Selection of habitats by two closely-related shorebird species wintering on the French Atlantic coast : Study of the bar-tailed and black-tailed godwits

Clément Jourdan

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Selection of habitats by two closely-related shorebird species wintering on the French Atlantic coast

Study of the bar-tailed and black-tailed godwits

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- Thesis Manuscript -

Clément JOURDAN

Selection of habitats by two closely-related shorebird species wintering on the French Atlantic coast

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« Comment peut-on préférer mettre les oiseaux dans la mire d'un fusil plutôt que dans le verre d'une jumelle ? »

Sylvain Tesson, Dans les forêts de Sibérie (2011)

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The photographs illustrating the chapters were mainly taken during my PhD. I would like to thank all the people who participated in the illustration of this manuscript.

General introduction

Selection of habitats in animals

Foraging (patch)

In the natural selection theory, the use of higher quality habitats maximizes the fitness of individuals, i.e. their survival and reproduction (Fretwell and Lucas 1969; Doligez and Boulinier 2008). The habitat selection by wildlife occurs at several scales (Rachlow 2008), and the foraging patches selection is considered to best explain the structure of animal communities (Paine 1980), and their dynamics and distribution (MacArthur and Pianka 1966; Charnov 1976). Indeed, the availability and quality of food resources fluctuates in space and time (Begon et al. 2006; Doligez and Boulinier 2008), even inside homogeneous habitats, and the animal feeding performances, which depend on it, too (Roese et al. 1991). Hence, the spatiotemporal variability of access to food supplies will then determine the animal population densities, so that to achieve a balance between number of prey and predators. Within a population, the spatiotemporal variability of feeding performances appears critical for the individual survival (Roese et al. 1991). Individuals will adapt their use of space and foraging decisions to optimize their net energy intake per unit of time (Breed and Moore 2012), according to the « optimal foraging » theory (MacArthur and Pianka 1966; Charnov 1976). Thus, the spatio-temporal use of habitats by animals generally highlights the preferential selection of foraging patches of higher quality over poorer quality patches (Charnov 1976), in order to maximize the net energy intake rate. Animals will adapt their use of foraging patches over time according to the evolution of its net intake rate which depends on the « carrying capacity » of the environment (Charnov 1976). However, beyond the spatio-temporal distribution of food resource and its available quantity and quality, the suitability of foraging patches for an animal also depends on intrinsic characteristics of the species, such as the level of intra or inter-specific competitions for resources or predation risk (Doligez and Boulinier 2008). Animals facing interspecific competition in foraging patches of high resource quality, synonym of a reduced net energy intake according to the theory of ‘density-dependence’ (van der Meer and Ens 1997; Begon et al. 2006), could then prefer to select poorer resource quality patches less subject to competition and allowing them to meet their daily energy needs. Similarly, intraspecific competition can lead to the use of different feeding areas between individuals, resulting sometimes in significant differences in the size of individual prospecting areas between high and low quality patches (Tingley et al. 2014). These direct response behaviours, facing to intra and interspecific competition, can be explained by the concept of « Ideal Free Distribution » (Fretwell and Lucas

1969) which predicts the density-dependent's distribution of individuals in habitats so that everyone could achieve equal intake rates, and finally equal fitness (Fretwell and Lucas 1969). On a larger temporal scale, natural selection and evolutionary events, leading to changes in morphology of organisms, can allow to maintain differences between species and reduce competition through resource partitioning, as observed in Darwin' finches (Grant 1986). Feeding resource partitioning appear in sympatric predators which exhibit interspecific interactions and competition on common habitats and trophic resources, and result in specialisation and co-evolutionary changes (Schoener 1974). Shorebirds, which use intertidal feeding areas in multispecies groups during the non-breeding period, well illustrate the evolutionary responses to resource competition and the resource partitioning concept, with a marked inter- and intra-specific variation in bill shape and bill length (Durell 2000; van de Kam et al. 2004; Nebel et al. 2005).

Dispersal (habitat)

Beyond the foraging patches, a density-dependent habitat selection also occurs at a larger scale through 'dispersal' process, and influences population dynamics and community organizations (Rosenzweig 1985; Pulliam and Danielson 1991). Dispersal is linked to the capacities of animals to disperse, relative to the size, shape and distribution of habitats in the landscape and successfully relocate their home ranges (Morris 1992). The dispersal movements constitute direct time, risks and energy costs for individuals, but the strategy finally aims to sufficiently increase the individual fitness to compensate the costs (Bowler and Benton 2005). It therefore occurs when animals face to decreasing of net intake rate, due food resource depletion or higher competition level on foraging patches of their respective home range (Sutherland 1996), and lead individuals to move and reach another suitable site. From these habitat-scale changes in distribution of individuals emerges the 'buffer effect', due to the density-dependent dispersal, notion according to which sites of poorer quality are often overused (in disproportional high population densities; Brown 1969; Kennedy and Gray 1993; Gill et al. 2001). Hence, connectivity between sub-populations and groups that results from dispersal also influence the demography and genetic structure (Lenormand 2002; Hanski and Gaggiotti 2004; Hastings and Botsford 2006) as well as the species distribution (Gonzalez et al. 1998). Habitat selection studies which helps in the management and conservation of populations and species must therefore consider individual dispersal for accurate assessment.

Migration (landscape)

On the larger scale, migration also appears as major habitat selection process and corresponds to home range shifts on a landscape scale (Morris 1987; Morris 1992). Migration is a time limited event in the annual cycle of an animal, and generally aim to take advantage of spatially distributed resources, to accede to rich but seasonal/temporary resources (Baker 1978) or to find suitable habitats for different life stages (Milner-Gulland et al. 2011). The schedule of migration events could thus be driven by multiple indicators such as food resource availability, temperature, day length (Morellet et al. 2013). In order to maximise the benefits of migration, animals could also adjust their timing of migration according to the arrivals of competitors (Møller 1994; Drent et al. 2003). Indeed, earlier arrival gives access in priority to territories of higher resource quality which improve both the survival on wintering grounds and reproductive success on breeding grounds of individuals (Senft et al. 1987). According to the species, migratory movements can represent long-distance travel with associated risks and energy costs, and only individuals in best condition could survive higher costs associated with early arrival (Kokko 1999).

Lifecycle of migratory shorebirds

Shorebirds, for most long-distance migrants, are a good example of the magnitude of migration process, as they fly from their wintering grounds in tropical and temperate latitudes to their breeding grounds in subarctic and artic regions (O'Reilly and Wingfield 1995) to benefits of most suitable habitats according to their life stage. During these seasonal long trips connecting breeding and non-breeding areas, shorebirds use migratory stopover sites where they rest and refuel.

Breeding season

The spring arrival schedule of migratory birds on their breeding sites depends on the timing of migration related to the timing of moult, and mainly controlled by environmental factors during non-breeding such as photoperiod (Gwinner 1996; Coppack and Both 2002), habitat quality (Marra et al. 1998) and weather conditions (Gordo et al. 2005). This timing of spring arrival on breeding sites seems to highly condition the breeding success of birds (Both and Visser 2001; Gunnarsson et al. 2005; Smith and Moore 2005), so as to stay ahead of competitors in the access of better quality sites. With breeding areas ranging from vast expanses of open tundra, steppes, to meadows or wetlands (van de Kam et al. 2004) from temperate to arctic areas, the density of pairs and associated competition largely varies according to areas and species, and is sometimes very low (Andres 2009). However, the territoriality in breeding shorebirds (Pitelka 1959; Edwards 1982; Mundahl 1982) and their site fidelity (Lourenço et al. 2011; Conklin et al. 2013; Kentie et al. 2017) emphasizes the interest of early arrival to accede to preferential territories and nest sites (Drent et al. 2003). Some individual strategies can thus appear such as speed the migration for early arrival benefits (Morrison et al. 2019) or slow down the migration (Johnson et al. 2016; Carneiro et al. 2019) to ensure advantageous high body conditions (Williams 1994; Morrison et al. 2007). Individuals arriving too early could face to snow cover making sites and food resources inaccessible (Madsen et al. 1998; Drent et al. 2006) and a late arrival can reduce the possibilities in the choice of the partner and the quality of the habitat (Gunnarsson et al. 2005). Birds will thus make a trade-off between both strategies, considering in particular the level of competition for breeding territories to adjust their schedule of arrival (Bauer and Klaassen 2013). Once on breeding areas, the prevailing theory suggests that animals exhibit habitat preferences in selection of nesting-site, in order to maximize their fitness (Hildén 1965; Martin 1998). Multiples factors are considered in the selection of habitats in order to balance the costs (e.g. risk of predation or competition) and benefits (e.g. food availability or favourable nest microclimate) of a territory (With and Webb 1993; Clark and Shutler 1999; P. A. Smith et al. 2007). Breeding sites of high quality are need by birds to correctly achieve the whole reproductive process (build nest, lay eggs and raise chicks), especially in high latitudes where the summer season is short (few months), and to ensure a high breeding success (Smith and Moore 2005). After rearing the young, the timing of departure from breeding sites is also crucial for birds, and mainly dependent on trophic depletion and weather deterioration, not specifically at the breeding site but at staging areas along the migratory route (Schneider and Harrington 1981; Duijns et al. 2019).

Migration and stopover

The seasonal migration process allows organisms to take advantage of fitness benefits provided by a breeding territory of high quality, without suffering the costs in the bad season (e.g. resource-depleted and harsh conditions; Alerstam et al. 2003; Winger et al. 2019). Shorebirds will thus seasonally migrate twice a year: in spring, from non-breeding to breeding grounds through a ‘pre-breeding’ migration, and in autumn, from breeding to non-breeding areas through a ‘post-breeding’ migration. In some species, movements of individuals occur at the end of the winter, consisting to reach other sites already used for wintering by other individuals of the same species. These exchanges of sites constitute the beginnings of migration, and the challenges of habitat selection on these sites are similar to those on wintering grounds, but require more energy to refuel. In the same way, during their two annual migratory events, shorebirds will use stopovers sites to refuel after the energy expenditure of the first migratory flights, and in view to achieve the rest of the migration journey (Baker et al. 2004; Kam et al. 2004). These stopovers can be crucial, especially for shorebirds species using a ‘jumping’ migration strategy, consisting on long distance flights interspersed with a few replenish staging (Piersma 1987; Warnock 2010). However, species using more stopovers through a ‘hopping’ strategy as alternate (Piersma 1987; Skagen and Knopf 1994) also depend on a high quality of their refuelling sites. Common staging areas are used, at high bird densities (Howell et al. 2020), and consistently by the same individuals from year to year (Warnock 2010; Chan et al. 2019; Verhoeven et al. 2020). However, the differences in time-constraint that experience shorebirds between the ‘pre-breeding’ and ‘post-breeding’ migrations, leads to differences in migration timing strategies between both (Duijns et al. 2019). Indeed, being more time-limited during the ‘pre-breeding’, due to the ‘time of arrival’ competition, the importance to meet food abundance peaks and the need of early breeding to allow re-nesting possibilities (Duijns et al. 2019), shorebirds are assumed to favour a time-minimizing strategy (Alerstam and Lindström 1990) with fewer staging sites and longer step lengths (Zhao et al. 2017). Seasonal migrations represents multiple risks and constraints for birds, such as predation risk (Lank et al. 2003; Ydenberg et al. 2007), physiological constraints and hazardous weather conditions (Richardson 1990; Newton 2007) on which birds could be more exposed during a time-minimizing migration strategy (Duijns et al. 2019). Conversely, with a lower selective pressure on wintering sites, shorebirds adopt an ‘energy-minimizing’ strategy during the ‘post-breeding’ migration (Alerstam and Lindström 1990), taking more time to complete their migration (Nilsson et al. 2013; Zhao et al. 2017) and ensure higher survival rate and body condition upon arrival. Without speaking of competition, the timing of arrival on non-breeding may be assumed to influence the wintering conditions, so that birds arriving later do not have access to better sites linked with the capacity support and carry over effect on sites of lower quality (e.g. in ruddy turnstone *Arenaria interpres*, Whitfield 2002).

Wintering period

After the reproduction, the ‘post-breeding’ migration in shorebirds consists in reaching lower latitudes, ranging from tropical to temperate areas, to spend the non-breeding period (van de Kam et al. 2004). During this life stage, shorebirds mainly distribute on coasts and estuaries

(Evans 1976), and exploit wetlands, marshes and intertidal areas (Harrington 2003; Taft and Haig 2006). The non-breeding period represents most of the annual cycle (up to three quarter) of shorebirds (Recher 1966; Taft and Haig 2006), and the environmental conditions encountered by birds on their wintering grounds are thus of major importance for survival. Indeed, upon their arrival from the ‘post-breeding’ migration, shorebirds will search for high quality sites allowing to refuel their reduced energy stocks (Piersma 1994). Then, throughout the winter, when food resources appear to be scarce and easily depleted (Goss-Custard et al. 1977), the availability of high quality areas are crucial for birds to meet their daily energy needs and to prepare the following ‘pre-breeding’ migration (Evans 1976; Kersten and Piersma 1987). Thus, during the winter, shorebirds devote most of their time to foraging, resting and maintenance activities (Nol et al. 2014), waiting for a new breeding season. However, the wintering cannot be reduced to a ‘waiting period’ between two breeding seasons. Indeed, beyond their importance in the pre/post-migration supply and the winter survival, the wintering conditions experienced by birds also influence their subsequent annual life-stages through carry over effects (Norris et al. 2004; Gunnarsson et al. 2005). Hence, the search for the best wintering conditions by shorebirds, to maximize their survival, will also condition their future migration and reproduction. Most of non-breeding shorebirds depend on intertidal areas (Burton et al. 2006; Piersma 2007; Colwell 2010), habitats which offer high invertebrate quality during the winter (Piersma et al. 1993; Bowgen et al. 2015; Chan et al. 2019). Although several shorebirds species prospect regularly together on intertidal feeding areas, trophic segregations allow to reduce the intra- and interspecific competition through distinct feeding methods, diet or bill morphology (Nebel et al. 2005; Nebel and Thompson 2011; Bocher et al. 2014). Some species, such as red knot *Calidris canutus*, are specialists and depend on very specific prey species and habitats (Quaintenne et al. 2010), while other are more generalists such as dunlin *Calidris alpine* (Dierschke et al. 1999) and redshank *Tringa tetanus* (Bocher et al. 2014). Some species are even able to exploit terrestrial habitats, as observed in individuals of Eurasian curlew *Numenius arquata* specialized on meadows (P. Bocher, *Pers. Com.*), or to both prospect on marine and terrestrial habitats during the winter, such as redshank (Sánchez et al. 2005), black-tailed godwits (Alves et al. 2010) or dunlins (Bocher et al. 2014). Beyond the habitat scale, differences at ‘landscape’ scale selection are mentioned between species, with for example very few movements and an extreme fidelity of individuals for their wintering areas in Eurasian curlew (P. Bocher, *Pers. Com.*), while other species, such as black-tailed godwits, are very mobile and can exploit new sites and thus potentially new habitats (F. Robin, *Pers. Com.*). Multiple factors are thought to explain bird movements during the wintering period, and the limited access to food resources, due to competition (Goss-Custard 1970; Sutherland 1983) or seasonal resource depletion (Gill et al. 2001a; Masero 2003), especially causes birds to switch for alternative sites or habitats. Shorebirds are also known to adjust their site choice and habitat use according to the predation risks, both during feeding (Cresswell 1994) and roosting (Rogers et al. 2006), as well as depending on abiotic factors (Burger 1984).

Preservation issues for shorebirds and their habitats

Conservation concern of shorebirds

Shorebirds constitute a group of birds of particularly high conservation concern (Piersma 2007) with populations submitted to strong declines throughout the world (Stroud et al. 2008; Studds et al. 2017; Hope et al. 2019). Observations report a declining situation for 52% of the populations with trend data, against only 8% which increases (Nebel et al. 2008). For migratory shorebirds, population changes have been observed from North and South America, Australia, Africa and Eurasia (Milton 2003; Stroud et al. 2008; Galbraith et al. 2014), even if some trend differences are observed between the main flyway systems. The East Asian-Australian Flyway appear especially under threat (Piersma et al. 2016) with a population declining for 88% of the shorebird species with known population trends (Hua et al. 2015). The others flyways are also concerned by important population changes, such as the Black Sea/Mediterranean Flyway and the West Asian/East African Flyway with 65% and 53% of the populations declining, respectively (Stroud et al. 2008). In comparison, the East Atlantic flyway seems less affected, but still in significant proportions since more than one-third of the populations is affected by a decline (37%, Stroud et al. 2008). The recent degradation of wetlands habitats worldwide, on which migratory shorebirds largely depend throughout their lifecycle, added to long migrations and low breeding rate, explain the particular conservation concern of shorebirds (Bildstein et al. 1991; Bart et al. 2007; Fernández and Lank 2008; Murray et al. 2018). Determining precisely the underlying drivers of population trends is crucial to develop effective measures for the conservation of the threatened species. However, it appears difficult to precisely understand which threats are most likely to impact shorebird populations since the factors are potentially numerous and sometime at a global scale. Indeed, due to the wide distribution of migratory birds, which cover a large geographic range through their long migrations, many potential drivers of change may exist and could be difficult to identify and distinguish (Webster et al. 2002; Piersma et al. 2016).

Main causes and threats

Some major threats and causes are still thought to mainly affect shorebird populations, among which the habitat loss and degradation (Murray and Fuller 2015; Clemens et al. 2016; Studds et al. 2017) as well as the human disturbance (Gill and Sutherland 2000; Dhanjal-Adams et al. 2016). Indeed, considerable modifications of wetlands affecting shorebird populations occurred worldwide (Ma et al. 2010), including loss of intertidal wetlands which affect shorebirds on their non-breeding range and "essential" stopovers (Fernández and Lank 2008; Hua et al. 2015). The conditions experienced by birds on non-breeding sites and staging areas are suggested to control the following lifecycle, including survival and breeding (Piersma 1994; Kam et al. 2004), the degradation of intertidal wetlands could thus account for a large part in the decline of shorebird populations. For instance, shorebirds needs a continued existence of few crucial staging areas of high quality, such as intertidal mudflats found in the Wadden Sea in Europe, to ensure their pre-breeding migration (Stroud et al. 2008;). Previous studies have shown that the loss of such intertidal wetlands in the Yellow Sea constituted the main cause of population declines in the East Asia-Australian Flyway (Rogers et al. 2008; Wilson et al. 2011; Hua et al. 2015). Beyond the loss of suitable habitats, others main threats affect shorebirds on their wintering grounds, among which the increased human disturbance (Lafferty 2001; Joanna Burger et al. 2004; Senner et al. 2016), the hunting pressure (Duriez et al. 2005; Ottema and Ramcharan 2009; Morrison et al. 2012), the lack of access to high quality roosts (Dias et al. 2006), as well as the exposure to pollutants (Strum et al. 2010; Pandiyan et al. 2020).

Role of management measures and protected areas

As wildlife habitat decreased worldwide, and especially wetlands, wildlife management turned to acquiring wetlands to manage them as wildlife reserves, and shorebirds particularly benefited from it (Harrington 2003). The practice of wetlands management aims to provide habitats of high quality for diverse waterbirds, including shorebirds, and thus requires an integrated knowledge about needs at the ecosystem-scale, considering spatial and temporal variabilities (Reid 1993; Ma et al. 2010). For shorebirds, most effective measures can reside in the reduction of disturbance on both feeding and roosting areas, but a priority for action on roosts appear essential. Indeed, even if human activities on intertidal areas can cause significant disturbance at low tide, birds have more space to avoid the danger and disperse than on specific and localised high tide roosts (Harrington 2003). The creation of protected areas, were human disturbance and predators could be reduced on these key areas, are assumed to help to maintain or even increase some bird populations through increasing the carrying capacity (Jackson et al. 2004). Some examples of efficient management exist, such as the development of nature reserves and protected areas in the last decades in France which contributed to the preservation of suitable habitats for the Icelandic Black-tailed godwits, and the increasing of numbers (Bocher et al. 2013). To multiply such example of successful management, research activities are needed to increase our fundamental knowledge of shorebird biology and ecology, and finally implement suitable conservation actions.

Conservation issues in Shorebirds habitat selection research

The identification and designing of necessary conservation actions to limit the decline of shorebirds requires a good understanding of life history of birds. Indeed, researches exploring the limiting factors of population, the distribution and abundance of birds, their foraging ecology and spatiotemporal habitat use, as well as the possible intra and interspecific differences appear essential to ensure the maintain and self-sustaining of shorebirds populations (Oring et al. 2000; Hua et al. 2015). Finally, habitat selection studies allow to both integrate habitat and demographic information, and thus appear of major importance into wildlife conservation planning (Caughley 1994; Morris 2003). Habitat selection analysis allows to describe the spatial distribution of birds in relation to the distribution of resources (Hutto 1985; Manly et al. 2002). This approach finally aims to explain the preferential use of certain habitat types also considering the possible effect of disturbance, predation or other environmental factors and not only the habitat quality (Jones 2001). Habitat selection studies are thus of major importance to inform about organism-habitat associations, and appear as priority researches for the management and conservation of shorebirds species.

Bar-tailed godwit and black-tailed godwit

The bar-tailed godwit *Limosa lapponica* and the black-tailed godwit *Limosa limosa,* both mainly breeding in Europe and Asia, are two closely related species of migratory shorebirds belonging to the order Charadriiformes and the Family Scolopacidae. Two more godwit species exist, the Hudsonian godwit *Limosa haemastica* and the marbled godwit *Limosa fedoa* which only breed in North America (Andres et al. 2012; Swift et al. 2017). These four godwit species form a species complex, i.e. a group of species having very recently diverged from each other (Trimbos et al. 2014), and belong to the Numeniini taxonomic group, a tribe of thirteen wader species (Dyson 2010; Pearce-Higgins et al. 2017). Closely-related species generally exhibit very close physical appearances, retaining common ancestral traits, as well as identical responses to environmental conditions (Peterson et al. 1999; Wiens and Graham 2005). However, beyond theses similarities, the existence of unique niche properties and species-specific ecological needs have been usually described in closely related species (Moritz et al. 2008; Costa et al. 2016; Silva et al. 2020). It is the case for bar-tailed godwits and black-tailed godwits which have distinct breeding distribution, respectively in North Eurasia and Alaska, and from Iceland to East Siberia, but share common non-breeding distribution (in Europe, Central West African coasts, South Asia and Oceania) where ecological disparities (diet, social organisation, site fidelity) have been reported.

Ecology and population

◗ **Bar-tailed godwit** *(Limosa lapponica)*

Bar-tailed godwit with inter-breeding plumage
© T. Guyot

The bar-tailed godwits mainly use marshy areas in lowland moss and shrub tundra (Flint et al. 1984; Hoyo et al. 1996) and swanpy heatlands near the Arctic treeline (Johnsgard 1981) as breeding grounds. On its wintering range, the species is mainly associated with intertidal areas of muddy coastlines, estuaries and mangrove-lined lagoons, using tidal mudflats or sandbanks (Johnsgard 1981; Hoyo et al. 1996).

The morphology of the bar-tailed godwits is characterized by long legs, a long bill (7-11 cm) slightly curved and a wingspan ranging from 62-72 cm, with a marked dimorphism between the sexes (Svensson 2015). Indeed, males are smaller, with an average weight of 290 g against 370 g for females, and have a shorter bill length. These physical characteristics can also vary between subspecies. During the breeding season, the species has a various diet, consisting mainly of insects, annelids, molluscs (Hoyo et al. 1996). On their wintering grounds, the bar-tailed godwits feeds mainly on marine preys, i.e. annelids, bivalves and crustaceans (Hoyo et al. 1996), but especially in polychaete worms in Europe (Duijns et al. 2013).

In total, four subspecies of bar-tailed godwits have been described, with breeding populations extending along Arctic Circle, from Northern Europe to Alaska:

Limosa lapponica lapponica, the nominal sub-species, breeds from Fennoscandia to Kanine Peninsula, and spends the winter in Western Europe, especially in UK, Ireland and Netherland (Prokosch 1988; Meltofte 1994), as well as on French coasts, Iberian Peninsula and Western Africa, in a lesser extent.

Limosa l. taymyrensis has breeding grounds mainly localised in Yamal and Taymir Peninsulas, in North Siberia, and migrates through Europe to join their wintering areas on West African coasts, in particular in the Banc d'Arguin and in Guinea Bissau (Drent and Piersma 1990). The species mainly use European coasts as stopover on the migration route, and can overlap with the subspecies *L. l. lapponica* during this period, such as in the Wadden Sea (Netherlands), an important stopover site.

Limosa l. baueri has a breeding range which extends in north-east Siberia, between Kolyma River and the Chukotka Peninsula, and in West Alaska (Higgins and Davies 1996). During the non-breeding period, the sub-species joins the northern and eastern Australia and New Zealand to spend the winter (Bamford et al. 2008; Garnett et al. 2011), stopping especially in the Yellow Sea region (East Asia) during the migration.

Limosa l. menzbieri also distributes in northern Siberia during the breeding season (Woodley 2009; F. Gill et al. 2021), and spends the winter in northern Australia (Higgins and Davies 1996; Battley et al. 2012). The Yellow Sea region constitutes a key staging site for *L. l. menzbieri*, but it is assumed that the sub-species has a more westerly migration pathway than *L. l. baueri* (Barter 2002).

◗ **Black-tailed godwit** *(Limosa limosa)*

Black-tailed godwit with inter-breeding plumage
© T. Guyot

On its breeding range, the black-tailed godwit use areas with short to high grass and soft soil (Hoyo et al. 1996; Laursen and Hald 2012), and preferentially select meadows habitats including pastures, wet grasslands, as well as grassy marshlands, raised bogs or grassy depressions in steppes (Hoyo et al. 1996). During the wintering season, the species use as well freshwater habitats (flooded grasslands and rice fields) as saline habitats (estuaries, salt-marshes and salt pans (Johnsgard 1981; Hoyo et al. 1996), with differences between sub-species.

The black-tailed godwit present physical characteristics close to those of the bar-tailed godwit, with a wingspan of 63-74 cm, a bill length of 8-11 cm and long legs (Svensson 2015), but some differences allow to differentiate them (Table 1). A huge sexual dimorphism also exists in this species, the female having a longer bill length and being larger than males, with a respective average weight of 340g (females) and 280g (males). Its breeding diet is mainly made of insects and annelids worms (Johnsgard 1981; Hoyo et al. 1996), while during the winter the species feeds on wide variety of prey, including molluscs and especially bivalves (Moreira 1994), insects (Estrella and Masero 2010), polychaete worms or even plant material such as rice seeds (Lourenço and Piersma 2008; Lourenço et al. 2010) or seagrass beds of *zostera noltei* (Robin et al. 2015).

From Western to Eastern Palearctic, breeding populations of three subspecies of black-tailed godwit are identified (Höglund et al. 2009):

Limosa limosa islandica: The 'islandic' sub-species almost exclusively breeds in Iceland (Wernham et al. 2002; Bauer et al. 2005), and to a much lesser extent in Northern Scotland, Faroe Islands and Western Norway (Bauer et al. 2005). Its wintering grounds mainly extend in Western Europe, from UK and Ireland to North West African coast, including France and Iberian Peninsula (Bauer et al. 2005).

Limosa l. limosa: The breeding grounds of the nominal sub-species, known as 'continental', extend from Western Europe to Central Asia (Groen and Yurlov 1999), with different wintering grounds for individuals depending on their breeding areas. Individuals breeding in Western-Central Europe will migrate through France to reach wintering grounds located from Central West African coasts to Southern Europe, with the Iberian Peninsula as northern limit. Individuals with breeding grounds located in Central-Eastern Europe join the Sahel to spend the winter, and those coming from West-Central Asia redistribute on the Eastern African coasts (Delany et al. 2009).

Limosa limosa melanuroides: This last subs-species of black-tailed godwit breeds in Eastern Siberia (Wernham et al. 2002) in small populations, and spends the wintering period in areas extending from Bay of Bengal to Taiwan, and Philippines to Australia (Piersma et al. 1996; Wernham et al. 2002).

In addition to these three recognized *Limosa limosa* subspecies, a Bohai godwit has been recently described as a potential new one, based on morphological and genetic characteristics of birds captured in northern Bohai Bay (China; Zhu et al. 2020).

Table 1 Morphological differences between *Limosa lapponica* and *Limosa limosa.*

Bar-tailed godwit *(L. lapponica)*	**Black-tailed godwit** *(L. limosa)*
 *Bar-tailed godwit with breeding plumage* *© P. van Giersbergen*	 *Black-tailed godwit with breeding plumage* *© T. Guyot*
◗ **General:**	◗ **General:**
Bill length: 7-11 cm	***Bill length:*** 8-11 cm
Wingspan: 62-72 cm	***Wingspan****:* 63-74 cm
Lenght: 33-41 cm (from bill to tail)	***Lenght:*** 37-42 cm (from bill to tail)
Mass: ~290 g (males), ~370 g (females)	***Mass:*** ~280 g (males), ~340 g (females)
Bill slightly shorter and noticeably upturned	Bill longer and straighter
Stockier build	More slender and elegant looking
Slightly shorter legs	Longer legs
Barred tail	Black tail (non-barred)
◗ **Non-breeding characteristics:**	◗ **Non-breeding characteristics:**
More obvious supercilium	Uniform plain smoky grey with no streaking
Curlew-like streaking on upperparts (for non-breeding plumage)	Black tail with square white rump
Elongated white rump patch	Obvious black-and-white wing pattern
No wing bar	

(Source: Svensson 2015)

Phenology of both species on French coasts

In France, two subspecies of bar-tailed godwit and two of black-tailed godwit are present on the East-Atlantic Flyway (EAF).

L. lapponica lapponica and *L. lapponica taymyrensis* are the only two subspecies of bar-tailed godwit observed, in distinct contexts, each year on French coasts. *L. l. lapponica* spend the wintering period in Western Europe, with most important sites located in UK, Ireland and The Netherlands (Wetlands International 2017), but France also hold more than 5% of the global population during the winter (Triplet et al. 2010). Hence, the nominal sub-species *lapponica* can mainly be observed between August and March on French coasts. When they leave French coasts, birds firstly reach the Wadden Sea, where they stay for a long time to refuel before the migration departure. On the other hand, *L. l. taymyrensis* is almost exclusively present during the pre-breeding (February-March) and post-breeding (August-October) migrations. Indeed, although some *L. l. taymyrensis* individuals appear to spend the entire winter in France, the sub-species mainly use French coasts as migratory stopover between breeding sites further north and wintering areas in western Africa.

Only two distinct sub-species of black-tailed godwit are also observed during the non-breeding period in France: *L. limosa islandica* and *L. limosa limosa*. The Icelandic sub-species *islandica*, almost exclusively coming from breeding sites in Iceland, redistributes in Western Europe, from August to March, to spend the winter. French coasts hold each year around 28% of the global population, with sites of international importance (Bocher et al. 2013). Besides, the continental sub-species *L. l. limosa* do not spend the winter on Atlantic French coasts. *L. l. limosa* is only observed during the northward migration (February-March) to breeding sites in The Netherlands and Central Europe, or during the southward migration (August-October) to the West African coasts. Otherwise, a small breeding population of *L. l. limosa* breeds in France with 146 to 170 pairs (Robin et al. 2012; Robin et al. 2016).

L. lapponica lapponica and *L. limosa islandica* in France and in the Pertuis Charentais

The number of birds wintering in France differs widely between the bar-tailed godwit and the black-tailed godwit, with respectively around 8,000 ind. (7,124 ind. in 2020) and 32,000 ind. (41,643 in 2020) counted each year during the mid-January Wetlands counts (Mahéo et al. 2020). With a population of *L. lapponica lapponica* estimated to 150,000 ind. (Wetlands

International 2017), the French coasts hold ~5.3% of the global population during the winter, against ~28% for *L. limosa islandica* (population estimated to be between 98,000 and 125,000; Wetlands International 2017). However, the two species are present in several sites along the French coasts, and overlap on a part of them. Ten sites are of national importance for bar-tailed godwits, holding more than 1% of the national population, and one site of international importance, representing >1% of the global population (Mahéo et al. 2020; Table 2). For black-tailed godwits, eight wintering sites along French coasts are of international importance (>1% global population), as well as one site of national importance (>1% national population; Table 2). The two species mainly overlap on five of these different sites: Mont-Saint-Michel Bay, Bourgneuf and Noirmoutier Bay, Aiguillon-Arçay Bay, Ré Island and Moëze Nature Reserve-Oléron Island. Three of these sites are located in the Pertuis Charentais, a region of the Central Atlantic French coast.

Table 2 Number of individuals of *L. lapponica lapponica* and *L. limosa islandica* counted on wintering sites during the mid-January Wetlands counts 2020. Only sites of international* or national** importance are mentioned.

Bar-tailed godwit (*L. lapponica lapponica*)	**Black-tailed godwit** (*L. limosa islandica*)
Mont-Saint-Michel Bay**: 438	**Mont-Saint-Michel Bay***: 2,560
Bourgneuf Bay and Noirmoutier*: 2,005	**Bourgneuf Bay and Noirmoutier***: 2,053
Aiguillon-Arçay Bay**: 1,197	**Aiguillon-Arçay Bay***: 12,271
Ré Island**: 637	**Ré Island***: 3,131
Moëze NR and Oléron Island**: 590	**Moëze NR and Oléron Island***: 9,249
Arcachon Bay**: 168	**Arcachon Bay****: 981
Marais d'Yves NR and surroundings**: 400	Morbihan Gulf*: 2,784
Saint-Brieuc Bay/Yffiniac/Morieux**: 320	Vilaine Bay*: 1,336
Goulven Bay, Kernic anse**: 306	Guérande Peninsula*: 6,244
Veys Bay**: 210	
West Cotentin littoral**: 383	

(Source: Mahéo et al. 2020)

How they depend on coastal habitats and protected areas in winter?

During the wintering period, godwits, as most of shorebirds, depend on coastal habitats for intertidal feeding areas and supratidal roost sites (Rogers et al. 2006; Zharikov and Milton 2009; Alves et al. 2010). Indeed, shorebirds have specific adaptations to forage on soft-bottom substrates, and especially a long bill in Scolopacidae which allow godwits to catch prey deeper in the sediment (Cunningham et al. 2013). Due to their high energetic requirements, and considering the tidal rhythm limiting the access to food resources, the godwits density highly depends on the availability and productivity of intertidal areas. At rising tide, godwits are forced to leave their feeding areas and join high-tide sites to roost. Thus, the availability of roosting areas also appears of major importance, and seems to influence the access to foraging grounds (Morrison and Harrington 1979) through the energetic expenditure during flights between both (Si et al. 2011; Novaes and Cintra 2013). Hence, the existence of functional areas able to provide highly productive mudflats, and secured roosts in proximity, are needed for godwits during the winter. The establishment of management measures, such as protected areas, can help to provide coastal areas of high quality for shorebirds, by reducing human disturbance and predators.

Study sites: the Pertuis Charentais

The pertuis constitute sea areas sheltered and generally bounded by one or more islands and a continent. The Pertuis Charentais are located on the Central French Atlantic coast (around La Rochelle), and includes a set of three pertuis: the Pertuis Breton, the Pertuis d'Antioche and the Pertuis de Maumusson. A huge variety of natural coastal habitats are present in this area, among which some particularly rich and productive habitats due to important sediments inputs coming from the surrounding rivers (Charente, Seudre and Gironde). Hence, the bays of the Pertuis Charentais shelter large mudflats with loose substrate which will constitute intertidal habitats of quality for shorebirds. In addition, four national nature reserves (NNR of Lilleau des Niges, NNR of Aiguillon Bay, NNR of Marais d'Yves and NNR of Moëze-Oléron) covering both intertidal areas and coastal marshes, are included in the Pertuis Charentais. These multiples and relatively closes wintering sites offer a significant reception capacity for birds, with important possibilities of connectivity/exchanges. Moreover, most of main roosts exploited by shorebirds, including godwits, are located inside the perimeters of national nature reserves. The recent development of these protected areas in the region, thus providing high quality roost sites (coastal marshes) with direct access to intertidal feeding areas, are even assumed to support the increasing trend of Islandic godwits on the French coasts (Bocher et al. 2013). Hence, the Pertuis Charentais appear to both provide natural coastal habitats of high quality with a high level of protected areas, which could explain that the region is the first wintering area for shorebirds in France (Mahéo et al. 2020). Therefore, the Pertuis Charentais are of major interest to study the habitat use in wintering shorebirds, and especially wintering godwits, in order to explore their dependence to intertidal areas (for feeding) and coastal marshes (for roosting) of high quality (protected areas).

Problematic of the Thesis

This thesis is carried out in the framework of a study program aiming in a precise description, understanding and comparison of the various winter survival strategies of main shorebirds species on the French Atlantic coast. The recent miniaturization of GPS tracking loggers allow to lead a fine-scale telemetry monitoring of medium size species, accessing to daily and seasonal movements of birds with a great spatial and temporal precision. Such approach can help to significantly improve our knowledge on the biology of shorebirds, their dependence on coastal habitats and their links with protected areas. Among the numerous shorebirds species spending the winter in the region, especially two of the main were retained for their great phylogenetic and morphologic proximities questioning on their ecological differences: the bar-tailed godwit *Limosa lapponica* and the black-tailed godwit *Limosa limosa.* Hence, this work, based on a GPS monitoring, wants to explore the selection of food resources (preys and habitats) by godwits, in relation to the use of rare roosts located in or outside the nature reserves. It will be possible to precisely describe the spatial and temporal use of functional areas by individual of the two species. The identification of precise feeding areas, thanks to GPS locations of birds during low tide periods, will allow to sample benthic macrofauna as potential preys, in order to estimate the energy qualities of the patches prospected and to define the corresponding habitats. Analysing the rhythm of bird's activity, their selection of habitats, the extent of the prospected areas and the choice of high tide roosts could precisely inform on the respective needs of the two godwit species during the winter. As the selected species have a marked sexual dimorphism, it also appears interesting, as much as data allows, to explore the existence of sexual segregations in term of wintering survival strategies.

Thesis outline

The present thesis is composed of 3 sections of two chapters through which we develop multiples approaches of habitat use analysis in wintering bar-tailed and black-tailed godwits, also investigating the role of protected areas in their conservation. The Section I explores the selection of habitats and the use of space by godwits throughout the wintering period. Firstly, we studied how resource availability can influence the habitat selection in bar-tailed godwits on Ré Island, a site characterized by a high diversity of intertidal habitats (Chapter 1). A second study examines the use of multiple habitat types at landscape scale in black-tailed godwits, both as response to the seasonal resource depletion and as complementation or supplementation strategies (Chapter 2). Then, in the Section II, we explore the effect of daytime on godwit movements and habitat use. To this end, we analyse the nycthemeral differences in the use of feeding and roosting areas in bar-tailed godwits on Ré Island (Chapter 3). In a similar approach, we examined the influence of the time of the day on the wintering habitat use by black-tailed godwits, also considering the effect of tidal periodicity and protected areas (Chapter 4). Section III focuses on the interactions between individuals during feeding activities, with a different approach between the two godwit species. In the first part, we explore in bar-tailed godwits, whose individuals have previously assumed an individual feeding pattern, a sex-specific spatial segregation and diet individual specialization (Chapter 5). Then, a second part investigates in black-tailed godwits, whose individuals have previously shown a gregarious feeding pattern on intertidal areas, the individual associations through an analysis of fusion-fission events in foraging flocks (Chapter 6). Finally, the two species are not directly compared in the different chapters, due to too few birds of both species caught on the same sites. Hence, the final discussion try to relate the different results respectively observed for bar-tailed and black-tailed godwits through this study, and compare the two species in term of selection of prey and habitats, also considering previous works. At last, we try to highlight the recommendations that this work can provide in terms of conservation of the two species, and to underline the limits of our study, looking for improvements.

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SECTION I

Selection of habitats and use of space by godwits throughout the wintering period

Chapter 1

Highly diversified habitats and resources influence habitat selection in wintering shorebirds

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Abstract

Habitat selection is an important process in birds that influences individual survival and fitness, and ultimately shapes population dynamics. As a consequence, strong selective pressures apply to favor strategies allowing individuals to choose high-quality habitat for foraging while reducing predation risk and competition. In long-distance migratory birds, such as shorebirds, the non-breeding period is considered as a key period of their annual cycle with reported effects on individual survival and subsequent reproduction. Site selection by non-breeding shorebirds should depend on habitat quality in order for them to ensure survival until the next breeding season. More specifically, birds should distribute in space and time according to their resource availability and specialize on feeding habitats or/and prey to reduce intraspecific competition. To test this hypothesis, we studied bar-tailed godwits (*Limosa lapponica*) at one of their main non-breeding sites along the French coast. We first used GPS tracking to investigate their foraging and roosting home ranges as well as core sampling to define the diversity of available habitats and their quality as feeding resources. We then compared individual habitat selection in relation to feeding home range sizes and benthic macrofauna abundances. Our results provide the first fine scale definition of shorebird movements and distribution along the non-breeding period. We found that godwits showed an extreme fidelity to restricted feeding areas (about 3.4 km^2) during winter, with low overlap between individual feeding home ranges. Each bird appeared to mainly use four to six of the 11 available foraging habitats, with a specialization on one to two main habitats and their associated prey. However, our results did not emphasize a clear relationship between home range sizes and the quality of bird feeding sites. This study thus demonstrates the high specialization of individual non-breeding bar-tailed godwits relying on specific foraging grounds and habitats, with important implications for the conservation of this species.

Keywords: Avian ecology, GPS tracking, Wintering strategy, Coastal habitats, Home range, *Limosa lapponica*

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Introduction

In spatially and temporally heterogeneous environments, habitat selection is a decision-making process where individuals are faced with choices not only resting upon habitat quality, but also on a trade-off between costs and benefits to acquire space for feeding (Fretwell and Lucas 1969; Kennedy and Gray 1994). Hence, the quality and availability of local habitats vary along with abiotic (e.g. feeding substrate), biotic (e.g. food resources, predators, parasites) and social (e.g. intraspecific competition) factors (Bruggeman et al. 2016; Philippe et al. 2016). Habitat selection ultimately influences the survival and reproduction of individuals (Hutto 1985; Block and Brennan 1993). Therefore, strong selective pressures apply to favor strategies that allow individuals to select high-quality habitats for foraging while avoiding predation and competition (Garabedian et al. 2019; Abdulwahab et al. 2019). The first step to study habitat selection is to define spatial habitat use, investigating animal movements and individual home ranges (van Moorter et al. 2016). The home range is defined as the area used by mobile animal during its regular activities (i.e. foraging, roosting, mating, caring for young; Burt 1943; Powell 2000). By affecting their physiology, energetics and behaviour, many factors are known to directly affect animal home ranges (size and shape; reviews in Mace et al. 1983; Rolando 2002, McGarigal et al. 2016), such as age, sex, body condition, habitat structure or weather conditions. Nonetheless, they are primarily driven by the distribution and availability of food resources (Brown 1975; Schoener 1983).

For long-distance migratory birds, such as many shorebird species, the non-breeding period is considered as a key period of their annual cycle with reported effects on individual fitness and population dynamics (Pienkowski and Evans 1984; Marra and Holmes 2001). Site selection by individuals during this period thus depends on habitat quality in order for them to ensure survival until the next breeding season (Evans 1976; Hutto 1985). At their coastal wintering sites, shorebirds are expected to face challenging weather conditions (Evans 1976; Clark 2009), high predation risks (van den Hout et al. 2008) and strong intraspecific competition (Beauchamp 2007). Most of them also have to deal with the characteristics of intertidal ecosystems where the tidal cycle reduces the time-window during which individuals can access their foraging grounds (Fonseca et al. 2017). In addition, birds must ensure their molt during this period, a particularly energy-demanding process (Murphy 1996). Consequently, wintering shorebirds have to balance their different energy gains and costs, especially the risk of starvation against the risk of predation (Evans 1976; Lima 1986), weighting the time spent in secured roosting sites against the time spent foraging in challenging feeding habitats (to acquire energy and maintain their body condition).

A large number of shorebirds winter along the French coasts (Gaudard et al. 2018), and particularly in the Pertuis Charentais (Central Atlantic French Coast, Fig.1), a region offering large areas of intertidal mudflats, essential feeding habitats for these species (Bocher et al. 2014; Robin et al. 2015). The Pertuis Charentais is the most important wintering area for shorebirds in France and is recognized as a site of international importance for these species (Delany et al. 2009). The bar-tailed godwit *Limosa lapponica* is one of them with a maximum of *c.* 4,000 individuals recorded in January (F. Robin, com. Pers.). Two subspecies of bar-tailed godwit are present in western Europe but only *L. l. lapponica* overwinters in this region (Duijns et al. 2012), from the Netherlands and British Islands to the Iberian Peninsula, with a population estimated to 150,000 individuals (Wetlands International 2017). The species predominantly feeds on polychaetes whatever their wintering site in Europe during non-breeding period (Duijns et al. 2013). *L. l. lapponica* is characterized by stable population trends at the European scale. Nonetheless, important decreases of wintering populations were observed in France during 1980s and 1990s (Triplet et al. 2010), likely due to degraded wintering habitats and increasing human disturbance during this sensitive period (Verger 2005; Delany et al. 2009; BirdLife International 2017), when godwits are known to occupy a few small areas (Delany et al. 2009). The creation of Nature Reserves in the Pertuis Charentais (Fig. 1) highlighted positive effects on bar-tailed godwits by reducing disturbance at their high tide roosts, resulting in a significant increase in bird numbers over the 1985-2009 period on Ré Island, Yves Bay and Marennes-Oléron Bay, reaching national or international importance threshold (Triplet et al. 2010). In that context, understanding the spatial distribution of wintering bar-tailed godwits is essential to refine conservation measures (Morris 2003; Klar et al. 2008). Likewise, characterizing their habitat use is crucial, not only for a complete understanding of ecosystem functioning, but also to develop appropriate management strategies bound to protect this Near Threatened species (BirdLife International 2017). In the present study, we tested the hypotheses that in a context of high bird densities, 1) female bar-tailed godwits specialize on feeding habitats and prey to avoid conspecific competition during the non-breeding period (Duijns and Piersma 2014), and 2) individuals using habitats with higher food abundances are predicted to have smaller home ranges. We first defined individual home ranges and more specifically feeding home ranges using tracking devices. Second, we determined available foraging habitats and benthic prey availability on accessible mudflats at low tide and their respective surfaces by in situ sampling. Finally, we compared individual habitat selection in relation to feeding home ranges size and prey abundance.

Methods

Study site

The study was carried out on Ré Island (Central French Atlantic coast) during non-breeding periods (from August to March) of 2015-2016 and 2016-2017. Ré Island is a part of the Pertuis Charentais area (Fig. 1), a region including the largest surface of intertidal mudflats on estuarine systems in France (Verger 2005). Two main feeding areas are available for bar-tailed godwits (hereafter godwits) on soft substrates on the Island (Aubouin 2014; Duijns et al. 2014). The first site is a mudflat inside a semi-enclosed bay, the 'Fier d'Ars' (46°13'18''N; 1°30'29''W), and the second site is sandflat on an exposed coast in the north of the Island, 'La Loge' (46°14'25''N; 1°28'42''W).

The 'Fier d'Ars' is a bay of about 800 ha bordered by 1,600 ha of saltpans or brackish marshes. This wetland has been classified according to the Ramsar Convention since 2003, and part of it (the western part of the bay and the high tide roosts in saltmarshes) is part of the National Nature Reserve 'Lilleau des Niges' since 1980. The 'Fier d'Ars' is divided by a central creek, with a mainly bare muddy substrate on the edges or covered by seagrass beds *(Zostera noltei)* at the center, and a restricted sandy area along the stream to the north.

'La Loge' extends over *c*. 100 ha. The foreshore remains uncovered by the tide for about 4 hours only, and the period of food availability is therefore limited for birds compared to the 'Fier d'Ars'. 'La Loge' is part of the Ramsar site 'Marsh of the Fier d'Ars' as the only protection status, and tourist activities on the beach during summer are frequent during daylight.

Coastal shorebird survey data

Counts of shorebirds were carried out by the staff of the National Nature Reserve, year-round, around the 15th of each month on the whole Ré Island from 2000 to 2016. The census targeted all the known high tide roosts during the highest water levels during spring tide. Birds were counted with telescopes, simultaneously by 5 observers distributed on the main spots of Ré Island, from 2 hours before and until the high tide.

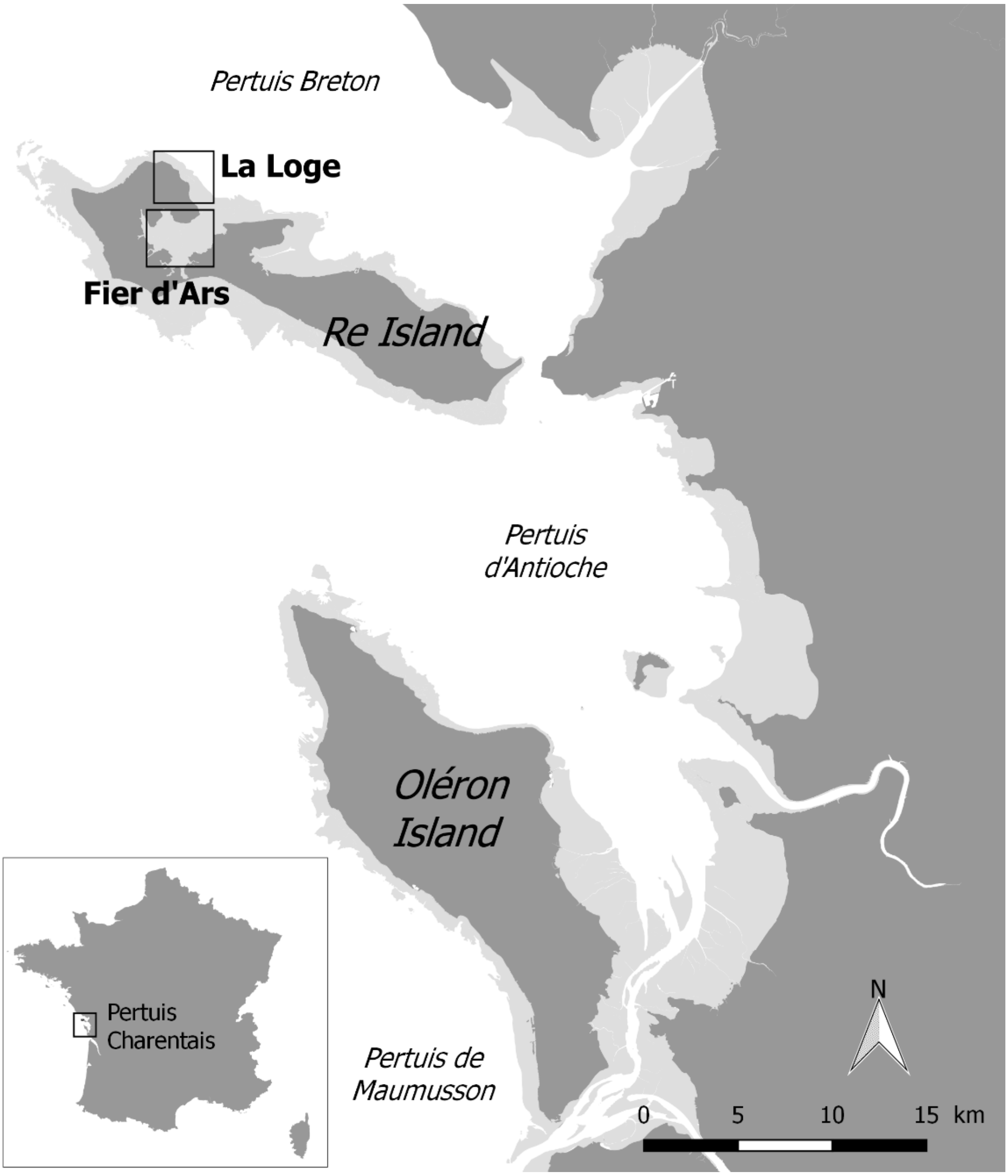

Fig. 1 Map of the Pertuis Charentais (Central French Atlantic coast) and localisation of the study areas on Ré Island. Dark grey corresponds to the mainland and light grey to the intertidal area.

Godwits captures and tracking

Godwits were captured using mist nets on high tide roosts between October 2015 and November 2016. Catching sessions took place during non-moonlight nights inside the National Nature Reserve. Individuals were marked with a metal ring and a unique color rings combination. The sex of individuals was determined based on their body mass (230-383 g for males and 280-455 g for females) and bill length (69-90 mm for males and 86-110 mm for females; Demongin 2016); and the age defined according to their plumage pattern (Demongin 2016).

A total of 15 godwits (11 in 2015 and 4 in 2016) were fitted with a GPS-VHF logger (STERNA VHF-SRD with solar charger, Ecotone, Gdánsk, Poland; 35 x 16 x 10 mm, 7.5 g). Birds were chosen so that the mass of the logger was less than 3% of the bird body mass. Consequently, only adult females (bill length > 86 mm) were selected for the study, considering that males were too small and that juvenile females were possibly not faithful to the study site during winter. Loggers were attached on the lower part of the back with a 2 mm Teflon harness according to the 'leg-loop' method (Mallory and Gilbert 2008). Tags recorded GPS locations (tested mean accuracy of ± 10 m) every 30 minutes. Out of the 15 females tagged, six recorded a sufficient number of positions during all the winter period. Among the others, four birds never contacted after the logger deployment and probably moved outside of the area, four birds had a tag which progressively stopped working because of misfunctioning in battery recharging and gave less than 300 locations in total over a short period of the winter, and one bird was found predated shortly after release. Among the six females, three (BTG01, BTG02 and BTG03) recorded locations for two consecutive winters (2015-2016 and 2016-2017). The three others birds provided only one winter of data in 2015-2016 (BTG04 and BTG05) or 2016-2017 (BTG06).

Prey availability and habitat description

The availability and quality of trophic resources at the feeding areas used by tagged godwits (distribution, density and biomass of benthic macrofauna) were investigated by sediment core sampling. Sampling was performed at the centroid of each predefined individual Feeding Core Area (hereafter FCA), based on GPS locations recorded over the first two months of deployment. Indeed, in order to determine the benthic macrofauna potentially available for birds during winter, the sampling of sediment was carried out during the course of the winter. Given the high fidelity of godwits to foraging sites, these sampling stations based on birds' FCA after two months were considered to be representative of the entire winter. The number of core sampling stations per bird ranged from two to nine, depending on the size of its FCA and the number of core areas which composed it, in order to apply the same sampling pressure per feeding surface between the different birds. These samples were collected between January and February, by foot and at low tide according to methods described in Bocher et al. (2007) and Kraan et al. (2009). At each point, a 15 cm diameter sediment core (0.018 m^2) was collected at a depth of 15 cm (depth of sediment containing almost all polychaetes available for foraging birds according to mean bill length of females). These samples were sieved over a 1 mm mesh size on site. Annelids were separated and preserved in 70° Ethanol. Molluscs were stored at -20°C until sorted at the laboratory. Although mudsnails *Hydrobia ulvae* are rare in the godwits diet, they were sampled by taking one additional core (70 mm diameter) of 0.0037 m² to a depth of 5 cm and sieved over a 0.5 mm mesh, in order to differentiate between present and available abundance. Mudsnails were a potentially abundant and small prey that would require too long processing time for a larger sediment core sampling. In the laboratory, all organisms were identified to the species level, if possible, and the molluscs were measured to an accuracy of 0.1 mm. The Dry Mass (DM) of flesh for each prey was measured after 72 hours of drying at 55°C. Dried specimens were then incinerated at 550°C for 5 hours to determine their ash mass and then a proxy of their energy content: the ash free dry mass (AFDM; Zwarts and Wanink 1993). For annelids damaged or cut during sieving, anterior part of the body, when remaining, was measured and DM and AFDM estimates were determined from allometric relationships specific to each species and established in a related study (Aubouin 2014).

A sediment sample was collected to a maximum depth of 5 cm for granulometric characteristics. Medium Grain Size (mm) and the percentage of silt (fraction < 0.063 mm) were determined using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2,000 mm). Results on granulometric characteristics of sediment were used as complement data to define the habitat type at each sampling station and to draw the map of habitats available to godwits.

A fine scale cartography of intertidal habitats was drawn by combining benthic macrofauna and sediment sample results with field observations, and using the Eunis classification of coastal habitats as a reference (Bajjouk et al. 2015). Seagrass beds delimitations were achieved during summer 2012 on field with GPS (Trimble GeoXH).

Home ranges and habitat selection

Space use during the winter period was analyzed through the estimation of the Utilization Distribution (UD), *i.e.* the probability density to found each bird at any place according to the location of this place (Calenge 2015). The UDs were computed with the Kernel Density Estimates (KDE; van Winkle 1975; Worton 1989) using the function ‘kernelUD’ (package ‘adehabitatHR’, Calenge 2020) on the statistical software R (3.6.1, R Core Team 2020). KDE takes into account the spatial distribution of locations, and corresponding time spent by birds in an area, to estimate, at the individual scale, their home range (at 95% isopleth) and core area (at 50% isopleth; Worton 1989). We used a fixed-kernel method with a smoothing factor of 70% the minimum reference value computed by the ‘ad-hoc’ bandwidth over all individuals, a compromise between under-smoothing of Least-Square Cross-Validation (LSCV) and over-smoothing of reference bandwidth (Kie et al. 2010; Schuler et al. 2014). Using a single value of smoothing factor allowed us to compare individuals. Cell size was set to 20 m considering the accuracy of GPS positions.

As the number of recorded positions differed between birds, we checked that data quantity had no effect on the estimation of home ranges size. To this end, we calculated wintering home range size (95% isopleth) of each individual using the kernel method for position samples successively increased by 50 locations chronologically, from n=50 to n=max number of positions collected (Supplementary material Fig. S1). For most of birds, the size of the home range showed a significant increase until c. 1000 GPS fixes, beyond, it no longer changed significantly and then reached a plateau. This confirmed that the number of GPS fixes recorded was sufficient for all individuals to provide reliable estimates of home ranges size.

The UDs were analysed at the global frame for each bird to estimate the individual Home Range (HR) and Core Area (CA) using all GPS locations. Then, we calculated separately UDs on feeding positions (i.e. when birds were foraging on intertidal areas at low tide, below a water height of 3.3 m relative to the hydrographic zero) and roosting positions (i.e. when birds were roosting on salt marshes, upper intertidal areas or pond when the water height exceeded 3.3 m). We thus estimated the complete Home Range (HR, 95% kernel density contour) and Core Area (50% kernel density contour) during Feeding (FHR and FCA) and during Roosting (RHR and RCA). For the three birds for which two consecutive wintering periods were recorded, we investigated the inter-annual fidelity to their wintering feeding areas. The high fidelity observed in these three individuals allowed us to assume the absence of a ‘year’ effect on the feeding UDs, and thus to compare the six individuals by retaining the winter 2015-2016 data for BTG01, BTG02, BTG03, BTG04, BTG05, and winter 2016-2017 data for BTG06.

In another study on Ré Island (Aubouin 2014) 64 droppings of godwits were sorted of and there were found almost exclusively remains from polychaetes, and very anecdotally shell fragments of molluscs. Hence, considering that godwits predominantly feed on polychaetes whatever their wintering sites in Europe (Duijns et al. 2013), including Ré Island

Table 1 Feeding and roosting home ranges sizes of bar-tailed godwits per winter. CA= Core Area (kde 50%); HR= Home Range (kde 95%).

					FEEDING			ROOSTING		
Bird Id	**Bill lengh (mm)**	**Year**	**Period**	**Nb. of days**	**GPS fixes**	**CA - 50% (ha)**	**HR - 95% (ha)**	**GPS fixes**	**CA - 50% (ha)**	**HR -95% (ha)**
BTG01	91.5	2015-2016	Oct.-Mar.	156	1388	69	478	1247	45	214
		2016-2017	Aug.-Mar.	208	4045	73	408	3469	34	210
BTG02	105	2015-2016	Oct.-Mar.	170	1347	22	363	1138	48	250
		2016-2017	Jun.-Feb.	247	1627	34	233	1786	26	149
BTG03	99	2015-2016	Oct.-Mar.	153	824	51	287	740	30	175
		2016-2017	Aug.-Mar.	227	761	49	297	672	34	172
BTG04	101	2015-2016	Nov.-Mar.	136	2171	54	396	1663	36	234
BTG05	95	2015-2016	Nov.-Mar.	139	1823	13	167	2063	19	161
BTG06	101	2016-2017	Nov.-Mar.	137	3524	49	350	2383	21	231

(Aubouin 2014), we tested the hypothesis that the size of individual FCA was negatively related to the abundance of polychaete biomass (excluding small species with individual biomass < 0,001g AFDM) inside the FCA. To investigate the use and importance of foraging habitats, a habitat selection analysis was then performed with the R package ‘adehabitatHS’ (Calenge 2011). To this end, we considered the estimated Minimum Convex Polygon (MCP) of foraging locations from all equipped godwits to define the available foraging areas. Habitat selection analysis was performed overlaying the FCA and the habitat typology using the method of selection ratios (Manly et al. 2002) for design II (second order selection), where the availability of habitats is the same for all 6 monitored birds and the habitat selection is analyzed at the individual level (Johnson 1980). In order to explain variations in habitat selection among individuals, we used an Eigen analysis of selection ratios (Calenge and Dufour 2006), an extension of principal component analysis were birds are projected in the factorial plane describe by the habitat types and which best explains the heterogeneity of the selection. This multifactorial method is suitable for the exploration of habitat selection and identification of groups of animals using habitats in a same or different way.

Results

Phenology and abundance of godwits

The wintering period at the study site spanned over a maximum of eight months from August to March, with a maximum number of birds recorded in January with a mean of 641 ± 85 individuals over 2000-2016 (Supplementary material Fig. S2). The last birds arrived in late-October / early-November and most of the birds left the site for pre-nuptial migration during March. Very few birds were present from April to July, *i.e.* during the migration period.

Home ranges variability

HR of the six birds over the two winters of study varied between 248 and 581 ha (mean = 461 ± 48 ha, n = 6). Despite a different number of total recorded locations, the size evolution of the HR of most of birds shown a plateau beyond which the additional locations bring no significant variation (Table 1, Supplementary material Fig. S1).

Inter-annual fidelity to feeding areas

For the three birds displaying two successive non-breeding periods, FHR overlapped by 83%, 74% and 71% between both winters (Supplementary material Table S1), while the average

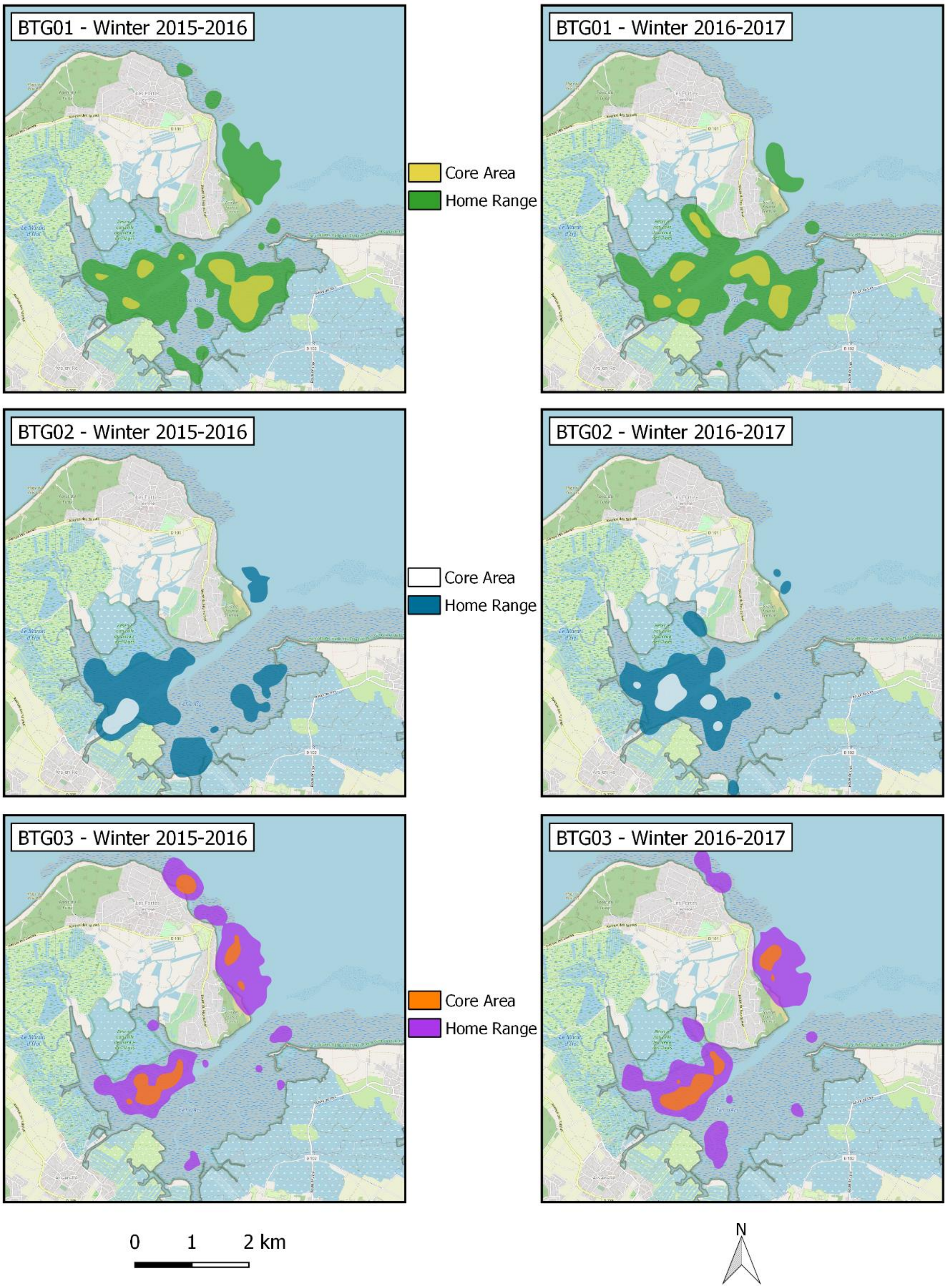

Fig. 2 Feeding Home Range (FHR) of three bar-tailed godwits during two successive wintering periods on Ré Island. Home ranges were calculated as 50% (Core Area) and 95% (Home Range) kernel density contours.

inter-individual overlap of FHR was 43% (Supplementary material Table S2). Individual BTG01 had the largest FHR (478 ha in 2015-2016; 408 ha in 2016-2017) and used both winters a large part of the bay with multiple FCA (Fig. 2). BTG02 foraged mainly in the 'Fier d'Ars', with only a few visits on 'La Loge'. The difference in FHR between winters for BTG02 (363 ha in 2015-2016; 232 ha in 2016-2017) was explained by the sporadic visit of a supplementary area during the first winter located outside the study site ('Fossé de Loix' not represented on Fig. 2). The FHR of BTG03 during both periods were very similar (287 ha in 2015-2016; 297 ha in 2016-2017). The estimated size of FCA between both winters was also close for BTG01 (69 ha in 2015-2016; 73 ha in 2016-2017), BTG02 (22 ha in 2015-2016; 34 ha in 2016-2017) and BTG03 (51 ha in 2015-2016; 49 ha in 2016-2017), but their location slightly changed with an overlap of 55%, 16% and 63%, respectively.

Feeding and roosting home ranges

For each bird, the number of GPS fixes at roost and on feeding areas were similar, allowing us to compare the size of FHR and RHR (Table 1). The number of GPS locations between birds were not comparable both for roosting and for feeding fixes, but our data set is large enough not to bias the estimation of the utilization distributions between birds (see above). The mean size of RHR (kde 95%) and RCA (kde 50%) were 211 ± 35 ha (min-max: 161-250 ha) and 33 ± 12 ha (min-max: 19-48 ha), respectively (Fig. 3). The birds used between six to 10 different roosts all around the bay according to individual. During neap tide, they remained in the upper part of the intertidal area but during spring tide, they only roosted in marshes within the Nature Reserve or in saltpans. The mean size (±SE) of FHR (kde 95%) and FCA (kde 50%) were 340 ± 105 ha (min-max: 167-478 ha) and 43 ± 21 ha (min-max: 13-69 ha), respectively (Fig. 2). The FHR and RHR overlapped only on the upper part of the intertidal area during neap tide, particularly on an elevated sandflat in front of the Nature Reserve.

Rhythm of feeding activity

According to GPS fixes located on potential feeding areas, godwits fed during approximately 6-7 hours by tide cycle (Fig. 4). The presence time of birds on the mudflats was not symmetrical around low tide, with a feeding period of 2-3 hours before low tide and 3-4 hours after. Beyond this general pattern, the duration of use of the mudflats seems to differ between individuals, with an arrival of birds on the feeding areas generally more synchronous (between -4h and -2h in tidal cycle) than the return towards roosting places (between 2h and 5h in tidal cycle). BTG05

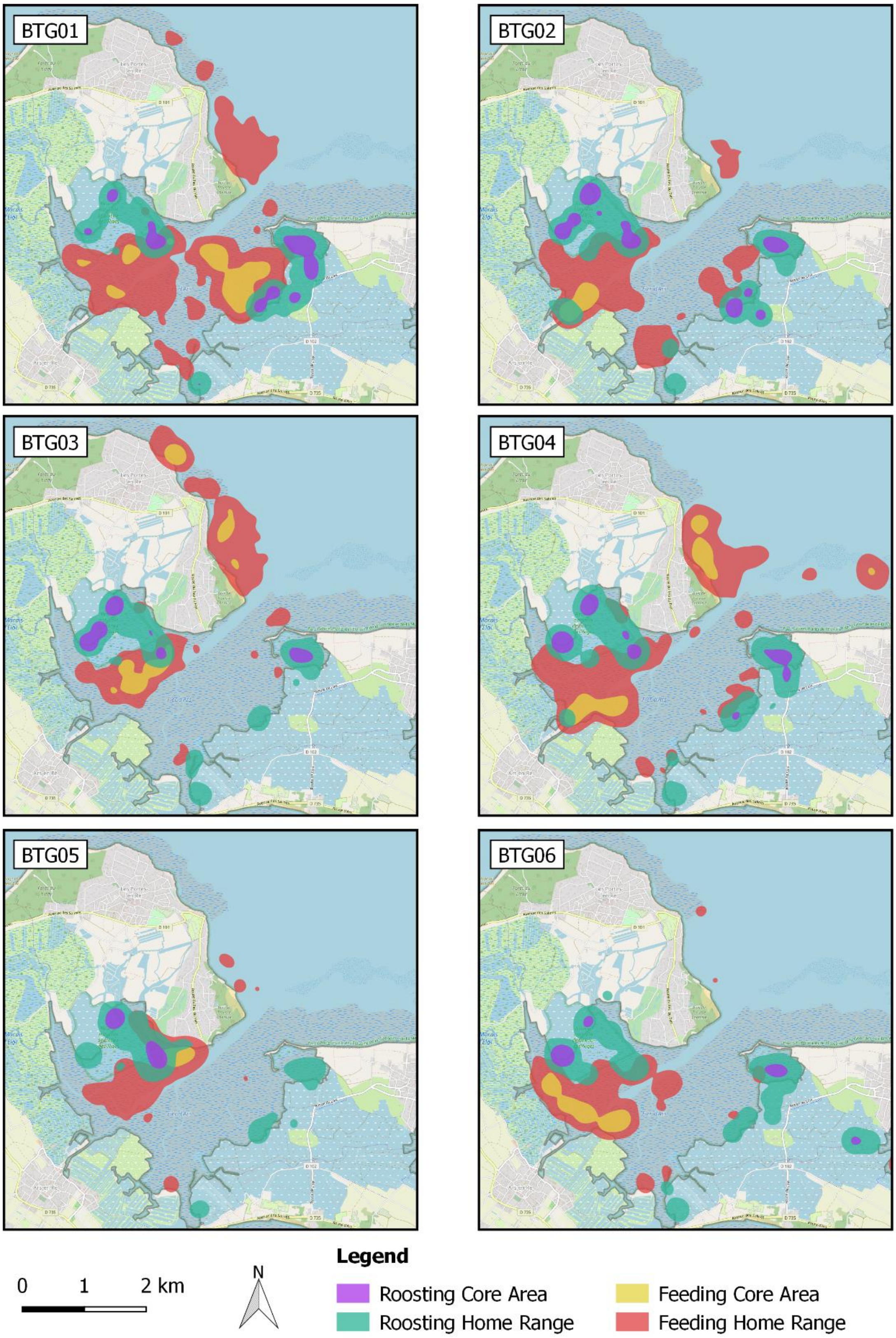

Fig. 3 Feeding Home Range (FHR) and roosting home range (RHR) of six bar-tailed godwits monitored during the non-breeding period on Ré Island. Home ranges were calculated as 50% (Core Area) and 95% (Home Range) kernel density contours.

spent less time than other birds on feeding areas, with a maximum value of 80-85% of its time on intertidal areas during the low tide.

Prey availability and feeding home ranges

A total of 19 stations located in FCA were retained to describe habitat quality within the FHR (between 2 and 9 stations per FCA per bird). A total of 16 bivalve, five gastropod, 32 annelid and one nemert species or taxa were identified for all sampled stations (Table 2). Three bivalve species were largely abundant: *Cerastoderma edule* (mean minimal and maximal densities for individual FCA: 98-274 ind.m^{-2}), *Ruditapes* spp. (12-62 ind.m^{-2}) and *Scrobicularia plana* (0-154 ind.m^{-2}); but differed between habitats. Among gastropods only *Hydrobia ulvae* was largely abundant (22-468 ind.m^{-2}). Among annelids, the most abundant species were Capitellidae sp. (0-180 ind.m^{-2}), *Cirriformia tentaculata* (0-25 ind.m^{-2}), *Hediste diversicolor* (0-117 ind.m^{-2}), *Nephtys hombergii* (11-41 ind.m^{-2}), *Notomastus latericeus* (2-82 ind.m^{-2}), *Owenia fusiformis* (8-46 ind.m^{-2}), *Scoloplos armiger* (0-462 ind.m^{-2}) and *Arenicola marina* (2-10 ind.m^{-2}). The size of bird FCA was not related to the mean abundance of polychaete biomass inside predefined core areas (t= 0.80189, df= 4, p-value= 0.4676, Fig. 5).

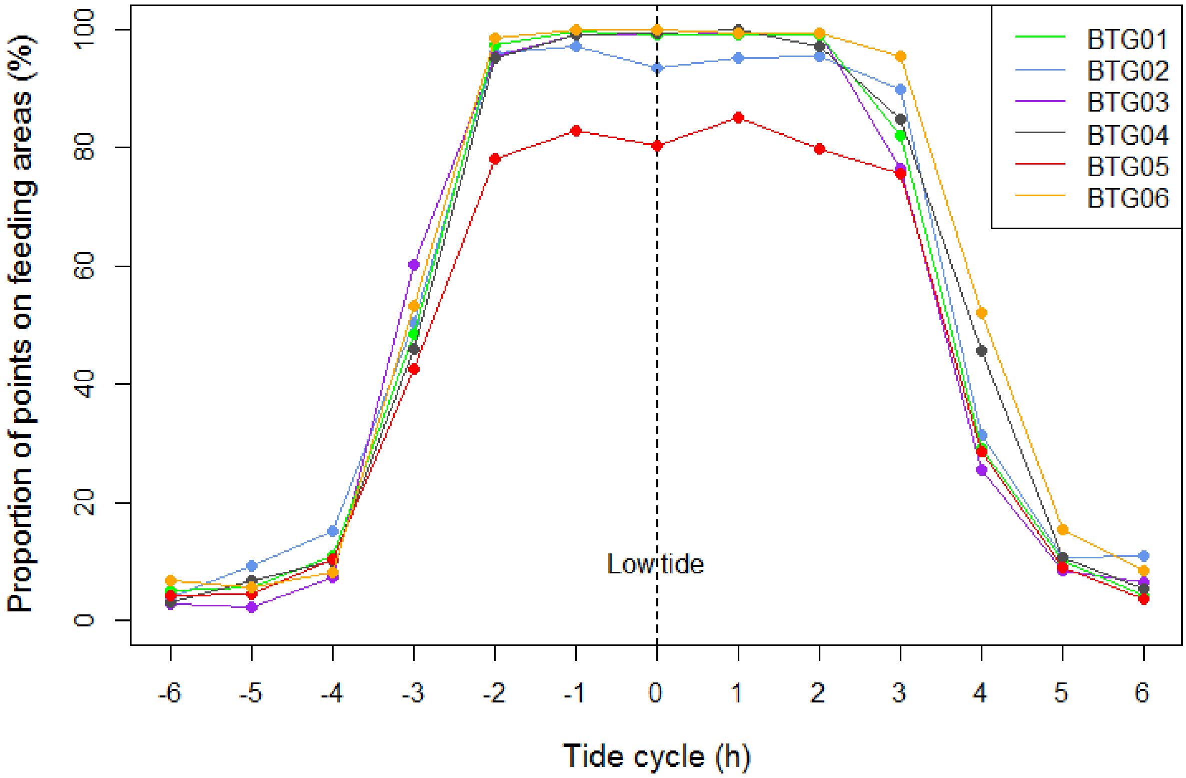

Fig. 4 Proportion of time spent by six bar-tailed godwits on mudflats, i.e. feeding, during the tidal cycle.

Table 2 Mean density (Dens.) and mean AFDM (Ash Free Dry Mass) of main macrofaunal species in Feeding Core Area (FCA) per bird.

	BTG01		**BTG02**		**BTG03**		**BTG04**		**BTG05**		**BTG06**	
Macrofaunal species	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})	Dens. (ind.m-^{2})	AFDM (mg.m-^{2})
Bivalvia	**167**	**8099**	**401**	**13144**	**264**	**8051**	**232**	**9640**	**296**	**16496**	**414**	**17862**
Abra tenuis	25	12	83	41	19	14	28	14	19	8	23	8
Cerastoderma edule	116	6932	99	5928	182	6644	104	6677	265	15871	274	13527
Corbula gibba	0	0	0	0	0	0	0	0	0	0	4	3
Kurtiella bidentata	0	0	0	0	0	0	0	0	0	0	10	1
Loripes lucinalis	0	0	0	0	0	0	0	0	0	0	2	35
Macoma balthica	0	0	3	2	26	201	5	82	0	0	2	7
Mytilus edulis	0	0	0	0	0	0	0	0	0	0	4	77
Nassarius sp.	0	0	0	0	0	0	0	0	0	0	0	0
Ruditapes sp.	12	1146	62	6582	20	1148	32	2632	12	617	29	2493
Scrobicularia plana	14	9	154	591	17	44	61	223	0	0	62	1629
Tellina tenuis	0	0	0	0	0	0	2	12	0	0	4	82
Gastropoda	**30**	**49**	**104**	**188**	**473**	**565**	**36**	**116**	**29**	**4**	**327**	**299**
Akera bullata	5	16	22	62	0	0	7	21	0	0	21	69
Cyclope neritea	3	7	6	14	0	0	2	5	0	0	2	112
Hydrobia ulvae	22	26	73	95	468	491	24	32	29	4	302	106
Littorina littorea	0	0	3	17	5	74	2	58	0	0	2	12
Gastropod sp.	0	0	0	0	0	0	1	0	0	0	0	0
Annelida	**195**	**1060**	**512**	**1071**	**374**	**1435**	**674**	**1625**	**92**	**608**	**339**	**1688**
Alitta succinea	0	0	3	14	0	0	1	5	0	0	2	9
Ampharete acutifrons	0	0	0	0	0	0	0	0	0	0	0	0
Arenicola marina	2	49	0	0	2	49	2	76	6	197	10	484
Capitella capitata	2	1	0	0	0	0	0	0	0	0	0	0
Capitellidae sp.	3	1	180	72	2	1	63	25	0	0	53	21
Cirriformia tentaculata	2	11	9	69	0	0	3	23	0	0	25	183
Eteone longa	3	17	3	17	5	25	1	6	12	68	4	23
Capitomastus minima	2	1	0	0	0	0	0	0	0	0	0	0
Eteone picta	2	0	31	6	0	0	10	2	0	0	6	1
Glycera tridactyla	2	5	9	31	3	10	16	56	0	0	8	28
Hediste diversicolor	12	33	83	188	5	7	32	72	0	0	117	204
Heteromastus filiformis	8	28	22	79	0	0	10	37	0	0	2	7
Lagis koreni	2	2	3	4	0	0	1	1	0	0	16	21
Magelona sp.	0	0	0	0	0	0	1	9	0	0	0	0
Maldanidae sp.	3	9	3	9	0	0	2	6	0	0	0	0
Marphysa sanguinea	3	278	0	0	0	0	0	0	0	0	4	370
Mediomastus fragilis	9	4	0	0	0	0	0	0	0	0	0	0
Melinna palmata	3	0	6	0	0	0	2	0	0	0	0	0

Nephtys assimilis	0	0	0	0	2	0	0	0	0	0	0	0
Nephtys cirrosa	0	0	0	0	2	10	0	0	0	0	5	27
Nephtys hombergii	19	163	15	141	11	96	16	84	31	236	41	253
Nephtys sp.	0	0	0	0	5	9	3	6	0	0	0	0
Notomastus latericeus	82	402	74	364	3	15	30	147	12	61	2	10
Owenia fusiformis	17	19	46	52	8	9	17	20	19	20	21	24
Phyllodoce mucosa	3	6	0	0	3	6	0	0	12	26	0	0
Scoloplos armiger	12	12	25	25	323	1198	462	1045	0	0	23	23
Spiochaetopterus sp.	2	13	0	0	0	0	0	0	0	0	0	0
Streblosoma bairdi	2	6	0	0	0	0	0	0	0	0	0	0
Oligochaeta	0	0	0	0	0	0	2	5	0	0	0	0
Nemertea	**6**	**99**	**3**	**49**	**5**	**74**	**3**	**49**	**19**	**296**	**0**	**0**

Foraging habitat selection

Eleven habitats were identified and delimited on the intertidal areas of both study areas, with marked differences between ‘La Loge’ and ‘Fier d’Ars’ (Fig. 6). On ‘La Loge’, two habitats of intertidal muddy sand (A2.242 and A2.231; Eunis Typology) and one habitat of barren littoral coarse sand (A2.221) were described. Outside the ‘Fier d’Ars’ a last type of intertidal habitat, mainly composed of rocky elements, was represented on the area of ‘La Loge’ composed by littoral rockpool communities: A1.41 (Fig. 6a). The ‘Fier d’Ars’ was muddy prevailing facies, largely dominated by seagrass beds on muddy sand (A2.6111) and oyster parks on muddy foreshore (A2.32). The rest of intertidal areas on ‘Fier d’Ars’ was characterized by bare muddy sand habitats (A2.242 and A2.313) and rocky habitats (A1.11 and A1.4; Fig. 6b).

There was a strong habitat selection by the six godwits ($\chi^2 = 86441.52$, df = 54.0, $p < 0.001$) and habitat selection was not identical among all individuals ($\chi^2 = 9618.85$, df = 45.0, $p < 0.001$; Supplementary material Table S3). Three habitats were preferentially used by females: seagrass beds in muddy sand (A2.6111) dominated by polychaetes, oligochaetes and molluscs; sandflat dominated by *C. edule* and polychaetes (A2.242); and Mudflat dominated by *H. diversicolor* and *S. plana* (A2.313; Global Selection Ratios > 1; Fig. 7, Supplementary material Fig. S3). Conversely, the habitats of muddy sand dominated by polychaetes *Nephtys cirrosa* and *S. armiger* (A2.231), fucoids on sheltered marine shores (A1.31) and oyster parks (A2.32) were globally avoided (Global Selection Ratios < 1), but confidence intervals indicate their marginal use by some few birds (Fig. 7, Supplementary material Fig. S3). The four remaining habitats were clearly avoided (Global Selection Ratios and IC < 1).

The Eigen analysis highlighted that two factors mainly explained the habitat selection, with 90.2% of information explained by the first axis and 6.2% by the second one. The results show that birds much more frequently used habitats A2.6111, A2.242 and A2.313. BTG01, BTG03 and BTG06 used preferentially the seagrass beds (A2.6111; Fig. 8), BTG04 favored sandflat (A2.242), and BTG02 and BTG05 did not selected one specific habitat but combined the use of A2.611, A2.242 and A2.313 (intertidal muddy sand dominated by *H. diversicolor*, *M. balthica* and *S. plana*). Without highlighting groups of birds, the Eigen analysis underlies a variability in habitat selection between individuals, with a 'continuum' along the second axis between habitats A2.6111, A2.242 and A2.313. Differences in the proportion of each habitat in the FCA confirmed a specific pattern of habitats combination for each individual, all-different from each other (Fig. 7).

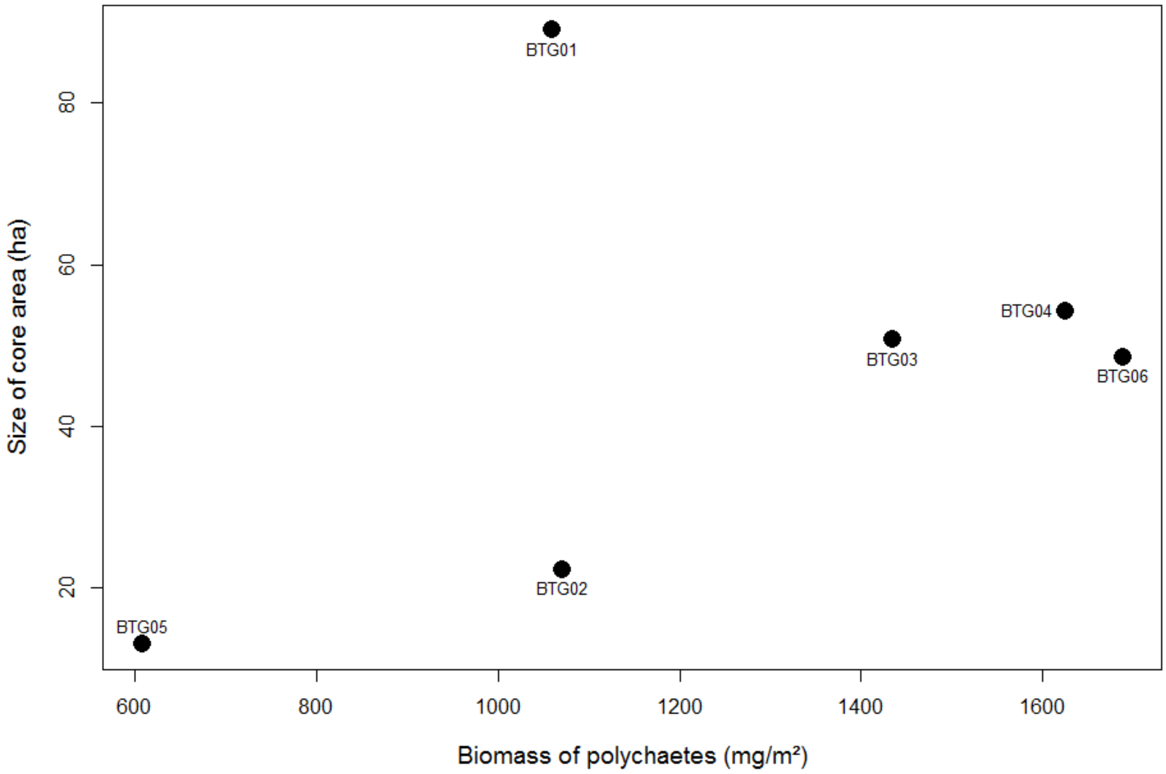

Fig. 5 Size of individual Feeding Core Area (FCA – core area) as a function of the mean polychaete biomass at each individual core area.

Discussion

This study on bar-tailed godwits, enabled by GPS tracking technology recently adapted to medium size shorebirds, highlighted the individual use of foraging patches during the almost entire non-breeding period, sometimes consistent from year to year, and showing a specific combination of habitats used among all suitable ones. Although our analysis was based on six birds, thus calling for further research to strengthen our conclusions, it underlines the high fidelity of some individuals of godwits to their feeding grounds during the non-breeding period. Indeed, on a small wintering site, tracked godwits were restricted to small foraging areas and did not exploit all suitable areas. In addition, at least three of the six monitored birds used the wintering site for two consecutive years, and with a high fidelity for their respective foraging home ranges. It also demonstrates a specific combination of foraging habitats used by each bird monitored, supporting the idea of a specialization on preys at the individual scale (Sutherland et al. 1996; Durell 2000). Previous studies showed that during winter, godwits feed predominantly on worms, wherever their distribution along the European costs (Evans 1976; Scheiffarth 2001; Duijns et al. 2013). On Ré Island, other studies confirmed a diet largely composed of worms, whether on the site of ‘La Loge’ or ‘Fier d'Ars’ (Aubouin 2014; Bocher et al. 2014; Duijns et al. 2014). Consequently, the spatial distribution of birds on mudflats could be linked to a specialization on feeding habitats, and more precisely on particular species of annelids, the largely dominant prey in their diet.

Adult godwits were overwintering on Ré Island between August and March. The peak number of birds at the study site was observed in mid-January, with a mean of 641 ± 85 individuals (over the period 2000-2016). Considering a total feeding functional area estimated to 900 ha on Ré Island (Aubouin 2014), the density of godwits on the island is then estimated to ca. 0.7 individual.ha^{-1} in the middle of winter. This density is the highest (by 2 to 7 times) of the four main wintering sites located inside the Pertuis Charentais area: Aiguillon Bay (0.3 ind.ha^{-1}), Yves Bay (0.1 ind.ha^{-1}) and Marennes-Oléron Bay (0.3 ind.ha^{-1}). The mean godwit densities measured in the Dutch sectors of Wadden Sea was estimated to 9.5 ± 1.5 ind.ha-1 in May (Duijns and Piersma 2014) and around 1.5–4.5 ind.ha-1 between July and September (Folmer et al. 2010, van den Hout and Piersma 2013). During these pre- and post-migration periods, both subspecies are present and denser than during the winter period. Therefore, although the carrying capacity appears lower than observed at other times of the year in the Wadden Sea, the site of Ré Island seems to offer habitats of good quality for godwits at the

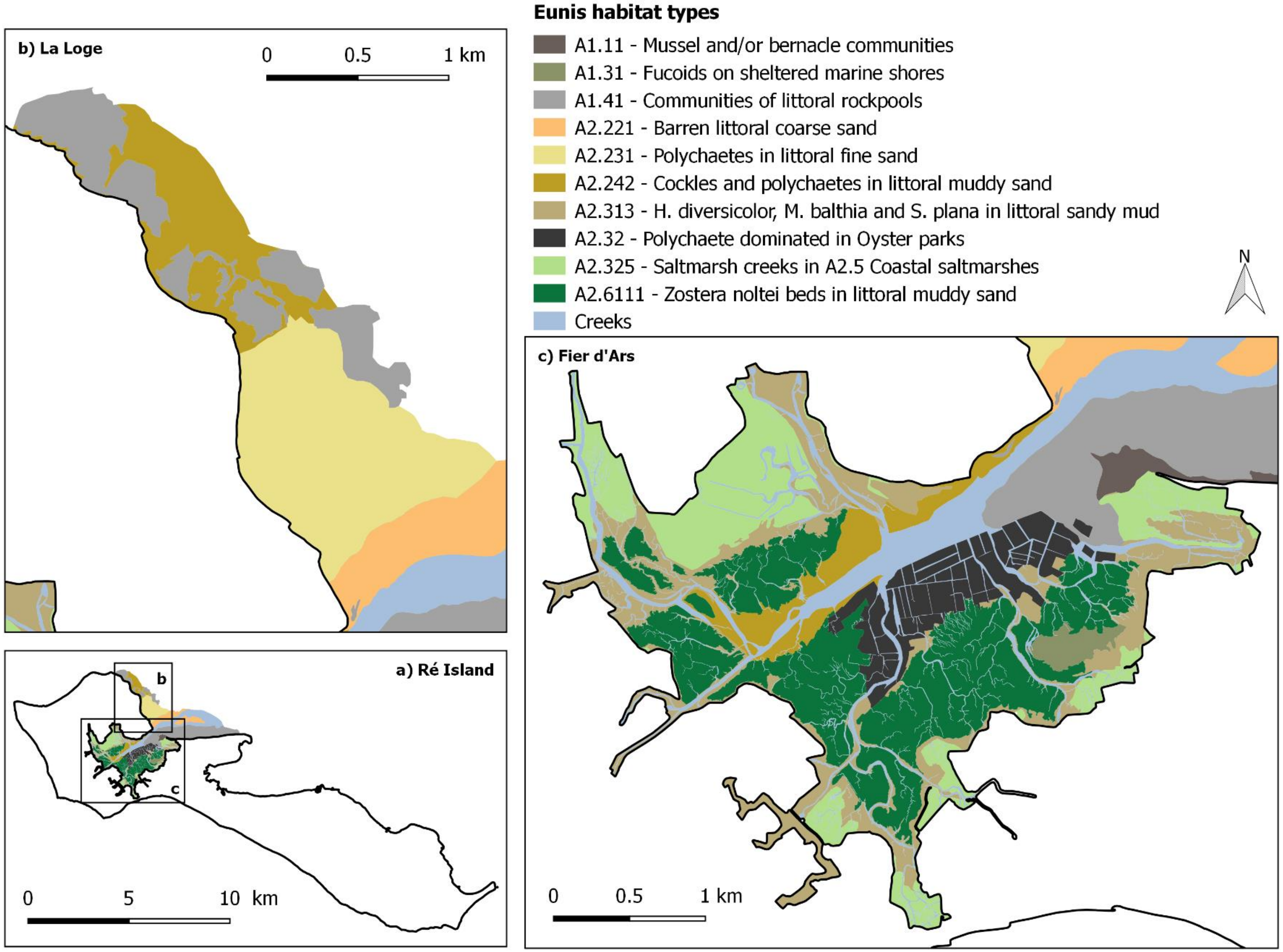

Fig. 6 Habitat typology at **(a)** Ré Island, **(b)** ‘La Loge’ and **(c)** the ‘Fier d’Ars’.

local scale. More specifically, despite the restricted surface of sand and mudflat areas, the quality and availability of trophic resources on Ré Island appear high enough to allow high bird densities. The observed fidelity of individuals to their feeding grounds on such a small site with a patchwork of diversified habitats suggests that birds specialize in prey species to maintain sufficient energy intake rates and ensure their survival (Catry et al. 2014; Ceia and Ramos 2015). Indeed, such a specialization could reduce intraspecific competition and restrict individuals to specific FCA, explaining the low overlap observed (48%) between our tagged birds (Kouba et al. 2017). A higher number of birds monitored would most likely have resulted in an increased overlap between individual FHR. This is supported by the density of birds observed on site during the winter, especially on 'La Loge' were godwits are usually observed in flocks, unlike in the 'Fier d'Ars' (P. Bocher, *Pers. Com.*). Nevertheless, the distinct feeding distribution observed on six birds using the same roosts confirms the non-gregarious pattern of foraging godwits, at least inside the 'Fier d'Ars'.

In addition to use the same restricted feeding areas during the non-breeding period, godwits which provided locations for two consecutive winters (n=3) showed a high inter-annual overlap in their FHR. Previous studies have reported fidelity of shorebirds to their non-breeding site but only a few highlighted faithfulness to specific feeding and roosting sites, both within and between winters (Conklin and Battley 2011; Coleman and Milton 2012). Based on GPS telemetry, our study help to fill this gap at the patch scale. Indeed, in this study we show a high fidelity of godwits to their roosting and feeding home ranges, with a less marked but still important inter-annual fidelity to feeding core areas. This highlights the abilities of godwits to specialize on particular set of foraging habitats, and calls for future research studies to explore the high degree of individual specialization on preys, all along their life in long-lived species such as shorebirds.

Our results also highlight that the surface of wintering home ranges for godwits wintering on Ré Island was small (< 600 ha) in comparison to others shorebirds species as dunlin *Calidris alpina* and red knot *Calidris canutus.* For instance, the home range of dunlin ranged from 1,080 to 56,470 ha according to the study area (Sanzenbacher and Haig 2002; Shepherd and Lank 2004; Taft et al. 2008; Choi et al. 2014) and the home range of red knot could range from 1,000 to 80,000 ha (Piersma et al. 1993; Leyrer et al. 2006). This large home range size variability among dunlin and red knot are due to differences in habitats and feeding conditions (Piersma et al. 1993; Choi et al. 2014). Nevertheless, these species foraged in large

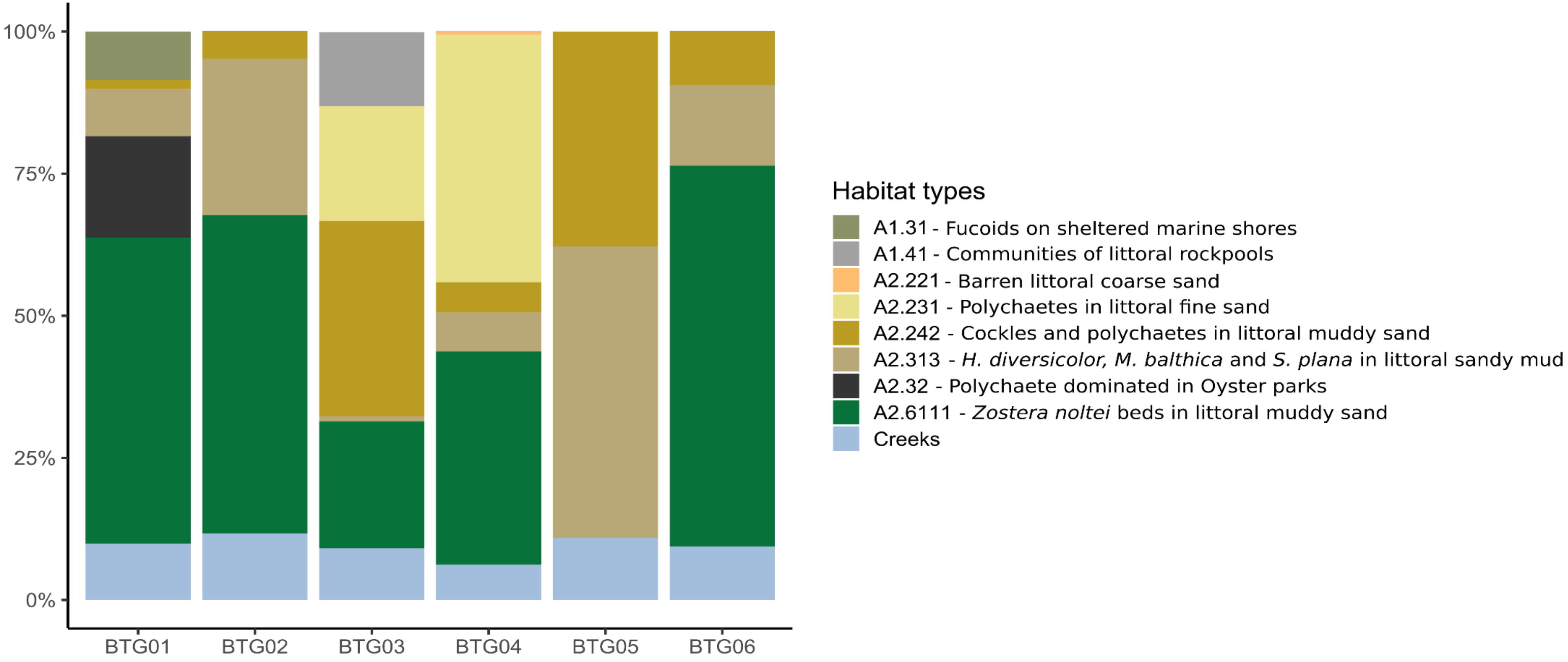

Fig.7 Proportion of habitat types in Feeding Core Area (FCA) of each bar-tailed godwit. The FCA estimated through the kernel method, was crossed with the typology of habitats, and give the surface proportion (%) of each habitat in this main spatial delimitation of foraging. This description of represented habitats inside the FCA is a proxy of the foraging habitat selection by each godwit.

flocks and birds moved according to group decision from one place to another (van Gils et al. 2015). Among close related species of godwit, the feeding home range of the marbled godwit *Limosa feoda* was estimated to 672 ha on Larnack Reef, a stable island near a highly dynamic intertidal area (Gulf of Mexico, Gabbard et al. 2001). In this study, the home range estimation was produced with minimum convex polygons, which differ from our method (kernel home range), but the order of magnitude is more similar to our results. FHR of godwits wintering on Ré Island thus appeared spatially restricted, reinforcing the idea of bird fidelity to their foraging areas and a supposed specialization on foraging habitats and prey species at the individual scale at Ré Island.

Estimation of FHR also showed a strong variability between individuals with low overlaps highlighting distinct areas prospected by godwits, while RHR showed a large mean inter-individual overlap (69%). Roost sites located at Western side of the study site mainly corresponded to former saltpans inside the Nature Reserve ('Lilleau des Niges'), known to hold most of the shorebirds at spring high tide (J-C. Lemesle, *Pers. Com.*). Roosting areas located at the Eastern side are not protected, and birds no longer use them during high water levels of spring tide. The alternating use of these roosts likely depends on the accessibility during the tidal cycle, as the roosts at Eastern side are located closer to the foraging sites. The short distances between roosting and feeding grounds could be one of the main factors driving the spatial distribution of wintering shorebirds (Morrison and Harrington 1979), reducing flight distance and associated loss of energy and predator exposure (Si et al. 2011; Novaes and Cintra 2013). Our results suggest similar processes in godwits on Ré Island. Feeding patterns identified in our study confirm that godwits start to feed between two and three hours after high tide, present on feeding areas for four to six hours before to join roosting areas (Lindisfarne, Northumberland – England; Smith and Evans 1973). Despite spatially restricted home ranges, godwits devote almost all of their time for foraging (>85%) during the complete access to mudflats, both day and night. This result suggests that birds have to optimize prey collection throughout their accessibility to achieve a sufficient intake rate and satisfy their energy needs.

Beyond the time spent foraging and according to the optimal foraging theory, godwits are predicted to optimize their prey intake rate by selecting specific feeding habitats of higher quality (Evans 1976). Godwits preferentially used three of the 11 identified habitats in our study site. Three birds preferentially selected habitat associated with eelgrass beds (A2.6111) where annelids abundance is high. Habitat composed mainly of *C. edule* and polychaetes (A2.242), and habitat composed mainly of *H. diversicolor*, *M. balthica* and *S. plana* (A2.313), were also selected by most of the birds. The inter-individual variability observed in habitat selection reinforces the hypothesis that individuals may specialize in particular polychaete prey species to limit competition (Durell 2000) and/or optimize intake rate by experience on catching abilities on particular prey species (Bolnick et al. 2003). Selection of specific prey or substrates could also explain the differences observed in the size of feeding core areas. However, and conversely to our hypothesis, our results did not show a significant negative relationship between the biomass of polychaetes and the size of bird feeding areas. An alternative hypothesis is that polychaete intake rates could not directly reflect worm abundance but rather the availability and catchability of certain species in the sediment. Thus, it could be more difficult for birds to extract polychaetes in some habitats due to the worm depth or the substrate hardness (Finn et al. 2008), or due to prey behavior (Duijns and Piersma 2014), which would lead to an increased foraging and prospecting effort in order to achieve sufficient intake rates to fulfill bird daily energy requirements.

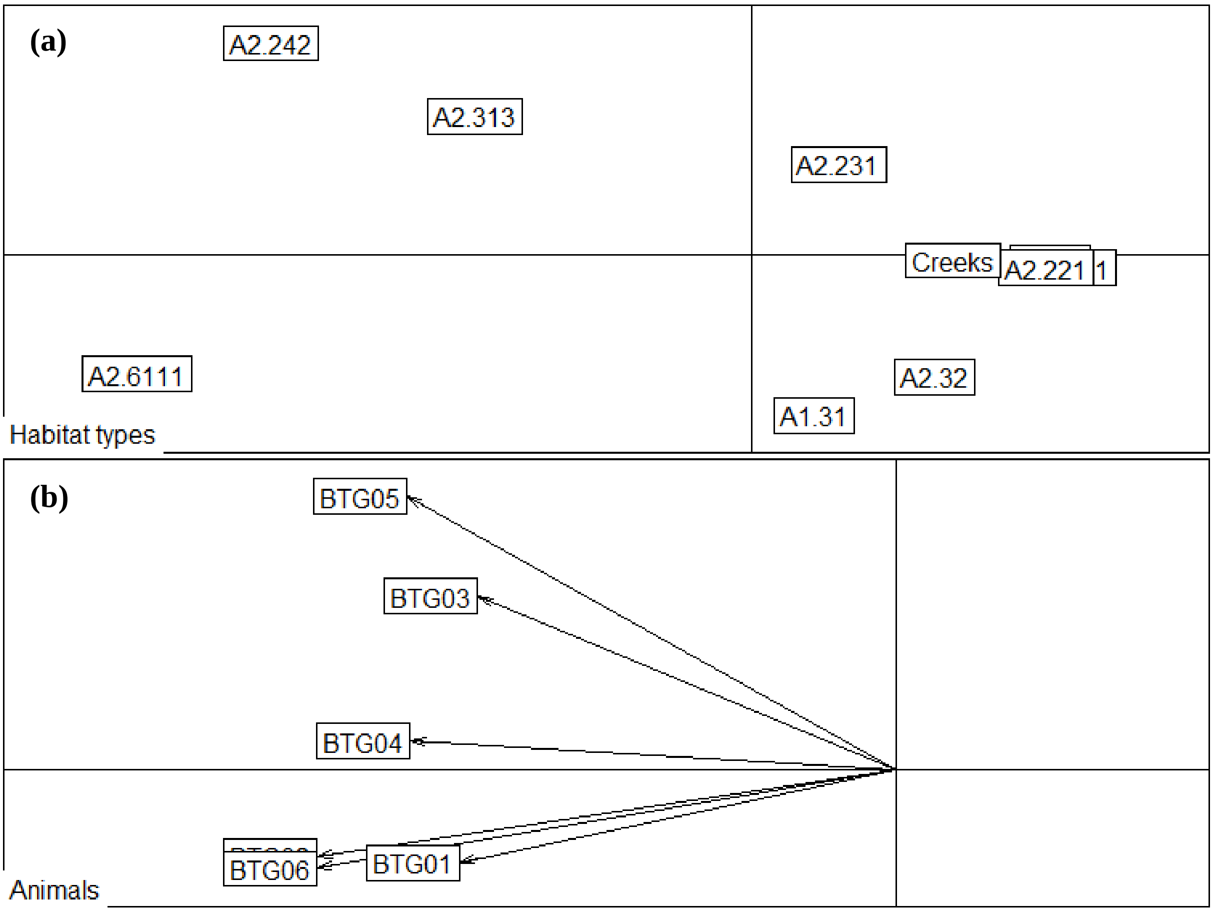

Fig. 8 Results of the Eigen analysis of selection ratios highlighting habitat selection by six bar-tailed godwits on 11 habitat types. **(a)** Habitat types projected along the first two factorial axes and **(b)** Bird scores on the first factorial plane. The analysis produced two factors (the two axis) to explain the heterogeneity of habitat selection. These two factors constitute the first factorial plane on which the habitats, which compose it, are projected, and birds are positioned in this plane described by habitats.

This study was carried out on female adults only, and results cannot be extrapolated to males. Indeed, a large sexual dimorphism exists in godwits with females being on average 1.25 times larger than males, leading to contrasting foraging strategies (Pierre 1994; Duijns et al. 2014). Similarly, juveniles show a lack of experience when arriving for the first time on unknown wintering site which might affect their foraging behaviour and habitat use (Durell 2000; van den Hout et al. 2014). Further investigations performed on different stages and including both sexes will thus be required when the miniaturization of GPS data logger will be improved, in order to have a complete understanding of wintering strategies in this Near Threatened species (BirdLife International 2017).

Bird specialization on particular prey or habitats implies knowledge of their distribution and the way to exploit those (Bolnick et al. 2003). Individuals can optimize their movement and maximize their foraging gain ratio. Thus, important changes in the quality and distribution of trophic resources, under the effect of anthropogenic disturbances, could modify bird energy intakes and jeopardize their winter survival and subsequent migration and reproduction (Gunnarsson et al. 2006). In a context of rapid environmental modifications of coastal habitats (Ivajnšič et al. 2018; Leo et al. 2019), expected degradations could result in an increased competition for the remaining resources. Consequently, any increase in bird density may have a marked effect on these habitats and individuals with specialized diet and feeding methods will be the first impacted, particularly if they are of lower social status (Durell 2000). This study thus confirms the importance of maintaining a good quality of wintering habitats, especially on intertidal habitats facing high human pressures such as professional or recreative on-foot fishing, roost-disturbing hunting activities, nautical activities and tourism.

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Supplementary material

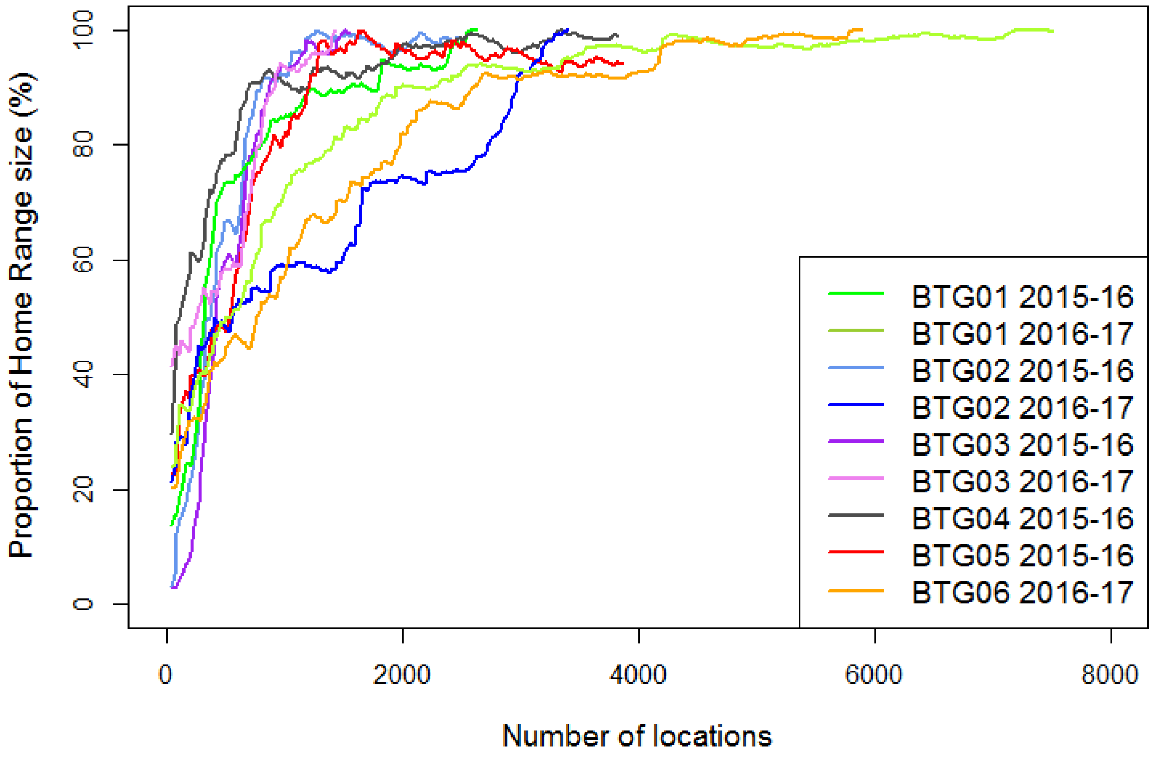

Fig. S1 Estimation of home ranges size (kde 95%) per individual and per year according to the number of locations recorded.

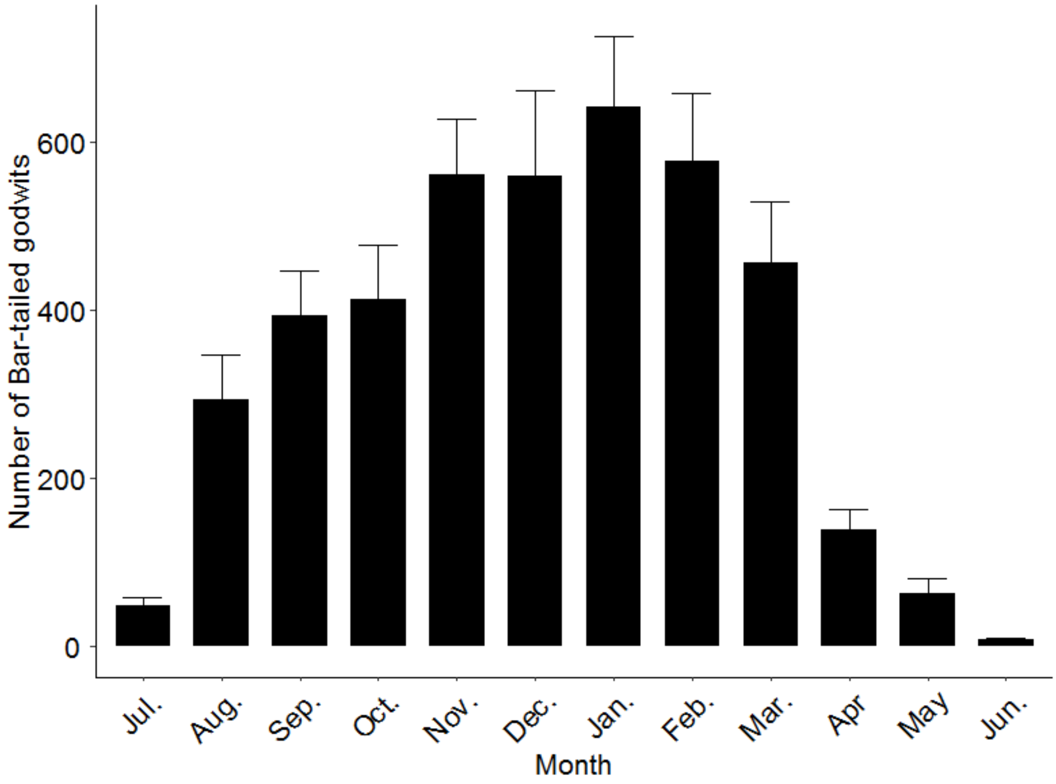

Fig. S2 Monthly mean abundance (± SE) of bar-tailed godwits on Ré Island (2000-2016).

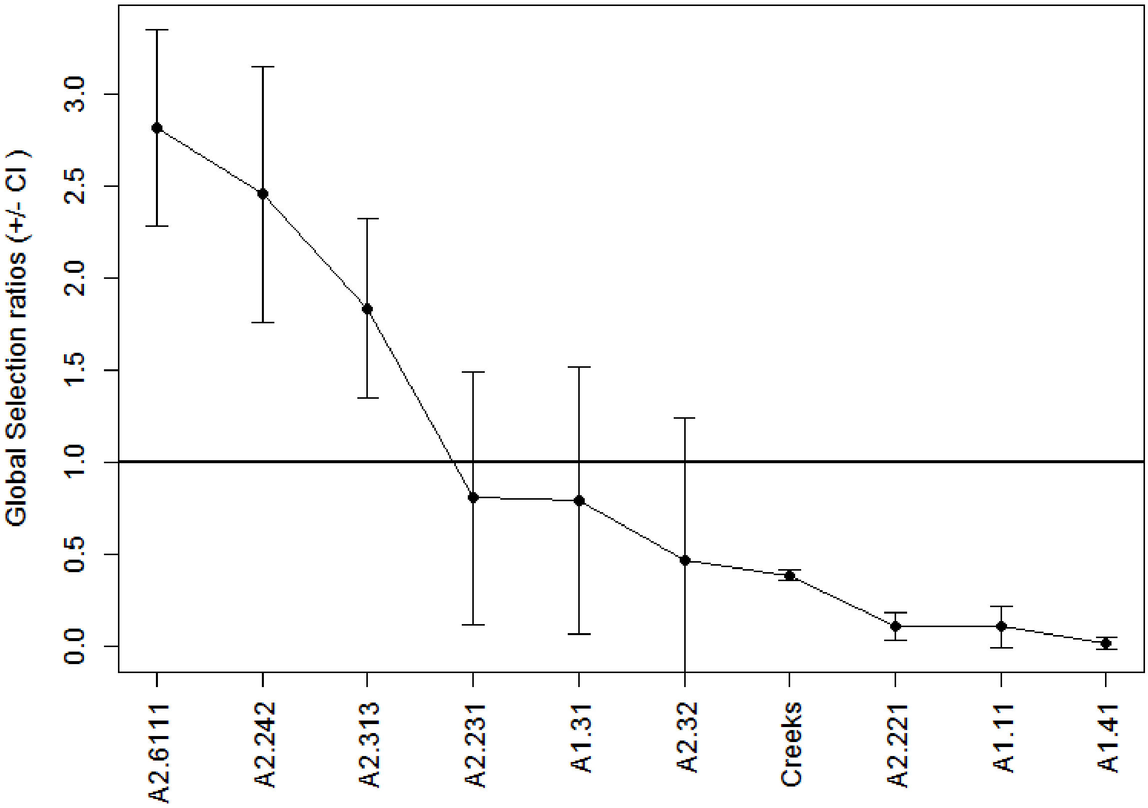

Fig. S3 Global selection ratios (+/- CI) for six bar-tailed godwits for 10 habitats types, using Manly's selectivity measure.

Table S1 Size of the wintering Feeding Home Range (FHR) and Feeding Core Area (FCA) per bird, in 2015-2016 and 2016-2017, and inter-annual overlap by individual.

Logger ID	FCA_{1516} *(ha)*	FCA_{1617} *(ha)*	*%* FCA_{1617} *in* FCA_{1516}	FHR_{1516} *(ha)*	FHR_{1617} *(ha)*	*%* FHR_{1617} *in* FHR_{1516}
BTG01	69	73	55	478	408	83
BTG02	22	34	16	363	232	71
BTG03	51	49	63	287	297	74

Table S2 Inter-individual overlap (%) of the Feeding Home Range (FHR).

	BTG01	***BTG02***	***BTG03***	***BTG04***	***BTG05***	***BTG06***
BTG01	-	39	37	47	22	26
BTG02	39	-	28	40	23	37
BTG03	37	28	-	46	36	20
BTG04	47	40	46	-	28	30
BTG05	22	23	36	28	-	22
BTG06	26	37	20	30	22	-

Table S3 Manly's selection ratio of the six bar-tailed godwits for the 10 available feeding habitats.

Logger ID	***A1.11***	***A1.31***	***A1.41***	***A2.221***	***A2.231***	***A2.242***	***A2.313***	***A2.32***	***A2.6111***	***Creeks***
BTG01	0.00	1.59	0.00	0.12	0.08	2.26	1.79	0.02	3.41	0.40
BTG02	0.27	0.00	0.10	0.18	1.82	3.09	1.74	0.06	2.13	0.37
BTG03	0.16	1.44	0.03	0.12	1.02	1.77	1.44	1.48	2.80	0.39
BTG04	0.18	0.70	0.01	0.18	1.25	2.18	2.00	0.05	2.79	0.37
BTG05	0.00	0.00	0.00	0.03	0.55	3.90	3.05	0.00	1.97	0.47
BTG06	0.00	0.33	0.00	0.00	0.03	2.49	1.51	0.71	3.41	0.36

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Chapter 2

Landscape supplementation in wintering black-tailed godwit allowed by quick shifts between marine and freshwater artificial habitats

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Abstract

At the landscape scale, animals distribute according to the spatial distribution of resources, including both substitutable and non-substitutable resources. The distribution of the non-substitutable resources is supposed to best explain the animal landscape use, so that the distance between patches of non-substitutable resources defines the level of landscape complementation. In shorebirds, after feeding on exposed mudflats, high tide roosts appear as non-substitutable resources on which birds depend for their winter survival. Beyond the 'landscape complementation', some species also show a 'landscape supplementation' consisting in the use of resources from different landscape elements, including different habitats types, in order to supplement their food intake rate. Migratory shorebirds, which have an energy-intensive lifestyle, must replenish their body reserves during the winter and ensure their survival. Hence, birds have to select wintering habitats providing the best net energy gain per unit of time, also considering the possible disturbances, predation risks, competition and resource depletion. Different foraging strategies can then emerge between species or individuals, with different degrees of site-fidelity, resulting in different distributions and movement patterns. By analysing the movements of 10 wintering black-tailed godwits (*Limosa limosa islandica*) monitored by GPS telemetry, our study aims to understand and describe their spatiotemporal use of wetlands, threatened habitats subject to major modifications. Obtained results highlighted a high plasticity of black-tailed godwits in term of habitat use. All godwits monitored used more than one site during the survey period, with site shifts at both small and large spatial scales, and showed the use of multiple habitat types within sites. Indeed, although a dominant use of intertidal areas was observed, birds highlighted seasonally and daily habitats shifts to prospect on inland marshes, saltpans and hunting ponds, with a rhythm of activity depending on the habitat. Finally, results support the importance of the protected areas and the management of artificial wetland habitats to ensure the preservation of high quality wintering areas for godwits.

Keywords: Avian ecology, GPS tracking, Habitat use, Landscape Complementation, Wintering period, *Limosa limosa*

In prep.

Introduction

The way animals use a landscape is undoubtedly influenced by the spatial distribution of their resources in heterogeneous environments (McIntyre and Wiens 1999; Illius and O'connor 2000; Roshier et al. 2008; Masello et al. 2017). At the landscape scale, resource limitation can result from the spatial distribution of patches and their intrinsic quality (Dunning et al. 1992; Mitchell and Powell 2004). Even if foraging resources are most of the time substitutables, animals also depend on non-substitutable resources for their survival at the level of the landscape, such as nesting sites for reproduction (Hansson et al. 2014; Michel et al. 2017), refuge from predators (Hamel and Côté 2007) or roost during high tide for shorebirds (van der Kolk et al. 2020). Landscape complementation is defined when non-substitutable resource patches are sufficiently close to one another for animals to successfully exploit them. The distance between patches of non-substitutable resources defines the level of landscape complementation of an area (Dunning et al. 1992). Consequently, animals will select areas with higher complementation to reduce travelling costs between non-substitutable areas. For instance, shorebirds depend on roosts at high tide after exploiting emerged intertidal areas (Rogers et al. 2006). Nevertheless, some species are able to supplement their food intake by using resources from different landscape elements with patches made of different habitats in the surrounding matrix, a process named 'landscape supplementation' (Dunning et al. 1992).

In migratory shorebirds, most of their annual cycle is taken away from breeding areas, generally in freshwater wetlands or coastal marine areas. Subsequently, the availability and suitability of these wetlands and their management strongly influence their survival and *in fine* their population dynamics (Ma et al. 2010). During the wintering period, shorebirds must restore body reserves lost during the breeding season and migration and must maintain sufficient reserves for ensuring winter survival (Morrison and Hobson 2004; Zwarts et al. 1990). In order to ensure winter survival, individuals would have to select the habitat and secondarily patches that provide the highest net gain of energy per time unit (Ge et al. 2006). Moreover, other factors as predation risks, human disturbances, site fidelity and social interactions may influence habitat selection during the wintering period (Yasué 2005; Folmer et al. 2010; van den Hout et al. 2017). A high degree of site fidelity can make birds more sensitive to local environmental conditions, including human activities, while mobile individual can reduce sensitivity by exploring new sites including possibly substitutable resources in other habitat types (Burger 1986; Martín et al. 2015).

Consequently, individual movements could reveal the mechanisms underlying foraging strategies of shorebirds and their distribution (Pyke 1983). Thus, foraging theory proposes that animals behave in a way that optimizes energy intake (Stephens and Krebs 1986), and Ideal Free Distribution (IFD) concepts predict that predator densities should be positively correlated with prey densities (Fretwell and Lucas 1969). Accordingly, changes in the distribution of predators resulting from large individual movements can reflect underlying differences in the availability or quality of prey between patches and/or habitats. If sites are submitted to temporal or spatial variability in resources availability, individuals must modify their behaviour and are constrained to move away. One important implication of this behavioural response by predators is the modification of distributions and movements, so that individuals move to occupy more profitable foraging areas when prey availability declines or is no longer accessible (Charnov 1976; Pyke 1983; Stephens and Krebs 1986). Predators will increase movement probability and enlarge their home ranges when resources are patchily spatially distributed, ephemerally available or depleted by competitors (Tufto et al. 1996).

Wetlands, used by shorebirds, are among the most threatened habitats on Earth (Ma et al. 2010). Wetland losses through drainage and other transformations have severe consequences for waterbird populations, leading to large-scale redistributions of birds and population declines (Weller 1999; Green et al. 2002). However, the creation of artificial wetlands can reduce the impact of the loss of natural ones. For some waterbird species, well-managed artificial habitats can even be more suitable than nearby natural wetlands, at least for some activities (Masero 2003; Lilleyman et al. 2020). Among shorebirds, the black-tailed godwit (*Limosa limosa islandica*) is a species breeding in Iceland that migrates south to the UK, Ireland, France and Portugal. The vast majority of Icelandic godwits use estuarine bare mudflats or seagrass during the autumn and some individuals move on grasslands during winter (Gill et al. 2007; Robin et al. 2018). In spring, most godwits from Portugal and France migrate to the Netherlands or eastern England, where they forage primarily on grasslands (Gill et al. 2007). At the same time, many godwits from coastal sites around the British Isles coast move inland to forage on flooded meadows (Gill et al. 2007). Studies of energetic intake rates on mudflats and grasslands suggest that godwits move to grasslands when estuarine food supplies are no longer sufficient to support them, and that they frequently use both mudflats and grasslands throughout winter and spring. This seems to be particularly common in the northern part of their range, where estuarine prey are often subject to strong seasonal depletion and where grassland foraging appears to be a necessary addition (Gill et al. 2001b; Jennifer A Gill et al. 2007). Hence, the present study aims to describe and understand the spatiotemporal use of wetlands habitats by Islandic black-tailed godwits during their wintering on the Central French Atlantic coast. To this end, we equipped godwits with GPS loggers, and analysed their movements and habitat use during the wintering survey. We first described the dynamic of individuals by analysing the number of sites used during the monitoring period. Then, after having characterized the typology of main habitats on the study areas, we explored the spatiotemporal habitat use by godwits through identifying, for each monitoring day, the most use habitat by each bird. This also allowed us to assess when birds changed of daily most-used habitat, and how many times over the survey period. Finally, a finer scale analysis aimed to evaluate the daily dynamic of individuals over a short time period, allowing to describe the rhythm of activity and possible habitat shifts within a day.

Methods

Study area

The study was carried out on the Central French Atlantic coast, including, from South to North, the Pertuis Charentais, the Vendee coast and the Loire-Bourgneuf area (Fig. 1). These areas include several functional sites, known to hold most of the non-breeding black-tailed godwits wintering in France.

In the north, the coast around the Loire Estuary (Fig. 1a) offers large intertidal areas for wintering shorebirds. It includes two important proximal roosting sites considered as two distinct functional sites: Bourgneuf Bay (46°58’N, 2°12’W), with roosts located on coastal marshes or upper intertidal area, and Noirmoutier Island (46°59’N, 2°13’W), with roosts located especially inside the National Nature Reserve of Müllembourg marshes. Both roosts recorded together c. 2,000 individuals according to the last Wetlands counts of mid-January (Mahéo et al. 2020). Further north, the Guérande Peninsula (47°17’N, 2°27’W) is another important site for wintering godwits, holding c. 6,200 individuals at last mid-January (Mahéo et al. 2020), characterized by a dominance of saltpans and a small bay with intertidal mudflats and sandflats.

In the south, the Pertuis Charentais (Fig. 1c) offers large intertidal feeding areas for wintering shorebirds, as well as coastal marshes for roosting. Four main wintering sites are identified: Ré Island (46°13’N, 1°30’W), Aiguillon Bay (46°17’N, 01°10’W), Yves Bay (46°02’N, 01°03’W) and Marennes-Oléron Bay (46°55’N, 01˚10’W). These sites are partly

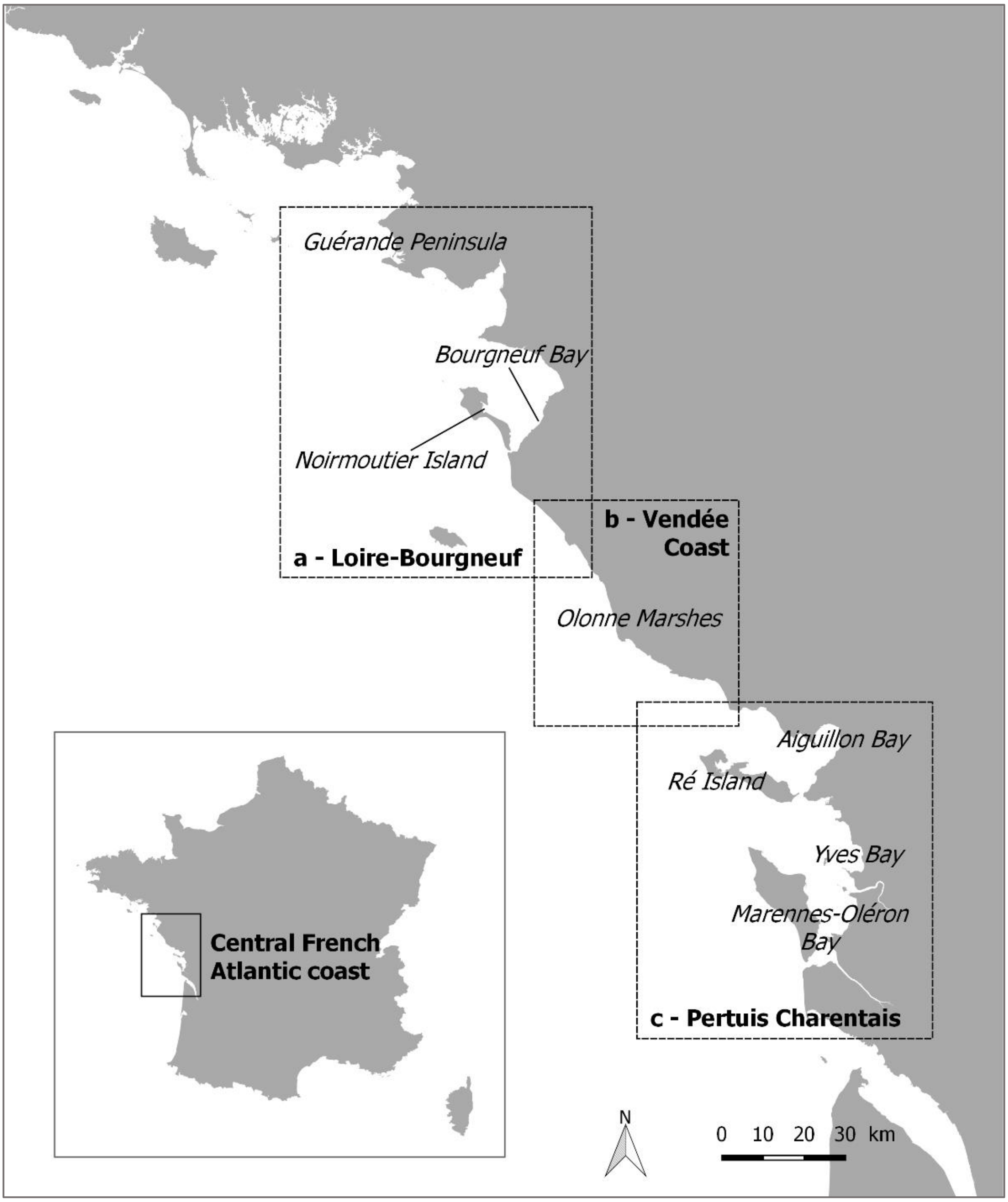

Fig. 1 Map of the Central French Atlantic coast and localization of the study areas: **(a)** Loire-Bourgneuf, **(b)** Vendée coast and **(c)** Pertuis Charentais. Dark gray corresponds to the mainland.

designed as protected area (National Nature Reserve) which generally covers a part of these surfaces. The Pertuis Charentais sites recorded nearly 25,000 wintering black-tailed godwits when combining the last counts of Wetlands survey on Ré Island (3,131 ind.), Aiguillon Bay (12,270 ind.), Yves Bay (106 ind.) and Marennes-Oléron Bay (9,249 ind.) at mid-January (Mahéo et al. 2020).

The Vendée Coast (Fig. 1b), mainly offers high quality sites for shorebirds during the breeding period. Indeed, the region is mainly composed of inland marshes, with wet meadows, and is a part of the Breton marshes known to hold most breeding pairs of black-tailed godwits in France. However, Olonne marshes (46°33’N, 01°47’W; Fig. 1b) are also exploited by wintering godwits, mainly as a transition site between the Pertuis Charentais and the Loire Estuary (only one ind. recorded on Vendée coast during the last mid-Januray Wetlands counts; Mahéo et al. 2020). Most of the coastline is a continuous sandy beach, not favorable to black-tailed godwit during winter.

Habitat description

The distribution and typology of habitats were described at the scale of the three study sites. The CORINE Land Cover data for the regions concerned (Büttner et al. 2012; CGDD - SOeS 2012) have been used to regroup continental habitats and described them in the following main categories: ‘cropping systems’, ‘inland marshes’, ‘coastal marshes’ and ‘saltpans’ (Fig. 2). In coastal and inland marshes, we secondly located and distinguished the hunting ponds, artificial ponds around which are installed “hard” constructions dedicated to accommodate waterbird hunters. Ducks are attracted on ponds and hunted at night between early August and late January. All other continental habitats, not suitable for godwits and known to not be used by birds (e.g. continuous or discontinuous urban areas and forests), were grouped in the ‘other habitats’ category. The distribution of habitats on intertidal areas was characterized according to previous studies on shorebirds. We secondly distinguished two habitats in intertidal areas: ‘bare mudflats’ and ‘seagrass beds’ of *Zostera noltei*, used as feeding habitat at the local scale (Robin et al. 2013). The mapping of study site and spatial distribution of individuals were produced with the software QGIS (2.18, Las Palmas - QGIS Development Team 2016).

Godwit captures and data collection

Between November 2016 and October 2018, several capture sessions of black-tailed godwits were carried out at different wintering sites within the Pertuis Charentais: Ré Island, Yves Bay

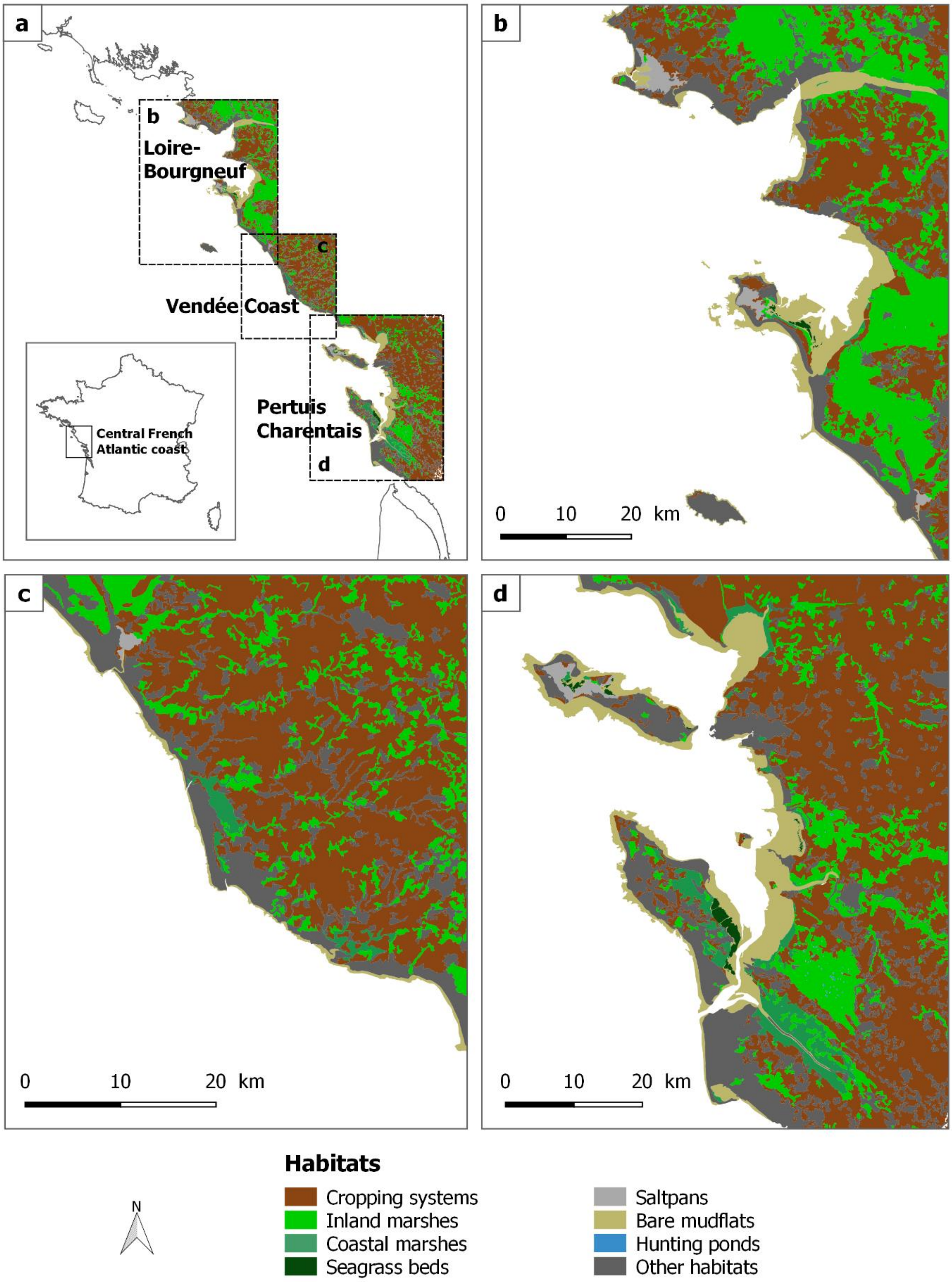

Fig. 2 Habitat mapping in study areas on the Central French Atlantic coast: **(a)** Loire-Bourgneuf, **(b)** Vendée coast and **(c)** Pertuis Charentais.

and Marennes-Oléron Bay. Godwits were caught when they came back from the feeding areas, with mist nets settled on their high tide roosts, inside the nature reserve. Non-moonlight nights were chosen for capturing to minimize the visibility of nets by birds, and maximize the capture possibilities. Once birds were captured, flattened wing length, tarsus length, bill length and body mass were measured using standard methods (Demongin 2016). The sex and age of godwits were also determined, through the allometric equation calculated by Gunnarsson *et al.* (2006) and according to the plumage pattern (Demongin 2016), respectively. Captured birds were then marked with a metal ring and a unique color ring combination. In order to not exceed 3% of the body mass of birds in marking equipment, only heaviest individuals were also fitted with a GPS-VHF tag (STERNA VHF-SRD with solar charger, Ecotone, Gdánsk, Poland; 35 x 16 x 10 mm, 7.5g). The device was fitted on the lower back of godwits according to the 'leg-loop' method (Mallory and Gilbert 2008) and using a 2 mm large Teflon thigh harness. The GPS's time step was set at 30 minutes, although it may vary depending on the sunshine and efficiency of each logger to recharge batteries. The mean accuracy of positioning (according to pre-deployment tests) is ± 10m. Among all birds equipped during these two years of capture sessions, we only retained godwits with at least one month of wintering data on the Central French Atlantic coast. These selected birds should allow to describe the habitat selection by black-tailed godwits during their non-breeding period over a large temporal scale. Hence, the present study focuses on 10 individuals, all monitored during the wintering period but over different periods and with different durations. We therefore do not seek to directly compare individuals, but we rather firstly describe the diversity of habitats used by godwits and their capacities to select them during the winter, and secondly their mobility throughout the Central French Atlantic Coast. Data were stored and processed from a PostgreSQL/PostGIS database, and their exploitation and descriptive analysis were then conducted with the software R (3.6.1, R Core Team 2020).

Habitat use

Over the entire tracking period

For each bird and over their entire tracking period, we considered for each day the dominant habitat among all locations recorded in a day, i.e. among 48 positions for a proper GPS functioning. At this global scale, only the six main gross habitats 'cropping systems', 'inland marshes', 'coastal marshes', 'saltpans', 'bare mudflats' and 'other habitats' were considered without differentiating the sub-habitats 'hunting ponds' and 'seagrass beds' (Fig. 2). The

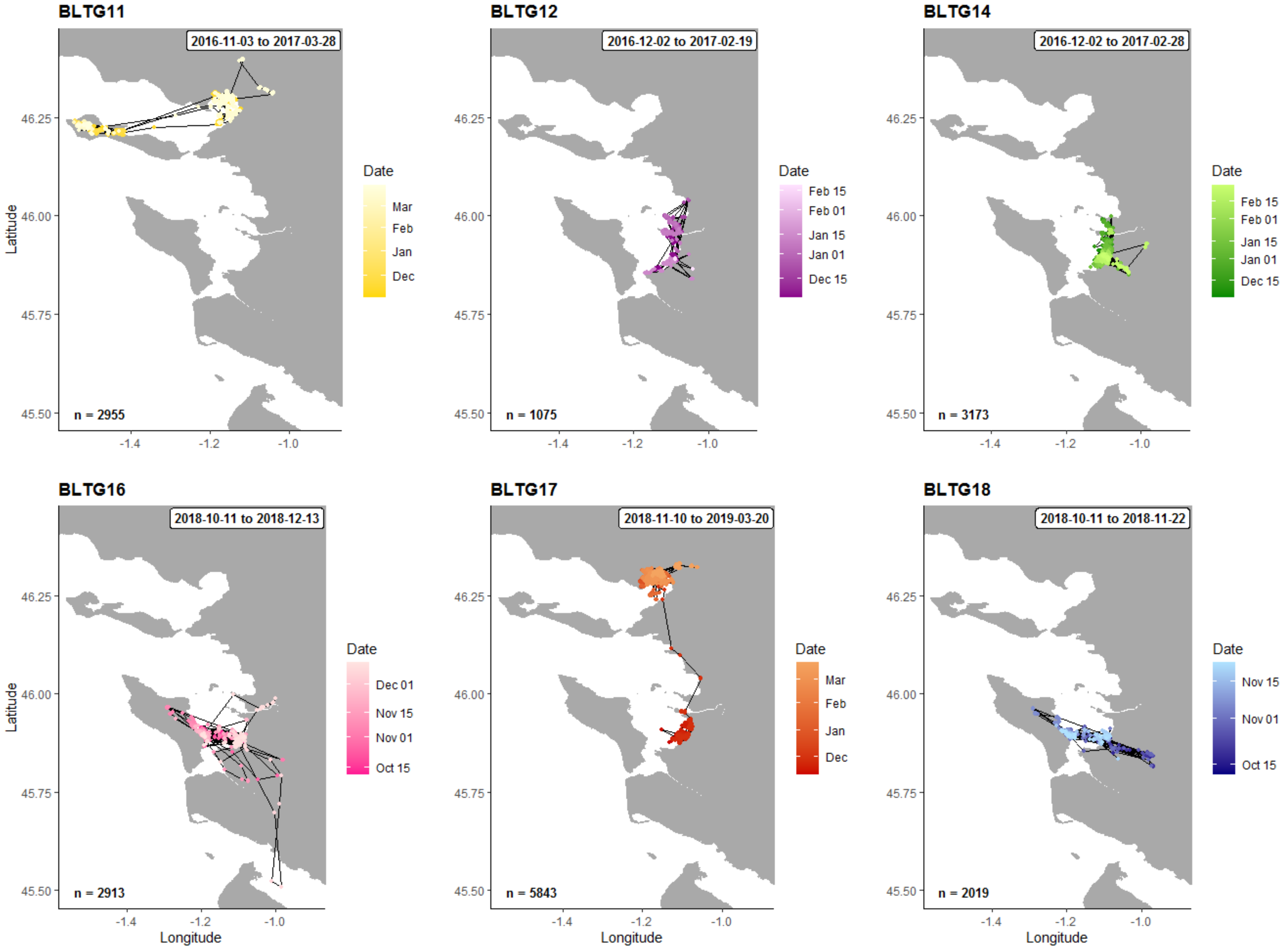

Fig. 3 Distribution and movements of 6 black-tailed godwits (BLTG11, 12, 14, 16, 17 and 18) which stayed in the Pertuis Charentais during their survey period.

missing data periods, as well as the migration/breeding periods for birds concerned, were illustrated in specifics colours**.**

At finer scale

Since day-to-day habitat use underlined the alternation of temporal periods when birds dominantly used one single main habitat, we explored the use of habitats at finer temporal scale considering all positions recorded per day on a period of 14 days. In this fine scale analysis, we distinguished the sub-habitats 'hunting ponds' among inland and coastal marshes and 'seagrass beds' on intertidal area. In order to describe the nycthemeral rhythm of habitat use, we also illustrated the diurnal and nocturnal periods and the tidal amplitude during periods of dominant use of intertidal habitats.

Results

Distribution and movements of birds

The 10 monitored black-tailed godwits provided from 1,075 to 13,115 locations per individuals, over a period ranging from 41 to 440 tracked days (Fig. 3, Table 1).

The six godwits BLTG11, 12, 14, 16, 17 and 18 stayed located inside the Pertuis Charentais area throughout their tracked period and exploited one or two distinct functional sites (20 to 200 km apart), with none to three changes per month according to individuals inside a unique wintering tracked period (Fig. 3, Table 1). Within wintering sites, some birds showed large distributional extent around their main roosts. All of them distributed along the coast, feeding on intertidal areas, but some of them prospected occasionally in a more sustained way in inland habitats.

After a part of the winter spent in the Pertuis Charentais, the four other birds (BTLG 13, 15, 19 and 20) suddenly moved to the north, directly from the Pertuis Charentais to the Loire-Bourgneuf area, or by stopping in Olonne Marshes on Vendée Coast (Fig. 4). BLTG13 and BLTG15, monitored during two successive years, shown some consistency in their distribution extent and their main sites used between their first (BLTG13-1 and BLTG15-1) and second (BLTG13-2 and BLTG15-2) wintering period. BLTG19, a bird equipped as juvenile, did not migrate to reproduce between the two non-breeding periods, and therefore remained a full year in the study areas. However, it migrated to breeding grounds in spring 2020, after its second

Table 1 Occurrence of site and habitat changes, and estimated frequencies per month, for each of the 10 individuals during their respective monitoring period.

			Sites		**Habitats**	
	Period	**Nbr. of tracking days**	**Nbr. changes**	**Changes/month**	**Nbr. changes**	**Changes/month**
BLTG11	2016-11-03 to 2017-03-28	76	4	1.58	9	3.55
BLTG12	2016-12-02 to 2017-02-19	41	4	2.93	4	2.93
BLTG13	2016-11-03 to 2017-10-01	253	4	0.47	50	5.93
BLTG14	2016-12-02 to 2017-02-28	82	4	1.46	16	5.85
BLTG15	2018-08-01 to 2020-01-22	440	24	1.64	78	5.32
BLTG16	2018-10-11 to 2018-12-13	64	2	0.94	9	4.22
BLTG17	2018-10-11 to 2019-03-20	131	1	0.23	12	2.75
BLTG18	2018-10-11 to 2018-11-22	43	0	0.00	6	4.19
BLTG19	2018-10-11 to 2020-04-24	401	16	1.20	81	6.06
BLTG20	2018-10-11 to 2019-02-05	94	4	1.28	25	7.98

winter. For this individual, we chose to not distinguish the two wintering periods since the bird did not leave the study area between both. Finally, BLTG20 only provided data during a part of the wintering period. All four godwits showed a chronology in their use of the different sites, exploiting the Pertuis Charentais in the middle of wintering while they mainly used Loire-Bourgneuf sites during the pre-migration and post-migration periods.

Typology of habitats

Intertidal habitats, coastal marshes and inland marshes are all present on the three study areas ‘Loire-Bourgneuf’ (Fig. 2b), ‘Vendée Coast’ (Fig. 2c) and ‘Pertuis Charentais’ (Fig. 2d). However, intertidal areas on Vendée Coast appear unfavourable since no large mudflats are available; the coast is only composed by sandy beaches. Conversely, the Loire-Bourgneuf area, especially around Noirmoutier Island and Bourgneuf Bay, and the Pertuis Charentais offer large surface of intertidal mudflats (Fig. 1 and Fig. 2). Habitats of ‘seagrass beds’ are found in Loire-Bourgneuf area, mainly restricted to the South-Eastern part of the Bay, and in Pertuis Charentais, widely on Fier d’Ars in Ré Island and Western part of Marennes-Oléron Bay, and in a lesser extent on Yves Bay. The coastline of most wintering sites is dominated by ‘coastal marshes’, in which shorebirds are known to roost. Exploited saltpans are found on Ré Island, Noirmoutier Island and Guérande Peninsula. We can note that Guérande Peninsula offers mainly ‘saltpans’ habitats for shorebirds since only restricted ‘intertidal areas’ are available, and coastal areas are surrounded by ‘cropping systems’ and urban area identified in the category ‘other habitats’. In all study areas, the general pattern of habitats further inland combines ‘cropping systems’ and ‘inland marshes’ in alternation, as well as not suitable ‘other habitats’ as especially observed on both islands. Some large marshes areas are observed in continental areas, with ‘inland marshes’ around Marennes-Oléron Bay (Brouage marshes), Yves Bay (Voutron marshes) and Bourgneuf Bay (Breton marshes), and ‘coastal marshes’ around Marennes-Oléron Bay (Seudre marshes). Otherwise, we note a landlocked ‘coastal marshes’, corresponding to Olonne marshes, which appears to be the unique suitable area for wintering black-tailed godwits in Vendée Coast study area. Finally, hunting ponds are found inside ‘inland marshes’ in very large numbers in the Pertuis Charentais, particularly in the Brouage marshes, as well as in the Breton marshes to a lesser extent.

Habitat use

The analysis of habitat use by godwits highlighted a variability of habitats selected over time. Indeed, at the individual scale, a temporality in the use of habitats clearly appeared for most of

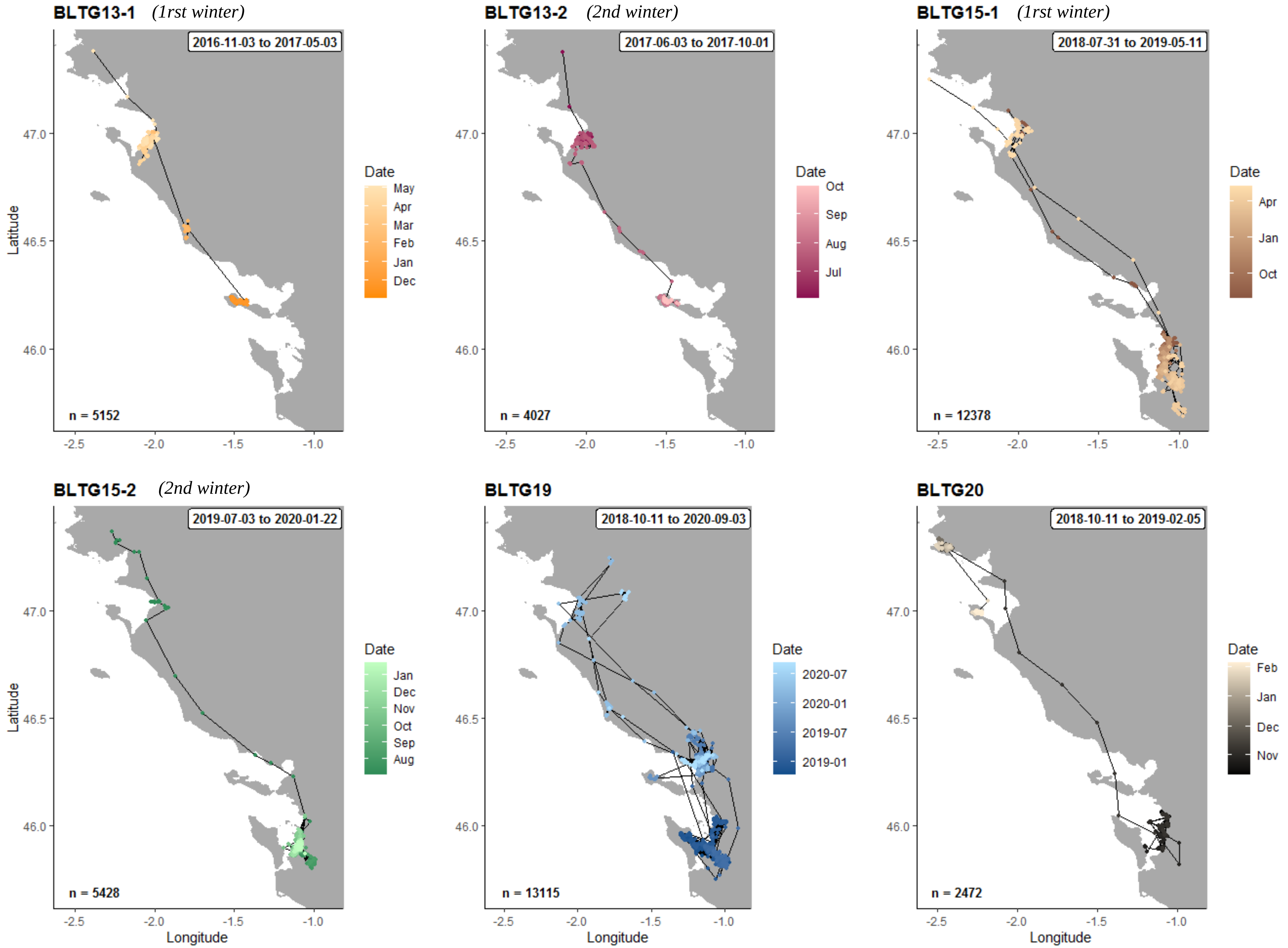

Fig.4 Distribution and movements of 4 black-tailed godwits (BLTG13, 15, 19 and 20) which move away from the Pertuis Charentais during winter.

birds (Fig. 5). Godwits with large datasets especially shown an alternate use of different gross habitats over time. Individuals tracked over a complete cycle, i.e. BLTG13 and BLTG15, have even showed a consistency in the habitat selection at the same time of year over two successive wintering periods (Fig. 5). Even if godwits were not monitored exactly over the same periods, we can examine the use of habitats at the same time of the year for all individuals. Godwits exploited four mains habitats during the non-breeding period, which were ‘bare mudflats’, ‘coastal marshes’, ‘inland marshes’, and ‘saltpans’. Hence, godwits showed an important variability in term of habitat use at their non-breeding grounds. An estimation of the most used habitat changes from day-to-day revealed 5 ± 2 changes/month in average (min: 3, max: 8; Table 1), also suggesting a high dynamism of habitat selection at finer temporal scale.

A focus on habitat selection at a finer scale, i.e. analysing 14 days within periods of a main habitat (‘bare mudflats’, ‘coastal marshes’, ‘inland marshes’, and ‘saltpans’), allowed to describe the exploitation of multiple habitats in a day. During periods of dominant use of intertidal areas (Fig. 6), the in-depth analysis highlighted, for all birds concerned, a successive alternation of mudflats as feeding habitat and marshes as roosting habitat. This pattern was regular over most of the two weeks period. It did not appear to be synchronized with the nycthemeral rhythm since, for instance, the use of mudflats occurred both at day and night. Birds were more likely paced by the tidal rhythm, which constantly evolving from day to day according to tide cycle variations. For three birds (BLTG12, BLTG15 and BLTG17), this alternation between marshes and intertidal mudflats was not obvious during few days, but finally become more visible. It appeared that the tide cycle, and particularly the water level of tides, could explain this change in habitat use, such as lower water height coincided with a possibility to stage on emerged upper intertidal areas at high tide (Fig. 6). All 10 birds presented an alternation pattern between ‘mudflats’ and ‘marshes’, but some birds used preferentially seagrass beds at the expense of bare mudflats as feeding habitats on Ré Island (BLTG 11 and 13) and on Oléron Island (BTLG 16, 17 and 19). Roosting habitats varied between ‘coastal marshes’ and ‘saltpans’ depending on the site.

During periods of a dominant use of ‘inland marshes’ (Fig. 7), no pattern appeared as common to all birds in the rhythm of habitat use. Birds used a multiplicity of habitats over the two weeks selected period, with many changes highlighting a dynamic and disorderly use of habitats for most of individuals. The godwits BLTG14 and 17 showed a kind of consistency in the way they used habitats over time. During the first week, BLTG14 rhythm seemed based on

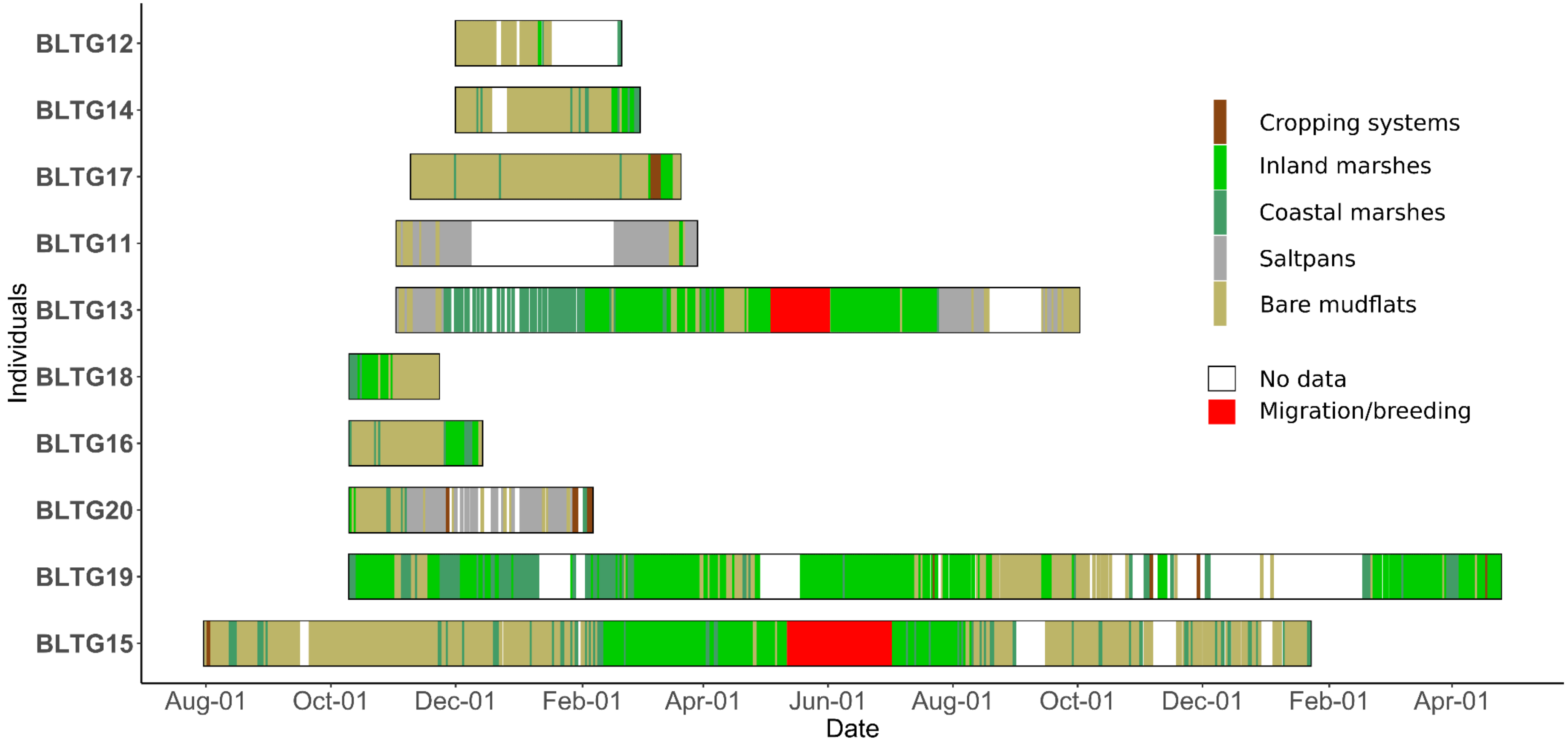

Fig. 5 Representation of the daily most used habitat over time, for each individual, during the entire monitoring period.

the tidal cycle, with alternation of feeding ‘intertidal areas’ and roosting ‘coastal marshes’, but it suddenly changed its behaviour to prospect in both inland and coastal marshes, hunting ponds and intertidal mudflats during the second week. On the other hand, BLTG17 appeared to follow a nycthemeral rhythm over the two weeks presented, using cropping systems at night and inland marshes during the day, although we were not able to distinguish feeding areas from roosts. Moreover, in ‘inland marshes’, godwits also used ‘hunting ponds’ in different time proportion according to individuals. The pattern of use of ‘hunting ponds’ also seemed to depend on the time of the year. Indeed, bird behaviour differed from ‘before’ and ‘after’ the official closing date for waterbird hunting, in late January. During the hunting season (before the end of January), observations in the field showed that godwits mainly used ‘hunting ponds’ occasionally and mainly during daytime (P. Rousseau, *Pers. Com.*), as observed for BLTG18 (Fig. 7). On the other hand, after the hunt closing (after the end of January), birds used ‘hunting ponds’ more intensively and both day and night, such as BLTG15 and BLTG14 (Fig. 7 and Fig. 8a). The distribution of godwits in ‘inland marshes’ (Brouage marshes) also illustrates the dynamic of their habitat use at the patch scale, with the use of many different hunting ponds and meadows (Fig. 8a).

Finally, the finer scale analysis for periods of ‘saltpans’ dominant use underlined a different pattern of use for this habitat, compared to previous observations during a dominant use of ‘bare mudflats’ (Fig. 9). Indeed, BLTG11 (as well as BLTG13), as previously mentioned, used the ‘saltpans’ as roosts on Ré Island, by alternation with intertidal feeding areas (Fig. 6). Here, on Ré Island again, BLTG11 still used intertidal areas, but to a lesser extent and only during the day (Fig. 8), and mainly prospected in ‘saltpans’, thus probably using them both for feeding and for roosting. In the same way BLTG20 exploit the ‘saltpans’ of Guérande Peninsula quasi-continuously for several days. It went from time to time on the intertidal areas, but only during the day. In addition, the day and night locations of BLTG20 underlined a particular pattern, with the use of few specific seawater reservoirs during the day, and a high dispersion on several other points at night (Fig. 8). During field observations on Guérande Peninsula, godwits appeared inactive during daylight, at rest on the upper foreshore or in few specific seawater reservoirs with shallow waters. These observations suggest a nocturnal feeding activity in other seawater reservoirs. The bird did not used directly active saltpans. The same pattern of ‘saltpans’ use is therefore assumed for BLTG11, although fields observations or further analysis are needed to more strongly confirm this behaviour for godwits on Ré Island ‘saltpans’.

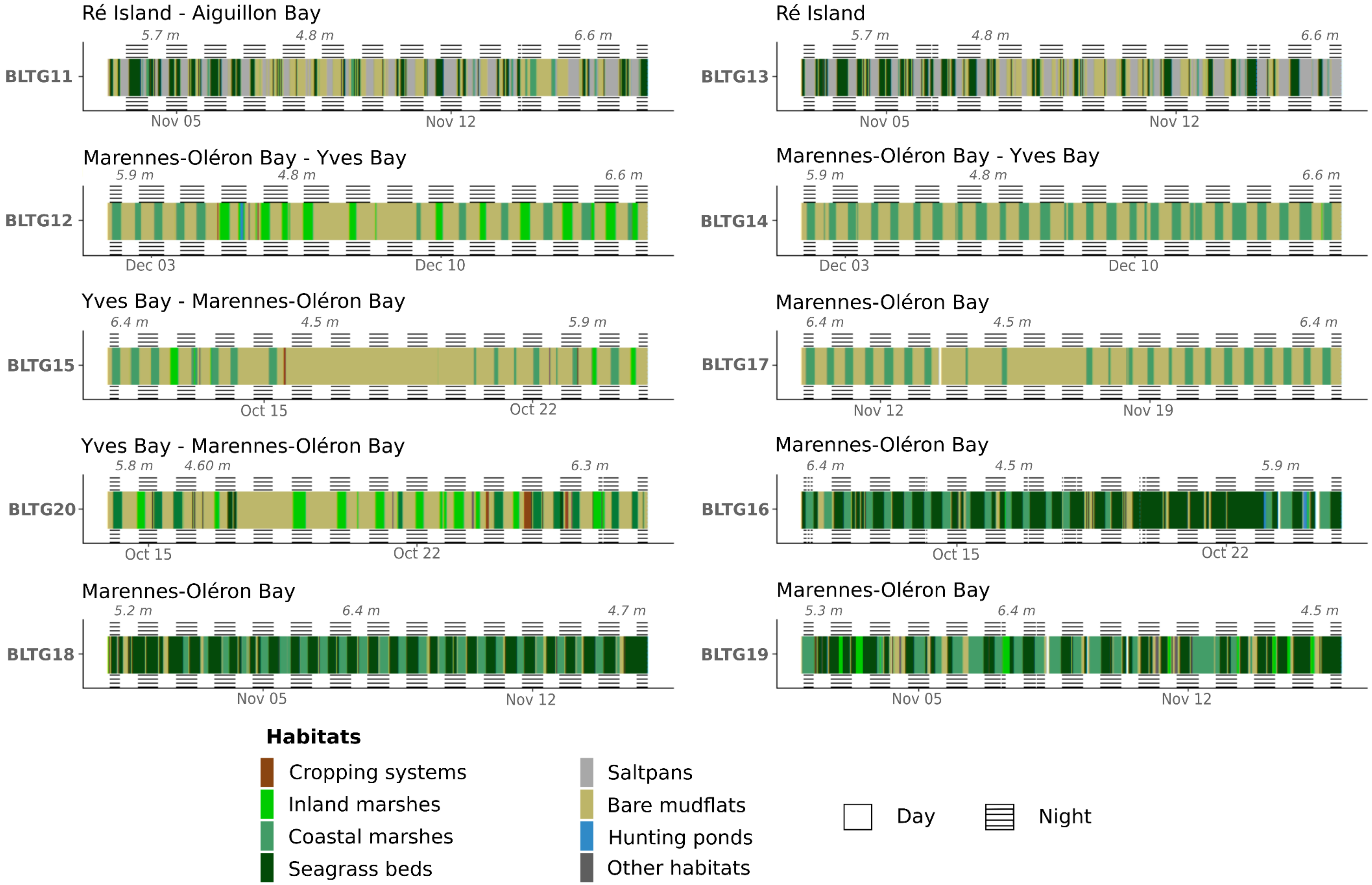

Fig. 6 Fine scale analysis of the habitat use by godwits during a two-week period of dominant use of intertidal habitats. For each individual, all the location data recorded during this 14-days period were considered (i.e. time step of 30 min.). Numbers in italic represent the extreme water heights (m) at the nearest tide gauge.

Discussion

Our results related only 10 individuals, and their unequal study periods do not allow us to generalize our observations. However, thanks to GPS telemetry and high frequency acquisition, we could describe at fine spatio-temporal scale the capacities of black-tailed godwits in terms of plasticity in habitat selection. The 10 monitored godwits showed a common use of more than one site during their wintering survey period on the Central French Atlantic coast. Site shifts were made at small spatial scale inside the Pertuis Charentais area, or at large spatial scale between the Pertuis Charentais and the Loire-Bourgneuf areas. At a finer scale, godwits also showed a large distribution extent around their main roosts within a wintering site. The movements at both local and large scale underlined the use of multiple habitat types, with a food prospecting as well on marine areas as in freshwater wetlands. Moreover, this spatial dynamism highlights the ability of birds to shift from natural habitats to artificial areas as saltpans or hunting ponds. For individuals with larger datasets, it appeared a clear dominant use of intertidal areas from autumn to mid-winter and then movement to inland marshes just before and after the migration, as previously described by Gill et al. (2007). Nevertheless, several habitat shifts occurred at finer temporal scale in inland marshes. Indeed, we observed an occurrence of changes in the daily dominant habitat of 5 ± 2 changes/month in average in monitored godwits, and these changes sometimes appeared quick and brutal. An exploratory analysis at very fine temporal scale, focusing on all locations of each bird over a chosen two weeks period, allowed to describe a high dynamism of habitat use by godwits with multiple habitats exploited by alternation within a day. It also highlighted different activity rhythms, from tidal to nycthemeral, especially depending on the dominant habitat used.

The black-tailed godwit is a gregarious species known to be highly mobile (Prater 1975) and weakly faithful to wintering sites compared to others shorebird species like the Eurasian curlew (*Numenius arquata)* (Bainbridge and Minton 1978; Sanders 2017). They widely explore new sites on their non-breeding grounds and can move from one site to another leading to a distribution according to the concept of the buffer effect (Gill et al. 2001a). Indeed, the quality of sites can change over time, due to depletion of food resources and the related density dependence of sites, leading birds to move to redistribute (Gill et al. 2001b; Gill et al. 2001a). In our study, all godwits changed of site at least once during their wintering on Central French Atlantic coast. As previously observed with godwits in the UK (Gill et al. 2001a), these site changes occurred both on a small scale, i.e. among the Pertuis Charentais sites in our study, and

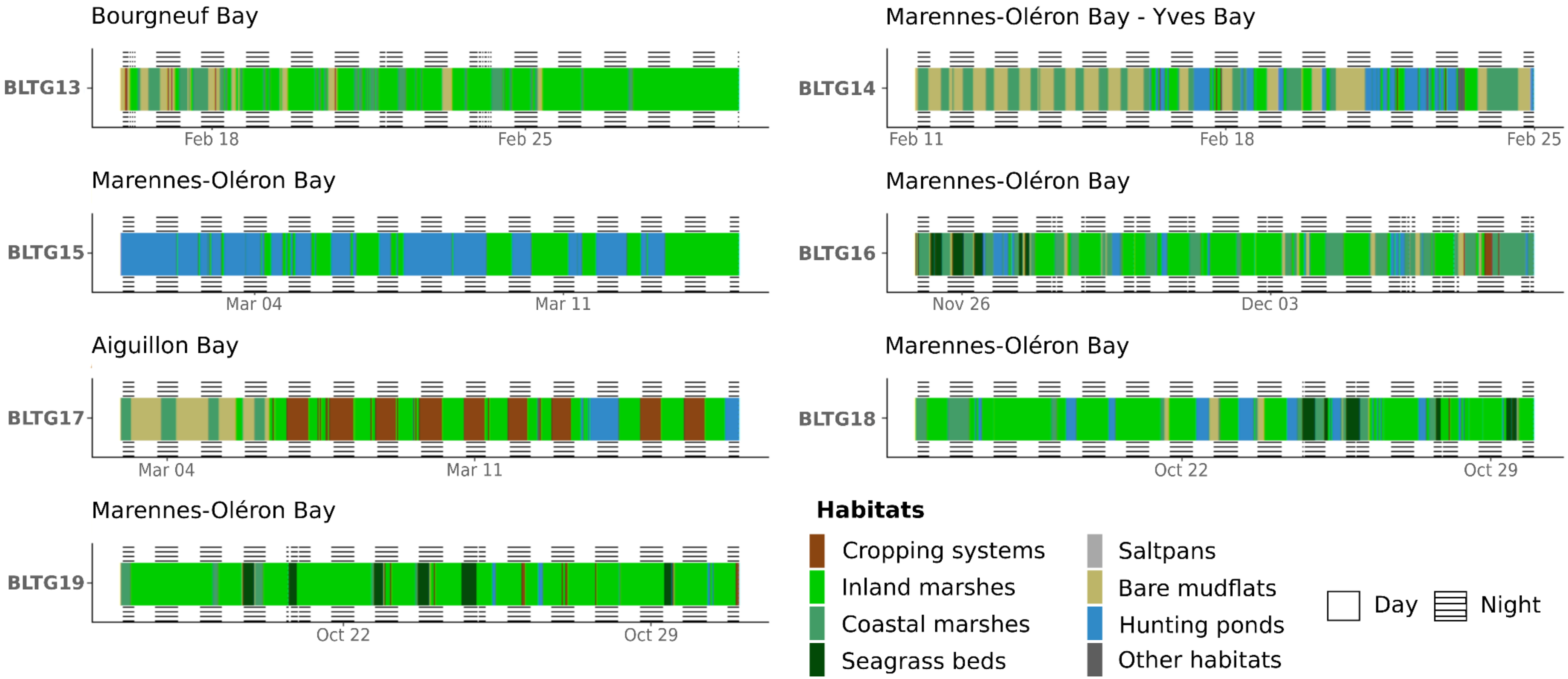

Fig. 7 Fine scale analysis of the habitat use by godwits during a two-week period of dominant use of inland marshes. For each individual, all the location data recorded during this 14-days period were considered (i.e. time step of 30 min.).

on a large scale, between the Pertuis Charentais and Loire-Bourgneuf areas. Godwits can even move at larger scale, joining other wintering sites in Europe, such as in the Iberian Peninsula or in the UK according to resighting of coloured marked birds (F. Robin, *Pers. Com.*). Within a wintering site, godwits also widely dispersed around their main roosts to prospect in several feeding areas. In the same way as site changes, such a local dispersion is thought to be influenced by the competition for food resources, especially interference causing decline in intake rates (Goss-Custard 1970; Sutherland 1983). Indeed, wintering survival of shorebirds critically depends on prey-intake rates, and birds will thus distribute on feeding areas according to the prey availability as well as their competitiveness in presence of competitors. As the seasonal prey depletion on intertidal areas progresses, the forager interference increases and birds could redistribute at patch or habitat scale by completely switching of feeding areas (Gill et al. 2001a).

Although the main trend in monitored godwits confirmed the predominant use of intertidal areas until mid-wintering (Delany 1996), birds were finally able to select four different gross habitat types during the non-breeding period: ‘mudflats’, ‘coastal marshes’, ‘inland marshes’ and ‘saltpans’. Intertidal mudflats constitute feeding habitats of high quality during the non-breeding period for shorebirds, most of which, including black-tailed godwits, are specialized and dependent on these habitats (van de Kam et al. 2004; Piersma 2007; Colwell 2010). Previous studies on godwits already underlined a shift in habitat use by birds to respond to the seasonal prey depletion on intertidal habitats, with a report on inland habitats such as meadows, marshes or saltpans (Gill et al. 2001a; Gill et al. 2007) also mentioned in other shorebirds (Masero et al. 2000; Masero 2003; Sánchez et al. 2005; Bocher et al. 2014). Such switches mainly occurred at the end of winter (during the pre-migration), as observed in our study for some individuals, and allowed birds to significantly increase prey-intake rates compared to intertidal mudflats that became of poorer quality (Gill et al. 2001a; Masero 2003). Indeed, invertebrate abundance in inland marshes and saltpans could be higher in spring and autumn (Casas 2001; Sánchez et al. 2006), explaining their main seasonal use by shorebirds, during pre-migration and post-migration. Beyond these seasonal changes, both related to fluctuations in habitat quality and energy needs of birds during the non-breeding period, our results also showed several habitat changes in the middle of wintering for some individuals. Facing competition for food, the use of alternative feeding habitats along the wintering may benefit for less competitive individuals.

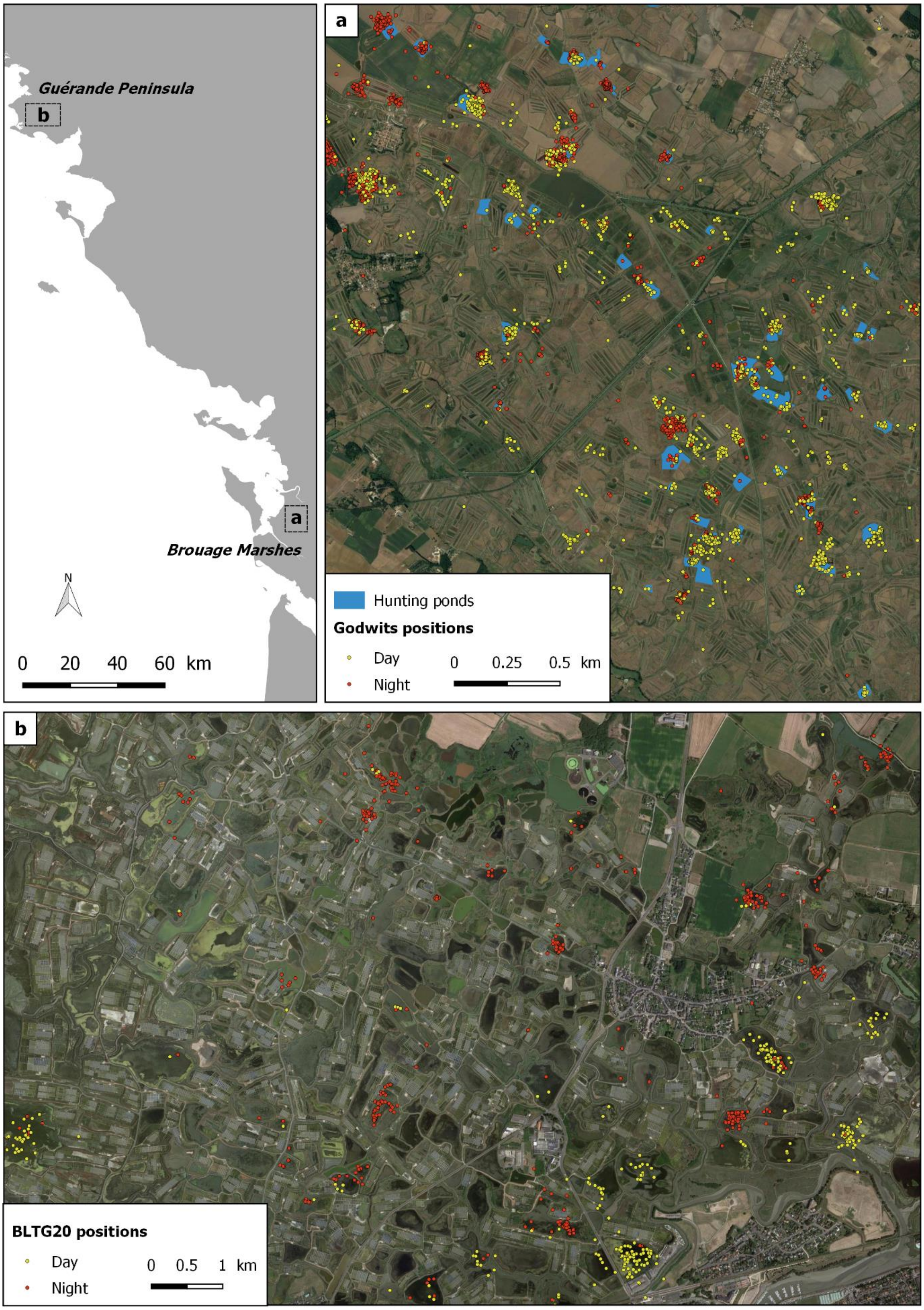

Fig. 8 Distribution of godwits in **(a)** Brouage marshes (inland marshes) and **(b)** Guerande Peninsula (saltpans). Hunting ponds used by godwits in Brouage marshes are represented in blue. Godwit positions in Guerande peninsula saltpans only concern one bird (BLTG20).

Shorebirds are known to adjust their diet depending on prey availability, with tendency to include less profitable prey when intake rate decreases with prey density (Zwarts et al. 1996). Less competitive birds, having therefore less access to high quality areas when interference increase, may have to complement their preferential diet by alternative prey and habitats, as observed in different species for part of individuals (Masero et al. 2000; Bocher et al. 2014). Previous studies carried out in the Pertuis Charentais showed that black-tailed godwits preferentially prospected on bare mudflats for *Macoma balthica* prey in Marennes-Oléron Bay, and mainly fed on seagrass beds on Ré Island (Robin et al. 2013; Bocher et al. 2014; Robin et al. 2015). However, our study underlined that some individuals, supposedly the least competitive, appeared to both combine the use of 'bare mudflats' and 'seagrass beds' on intertidal feeding areas. Moreover, and beyond the alternate use of intertidal feeding areas and inland roosts under the tidal influence, godwits also alternated, sometimes within a day, between intertidal habitats and inland habitats ('inland marshes' and 'saltpans') for feeding. Inside habitat types, monitored godwits also revealed a great variability in the location of feeding areas, prospecting for example in a large number of seawater reservoir in 'saltpans' of Guérande Peninsula, as well as in varied artificial drainage ponds and hunting ponds within 'inland marshes'. This highly dynamic use of habitats by godwits underlines the huge plasticity of birds to adapt to different habitats and diets, especially since the different habitat types also induce different activity rhythms.

Indeed, the tidal rhythm predominate when godwits mainly exploited intertidal habitats, while birds tended to follow a nychthemeral rhythm for a dominant use of inland habitats. Hence, black-tailed godwits used the intertidal feeding areas both during day and night, depending on their availability, and then reached the 'coastal marshes' to roost at high tide. On the other hand, during a dominant use of 'saltpans' or 'inlands marshes' birds were observed to roost during the day, suggesting that feeding activities especially occurred at night in these habitats (A. Gentric and F. Robin, *Pers. Com.*). In saltpans of Guérande Peninsula, and probably also on Ré Island, godwits roosted by day, on the upper foreshore or in few specific seawater reservoirs depending on the tide, and prospected in several pans by night when no salt workers were present or when diurnal birds of prey were not active. However, a particular pattern was observed in the use of 'hunting ponds' since during the waterbird hunting season, godwits seemed to mainly exploit them during the day. After the hunt closure, birds used the 'hunting ponds' day and night likely for roosting and feeding.

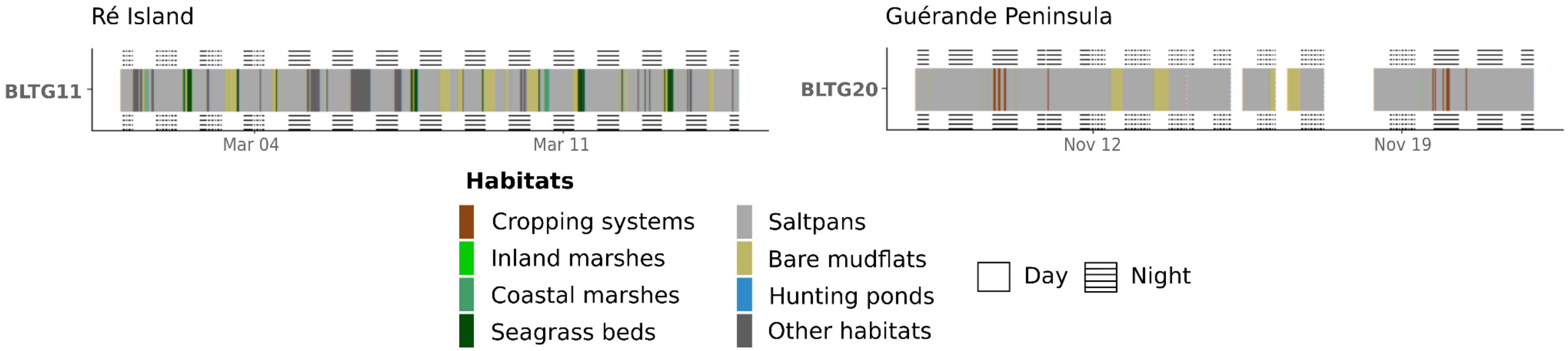

Fig. 9 Fine scale analysis of the habitat use by godwits during a two-week period of dominant use of saltpans. For each individual, all the location data recorded during this 14-days period were considered (i.e. time step of 30 min.).

Although limited to wetlands and meadows, black-tailed godwits are a generalist species (omnivorous) able to exploit multiple habitats. Godwits are able to move quickly to new sites and/or habitats to ensure their winter survival. At the scale of the study area, landscapes are able to provide this supplementation in terms of new substitutable resources, assuming that, on sites, the presence of secure roosts allow to provide a complementation. This is the case on most study sites, especially because roosts are located inside nature reserves, with exception of Guérande Peninsula. In addition, the use of the landscape changed after the closure of the hunt, with roosting areas available out of the nature reserves, and a nocturnal feeding possible on the hunting ponds for instance. These results highlighted that black-tailed godwit is a very plastic species and therefore able to adapt very quickly to environmental changes and to intra- and interspecific interactions. The Islandic black-tailed godwit has been increasing for recent decades, and such a demographic trend can favour the dispersal of part of individuals on multiple sites and habitats of lower quality, under the buffer effect (Gill et al. 2001a). Individuals which experience the worst wintering conditions will also be those which arrive later and in poorer body conditions at breeding sites. The survival and breeding success of individuals, as well as the associated population dynamics, could thus depend on the quality of wintering conditions. In order to maintain the population of *L. l. islandica*, it appears essential to ensure a good quality of such alternative sites and habitats that can be used by the exceeding individuals arriving on French coasts each winter.

To conclude, protected areas and the management of artificial habitats, such as hunting ponds and saltpans, appear crucial to support the preservation of the fragment of the population. Considering the intra winter movements of godwits within western European coast between British Isles and Portugal, such conservation actions could help both at the scale of the study site and at the scale of the wintering area.

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SECTION II

Effect of nycthemeral periodicities on godwit movements and habitat use


SERIE 180

Chapter 3

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 behaviours 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*

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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 behaviours. 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 night-time (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 behaviour 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 night-time 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 behaviours and distributions between day and night. Indeed, visual capacities, prey availability, predation risk, and human activities are all factors influencing the behaviour 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 movements (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 night-time.

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 semi enclosed 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 non-moonlight nights inside the Nature Reserve. Godwits were immediately marked with a metal ring and a unique color rings 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

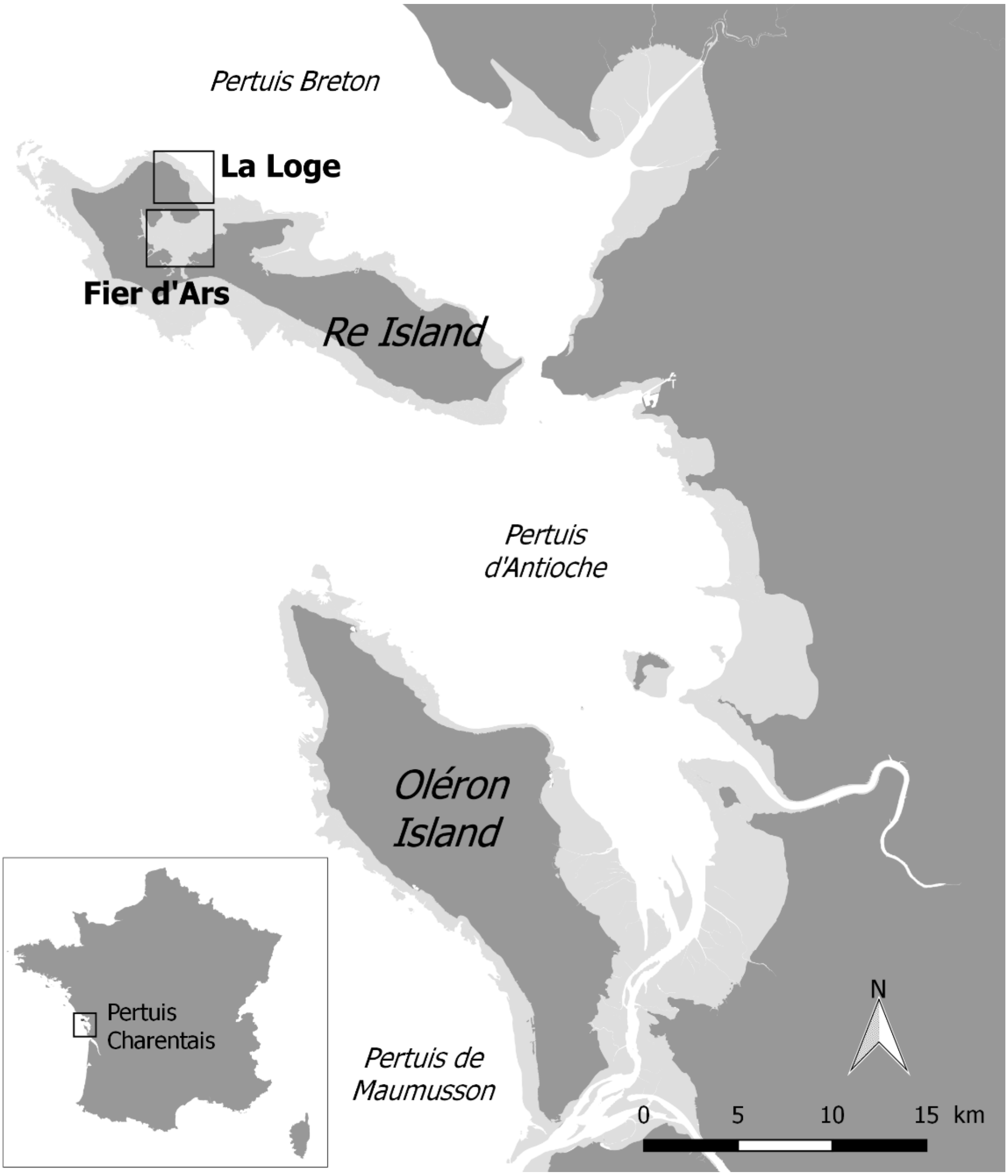

Fig. 1 Map of the Pertuis Charentais (Central French Atlantic coast) and localisation of the study areas on Ré Island. Dark grey correspond to the mainland and light grey to the intertidal area.

±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 m^2), 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 m^2, 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 < 0.063 mm) 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 mm) 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

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 (g)**	**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

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

UDs were then used to investigate the importance of foraging habitats through habitat selection analysis. For this, we considered a second-order selection (design II), that is, a same availability of habitats for all birds and an analysis of habitat selection at the individual scale (Johnson 1980). A minimum convex polygon (MCP) of foraging points from all monitored birds provided an estimation of available foraging habitats for godwits. Individual kernel home ranges and the habitat typology of the study area were then superimposed to perform habitat selection analysis through Manly's selection ratios (Manly et al. 2002) and using the R package

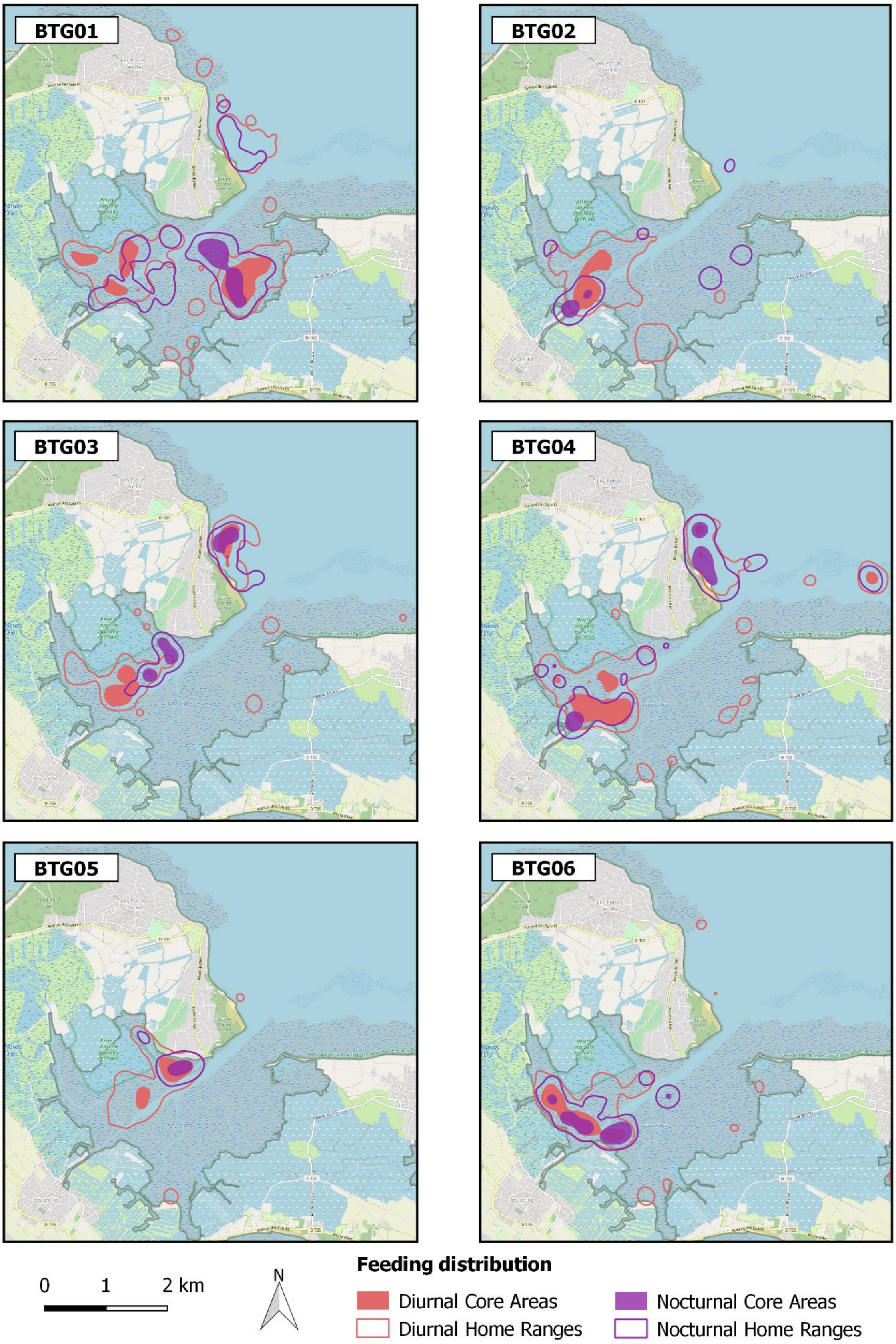

Fig. 2 Diurnal and nocturnal feeding home ranges of six bar-tailed godwits during the nonbreeding period on Ré Island. Feeding home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours.

“adehabitatHS” (Calenge 2011). We explored the interindividual variability of habitat selection through an Eigen analysis of selection ratios (Calenge and Dufour 2006), a multifactorial method. These analyses and other statistical tests (ANOVA, paired t-tests and chi-squared tests) were performed with the statistical software R (3.6.1, R Core Team 2020).

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

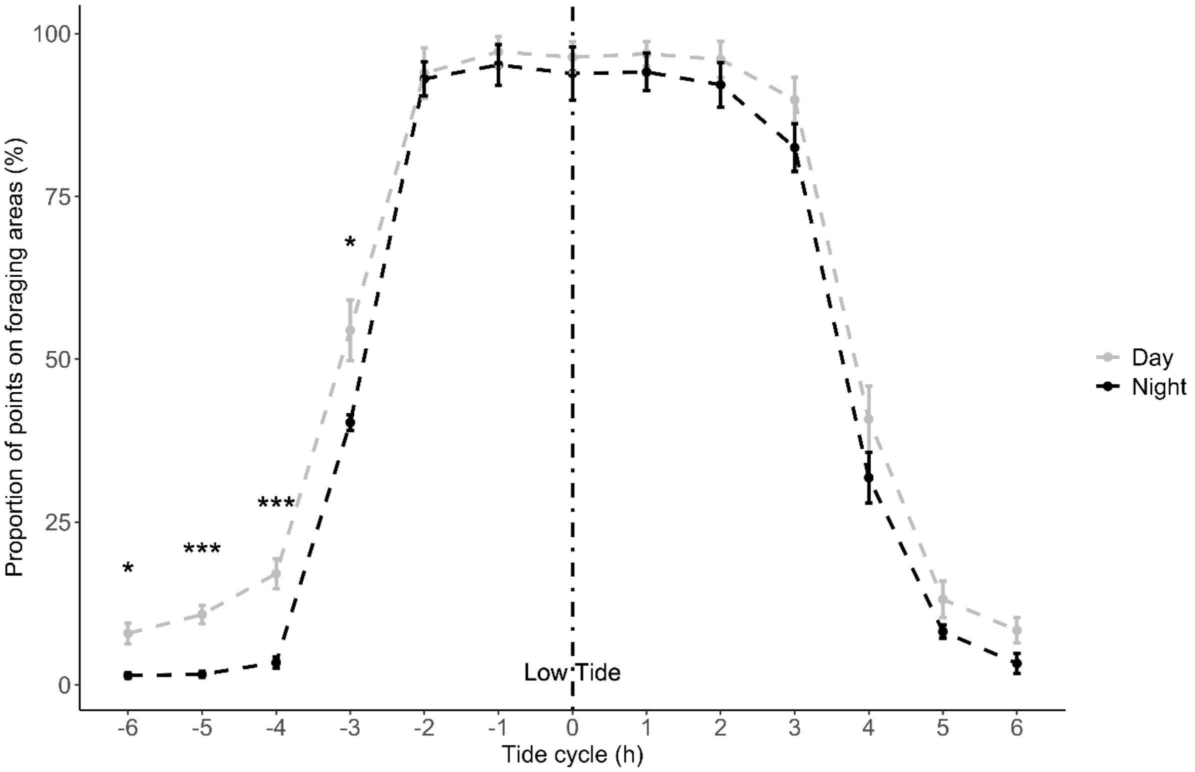

Fig. 3 Mean proportion of time spent by six bar-tailed godwits on mudflats, i.e. foraging, by day and by night during the tide cycle. Significant differences between Day and Night, for each slot time around the low tide, are illustrated by the symbols '*' when p<0.05 and '***' when p<0.001.

Daylight and night local movements

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

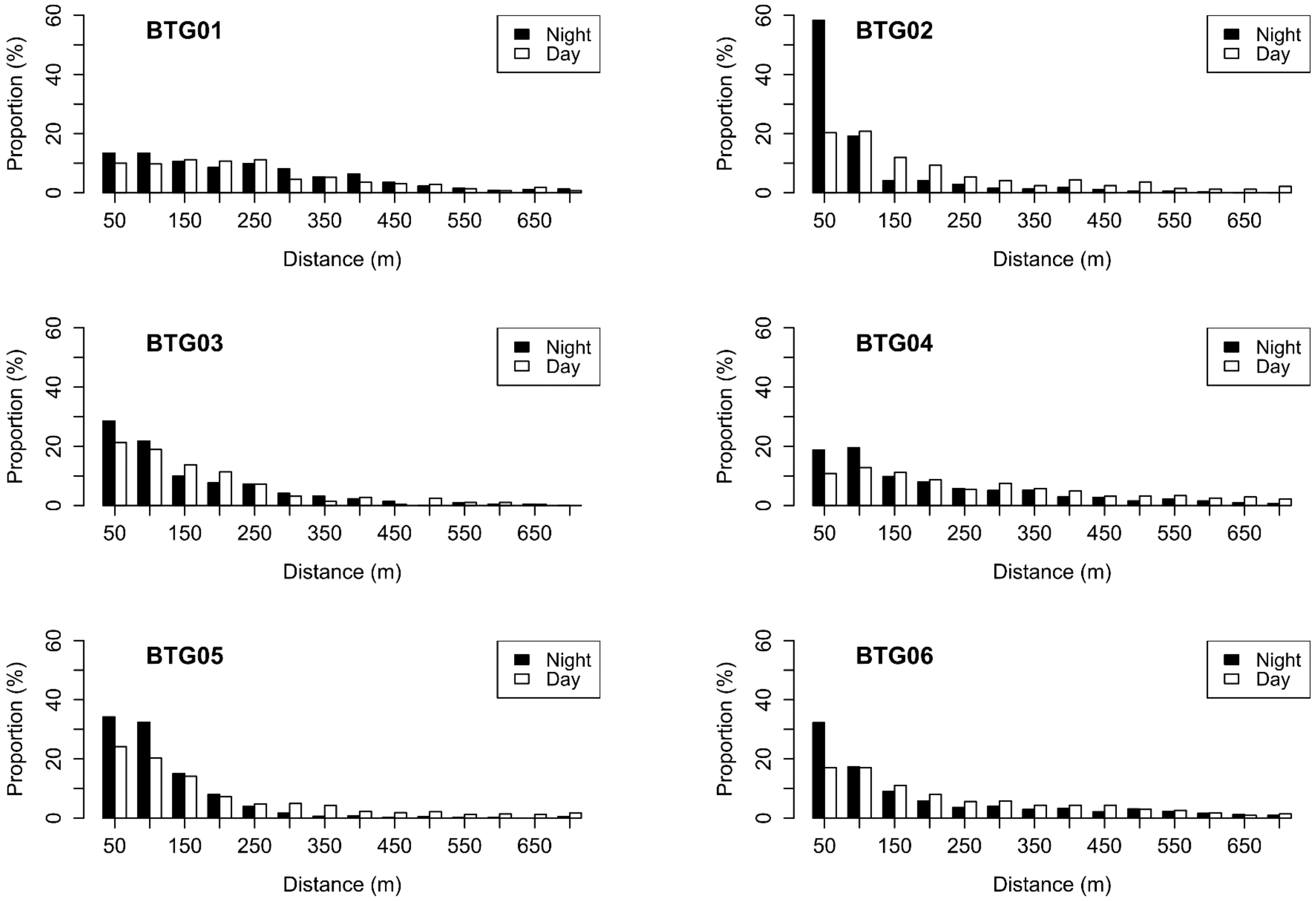

Fig. 4 Day and night distribution of distances between two successive locations (30 min.).

distances between points on the feeding area exceeded 100 m, and the most represented distance class was 100–150 m (Fig. 4).

Habitat diversity and structure

In total, 11 locations, as potential feeding habitats, were identified in the intertidal areas of the study site (Fig. 5). The "Fier d'Ars" area included a large diversity of habitats, with a clear dominance of seagrass beds (A2.6111 – 27% of the total intertidal site surface), bare mudflat (A2.313 – 19%), and oyster parks (A2.32 – 8%) on the muddy foreshore at the center of the bay (Fig 5.b). Habitat A2.6111 was characterized by a fine muddy sand substrate with an abundance of *Zostera noltei* and infaunal species dominated by polychaetes (*Scoloplos armiger* and *Arenaria marina*), oligochaetes, and mollusks (*Cerestoderma edule*, *Macoma balthica*, and *Hydrobia ulvae*). Habitat A2.313 corresponded to a littoral sandy mud, mainly characterized by polychaetes (*Hediste diversicolor*) and bivalves (*M. balthica* and *Scrobicularia plana*). A2.32 was a muddy substrate mainly characterized by a low diversity of polychaetes and oligochaetes, covered with artificial oyster grow-out tables. Another habitat well represented in the "Fier d'Ars" was an intertidal muddy sandflat dominated by polychaetes (*Eteone longa*, *S. armiger*) and capitellidae combined with the bivalve *C. edule* (A2.242 – 6%). Saltmarsh creeks in the A2.5 coastal saltmarshes (A2.325 – 17%) surrounded the muddy bay while rocky elements, that is, bedrock and boulders dominated by mussels and/or barnacle communities (A1.11 – 1%) and habitats with littoral rock features (A1.41 – 6%) characterized the bay entrance.

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

Foraging habitat selection

During daylight, godwits did not use available foraging habitats randomly but showed a significant habitat selection, both at an individual scale ($\chi^2 = 47563.98$, df = 9.0, $p < 0.001$) and when combining the six birds monitored ($\chi^2 = 51039.79$, df = 54.0, $p < 0.001$). In the diurnal

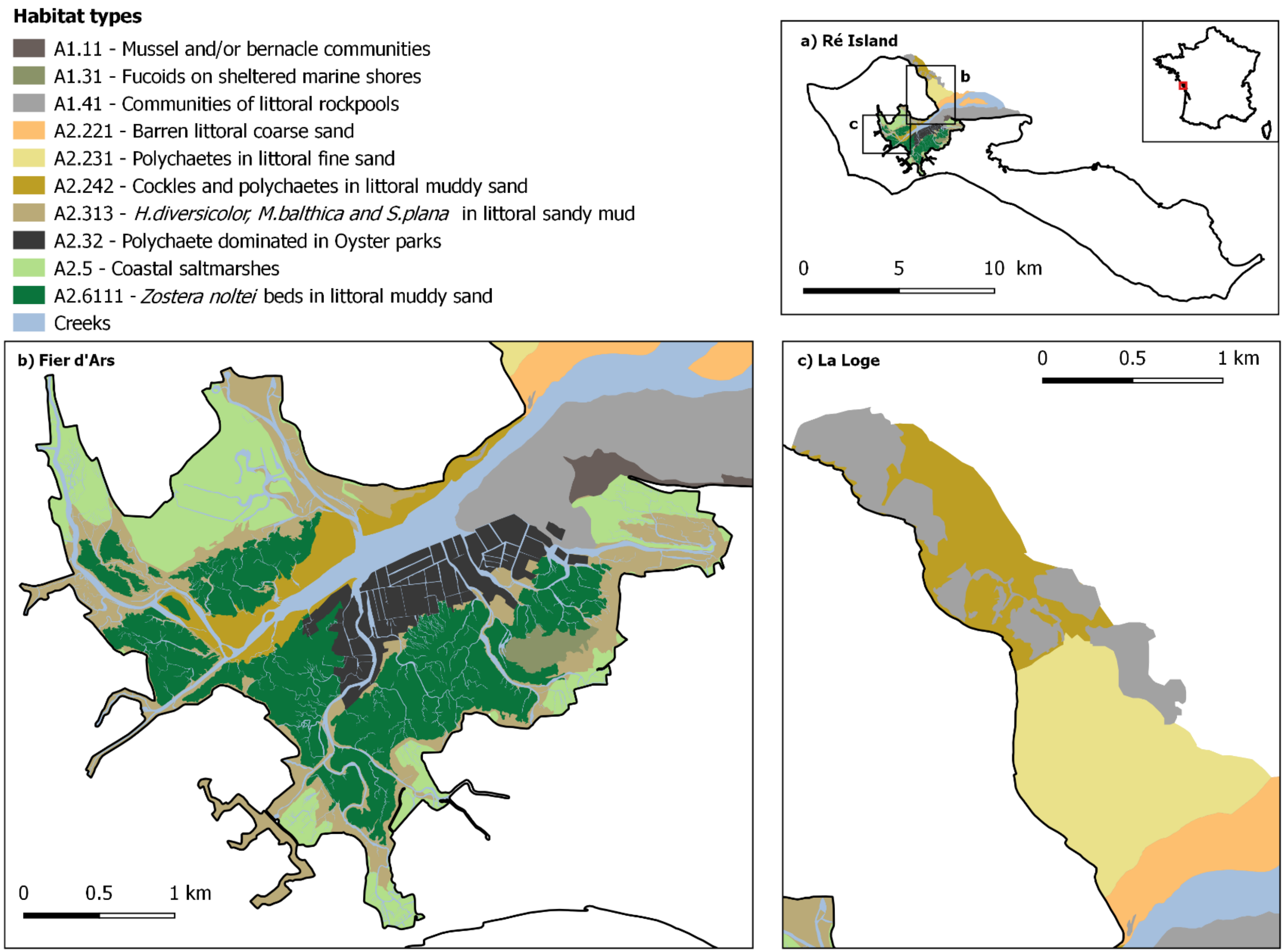

Fig. 5 Habitat typology at **(a)** Ré Island, **(b)** "La Loge," and **(c)** "Fier d'Ars".

feeding core areas, the seagrass beds habitat (A2.6111) was selected by four godwits (BT01, BTG02, BTG03, and BTG04; Fig. 6). For BTG05 and BTG06, the most represented habitats were the sandflat dominated by *C. edule* and polychaetes (A2.242) and the mudflat dominated by *H. diversicolor* and *S. plana* (A2.313), respectively. Habitat A2.313 was also a prevailing habitat in the core feeding areas of BTG02 and BTG05. Hence, habitat A2.6111 appeared preferentially used by godwits on average, followed by A2.242 and A2.313 (global selection ratios > 1; Fig. 7). Conversely, habitat A1.31 (fucoids on sheltered shores) was globally avoided by the studied birds (global selection ratios < 1) although standard errors indicate their marginal use by some birds. The six remaining habitats were clearly avoided (global selection ratios and SE < 1).

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

The Eigen analysis emphasized these differences between diurnal and nocturnal habitat 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

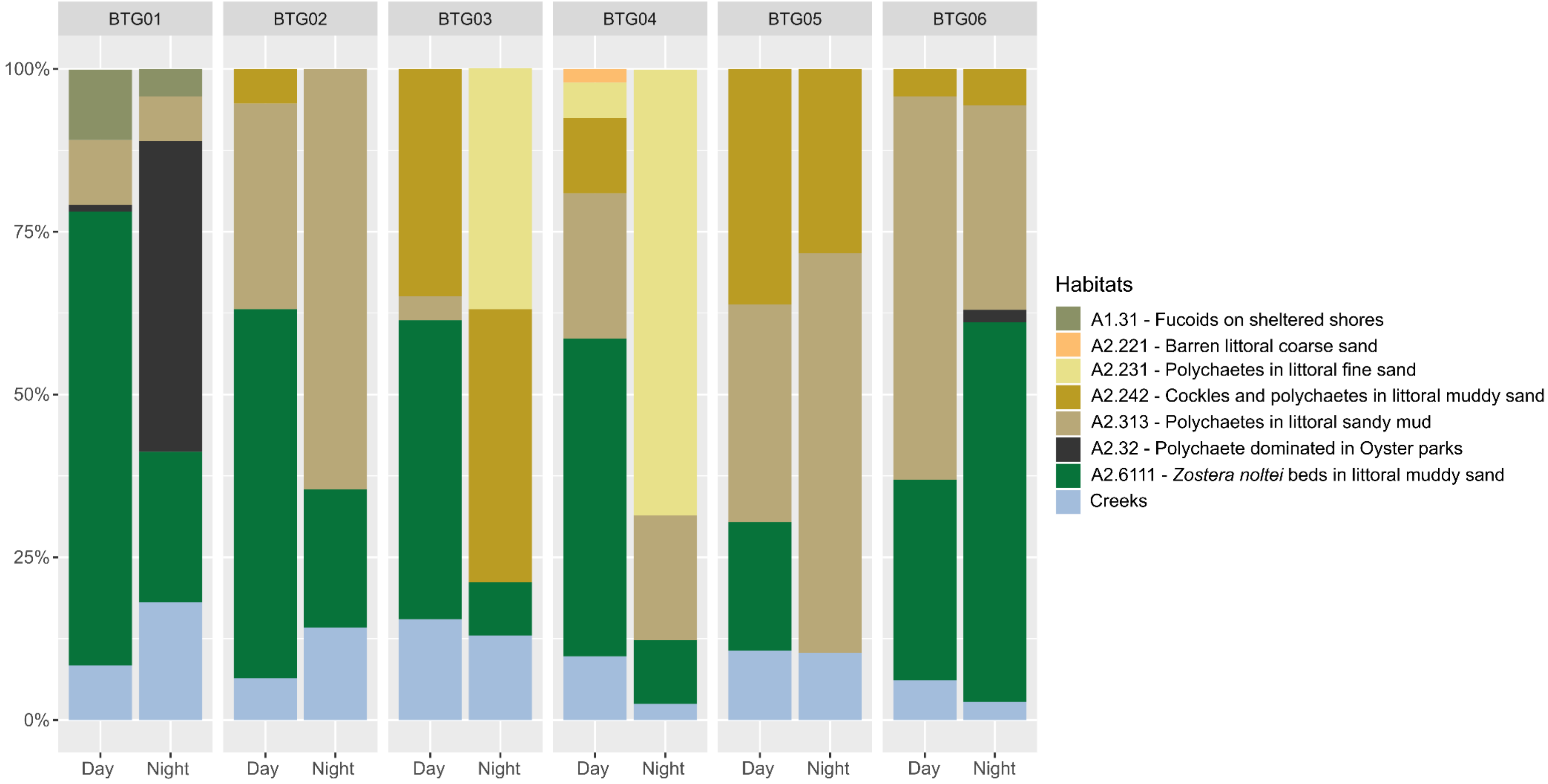

Fig. 6 Day and night proportion of habitat types on feeding core areas (50% kernel density contour) of each bar-tailed godwit.

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 night-time, with a relatively small feeding area per individual. 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

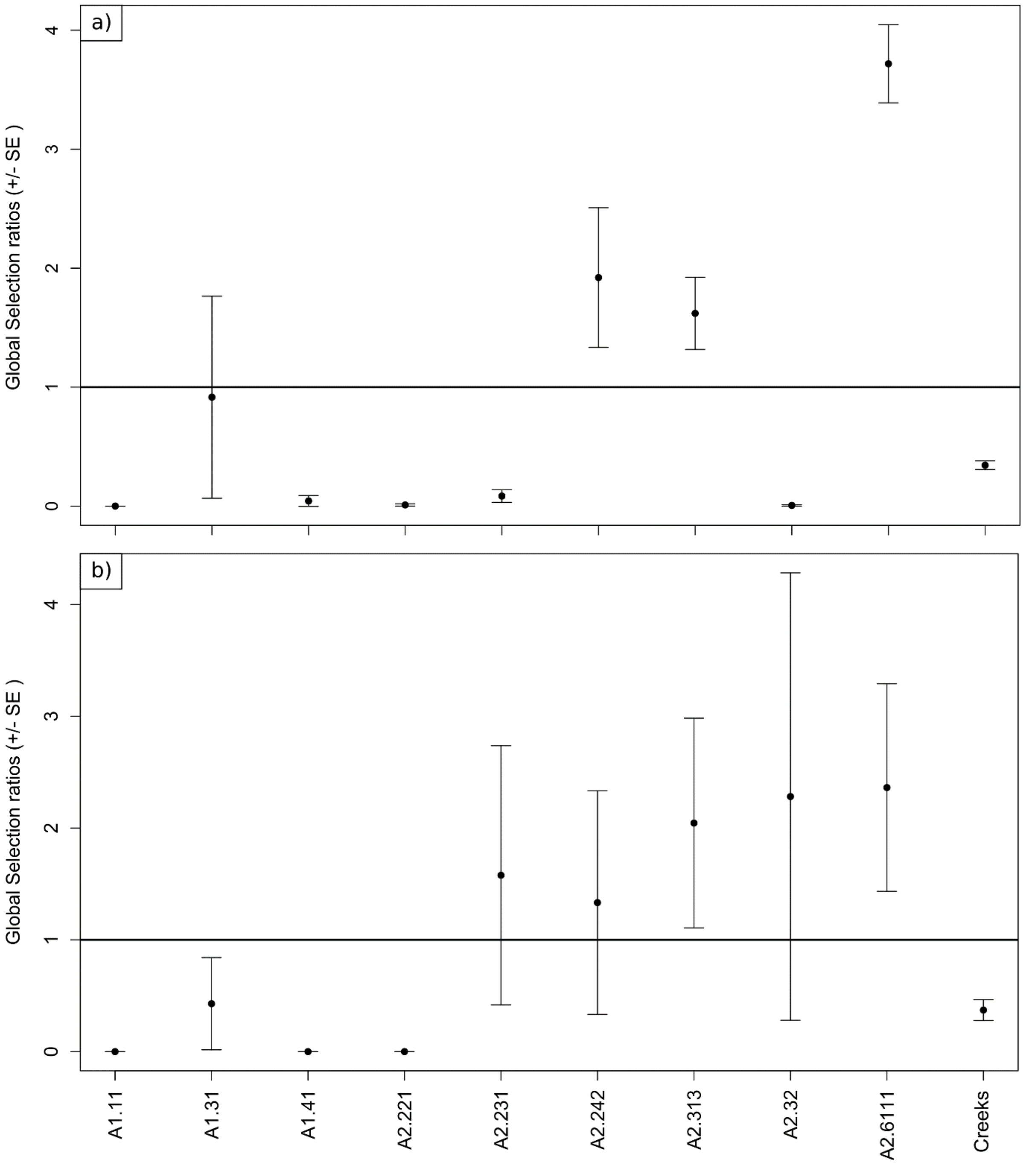

Fig. 7 Results of the selection ratio analysis highlighting habitat selection by six bar-tailed godwits on 10 intertidal habitat types by **(a)** daytime and **(b)** nighttime.

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; van de Kam et al. 2004; Lourenço et al. 2008). Night foraging was therefore mainly considered as "supplementary" in previous studies, that is, used when diurnal prey intake is not enough to offset the increased energy demands of less favorable wintering conditions (McNeil and Rodriguez 1996; Smith et al. 1999; Sitters 2000). However, some shorebirds could fill a significant part of their energy requirements during the night (Turpie and Hockey 1993; Lourenço et al. 2008) because of physiological adaptations such as better nocturnal vision for *Charadriidae* (high rod–cone ratio in the eyes; De Azuje et al. 1993; Rojas et al. 1999) or higher tactile sensitivity for *Scolopacidae* as in godwits (Cunningham et al. 2013), which facilitate nocturnal foraging.

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

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

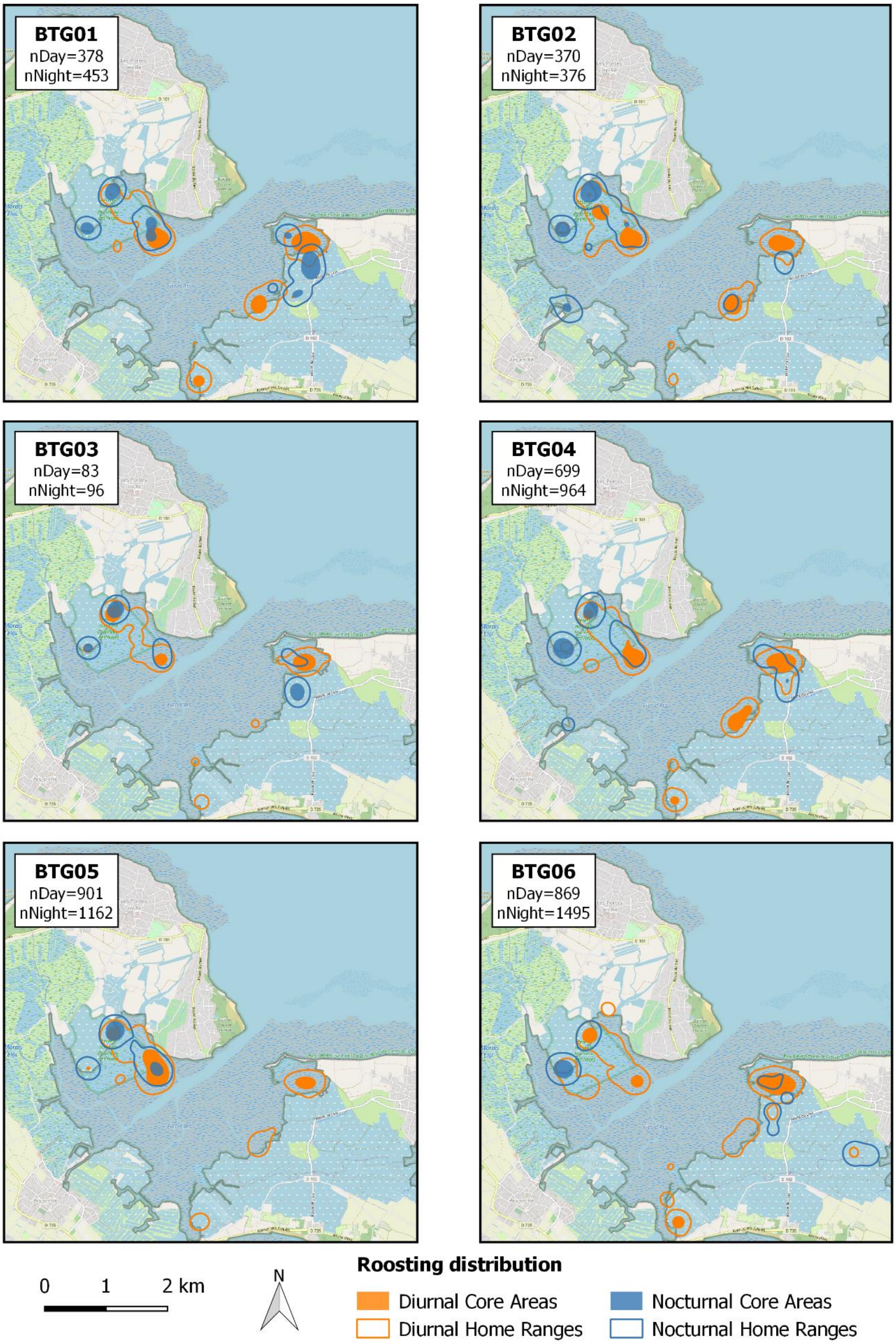

Fig. 8 Diurnal and nocturnal roosting home ranges of six bar-tailed godwits during the nonbreeding period on Ré Island. Roosting home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours.

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

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

Contrasting foraging methods between day and night were also found to affect the spatial distribution of shorebirds. For instance, Mouritsen (1993) found that the dunlin (*C. alpina*) switched from visual feeding during the day to tactile feeding during the night, as did black-tailed godwits which showed a higher rate of stitches and sweeps at night and a majority of pecks during the day (Lourenço et al. 2008). Generally, the bill of the Scolopacidae species benefits from a high number of touch-sensitive nerve endings which favors tactile feeding (De Azuaje et al. 1993). Hence, we can assume that bar-tailed godwits switch from sight feeding during the day to probing at night and, as observed in dunlins (*C. alpina*) by Mouritsen (Mouritsen 1994), this change in behavior may induce the use of distinct feeding habitats based on prey availability. This could be related to the dominance of polychaetes, more active and likely more available at night (Last and Olive 2004; Kuwae 2007) in habitats A2.32 and A2.231, which could explain the nocturnal use of these habitats by godwits. We did not have available data to compare diurnal and nocturnal prey density, but studies underlined that polychaete worms, the favored preys of bar-tailed godwits (Duijns et al. 2013), may be closer to the sediment surface at night (McNeil et al. 1992; Esser et al. 2008). Such a density of prey available in the top layer of the sediment could explain the nocturnal preference of polychaete-dominated habitats by godwits, as observed in dunlins and redshanks (Mouritsen 1994; Burton and Armitage 2005). Beyond their influence on the location of godwits' feeding areas, the differences in prey availability and foraging methods between day and night also seemed to affect the size of foraging areas.

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

At high tide, results showed marked differences in the use of roosts between day and night during neap and spring tides. Indeed, at daytime, godwits selected upper mudflat roosts as soon as they were available, that is, during neap tides. However, at night, birds always used saltpans in whatever tidal heights. In a previous study based on daytime observations, Rosa et al. (2006) showed that wintering shorebirds, including bar-tailed godwits, preferentially select mudflats to roost, and move to saltpan roosts when the upper foreshore became unavailable during highest tides. This study also highlighted the effect of both raptor presence, higher in saltpans than in mudflats, and visibility, lower in saltpans, on daytime shorebird roost choice (Rosa et al. 2006). Others studies reported the anti-predator strategy of shorebirds avoiding some specific roosting areas at night-time because of higher predation risks (Hilton et al. 1999; Rogers et al. 2006). Hence, in addition to their availability, the roost choice by shorebirds between day and night in the present study could be influenced by the predation risk (Handel and Gill 1992; Rohweder 2001). Birds would favor mudflats at day, less prone to overflying raptors and offering better visibility of approaching predators (Rosa et al. 2006), and saltpans at night, with a water barrier against nocturnal predators such as foxes or mustelids (Cramp et al. 1983; Sitters et al. 2001). Further studies are nonetheless needed to validate this hypothesis and better explain the pattern of use of roost sites on Ré Island, including the monitoring of predator activities.

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

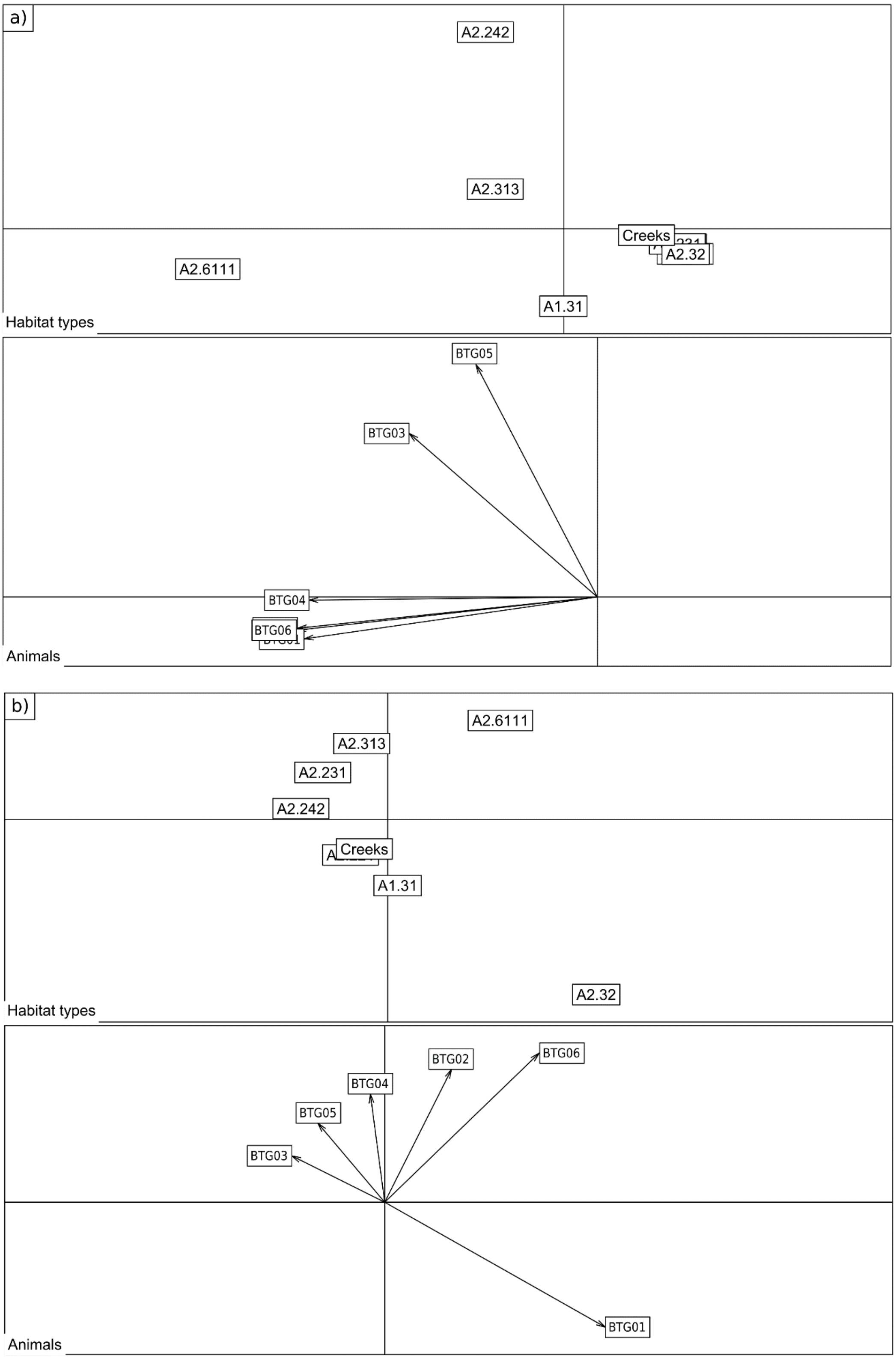

Fig. S1 Results of the Eigen analysis of selection ratios highlighting habitat selection by six bar-tailed godwits on 10 habitat types during **(a)** day and **(b)** night. Habitat types projected along the first two factorial axes, and bird scores on the first factorial pane.

Table S1 Size of diurnal and nocturnal roosting areas (RCA: Roosting Core Areas 50%, RHR: Roosting Home Ranges 95%), and their overlap rate.

	DAY			NIGHT				
Logger ID	**GPS fixes**	**dRCA (ha)**	**dRHR (ha)**	**GPS fixes**	**nRCA (ha)**	**nRHR (ha)**	**Overlape dRCA/nRCA (%)**	**Overlape dRHR/nRHR (%)**
BTG01	378	31.1	140.3	453	28.5	114.2	5.9	28.6
BTG02	370	33.1	137.8	370	16.9	104.0	0.8	33.8
BTG03	83	16.5	86.7	96	12.9	61.6	14.1	24.5
BTG04	699	35.4	148.0	964	14.6	108.3	4.2	34.2
BTG05	901	27.5	120.2	1162	11.6	64.8	23.7	35.3
BTG06	869	30.3	186.7	1495	7.7	76.8	0	32.1

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Chapter 4

Daytime, tidal amplitude and protected areas influence movements and habitat use by wintering black-tailed godwits

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Abstract

Integrating the specific requirements that might explain the foraging distribution of animals is of major importance in order to define conservation priorities for maintaining the quality of key habitats. During the wintering stage, most shorebirds depend on intertidal areas, as foraging grounds, and supratidal areas, as high tide roosting grounds. Accessibility of foraging areas and food resources is thus limited, and most wintering shorebirds have to forage whenever mudflats are available, both at day and night, to fulfil their daily energetic demands. However, the current knowledge about spatio-temporal use of foraging habitats by shorebirds is often restricted to the daylight period, during which visual observations are possible. In this context, we investigated the spatial distribution and selection of habitats by wintering black-tailed godwit *Limosa limosa islandica,* distinguishing day from night, in relation to environmental characteristics. We equipped wintering black-tailed godwits with miniaturized GPSs on two different sites of the Pertuis Charentais (Atlantic French coast). Concurrently, we sampled benthic macrofauna communities in order to map the distribution of habitats in mudflats. We then tested the hypothesis that black-tailed godwit feed both day and night, and show contrasting foraging behavior and distribution in response to different visual capacities, prey availability, predation risk and human activities. The results showed a high variability in the selection of feeding areas according to nycthemeral periodicities. Indeed, the estimated nocturnal feeding areas were two time smaller than daytime ones, and located closer to the coastline. Moreover, birds largely foraged inside the protected areas during daytime while most of them foraged outside at night. Finally, godwits with the smallest feeding home ranges stayed inside the Nature Reserve, both during day and night, while the others prospected more often outside the protected area, preferentially at night.

Keywords: Coastal ecology, GPS tracking, Habitat use, Nycthemeral movements, Protected areas, *Limosa limosa*

In prep.

Introduction

Understanding feeding habitat selection by animals and variations in their movements in space and time is crucial for the conservation of the biodiversity, especially in rapidly changing environments and increasing anthropogenic pressures (Pearl 2000; Fuller 2012; Davidson et al. 2020). The choice of where and which resources to forage is critical for individuals, and relies primarily on a trade-off between starvation and predation risk (Lima 1986; McNamara and Houston 1990; Quinn et al. 2012). Furthermore, integrating the specific requirements that might explain the foraging distribution of animals and their use of habitat is of major importance in order to define conservation priorities for maintaining habitat quality and their protection over the long-term. Shorebird populations are facing important modifications of their habitats as well as various threats from human activities, either on their breeding, migratory or wintering sites (Gill et al. 2007; Loss et al. 2012; Pearce-Higgins et al. 2017). As a consequence, most of large-size shorebird species have an unfavorable conservation status (Pearce-Higgins et al. 2017). During the wintering stage, most shorebirds are dependent on intertidal areas, accessible at low tide only as foraging grounds, and on supratidal areas, at high tide, used as roosting grounds (van de Kam et al. 2004). Accessibility of foraging grounds and of food resources is thus limited along the day, and most wintering shorebirds have to forage whenever mudflats are available, both at day and night, to fulfil their daily energetic demands (McNeil et al. 1992; Dodd and Colwell 1998; Lourenço et al. 2008). However, the current knowledge about spatio-temporal use of foraging habitats by these birds is often restricted to the daylight period during which they can visually be observed. Some rare studies have shown significant variations in shorebirds' behavior between day and night, constrained by temporal differences in food availability, predation pressure or human disturbance (Robert and McNeil 1989; Mouritsen 1994; Lourenço et al. 2008). This demonstrates that determining possible day and night differences in habitat use and selection in such dynamic and human-influenced environments is essential to define adapted protection areas and management measures.

In this context, we investigated the winter distribution and habitat use of the black-tailed godwit *Limosa limosa islandica* (hereafter 'godwit') both at day and night and in relation to the characteristics of their environment. To this end, we focused on one of the main mudflat areas of the European Atlantic coast: the Pertuis Charentais. This region is a set of large intertidal mudflats on the French coast of international importance for migrating and wintering shorebirds (Delany et al. 2009) and is considered as the first wintering area for shorebirds in France (Mahéo et al. 2020). The coastline of the Pertuis Charentais is subject to a strong urban pressure linked to tourism and the settlement of retired people (Zaninetti 2006). Leisure activities are carried out on the beaches mainly during school holidays, but there is still pressure during the rest of the year through nautical activities, shellfish fishing or hunting of waterbirds.

Godwits can reach a maximum of c. 14,000 individuals in mid-winter in the Pertuis Charentais (Mahéo et al. 2020), representing 28% of the population and 65% of the national counts (Bocher, et al. 2013a). The recent increase in *L. l. islandica* numbers in France since 1990-1991, after a decreasing period from 1977 to 1990, appears to be mainly due to a welcoming of more juveniles each year since the sustained increase of the population in Iceland (Bocher, et al. 2013b). Moreover, the design and implementation of Nature Reserves during the 1990s, with the protection of suitable habitats for wintering shorebirds, could have facilitated the arrival of these exceeding individuals and explain the recent population dynamics and distribution of wintering black-tailed godwits in France. Indeed, Nature Reserves insure the protection of these key habitats and associated resources for godwits, and reduce local human activities known to have disturbing effects on birds. However, these protected areas generally cover a small surface of the functional areas only, with limited support capacity, and sometimes only roosts or foraging areas.

The species was previously described locally as molluscivorous when feeding on bare mudflat and as herbivorous when feeding on seagrass belt (Robin et al. 2013). Nevertheless, diets were described only during daytime, ignoring possible prey shift during night. Previous studies, exploring the night foraging in wintering shorebirds on intertidal mudflats, estimated a more important diurnal foraging in black-tailed godwits which fed at night most likely when cold temperatures increased the energy requirements (Dugan 1981; Kersten and Piersma 1987; Lourenço et al. 2008). However, all other species needed to forage both during the day and night low tides (Lourenço et al. 2008). In this study we equipped wintering black-tailed godwits with miniaturized GPSs on two different sites of the Pertuis Charentais. Concurrently, we sampled benthic macrofauna communities in order to map the distribution of habitats in mudflats. We then tested the hypothesis that black-tailed godwit feed both day and night, and show contrasting foraging behavior and distribution in response to different visual capacities, prey availability, predation risk and human activities such as hunting. We predicted smaller foraging home ranges at night due to difficulties for birds to visually detect prey (Turpie and Hockey 1993), suggesting more probing of sediment and therefore less movements (Pienkowski 1983; Lourenço et al. 2008). We also predicted a stronger use of habitats

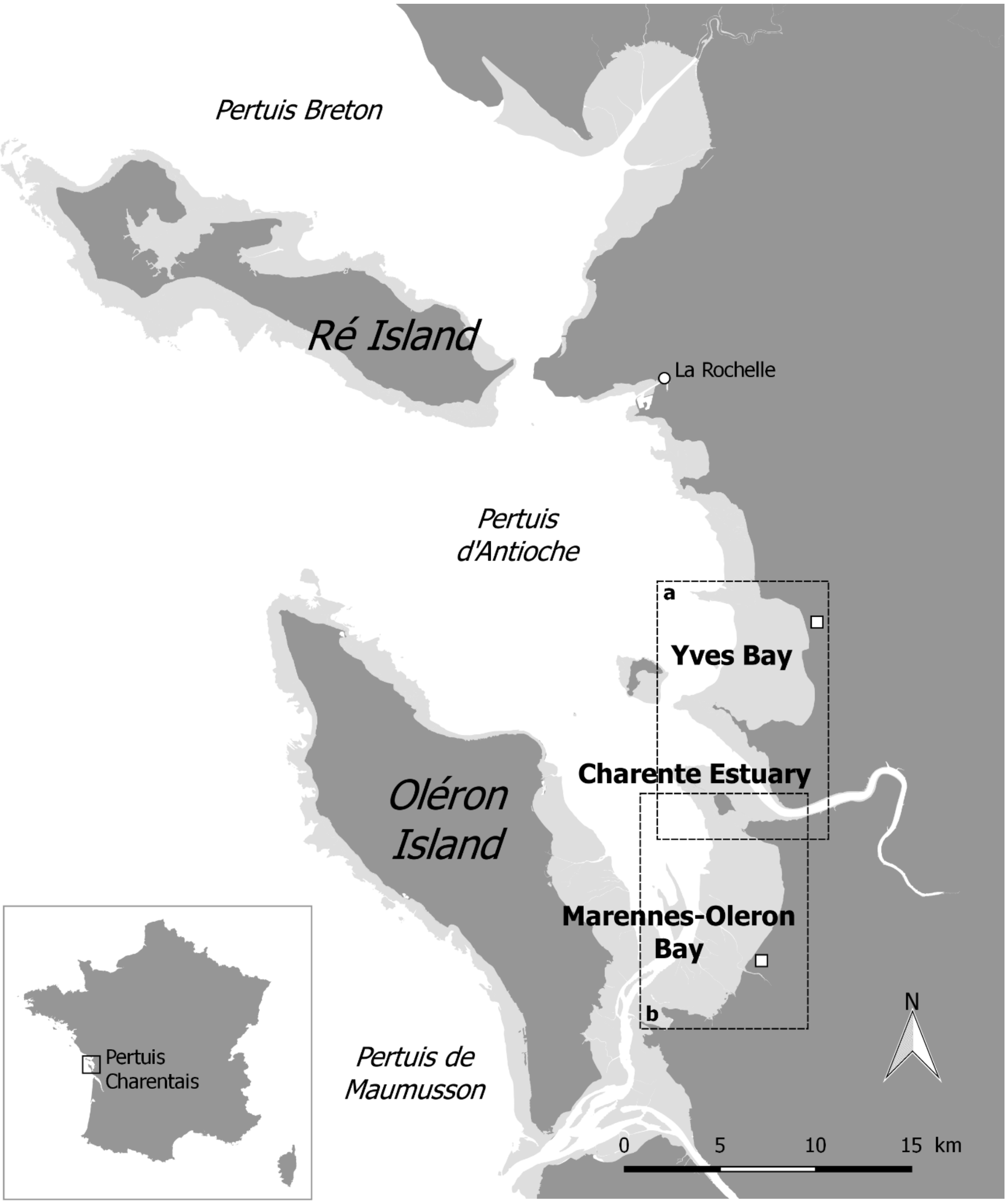

Fig. 1 Map of the Pertuis Charentais (Central French Atlantic coast) and localisation of the study sites. **(a)** Yves site corresponds to Yves Bay and Charente Estuary and **(b)** Moëze site corresponds to east side of Marennes-Oléron Bay. Dark grey corresponds to the mainland and light grey to the intertidal area.

distributed within the Nature Reserve during the day than at night, when human activities and disturbance are reduced.

Methods

Study site

Black-tailed godwits were surveyed and captured in September and October 2017, on two main wintering sites of the Pertuis Charentais: Yves Bay (Fig. 1a, 46°02’N, 01°03’W) and Marennes-Oléron Bay (Fig. 1b; 45°55’N, 01˚10’W). The Yves Bay includes an intertidal area of 2,300 ha with a marked north-south particle-size gradient (sandflats in the north and mudflats in the south; Philippe et al. 2016). The Marennes-Oléron Bay extends from continental coast to Oléron Island and covers 3,800 ha of intertidal areas, mainly characterized by bare mudflats on the mainland side and seagrass beds on the Oléron side. On these sites, godwits are known to roost in coastal marshes inside the National Nature Reserves of Marais d’Yves (192 ha, only marshes) and of Moëze-Oléron (6320 ha of sea and 320 ha of land surfaces). Hereafter, we distinguish the two study sites according to main high-tide roosts location: ‘Yves’ site including the Yves bay and the Charente Estuary (the largest estuary in the Pertuis Charentais located between both bays and mainly edged by 1,200 ha of bare mudflat) and ‘Moëze’ site including the mainland intertidal area of Marennes-Oléron Bay.

Godwit capture and tracking

A total of 12 black-tailed godwits were captured on Yves (n=4) and Moëze (n=8), during two sessions of non-moonlight nights. Mist nets were used to catch birds arriving at their high tide roost inside the Nature Reserves. For each bird, the biometry (flattened wing length, tarsus length and bill length) was measured using standard methods (Demongin 2016). Birds identified as *L. l. islandica* were sexed according to the allometric equation calculated by Gunnarsson *et al.* (2006). No individual with measurements located in the range of biometric overlap between males and females were found among the 12 individuals. The age was determined according to the plumage pattern (Demongin 2016). Godwits were then marked with a metal ring and a unique color rings combination, and equipped with a GPS-VHF tag (STERNA VHF-SRD with solar charger, Ecotone, Gdánsk, Poland; 35 x 16 x 10 mm, 7.5g), making sure that the weight of the tag did not exceed 3% of the bird body mass. GPS tags (tested mean accuracy of ± 10 m) were attached according to the ‘leg-loop’ method (Mallory

Table 1 Sex, age and biomass of tagged black-tailed godwit. Size of diurnal and nocturnal feeding areas (Convex Polygon, FCA feeding core areas 50%, FHR feeding home ranges 95%) and their overlap rate.

					Day			Night				
Site	Logger_ID	Sex	Age	Mass (g)	GPS fixes	dFCA (ha)	dFHR (ha)	GPS fixes	dFCA (ha)	dFHR (ha)	Overlape dFCA/ nFCA (%)	Overlape dFHR/ nFHR (%)
Yves	BLTG01	M	Ad.	292	465	428	1537	503	186	954	11	23
	BLTG02	M	Ad.	292	408	148	803	471	108	416	39	35
	BLTG03	F	Ad.	365	375	383	1495	391	207	936	13	18
	BLTG04	F	Ad.	345	369	412	1530	448	143	767	2	13
Moëze	BLTG04	-	-	-	354	346	1461	373	132	657	2	16
	BLTG05	M	Ad.	376	397	439	1722	446	209	864	2	19
	BLTG06	M	Ad.	290	370	311	1488	426	131	1043	19	42
	BLTG07	M	Ad.	298	273	283	1334	241	92	572	4	13
	BLTG08	M	Juv.	305	246	92	539	393	50	295	20	34
	BLTG09	F	Ad.	345	219	145	760	269	131	646	15	37
	BLTG10	M	Ad.	281	396	292	1596	286	123	781	25	18

and Gilbert 2008), with a 2 mm Teflon thigh harness (on the lower back), and recorded bird positions every 30 minutes. Among the 12 godwits equipped, two birds from Moëze were excluded from the analyses because their GPS provided data for one to two weeks only after which the battery failed, making them incomparable to other individuals. Data collected on the 10 remaining birds allowed the constitution of a first set of data for 4 individuals monitored simultaneously at Yves for one month (from 22nd September to 22nd October 2017), and a second set of data for 7 individuals (including one bird previously equipped at Yves) simultaneously tracked at Moëze for one month (from 22nd October to 22nd November 2017; Table 1). Data were stored and processed from a PostgreSQL/PostGIS database.

Habitat mapping

Habitat description at the two study sites was carried out by digitization of satellite images at the corresponding period for the habitats clearly identifiable (e.g. seagrass beds, oyster parks, littoral biogenic reefs, coastal saltmarshes, etc.), or by determination of the benthic macrofauna and granulometry of the sediment for mudflat habitats. Previous studies in Philippe *et al.* (2016) and Robin *et al.* (2015) provided a first description of the benthic macrofauna distribution on Yves and Moëze. Following the same sampling method, described in Bocher *et al.* (2007), 34 additional sediment core samples were carried out around the centroid of each foraging core area of monitored godwits during the present study, based on GPS locations. This additional core sampling consisted of a squared grid of nine replicates of sediment cores spaced by 10 meters and arranged around the central reference point of the station, that is, the centroid of the corresponding foraging area. Samples were collected on foot (during low tide) or by boat, depending on the accessibility of the area, both providing identical estimates (Bijleveld et al. 2012). Two specific sediment cores were collected for each replicate. For samples collected by foot, a first 15 cm diameter sediment core (0.018 m²), to a depth of 15 cm (maximum depth reached by foraging birds according to mean bill length of females), was sieved over a 1 mm mesh size to identify all living invertebrates, excluding *Hydrobia ulvae*. A second sediment core of 70 mm diameter (0.0037 m²), to a depth of 5 cm, was sieved in the laboratory over a 0.5 mm mesh to exclusively sample the potentially small and abundant mudsnail *H. ulvae.* For inaccessible points, covered by the tide or located on very soft sediments, the samples were collected from a boat (inflatable zodiac or small vessel) with two sediment cores of 10 cm diameter, covering 0.018 m² in total, to a depth of 15 cm. Only one core was processed to identify *H. ulvae*, and both were considered for all others species. Annelids were taken apart on site and stored in 70° Ethanol, and living molluscs were stored at -20°C until sorted at the laboratory. In the laboratory treatment, identification of organisms was done at the species level when possible, and length of molluscs was measured with an accuracy of 0.1 mm.

At each sampling station, an additional sediment core (depth of 5 cm) was collected to characterize the particle size of the substrate, by measuring the mean grain size (mm) and the percentage of silt (fraction < 0.063 mm) using a Malvern Mastersizer 2000 diffraction laser (particle sizes analysed from 0.04 to 2,000 mm).

The combination of benthic macrofauna data, particle size characteristics of the sediment, and digitization of hard substrate habitats from satellite images and field knowledge allowed to produce a fine-scale habitat typology on intertidal areas of study sites. Habitat determination is based on the European Nature Information System (EUNIS) classification of coastal habitats (Bajjouk et al. 2015).

Home ranges and habitat selection

To determine the spatial distribution of godwits, the Utilization Distribution (UD) was determined through the method of Kernel Density Estimates (KDE; Van Winkle 1975; Worton 1989; Laver and Kelly 2008), using the function 'kernelUD' (package 'adehabitatHR'; Calenge 2020). KDE method describes the UDs through estimation of a home range (95% isopleth kernel) and a core area (50% isopleth kernel) for each animal, from individual locations and time spent in the corresponding area (Worton 1989). Two main bandwidth methods exist for the estimation of kernel home ranges: the Least-Square Cross Validation (LSCV) and the reference bandwidth (ad-hoc) generally recognized as giving respectively an under-smoothing factor (h *LSCV*) and an over-smoothing factor (h *ad-hoc*) (Kie et al. 2010; Schuler et al. 2014). We retained an intermediate approach and used smoothing factor value h such as h *LSCV* $> h >$ h *ad-hoc*, with h *LSCV* and h *ad-hoc* the minimum values computed by 'LSCV' and 'ad-hoc' methods over all individuals monitored, and which resulted in a as contiguous as possible 95% kernel home-range polygon without including proximal areas known to not be used by birds (e.g. proximal supratidal resting areas during feeding distribution). Hence, we applied an identical smoothing factor $h = 120$ for all our monitored birds, in order to compare UDs between individuals. The grid resolution was set to 20 m, in accordance with the accuracy of locations provided by GPS loggers (± 10 m).

First, we estimated the global UD of each bird, from all locations collected during the monitoring period. Then, we considered the foraging distribution (when GPS positions were on intertidal areas at low tide) and the roosting distribution (when GPS positions were on supratidal lagoons and marshes) independently, also differentiating daytime and nighttime locations (sunrise and sunset data from the R package 'GeoLight'). Foraging distributions of godwits were then used to investigate the importance of foraging habitats through a habitat selection analysis using the Manly's selection ratios (Manly et al. 2002) with the R package 'adehabitatHS' (Calenge 2011). We analyzed the habitat selection as design II (second order), that is, at the individual scale and considering a same availability of habitats for all birds (Johnson 1980). The delineation of habitats considered as 'available' for birds has been determined from the Minimum Convex Polygon (MCP) of foraging points from all monitored birds. Finally, we explored the interindividual variations in the habitat selection, through an Eigen analysis of selection ratios (Calenge and Dufour 2006). This multifactorial analysis projects birds in a factorial plan described by the habitat types and best explaining the heterogeneity of the selection. The result should be able to highlight if groups of godwits using habitats in the same way exist. All statistical analyses where performed with the software R (3.6.1, R Core Team 2020).

Daily activity rhythm

To analyze the daily activity of godwits, which alternates between intertidal mudflats for feeding at low tide and coastal marshes for roosting at high tide, we measured the shortest distance to the coast of each bird over time and throughout the monitored period. We distinguished daytime and nighttime GPS locations, in order to explore differences in the shortest distance to the coast between diurnal and nocturnal foraging activities. We also considered the water height variation over time and changes in luminosity through moon phases (new, crescent, quarter, gibbous and full moon) to investigate their effect on the daily pattern of distance to the coast by foraging godwits (analysis of variance, ANOVA). The low number of high tides during which godwits remained on the intertidal areas to rest, and the difficulty in distinguishing roosting fixes from foraging ones, led us to consider for each bird all GPS locations over mudflats to estimate its foraging distribution.

Availability of main prey in used habitats

On the basis of dropping analyses collected during daylight in a previous study, godwits in Yves and Marennes-Oléron bays fed predominantly on bivalves (mainly *Macoma balthica*), whereas the godwits on Ile de Ré had a diet mainly of rhizomes of *Zostera noltei* (Robin et al. 2013). In this study, large worms (*Nereidae*) and small worms (*Capitellidae* and *Maldanidae*) accounted for less than 0.5% of the diet. The molluscivorous diet of godwits on these sites was

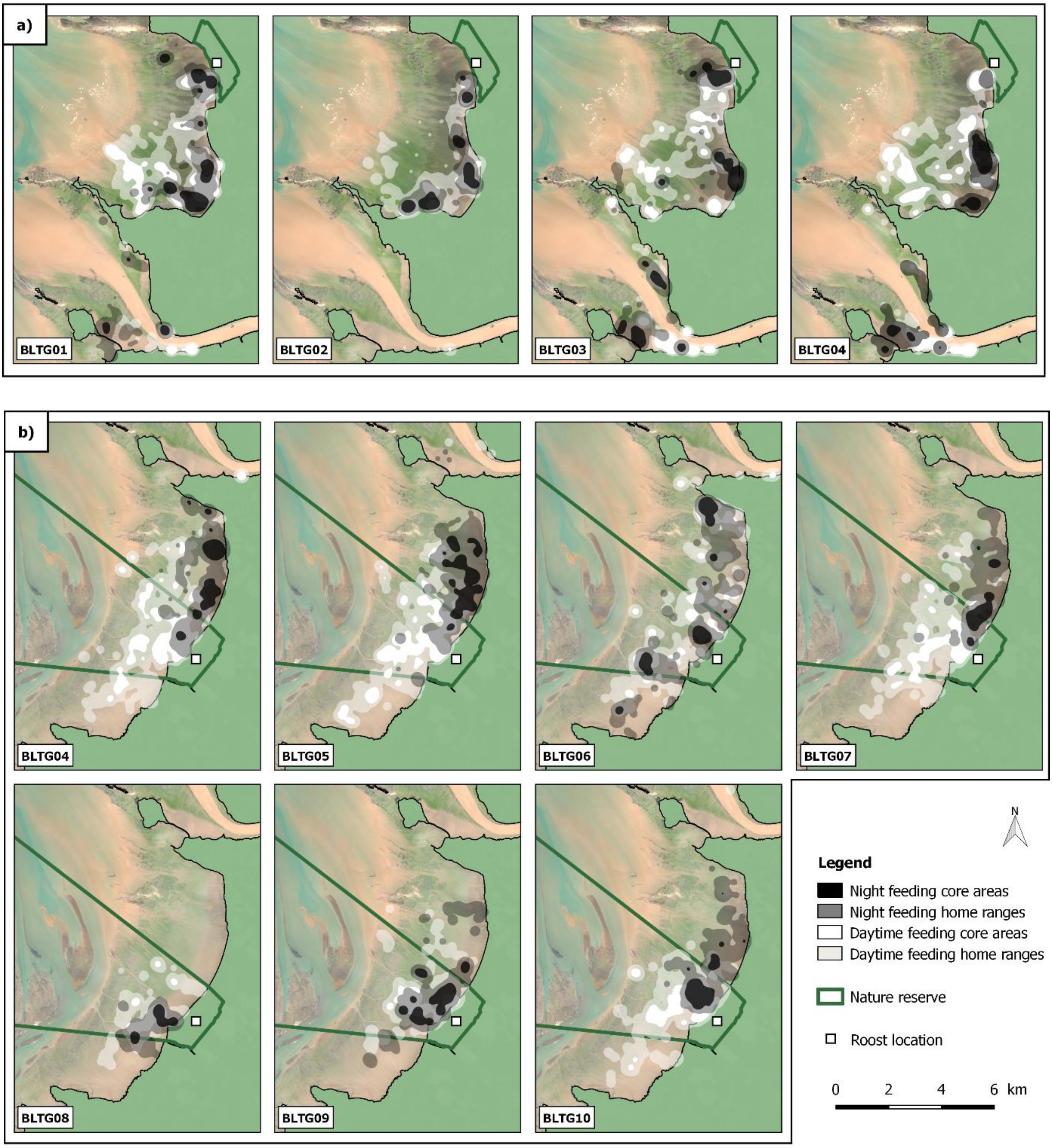

Fig. 2 Diurnal and nocturnal foraging home ranges of black-tailed godwits on **(a)** Yves site from mid-Sep to mid-Oct and **(b)** Moëze site from mid-Oct to mid-Nov. Foraging home ranges were calculated as 50% (core areas) and 95% (home ranges) kernel density contours.

confirmed by isotopic analyses of blood in a study on trophic resource partitioning within the local shorebird community (Bocher et al. 2014). Thus, we looked at the availability of bivalves *Macoma balthica* and *Scrobicularia plana* inside the most used habitats, that is, the most common habitats in the feeding core areas (FCA) of godwits. As the surface of the different habitats was not equal, the number of sediment core samples per habitat type was not similar. We therefore expressed the availability of preferential prey in terms of density per surface. In order to identify the availability of profitable prey for godwits, prey density by size class was also detailed.

Results

Day and night feeding areas

During the study periods, all monitored individuals fed exclusively on the intertidal mudflats of Yves and Moëze, except BLTG08 which foraged for six consecutive days in inland marshes on east of Moëze roost (Fig. 2). The main roosts were located inside both Nature Reserves, but godwits used also occasionally the intertidal mudflats to rest during high neap tide, when the upper foreshore remained emerged. Individual FCA presented different clear sizes between day and night, at both sites (Table 1). Diurnal FCAs, with a mean of 343 ± 131 ha (min-max: 148 – 428 ha, n = 4) at Yves and of 273 ± 118 ha (92 – 439 ha, n = 7) at Moëze, appeared more than two times larger than nocturnal ones at Yves: 161 ± 44 ha (108 – 207 ha; t = 3.54, df = 3, p = 0.04) and at Moëze: 124 ± 48 ha (50 – 209 ha; t = 4.60, df = 6, p < 0.01). The same magnitude of differences in size was observed for feeding home ranges (FHR) between day and night at both sites. Diurnal and nocturnal FRH were respectively of 1,341 ± 359 ha (803 – 1,537 ha) and 768 ± 250 ha (416 – 954 ha) for birds monitored at Yves (t = 7.45, df = 3, p < 0.01), and of 1,271 ± 446 ha (539–1,722 ha) and 694 ± 237 ha (295–1,043 ha) for those at Moëze (t = 4.98, df = 6, p < 0.01).

Thus, at both sites, spatial distributions of monitored godwits always corresponded to smaller feeding areas at night, and were also always located closer to the coast compared to daytime (Fig. 2). The day-night differences in the location of feeding areas was confirmed by the calculation of overlapping rates (Table 1), with a mean individual day-night FCA overlapping rate of 16 ± 16% (2-39%) at Yves and 12 ± 10% (2-25%) at Moëze. Day-night FHR also overlapped at low rates with 22 ± 10% (13-35%) at Yves and 26 ± 11% (13-42%) at Moëze. In addition, day and night feeding areas stood out on a north-south axis on Moëze

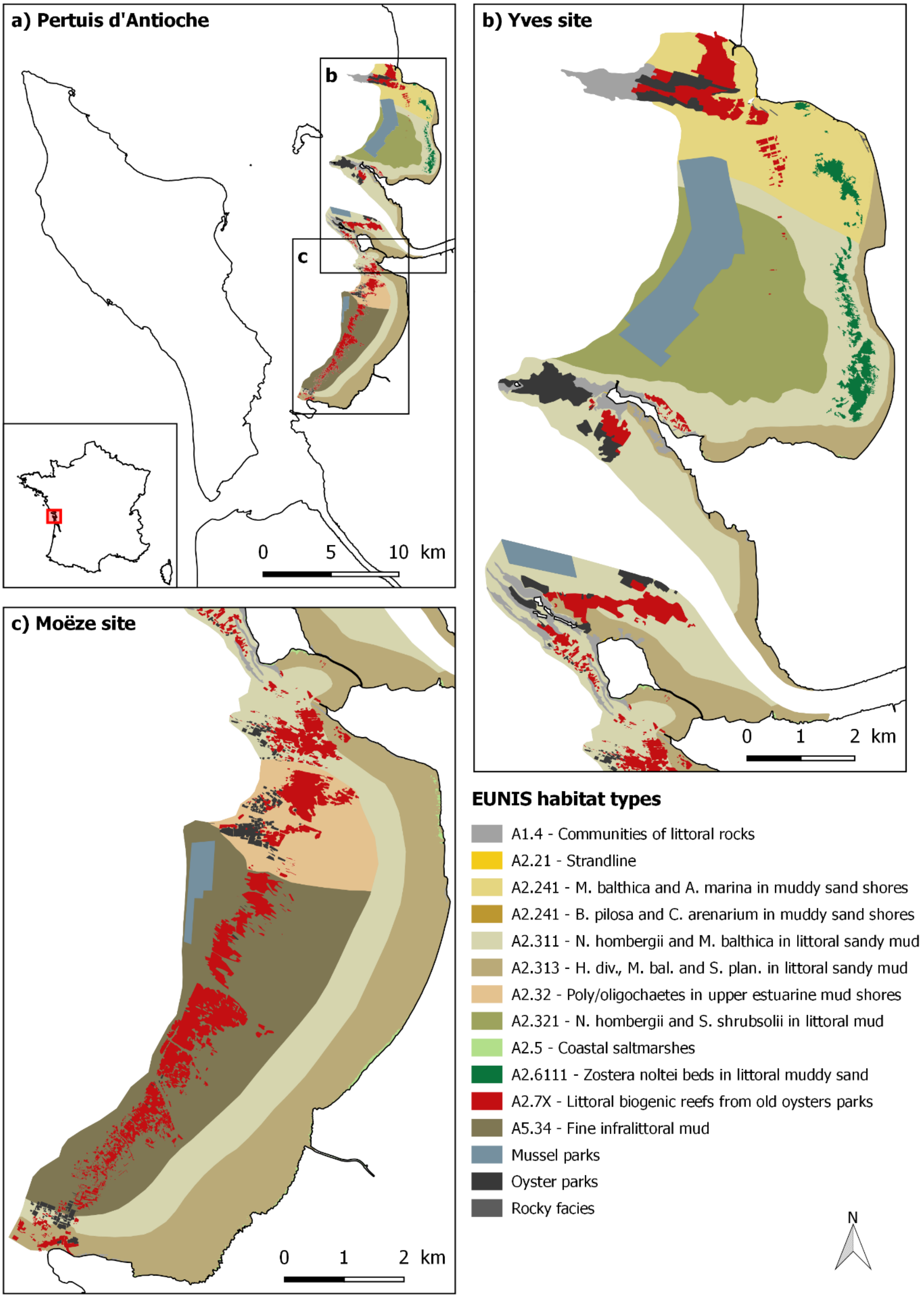

Fig. 3 Habitat typology at **(a)** Eastern area of Pertuis d'Antioche, **(b)** Yves Bay and Charente Estuary; and **(c)** Eastern area of Marennes-Oléron Bay.

mudflats, according to the border of the Nature Reserve. By day, tracked godwits were mainly restricted to the southern part of the mudflat, with a mean FCA of 83 ± 20% (43-100%) inside the Nature Reserve. By night, birds were located further north with only 51 ± 35% (5-92%) of FCA still located inside the Nature Reserve.

Habitat diversity and structure

In total, 15 intertidal habitat types were described on the two study sites (Fig. 3). Differences in habitat typology and distribution were described between Yves and Moëze and partially within site according to north-south gradient. At both sites, along the coastline, upper intertidal areas were bordered by habitats of strandline (A2.21), coastal saltmarshes (A2.5) or rocky facies, alternately. These micro-habitats are not considered in the habitat selection analysis. At Yves, the dominance of sandy habitats in the north of the bay (A2.241 and A2.244) and of muddy habitats in the south (A2.311, A2.313 and A2.321) illustrated the strong north-south particle size gradient (Fig. 3b). In the northern part, the main habitat A2.241 was characterized by the bivalve *Macoma balthica* and the polychaete *Arenicola marina*. The other habitat A2.244, more restricted, was dominated by crustaceans *Bathyporeia pilosa* and *Corophium arenarium.* Artificial oyster grow-out tables (oyster parks) and littoral biogenic oyster reefs associated (A2.7X) were dominant on the eastern and northern parts of the bay with also rocky substrates sheltering littoral rock pool communities (A1.4). In the south, the habitat A2.313 dominated by the polychaete *Hediste diversicolor* and the bivalves *M. balthica* and *Scrobicularia plana*; and the habitat A2.311 characterized by polychaete *Nepthys hombergii* and *M. balthica* were predominant. The muddy habitat A2.321 in the southeastern part of the bay, was mainly described by the dominance of the polychaetes *N. hombergii* and *Streblospio shrubsolii.* Finally, seagrass beds of the phanerogam *Zostera noltei* (A2.6111) were present in patches on the upper tidal area of the bay. The lower part of tidal areas was covered by mussel culture (mussel parks). In addition, the main habitats on the Charente Estuary were again habitats A2.311 and A2.313. Mussel and oyster parks or biogenic reefs were present on the lower part of the intertidal areas.

At Moëze, the particle size features of the sediment appeared more homogeneous over the site, with a dominance of muddy substrates (Fig. 3c). Habitats A2.311 and A2.313 were dominant at the upper tidal areas. Habitats A2.32 and A5.43, not observed at Yves, extended over large surfaces on medium and lower intertidal areas. The habitat A2.32 was composed by

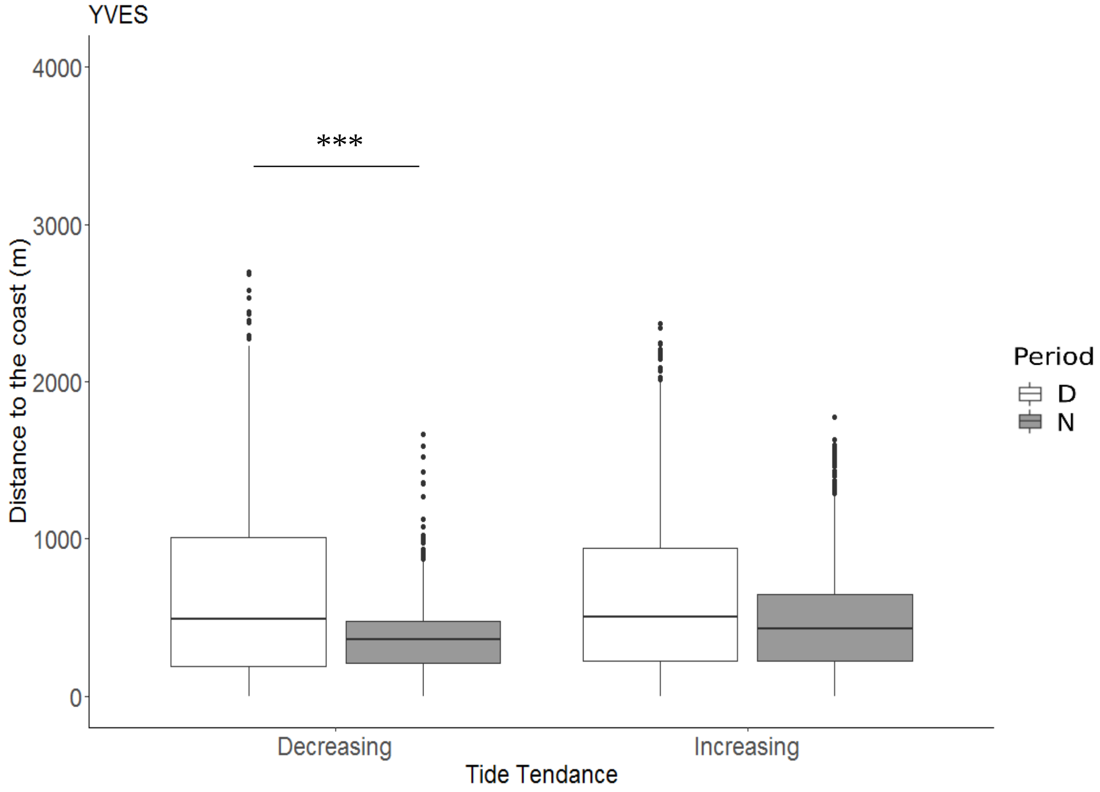

Fig. 4 Distance of godwits to the coast according to tendency of the tides (increasing or decreasing) and daytime period (day “D” or night “N”) at Yves site.

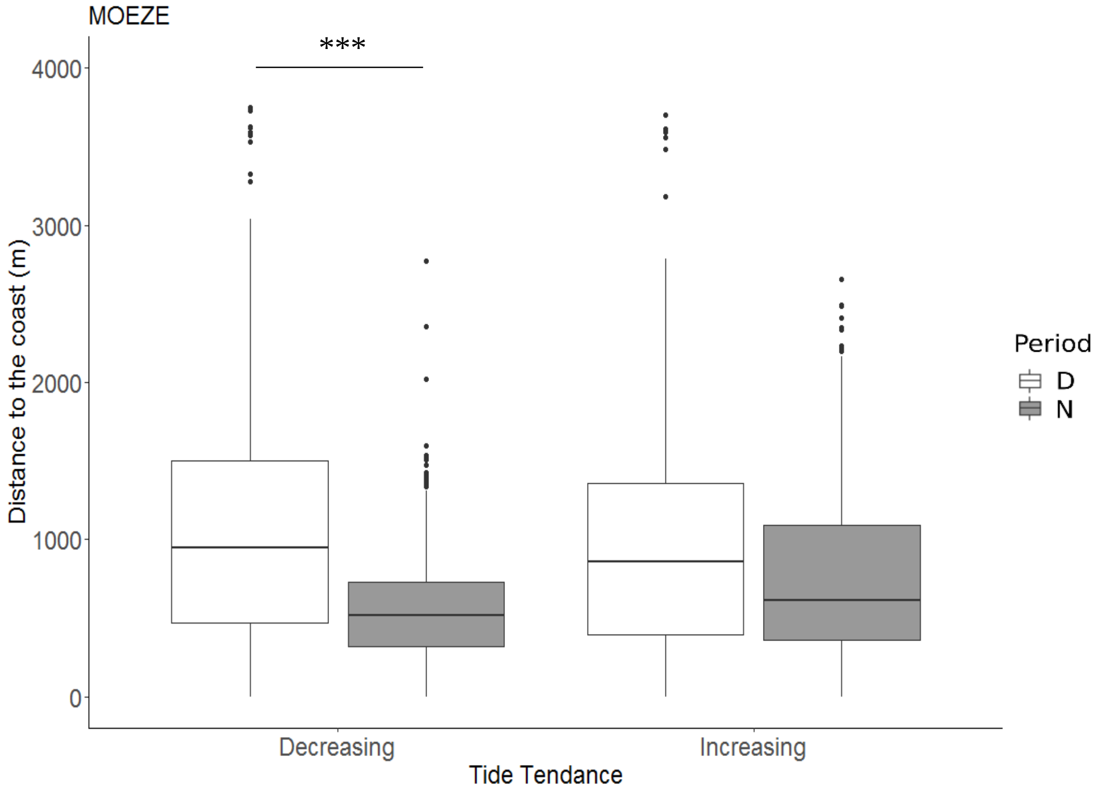

Fig. 5 Distance of godwits to the coast according to tendency of the tides (increasing or decreasing) and daytime period (day “D” or night “N”) at Moëze site.

a low diversity and abundance of polychaetes and oligochaetes, and habitat A5.34 by a fine mud holding a low invertebrates' abundance. Littoral biogenic reefs on abandoned oyster parks (A2.7X) were widespread at lower intertidal areas, as well as the still active oyster and mussel parks, but to a lesser extent.

Foraging distance to the coast

Analysis of monitored godwit positions over time and in relation to the coastline revealed a cyclical distribution pattern not only dependent of the tidal cycle. Schematically, godwits moved away from the coast during ebbing tide and were approaching the coast during rising tide to return to their roost during high tide. Nevertheless, movements from the coast to intertidal feeding areas during low tide underlined marked differences between diurnal and nocturnal movements. At both sites, the mean distance of feeding godwits to coastline were higher during daytime than nighttime. At Yves, the mean distance to the coast (429 ± 536 m) during the day was significantly higher than during the night (303 ± 327 m; KW χ^2 = 10.84, df = 1, p-value < 0.001). The difference in distances was more important at Moëze with a mean distance to the coastline at day of 611 ± 725 m and only of 380 ± 464 m at night (KW χ^2 = 121.45, df = 1, p-value < 0.001). These differences in nycthemeral distributions on mudflats depended on tidal amplitude, but being obviously particularly discernable during spring tides when more mudflat areas were available (Fig. S1 and Fig. S2). In addition, day and night differences of foraging distances to the coastline varied according to the tide amplitude tendency. There were significant differences of mean distances to coastline during decreasing water heights from one tide to the other at Yves (day: 436 ± 547 m; night: 256 ± 255 m; KW χ^2 = 15.62, df = 1, p-value < 0.001) and Moëze (day: 655 ± 769 m, night: 287 ± 367 m; KW χ^2 = 191.5, df = 1, p-value < 0.001). Conversely, no significant differences were observed in the distance to coast during increasing water heights at Yves (day: 422 ± 524m; night: 350 ± 381m; KW χ^2 = 0.32, df = 1, p-value = 0.6; Fig. 4) and Moëze (day: 565 ± 675m; night: 475 ± 528m; KW χ^2 = 2.78, df = 1, p-value = 0.09; Fig. 5). This general pattern observed at each site, pooling all equipped birds, was also observed at the individual level for most godwits (Fig. S3 and Fig. S4).

Foraging habitat use and selection

The monitored godwits foraged on several habitats at Yves (from 4 to 10) at Moëze (from 3 to 8) among all available ones (Fig. 6). Nevertheless, the proportion of habitat identified within FCA emphasized a predominant use of a few habitat types.

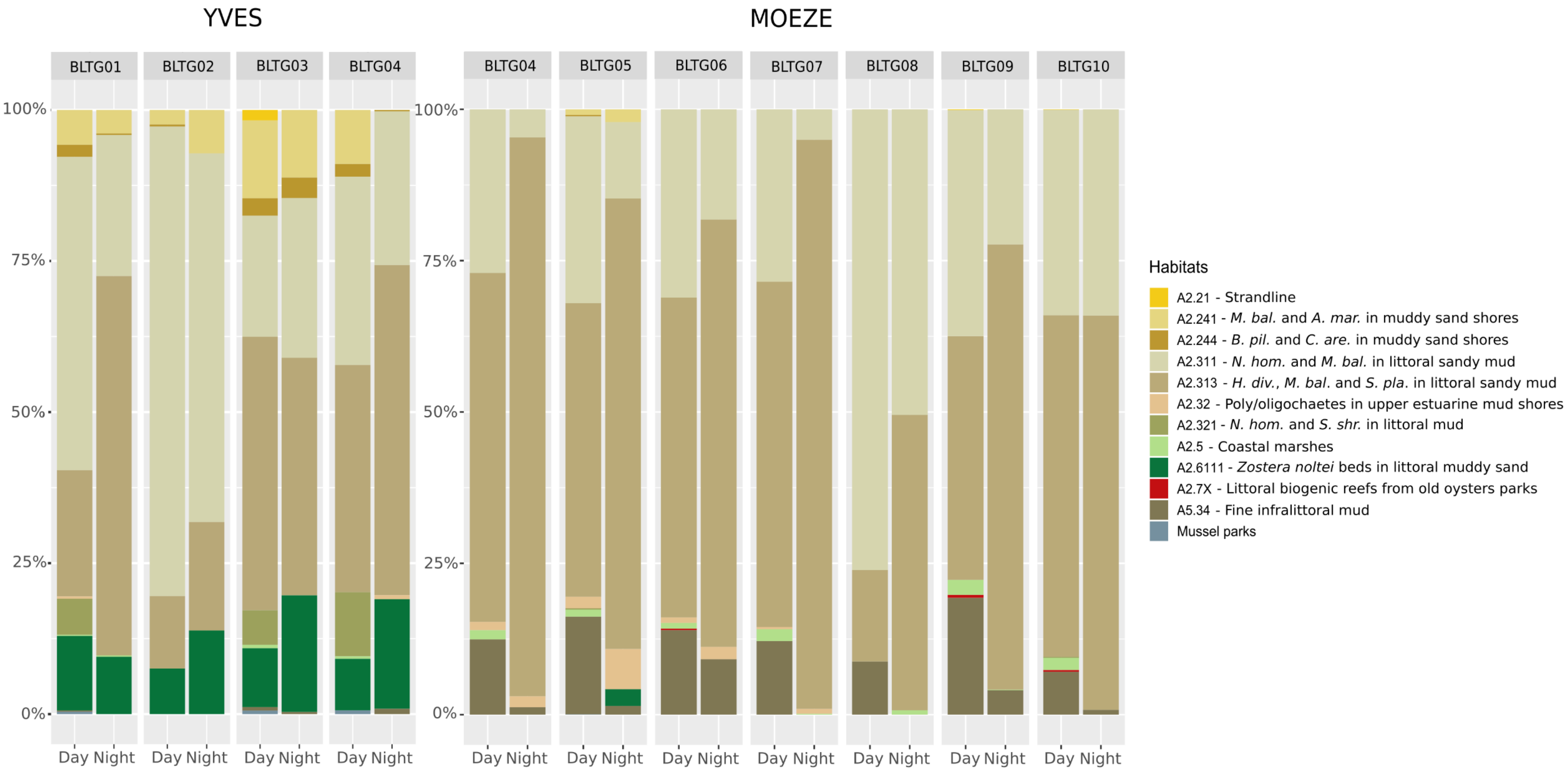

Fig. 6 Day and night proportion of habitat types on Feeding Core Areas (50% Kernel density contour) of each black-tailed godwit at Yves and Moëze.

At Yves, the habitats A2.311, dominated by *N. hombergii* and *M. balthica,* and A2.313 dominated by *H. diversicolor, M. balthica* and *S. plana,* were mainly used, both during day and night (Fig. 6). Seagrass beds (A2.6111) was the third habitat identified in FCA in terms of surface used. The habitat A2.241 with dominance of *M. balthica* and *A. marina* and the habitat A2.321 characterized by polychaetes *N. hombergii* and *S. shrubsolii* were secondarily used by birds. This selection of some specific habitats for foraging illustrated the diurnal and nocturnal non-random habitat selection, both when pooling the four monitored birds (Daytime: $\chi^2 = 919.9$, df = 44.0, $p < 0.001$; Nighttime: $\chi^2 = 2113.2$, df = 44.0, $p < 0.001$) and at the individual scale (Daytime: $\chi^2 = 810.2$, df = 11.0, $p < 0.001$; Nighttime: $\chi^2 = 2028.7$, df = 11.0, $p < 0.001$). All main habitats were selected (all global selection ratios > 1), except A2.241 (Fig. S5). The habitats A2.6111 (seagrass) and A2.313 (*H. diversicolor, M. balthica* and *S. plana*) had the highest selectivity indexes. Although selected by day, the non-use of the habitat A2.321 (*N. hombergii* and *S. shrubsolii*) at night, in favor of a greater use of habitats A2.313 and A2.6111, constituted the main differences between diurnal and nocturnal habitat selection by godwits at Yves (Fig. 6 and Fig. S5).

Diurnal and nocturnal FCA at Moëze were predominantly located in habitat A2.313, followed to a lesser extent by habitat A2.311. Godwits also foraged secondarily in habitat A5.34 during daytime, but no longer by night. At night, all monitored godwits reduced their prospection in habitat A2.311 and increased their presence in habitat A2.313. These results highlighted the significant selection of habitats by godwits, non-randomly used both day and night, considering individuals independently (Day: $\chi^2 = 853.8$, df = 7.0, $p < 0.001$; Night: $\chi^2 = 2091.9$, df = 7.0, $p < 0.001$) as well as combining all the seven birds monitored (Day $\chi^2 = 993.1$, df = 49.0, $p < 0.001$; Night: $\chi^2 = 2520.2$, df = 49.0, $p < 0.001$). The results of Manly selectivity measures confirmed a clear selection of habitat A2.313 (global selection ratio = 1.1) over habitat A2.311 (GSR = 1.9) by day (Fig. S6). At night, A2.313 (GSR = 2.1) appeared selected to a greater extent over A2.311 (GSR = 1.5), illustrating a shift at night in habitat preferences, previously observed with FCA (Fig. 6 and Fig. S6).

Within sites, despite the use of the same habitats for foraging, godwits showed inter-individual differences in the proportion of each habitat used for feeding (FCA) during daytime and nighttime, both at Yves (Fig. 5; Day: $\chi^2 = 109.7$, df = 33.0, $p < 0.001$; Night: $\chi^2 = 84.5$; df = 33.0; $p < 0.001$) and Moëze (Day: $\chi^2 = 139.3$, df = 42.0, $p < 0.001$; Night: $\chi^2 = 428.3$, df = 42.0, $p < 0.001$).

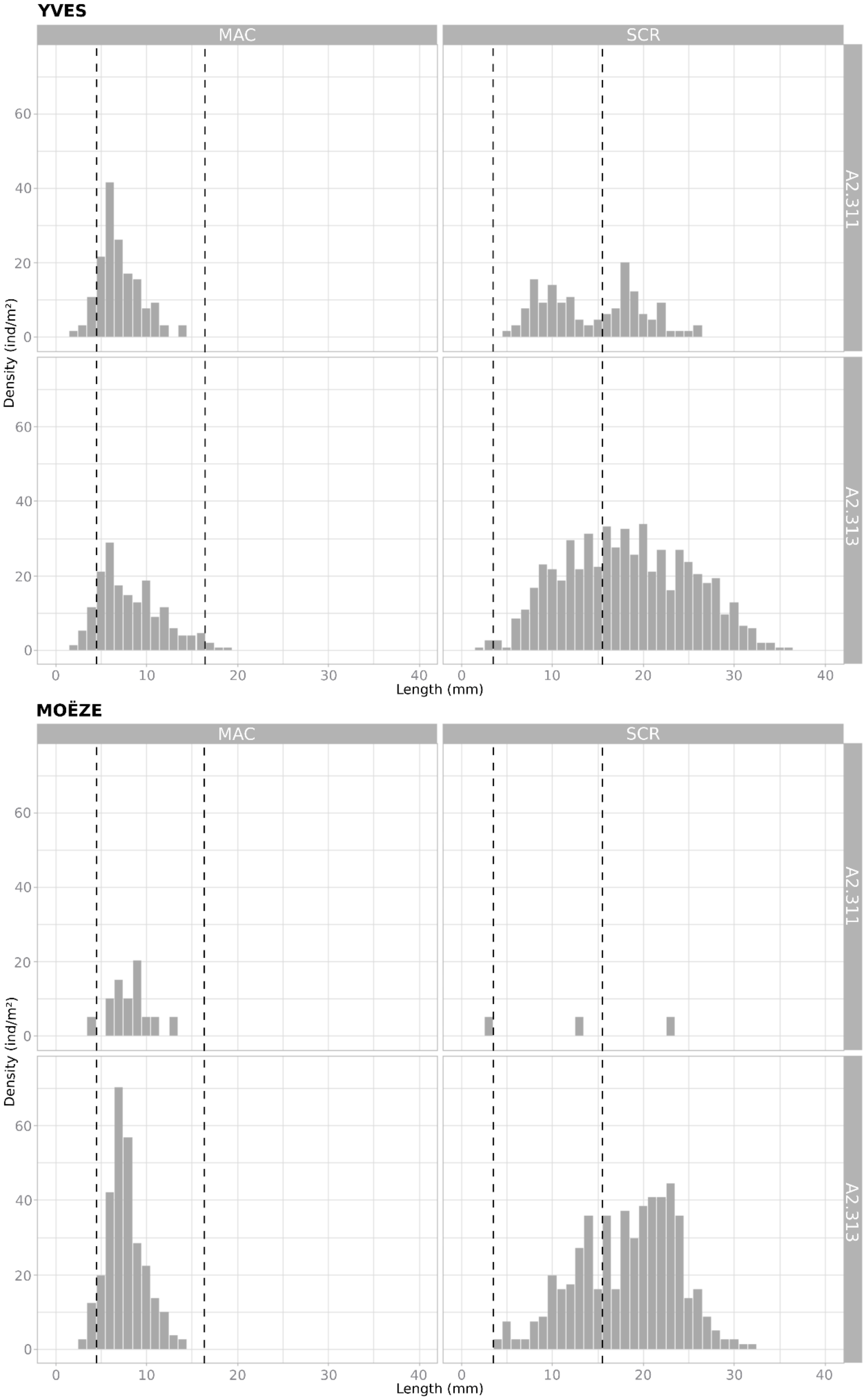

Fig. 7 Distribution of prey sizes for *Macoma balthica* (MAC) and *Scrobicularia plana* (SCR) in the two most represented habitats in the feeding core areas of godwits, i.e. A2.311 and A2.313. Dashed lines represent the range of optimal prey sizes of MAC (5-16 mm) and SCR (4-15 mm) for godwits.

Availability of bivalves as prey in the main used habitats

At both sites, the two main foraging habitats used by godwits were A2.311 and A2.313. In these habitats, the density of *M. balthica* and *S. plana* considered as the main prey differed in densities and size distribution (Fig. 7). At Yves, the size-class density distribution of *M. balthica* in the range of optimal prey sizes (5-16 mm, Robin 2011) did not significantly differed between A2.311 and A2.313 (t = 0.12017, df = 18.14, p-value = 0.906), but the density of *S. plana* underlined more individuals per square meter in the habitat A2.313 for optimal size classes (4-15 mm, Robin 2011 ; t = 4.43, df = 11, p-value = 0.001). At Moëze, the density of *M. balthica* and *S. plana*, in the range of optimal prey sizes for godwits, were widely higher in the habitat A2.313 (*M. balthica*: t = 2.66, df = 10.92, p-value = 0.022; *S. plana*: t = 4.2994, df = 11.42, p-value = 0.001).

Discussion

The analysis of habitat use and selection in wintering Icelandic black-tailed godwits highlighted, for the first time and at a very fine scale, the influence of the day time on their spatial distribution. The monitored godwits showed a high variability in the selection of feeding areas according to nycthemeral periodicities, with little changes in habitat types selected. Indeed, the size of feeding areas and their distance to the coast significantly differed between day and night, with nocturnal feeding areas being two time smaller than daytime ones, and located closer to the coastline. These day and night differences in the distance of foraging areas to the coastline also depended on the tidal cycle (neap tides *vs* spring tides) and tidal range tendency, with the most marked differences occurring during a decreasing tidal amplitude of spring tides. Moreover, the protected status of mudflat areas also showed an influence on the diurnal and nocturnal distribution of godwits. Hence, at Moëze, where both ‘protected’ and ‘not protected’ areas were adjacent on mudflats, birds largely foraged inside the protected area during daytime while most of them foraged outside at night. Finally, at both sites, a significant inter-individual variability in the size and the location of diurnal and nocturnal foraging areas was observed, although the same habitat types are used and in close proportions. Individuals at Moëze showed differences in their use of the Nature Reserve areas. Godwits with the smallest feeding home ranges stayed inside the Nature Reserve, both during day and night, while the others prospected more often outside the protected area, preferentially at night.

Lourenço *et al.* (2008) investigated the energetic importance of night foraging for shorebirds in intertidal mudflats, and concluded that wintering Icelandic godwits were able to fulfill their daily energy requirements on a single tide, while all other studied species needed to forage during both day and night low tides. Hence, in the Tagus Estuary in Portugal, godwits achieved much a higher energy consumption during the day and the species was seldom seen foraging at night except during coldest night. The authors explained this unusual activity at night by higher energy needs during cold spells (Dugan 1981; Kersten and Piersma 1987). Conversely, at our study sites, godwits also had to feed at night and we hypothesize that they could not meet their daily energetic requirements just feeding during daylight low tide. Hence, it is possible that individuals wintering in Europe with lower temperatures than along the coasts of Africa, may induce higher thermoregulatory costs and energy requirements (Wiersma and Piersma 1994).

Consequently, godwits were dependent of the availability of emerged mudflats according to tidal rhythm for feeding whatever the time of the day, as previously observed for many species of coastal shorebirds (McNeil et al. 1992; McNeil and Rodriguez 1996; Dodd and Colwell 1998; Lourenço et al. 2008; Jourdan et al. 2021). Nevertheless, the nycthemeral patterns of monitored godwits highlighted differences in space use between diurnal and nocturnal feeding activities. Piersma *et al.* (2006) already observed contrasting areas used between day and night in some foraging non-breeding shorebirds, but without exploring the characteristics of feeding areas. Burton and Armitage (2005) and Dwyer *et al.* (2013) also observed in wintering redshanks *Tringa totanus* the use of contrasting foraging areas between day and night, with larger foraging home ranges and core areas at night. Hence, our observations of distinct distributions between day and night in black-tailed godwits are consistent with previous studies, although the smaller-size pattern of nocturnal feeding home range (nFHR) and core areas (nFCA) differ from redshanks (Burton and Armitage 2005) but not from bar-tailed godwits (Jourdan et al. 2021). Such differences between diurnal and nocturnal foraging home ranges could be related to birds' feeding method. In black-tailed godwit in the Tagus estuary, Lourenço *et al.* (2008) showed a more frequent pecking behaviour during the day and the dominance of stitching and sweeping movements at night. These changes in foraging behaviour, also observed in dunlins (*Calidris alpine*) (Mouritsen 1994), are assumed to be an adjustment to visual conditions, birds preferring visual foraging methods (pecks) during daylight but need tactile capacities (stitches, swipes) to forage at night (Mouritsen 1994; Lourenço et al. 2008; Cunningham et al. 2013). Larger prospecting areas could then result from the higher step rate associated to direct visual searches by day, while reduced step rate during tactile methods could limit the size of night foraging range (Lourenço et al. 2008). Nevertheless, the predominant use of pecking at day is not consistent with birds' diet, made of bivalves at both our study sites (Robin et al. 2013; Robin et al. 2015). These preys being detected tactilely by probing, godwits need to walk longer to increase probability to detect them.

The size of foraging home ranges could consequently depend on the prey density at diurnal and nocturnal grounds. Results of habitat selection underlined that godwits selected the intertidal sandy mud habitat 'A2.313' both during day and night, but in greater proportion during nocturnal feeding. Compared to the second most used habitat 'A2.311', the density of the preferred prey *M. balthica* (Robin et al. 2013) in the optimal range size (5-16 mm) was significantly higher in the habitat 'A2.313'. In case of higher prey density on nocturnal foraging grounds, the intake and spatial turning rates is assumed to increase (Zharikov and Skilleter 2003; Dias et al. 2009), resulting in sinuous low-speed searches (Nolet and Mooij 2002) and lower size of prospecting areas. In addition, the higher surface activity of intertidal invertebrates by night, including bivalves such as *M. balthica*, could constitute better prey catching opportunities for godwits compared to daytime (Esser et al. 2008), and could amplify the prey availability dependent behaviour of birds (Evans 1987).

Further, although the preferred prey *M. balthica* was abundant in habitat 'A2.311', godwits selected habitat 'A2.313', which combined a higher harvestable prey density of *M. balthica* and *S. plana*. The presence of *S. plana* in habitat 'A2.313' could constitute additional feeding opportunities (Moreira 1994; Robin et al. 2013), with an optimal prey size (4-15 mm) well represented. Moreover, by night, godwits could feed on siphons of larger *S. plana* than initial optimal range size. Indeed, the increased surface activity of bivalves at night (Esser et al. 2008), would make *S. plana* siphons more abundant and available to birds in the nearshore habitat 'A2.313', making them to feed closer to the shoreline at night.

Indeed, and in contrast to previous observations which highlighted an avoidance of the nearshore by non-breeding shorebirds during nocturnal foraging due to an increased predation risk (Sitters et al. 2001; Piersma et al. 2006), godwits in the Pertuis-Charentais fed at a higher distance to the coast by day. In addition to the aforementioned prey availability, this pattern could arise from an increased human disturbance during daytime, such as recreational activities, which already showed an effect on feeding opportunities, flight movements and use/avoidance of some feeding areas in some shorebird species (Thomas et al. 2003; Navedo and Masero 2007; Burger and Niles 2013). By day, at Yves and Moëze, black-tailed godwits seem to move away from the coast, the likely source of disturbance, to join the less interesting but still suitable habitat ‘A2.311’. At night, with the decrease in human disturbance on coastline, godwits could benefit to get closer to the coast to reach the most profitable habitat ‘A2.313’ that provides a higher density of *M. balthica* and *S. plana*. In addition, the presence of public lighting around inhabited areas could allow a good feeding efficiency at night, as shown for the redshanks on the Forth Estuary in Scotland (Dwyer et al. 2013). However, the two study sites are not directly under the influence of artificial lighting except for the southern and northern ends of Yves Bay (https://lighttrends.lightpollutionmap.info) and the benefit of artificial lighting cannot solely explain the nocturnal feeding observed near the coast.

This distance of foraging birds to the coast was different between tidal cycles, i.e. neap tides or spring tides, but also between tidal trends, i.e. decreasing or increasing tidal amplitude. During neap tides, intertidal areas available at low tide were obviously limited and the selection of habitats further away the coast could not be prospected, reducing differences between day and night. Moreover, the upper foreshore remained available at high neap tides, and birds did not necessarily reached marshes for roosting. In spring tides, during which the low tides expose almost all the intertidal areas and the high tide completely covers them, the bird distance to the shoreline highlights an alternation between intertidal feeding period and supratidal roosting time. Thus, day and night differences in the foraging habitat selection, according to the aforementioned anthropogenic disturbance and prey availability, can easily appear. However, this behavior pattern depended on the tidal tendency, so that the significant distinct distribution of godwits between day and night during mid and spring tides was mainly observed during decreasing tidal ranges but not during increasing ones.

The influence of anthropogenic disturbances on the distribution of black-tailed godwits was also highlighted by the alternation of ‘protected’ and ‘unprotected’ foraging areas. Most of diurnal foraging areas were located inside the National Nature Reserve of Moëze-Oléron. Hunting is prohibited in the Nature Reserve, but authorized from August to January from the sunrise to 10 a.m. in its north and south sectors (Delaporte, *Pers. Com.*). Although the hunting activity was not measured during the study period, its related disturbance, in addition to the morning and recreational walks (with dogs) later during the day could explain limited tracked godwits inside the Nature Reserve. Additional studies must be undertaken to measure human activity and its disturbance impact on feeding areas, which would constrain bird ability to meet their energy needs on the long-term.

Supplementary material

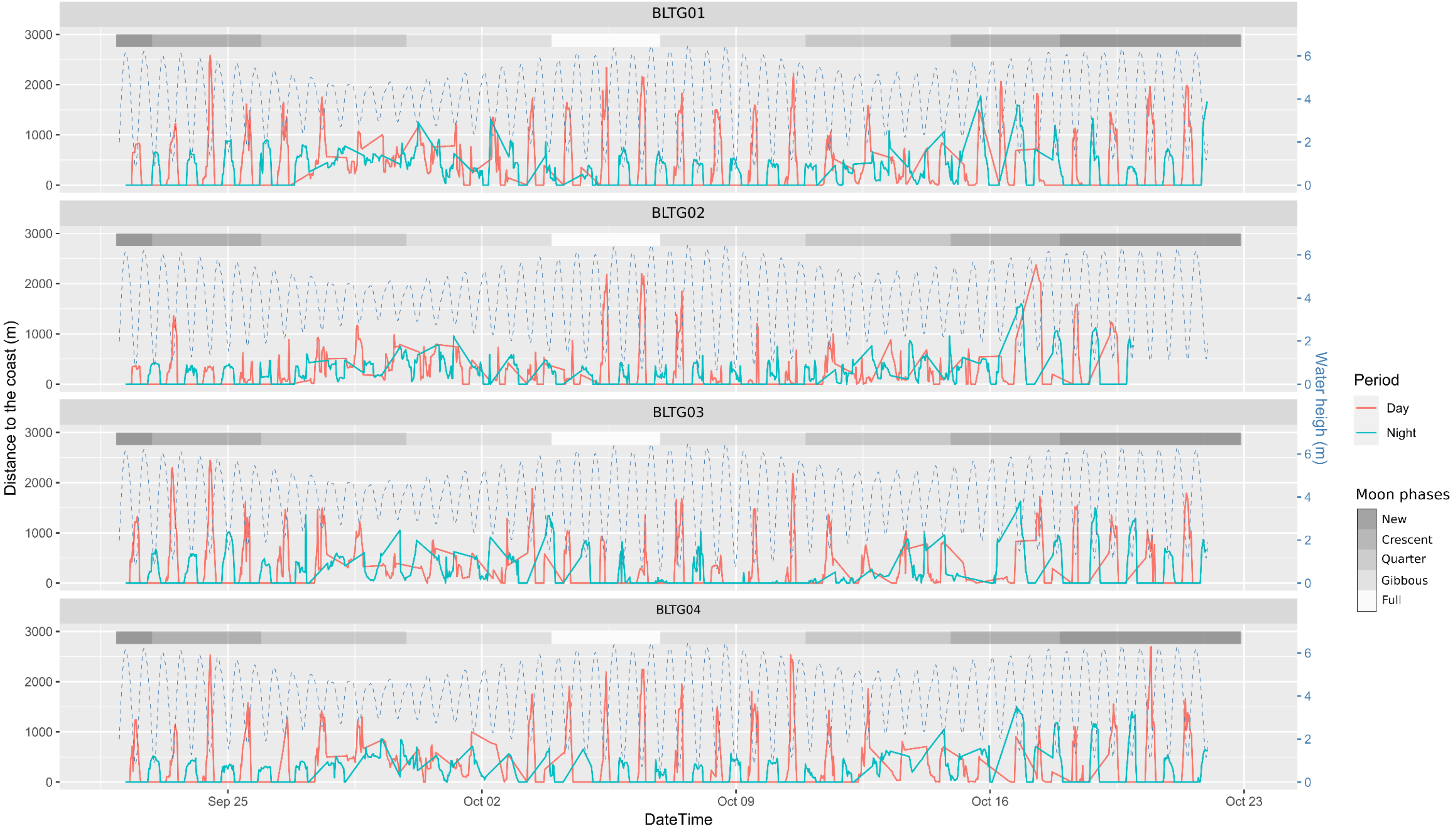

Fig.S1 Distance to the coast over time for individuals monitored at Yves site, according to the time period (day and night), moon phases (new, crescent, quarter, gibbous, full) and water height (dotted lines in blue). The grey scale represents the moon brightness during the different phases, although other environmental factors can alter this theoretical luminosity (e.g. cloud cover).

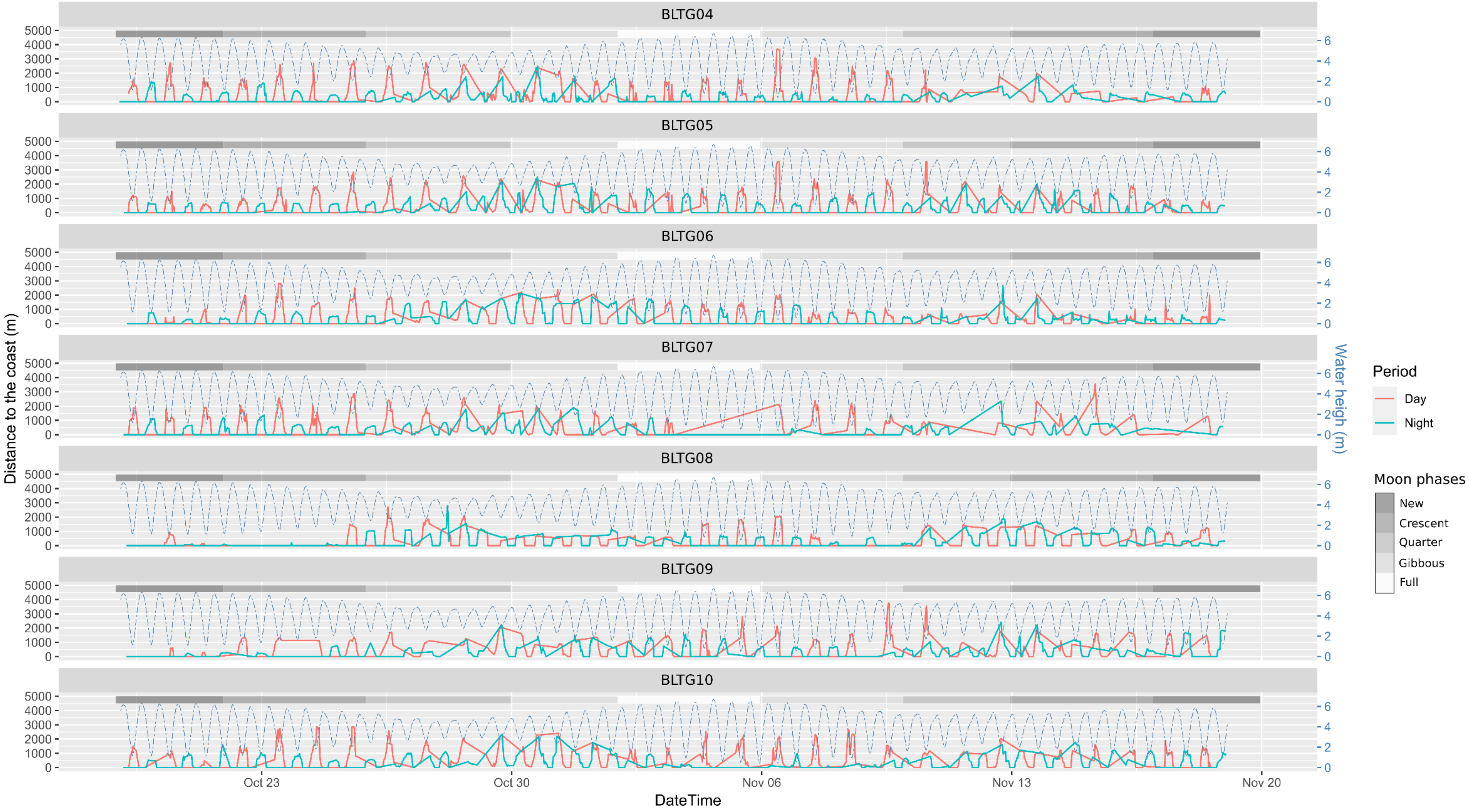

Fig.S2 Distance to the coast over time for individuals monitored at Moëze site, according to the time period (day and night), moon phases (new, crescent, quarter, gibbous, full) and water height (dotted lines in blue). The grey scale represents the moon brightness during the different phases, although other environmental factors can alter this theoretical luminosity (e.g. cloud cover).

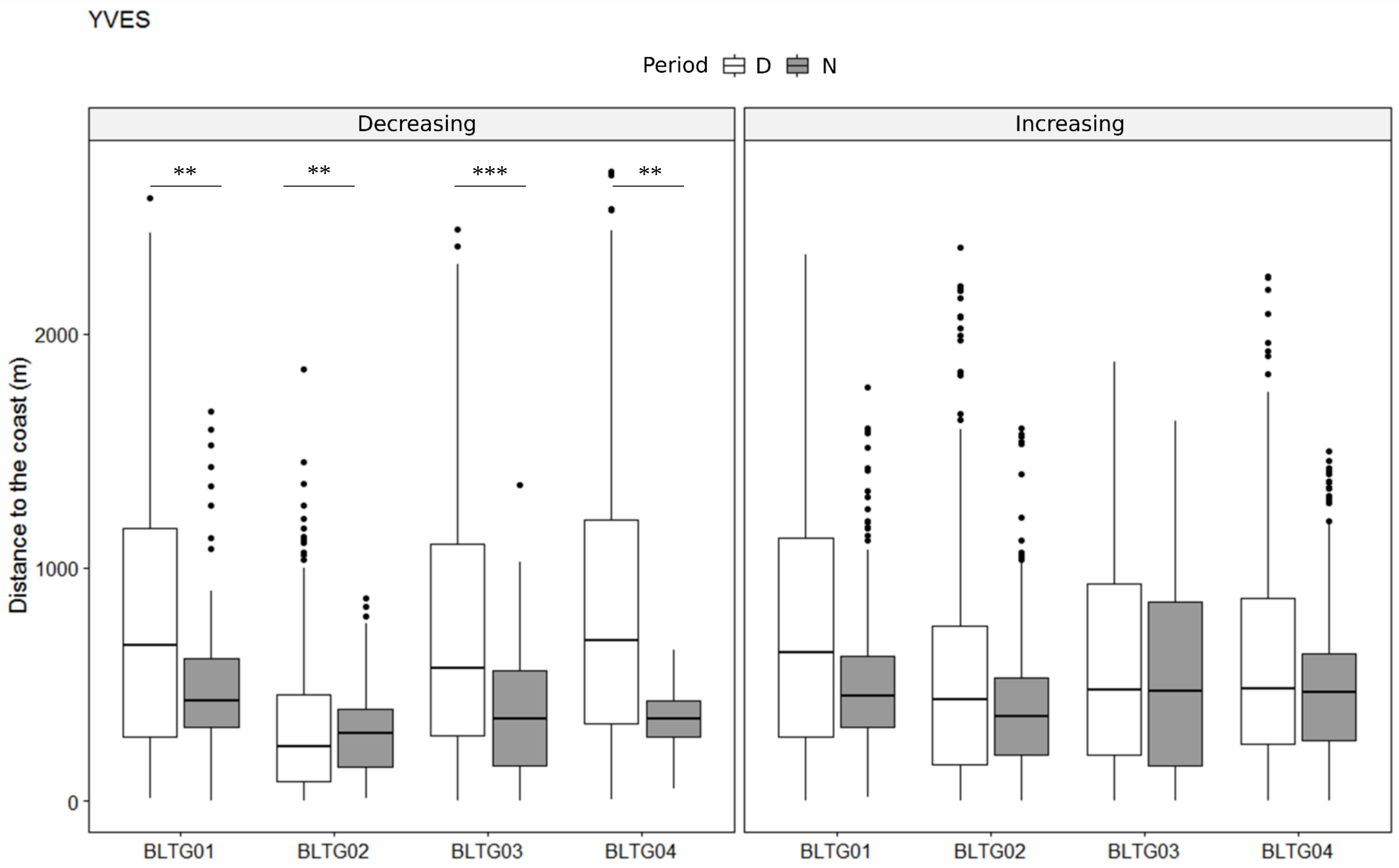

Fig. S3 Distance to the coast, for each individual, according to tendency of the tides (increasing or decreasing) and the daytime period (day “D” or night “N”) at Yves site.

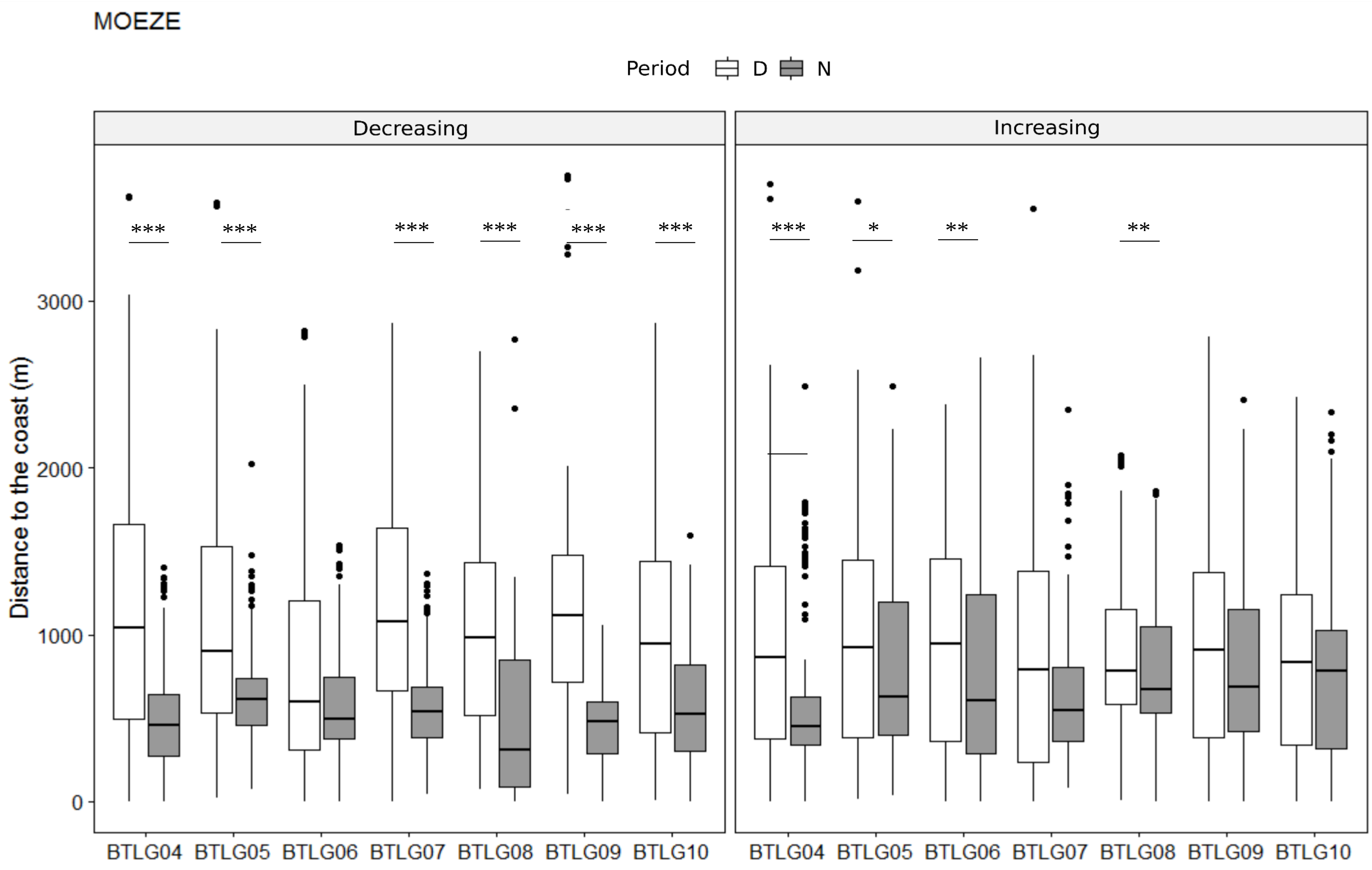

Fig. S4 Distance to the coast, for each individual, according to tendency of the tides (increasing or decreasing) and the daytime period (day "D" or night "N") at Moëze site.

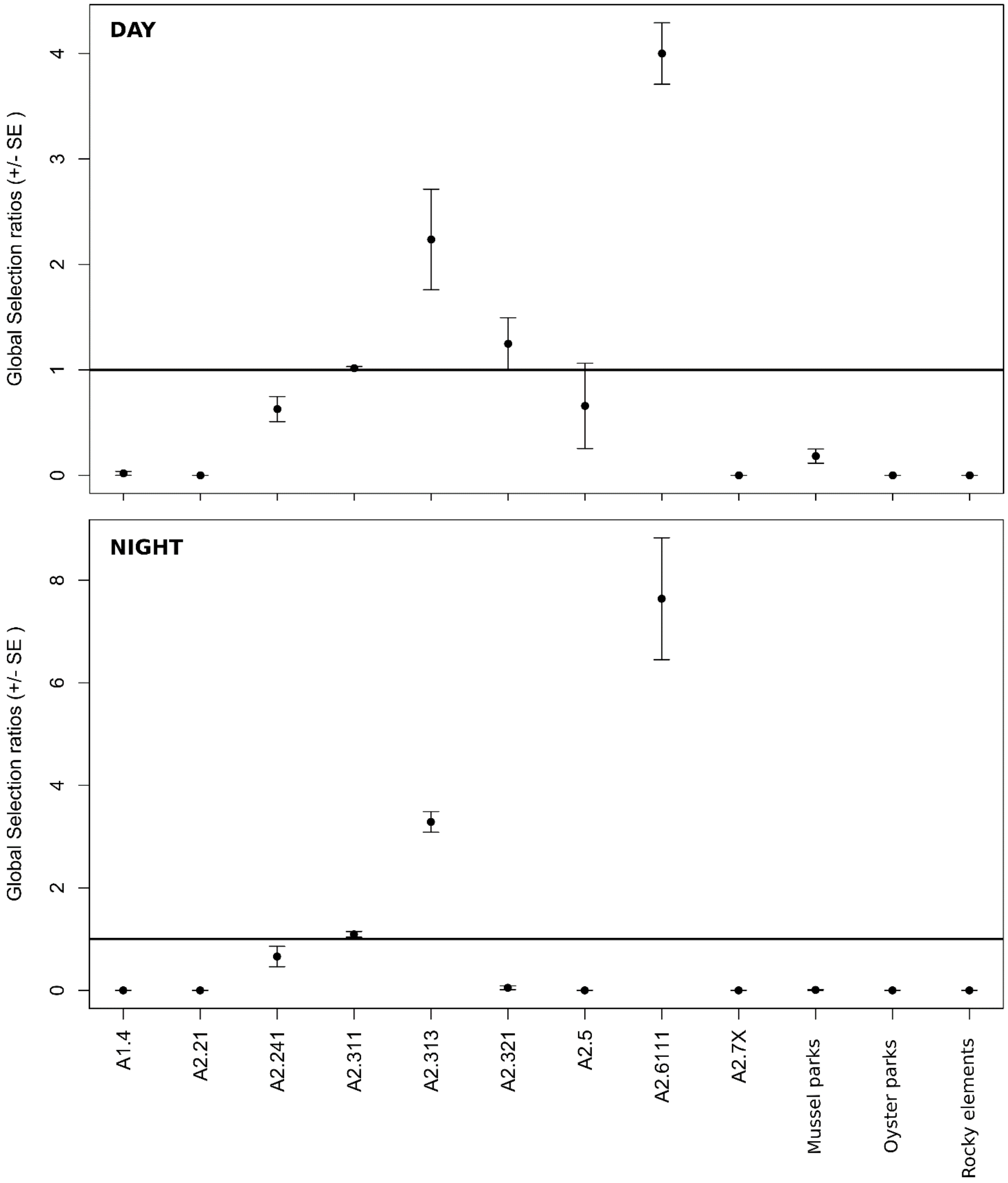

Fig. S5 Results of the selection ratio analysis highlighting habitat selection by four black-tailed godwits on 12 intertidal habitat types by day and night, at Yves site.

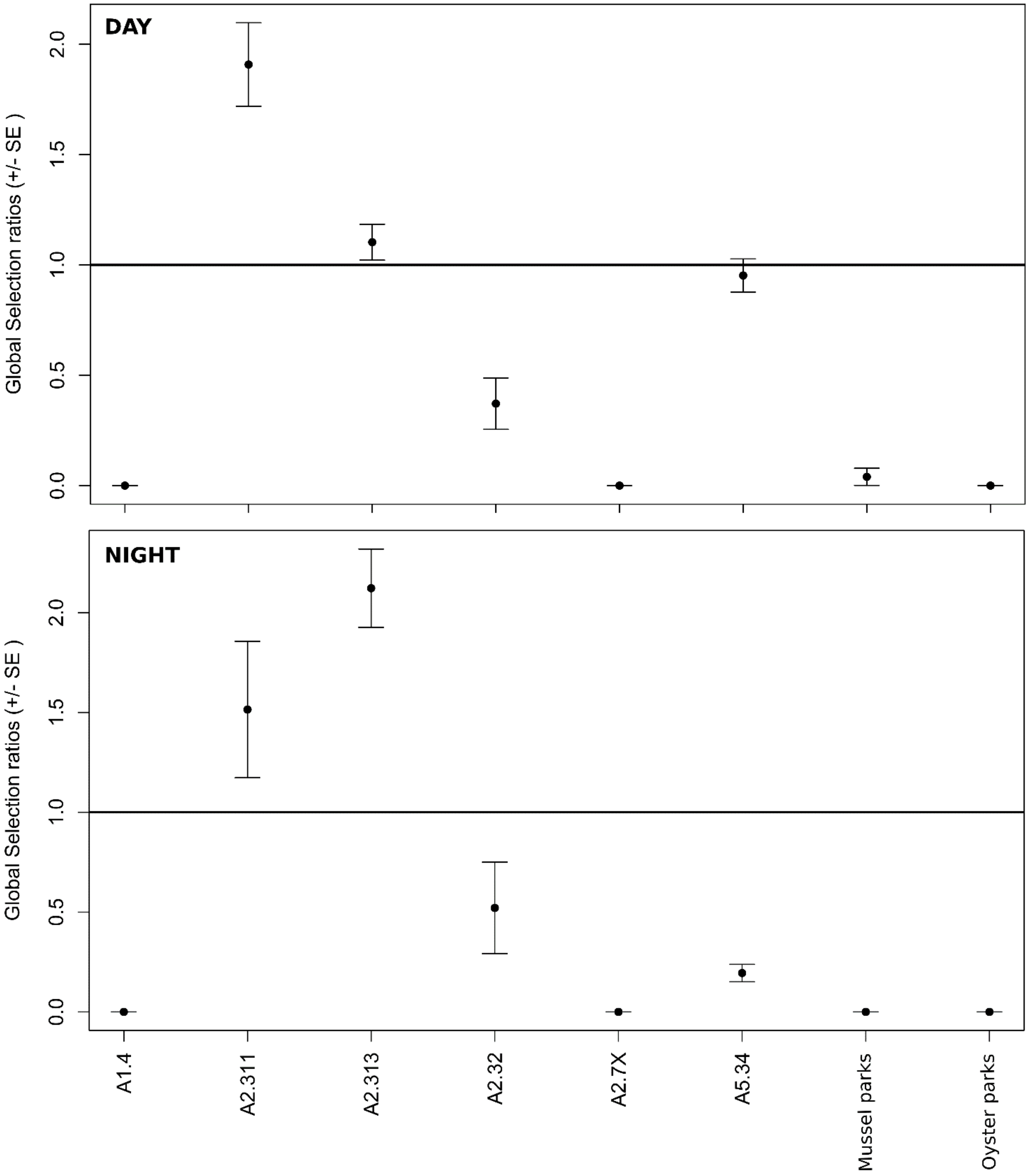

Fig. S6 Results of the selection ratio analysis highlighting habitat selection by four black-tailed godwits on 12 intertidal habitat types by day and night, at Moëze site.

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SECTION III

Interactions between individuals during feeding: sex-specific segregation in bar-tailed godwit and birds association in black-tailed godwit

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Chapter 5

Sex-specific spatial segregation and diet individual specialization in wintering bar-tailed godwits *Limosa lapponica*

P. Bocher, C. Jourdan, P. Delaporte, T. Guyot, J. Gernigon, J. Jourde, N. Lachaussée, J.C. Lemesle, P. Pineau, P. Rousseau and N. Aubouin

Abstract

For birds with clear sexual size dimorphism, males and females could face different trade-offs as feeding-site selections in winter. The dominant sex may outcompete the other sex in access to trophic resources. Here we aimed to test occurrence of spatial segregation in wintering feeding areas in a sexually dimorphic shorebird, the bar-tailed godwit *Limosa lapponica*. We quantified the occurrence of males and females and their benthic prey availability at two clear distinct feeding areas with contrasting habitats on a wintering site on coast of Western France. Females outnumbered males on sandflat habitats and individuals tended to forage in flock along the waterline, exhibiting a higher number of interactions. On the mudflat "habitats", males and females were evenly numerous with lower densities in terms of number of foraging individuals per hectare but with the benefit of a longer access time to the feeding areas. Males and females' diets differed at first by site selection rather by prey species selection. Although we were not able to describe the diet per sex at the scale of the feeding areas, we assume that shorter-billed males fed on the smaller and shallowly buried prey, and the longer-billed females predominantly fed on the larger and more deeply buried prey as *Arenicola marina* in mudflat or *Nepthys cirrosa* or *N. hombergii* in sandflat. We also confirm that females are more numerous in sandy habitats, where their longer and stronger bill allows them to penetrate deeper into the sediment compare to males. Consequently, the highest quality feeding area is predominantly selected by females while we could not distinguish differences between males and females in the poorest quality site.

Keywords: Sexual dimorphism, Sexual segregation, Benthic macrofauna, Isotopic signatures, Foraging behavior

In prep.

Introduction

Giving the ‘ideal free distribution’ concept, individuals distribute themselves such that everyone was able to achieve equal fitness (Fretwell and Lucas,1969). Among population, some individuals can differ in competitive abilities, and those with the highest competitive capacities would then occupy the best food patches, leading to hierarchical types of distributions (Houston and McNamara, 1988; Grand and Dill, 1999). Spatial foraging distributions can be predicted according to ‘generalized functional response models’ (Matthiopoulos et al. 2011) where intake rate and foraging distribution models combine prey density and interference effects. For species with clear sexual size dimorphism, males and females could face different trade-offs. These differences can affect migratory strategies, winter-site selections but most of the time, feeding-site selections (Catry et al. 2012). Consequently, the dominant sex may outcompete the other sex in access to trophic resource or shelter (Blanckenhorn 2005, Lindenfors et al. 2007). The sexual segregation during the non-breeding period has been documented for many migratory birds at different spatial scales (e.g., Marra and Holmes 2001, Catry et al. 2006, Catry et al. 2012, Nebel et al. 2013). If sexes differ in body size and bill length, they will not only differ in energetic requirements but also in use of different prey size or accessibility. This partitioning of the trophic resource can lead to the use of distinct feeding areas inducing strong spatial segregation (Schoener 1974). In many shorebird species, bill length has been used as a robust predictor of foraging niche (Selander 1966). The differences in bill structure and size can lead to differences in feeding methods and prey selections (Radford and du Plessis 2003, Navarro et al. 2009, Santiago-Quesada et al. 2009, Alves et al. 2013; Duijns and Piersma 2014).

Here we aimed to test occurrence of spatial segregation in wintering feeding areas in a sexually dimorphic shorebird, the bar-tailed godwit *Limosa lapponica*. The females are about 20% heavier and have 25% longer bills than males (Baker 1993, Duijns et al. 2014). Bar-tailed godwit feed preferentially on polychaete worms on most of its wintering sites in Western Europe (Scheiffarth 2001a, Duijns et al. 2013). Habitat use of the species was previously described as differing between the sexes, both at large spatial scales (Atkinson 1996; Scheiffarth 2001b) and at small scales (Smith and Evans 1973; Zwarts 1988; Both et al. 2003, Duijns and Piersma 2014). Sex-related diet differences have been observed in Wadden Sea (Scheiffarth 2001a) where females forage on the larger and deeper buried polychaetes, whereas males mainly forage on smaller shallower living polychaetes. Others studies have reported sexual segregation on feeding sites (Smith and Evans 1973) with males being distributed over the mudflat habitats, while the females were rather concentrated along the water line (Zharikov and Skilleter 2002) or on sandbank habitats (Smith and Evans 1973, Zwarts 1988, Both et al. 2003). Sex differences have also been highlighted regarding feeding techniques, as probing and pecking, as well as in ingestion rate in the subspecies *Limosa l. baueri* (Pierre 1994).

Considering sex-differences in bill size in godwits that feed in soft substrates, shorter-billed males would rely more heavily on shallowly buried prey from the sediment surface compared to longer-billed females, which are able to extract more deeply buried prey (Scheiffarth 2001a; Duijns and Piersma 2014). Benthic organisms in intertidal mud- or sandflat are distributed in sediment with the larger and more profitable prey (e.g., Alves et al. 2013; Duijns and Piersma 2014) occurring deeper and the smaller prey dwelling closer to the surface (Esselink and Zwarts1989, Zwarts and Wanink 1993). This would suggest that males should forage at feeding sites with a high density of prey available near the mudflat surface, whereas the females should forage in areas with a high density of deeper buried prey.

To address the mechanisms underlying this sex-specific spatial pattern, we have quantified the occurrence of males and females of godwits and their benthic prey availability at two clear distinct feeding areas with contrasting habitats on a wintering site on coast of Western France.

We hypothesize that bar-tailed godwit females will dominate on sites with better food quality, while males will be restricted to feeding areas of lower quality. If females have a privileged access to better feeding site, what are the criteria that determine these advantages of females: larger prey allowing a better instantaneous ingestion rate or better access to deep-sea prey due to the longer bills of females? What impact could this have on the population, knowing that conservation issues could thus go beyond the currently protected sites, and therefore concern sites that may be subject to strong anthropogenic pressures?

Methods

Study site

The study was carried out on Ré Island (Central French Atlantic coast) during winter 2013-14 (Fig. 1a). Two subsites were previously identified as main feeding areas for bar-tailed godwits on soft substrates on the Western part of the Island. The first subsite is a sandflat on exposed coast in the North of the Island, “La Loge” (46°14’25’’N; 1°28’42’’W) (Fig. 1b), and the second subsite is a mudflat inside a semi-enclosed bay, the ‘Fier d’Ars’ (46°13’18’’N; 1°30’29’’W) (Fig. 1c). The map of habitats according to EUNIS classification (Bajjouk et al. 2015) was previously established in Jourdan *et al.* (2021). The site of “La Loge” is a sandflat that extends over 101.0 ha on the Northern exposed coast of the island. The shorebirds can have an access to the intertidal sandflat for c. 4 hours only, and the period of food availability is therefore limited for godwits compared to the “Fier d’Ars”. The “Fier d’Ars” is a bay of about 800 ha bordered by 1,600 hectares of saltpans or brackish marshes. The bay is divided by a central creek, with a mainly bare muddy substrate on the edges and covered by seagrass beds *(Zostera noltei)* at the center. The study focused only on the Northwestern part of the bay (71.5 ha) with sandy-muddy substrate. The Northern part of this area is part of the National Nature Reserve of Lilleau des Niges. The feeding area on intertidal range is available for feeding birds for c. 6 hours per tide cycle.

Coastal shorebird counts

Exhaustive counts of shorebirds were operated by the staff of the National Nature Reserve year-round the ca. 15th of each month on the whole Island from 2000 to 2016. The census targeted all the known high tide roosts during the highest tidal coefficients. Birds were counted with telescopes from 2 hours before and until the high tide.

Spatial segregation on feeding areas

During the winter, counts were made on areas delimited on both subsites (Fig. 1b and c). Godwits were counted during 12 and 10 sessions for “La Loge” and “Fier d’Ars”, respectively. At each session, godwits were counted on all the subsite every 30 min during 3.5 hours. Depending on the time of low tide (LT) (and with the necessity of carrying out count during daylight), these sessions started either at LT (session on rising tide with counts every 30 min from LT to LT+ 3h) or 3h before LT (session on ebb tide with counts from LT-3h to LT). In this way, we counted over the entire diurnal emergence period when the study sites were available for feeding birds. Bar-tailed godwit is a marked sexual dimorphic species. The sex of each individual could be identified for most of individuals at distance, on the basis of overall body and bill sizes (Both et al. 2003, Djuins at al. 2009). Individuals with intermediate size of bill were recorded as indeterminate sex. The sex-ratio were expressed as % of females.

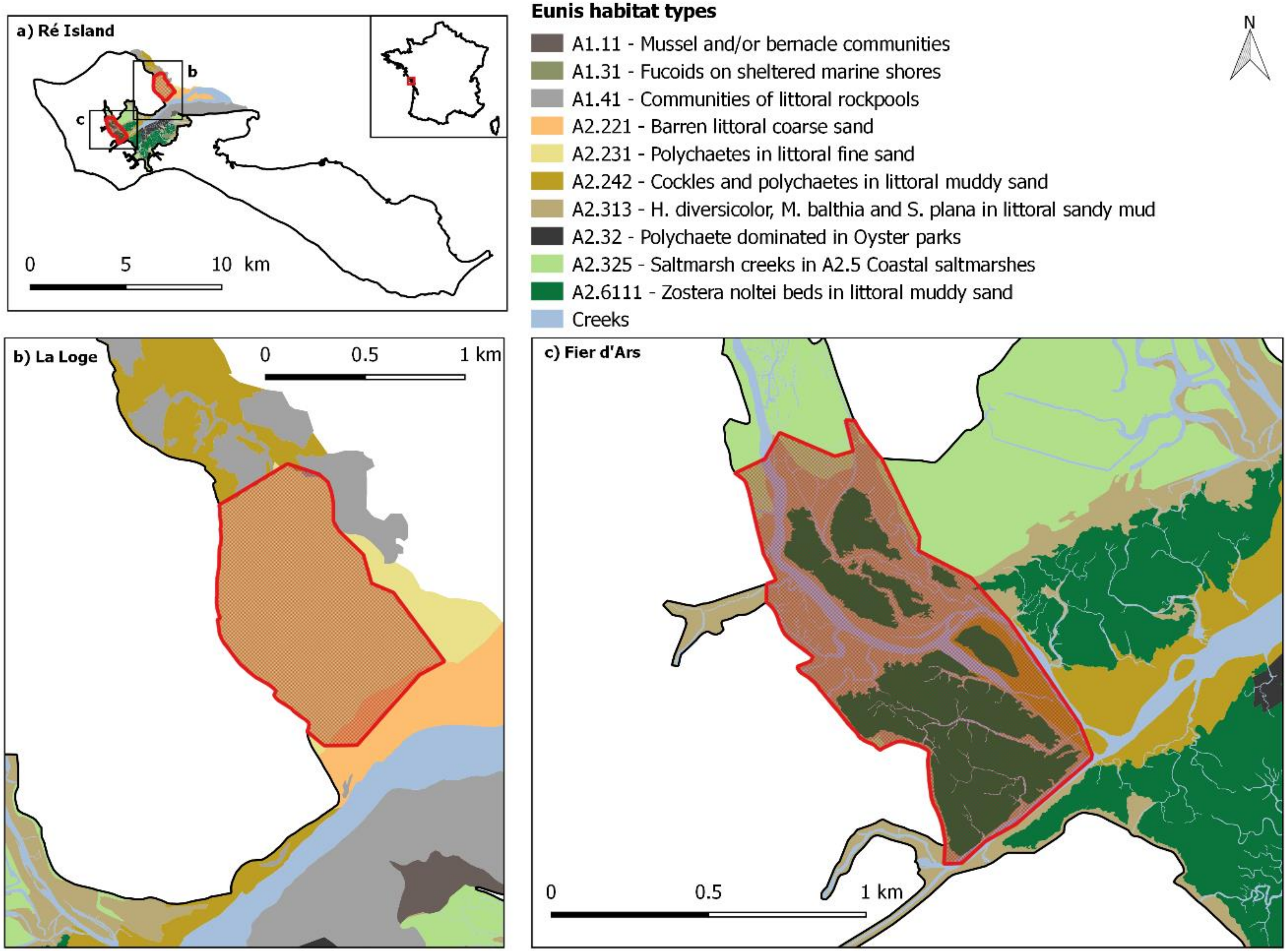

Fig. 1 Maps of (**a**) Ré Island and locations of the study sites of (**b**) "La Loge" and (**c**) "Fier d'Ars". Study areas are delimited by red line. Surfaces of habitats on study sites are characterized according to International Eunis classification (Bajjouk et al. 2015).

Godwits capture

Thirty-three godwits were captured using mist nets on high tide roosts between late December 2013 and early January 2014. Individuals were marked with a metal ring and a unique color rings combination. The sex of individuals was determined based on their body mass and bill length (Baker 1993) and the age defined according to their plumage pattern (Demongin 2016).

Food resource sampling and treatment

Considering the very clear dietary preferences of the bar-tailed godwit for polychaetes established by faecal analyses in previous studies (99.6% of the diet consisting of polychaetes according to Duijns *et al*. (2013)), we present here only the availability of polychaetes as prey for godwits. The distribution, densities and biomasses of polychaetes were determined by extracting sediment cores at predetermined stations (Bocher et al., 2007). The sampling grids were predetermined in order to cover all of the intertidal areas of the two study subsites. Gridlines were fixed at intervals of 100 m corresponding to 72 stations for “La Loge” and 69 for “Fier d'Ars”. The sampling stations were located by GPS (WGS84 as the map datum). During January and February, sampling stations were visited on foot. For each station one sediment core covering 0.018 (1/56) m² was extracted to a depth of 25-30 cm. The core was divided into three fractions, corresponding to depths accessible or not, according to the length of bill and consequently according to the sex of godwit. The "top" corresponded to the first 8 cm (accessible to males and females), the "middle" corresponded to the next 7 cm (accessible only to females) and the "bottom" to the rest of the core (inaccessible). Each of these parts was sieved separately on a mesh of 1 mm. The annelids were removed and preserved in alcohol at 70 °. In the laboratory, all organisms were identified to species level whenever possible and then counted. Since the polychaetes are regularly damaged during the sieving of cores, they were obtained most of the time in several fragments. To avoid multiple counts, only anterior fragments with mouth were counted. All organisms were measured to an accuracy of 0.1 mm. The Dry Mass (DM) of flesh for each prey was measured after 72 hours of drying at 55°C. Dried specimens were then incinerated at 550°C for 5 hours to determine their ash mass and then the ash free dry mass (AFDM) (Zwarts and Wanink 1993). For damaged or cut polychaetes during sieving, DM and AFDM measurements were determined from allometric relationships from size measure of anterior part of the body. We determined the precise harvestable fraction of the polychaete’s biomass per sex according to top fraction for male and top+middle fractions for females.

Reconstruction of godwit diet

The godwit's diet was reconstructed from faeces collected at low tide within each feeding area sampled (Table 1). The faeces analysis method was based on that established by Duijns *et al*. (2013) with some modifications. It takes an average of 28 min for a godwit to digest prey and evacuate the remains in faeces (Scheiffarth 2001a). We identified the faeces origins thanks to the footprint characteristics of godwit on mud or sand. Faeces were individually collected and frozen at -18 ° C. In order to be sure that the remains found in the faeces came from prey ingested by godwits and not from surrounding sediment, control samples of sediment around the faeces were taken. At the laboratory, the samples where defrosted at least 60 min before analysis. They were then cleaned for 60 min in an ultrasonic bath and sieved through a 64 µm mesh. The samples were sorted under a binocular magnifier. The teeth and jaws of polychaetes were set aside in alcohol and then identified and counted. The rest of the faeces was kept in alcohol at 70°. Many species of polychaetes, however, had neither jaws nor teeth, and their presence in faeces were then detectable only through their bristles, the only indigestible remains. To determine the species corresponding to these bristles, faeces were placed in an oven at 55 °c until the alcohol was evaporated so as to leave a faeces which was just moist (completely dried, the bristles were weakened and broken very easily). Five percent of the mass of this dropping was then removed and cleaned again, put in plastic tube, and mixed with a mixture composed of 100 µL of lysis buffer and 100 µL of detergent (dishwashing liquid). They were maintained at 65° C in a water bath for 12 hours. This process allowed to destroy the cell membrane of any flesh residue present in the faeces which only keeping the bristles. To carry out the identification of the taxa from which jaws, teeth and bristles were derived, a reference collection has been made. We simulated the digestion of previously identified individuals belonging to the main polychaete species present on the sites, using a mixture of lysis buffer and proteinase K. Prey species and number per faeces were described according to number of jaws, teeth or bristles.

Feeding behaviour

Videos of feeding godwits were carried out on the two subsites in order to compare behaviour of males and females (Scheiffarth 2001a; Zharikov and Skilleter 2002). Focal animal observations were recorded with camera Canon 5D mark2 equipped with Sigma 500mm f4.5 lenses (added to a Canon Extender EF 1.4x III) based on the method of Kuwae *et al*. (2010). The focal observations ranged from 1.4 to 2.3 minutes. Behaviours were distinguished at

Table 1 Frequency of occurrence (Occ.), mean density (Dens.) and mean biomass (Biom. in AFDM) of macrofaunal species per feeding area at the study subsites.

Species	**La Loge**			**Fier d'Ars**		
	Occurrence (%)	**Density (ind./m^2)**	**AFDM (g/m^2)**	**Occurrence (%)**	**Density (ind./m^2)**	**AFDM (g/m^2)**
Orbiniidae						
Orbinia bioreti	1.4	0.8	0.001	-	-	-
Phylo foetida	6.9	4.7	0.005	-	-	-
Scoloplos armiger	28.9	82.5	0.094	-	-	-
Spionidae						
Scolelepis sp.	1.4	11.8	0.047	-	-	-
Magelonidae						
Magelona johnstoni	1.4	0.8	0.007	-	-	-
Chaetopteridae						
Chaetopterus variopedatus	1.4	0.8	0.032	-	-	-
Cirratulidae						
Cirriformia tentaculata	-	-	-	7.2	9.0	0.067
Tharyx sp.	2.8	3.1	0.019	-	-	-
Cirratulidae	-	-	-	1.4	0.8	0.004
Capitellidae						
Capitella capitata	-	-	-	4.3	4.1	0.002
Heteromastus filiformis	-	-	-	4.3	2.5	0.001
Notomastus latericeus	12.5	7.8	0.003	31.9	109.1	0.04
Arenicolidae						
Arenicola marina	-	-	-	13	12.3	0.251
Maldanidae						
Euclymene oerstedi	4.2	4.7	0.001	-	-	-
Leiochone leiopygos	-	-	-	5.8	3.3	0.010
Phyllodocidae						
Eteone longa	-	-	-	1.4	0.8	0.004
Eteone picta	-	-	-	1.4	0.8	< 0.001
Phyllodoce lineata	1.4	0.8	0.001	-	-	-
Phyllodoce maculata	1.4	0.8	0.001	-	-	-
Sigalionidae						
Sigalion mathildae	1.4	0.8	0.012	-	-	-
Nereididae						
Hediste diversicolor	-	-	-	2.6	111.5	0.175
Neanthes nubila	1.4	0.8	0.001	-	-	-
Glyceridae						
Glycera tridactyla	4.2	2.4	0.006	4.3	2.5	0.018
Goniadidae						
Goniadella bobrezkii	1.4	0.8	0.00316	-	-	-
Nephtyidae						
Nephtys cirrosa	33.3	29.1	0.169	1.4	0.8	0.006
Nephtys hombergii	23.6	17.3	0.23	18.8	18.9	0.104
Lumbrineridae						
Lumbrineris latreilli	-	-	-	1.4	0.8	0.008
Oweniidae						
Owenia fusiformis	9.7	8.7	0.029	2.9	1.6	0.002
Nemert	4.2	3.1	0,050	10.1	6.6	0.104
Oligichaeta	-	-	-	2.9	1.6	0.006

laboratory using the free software CowLog 2.0 (Pastell 2016). Recorded behaviours were occasional (expressed in number of occurrences per minute) or periodic (expressed in seconds per minute). The ingestion rate was then calculated using the average frequency of the "swallowing" behaviour multiplied by the average biomass of prey calculated according to the site and accessibility. A total of 98 godwits were recorded on feeding areas, 57 individuals for “La Loge” (29 females, 25 males, 3 non-sexed) and 41 for “Fier d'Ars” (16 females, 17 males, 8 non-sexed).

Trophic niche from stable isotope analysis

Stable analyses were performed on 1 and 2 mm of toenail that were clipped from three toes of 12 males and 18 females during catches, using sharp scissors and stored in individual plastic bags. Recent captivity experiments with a small-sized shorebird, the dunlin (*Calidris alpina*), indicated half-lives of approximately one month (27-35 days) for both carbon (^{13}C) and nitrogen (^{15}N) isotope ratios in toenails, thus further validating the use of this tissue for studies of diet on short terms of migratory shorebirds (Lourenco et al. 2015). Samples were prepared according to method in Catry *et al*. (2016). Results are presented conventionally as δ values in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) for ^{13}C, and atmospheric nitro-gen (N2) for ^{15}N. Precision of the isotope ratio analysis, calculated using values from 6 to 9 replicates of laboratory standard material (casein) interspersed among samples in every batch analysis, were 0.11 to 0.25‰ for 13C and 0.05to 0.17‰ for 15N (SD).

Statistical analyses

Comparisons of sex ratio, food resource availability and feeding behaviour between males and females, within a site or between the two study subsites, were analysed on the software R (3.6.1; R Core Team, 2020) using various statistical tests (chi-squared tests, Wilcoxon tests, Kruskal-Wallis tests) and descriptive statistics. The mapping of study site, habitats and distribution of prey were produced with the software QGIS (2.18, Las Palmas - QGIS Development Team 2016).

Results

Number and phenology

The presence of bar-tailed godwit in wintering period on Ré Island expanded from early August to late March, with arrival of new individuals during the curse of autumn (Fig. 2). Throughout the wintering period (2001-2016), the mean number of godwits was at the maximum in January with 682 ± 320 individuals and at the minimum in June with 8 ± 11 individuals. Godwits were very uncommon from April to July. From November to February, the mean number of individuals was stable around 600 individuals over the period 2001-2016. Most of the birds left the site from late March to early April for pre-breeding migration (Fig. 2).

Godwit’s densities and sex ratio on feeding areas

On “La Loge”, the mean density of godwits according to emerged sandflat (n = 81counts), ranged between 1.5 ± 2.1 individuals/ha (LT+1h30 of emerged mudflat) and 3.0 ± 2.2 ind./ha (LT-3h00), but remained fairly stable (c. 2.0 ind./ha) until departure of most of the birds at LT + 1h30 (Fig. 3). The site was mostly available between LT-2h00 and LT+2h00 (c. 44 ha) and consequently visited during this narrow time window. Females represented 44.4 ± 19.7% and males 23.8 ± 10.9% of surveyed individuals (31.8 ± 30.4% of indeterminate sex). The mean number of females was significantly higher than number of males (Wilcoxon test: W= 1018, p-value<0.001) (Fig. 3). This trend was observed whatever the tidal range. On “Fier d'Ars”, the mean density of birds was highest when mudflat just emerged (LT-2h30, 20 ha) with 4.4 ± 1.3 ind./ha and the number suddenly increased at last time of the survey period around LT+3h00 (10 ha) with a mean of 24.2 ± 14.1 ind./ha. At LT (101 ha), the mean density was the lowest with 0.4 ± 0.3 ind./ha. From LT-2h30 to LT+1h30, there were no significant differences between both sexes on feeding site (Wilcoxon test: W = 863.5, p-value = 0.8346) (Fig. 3). Males represented 40.6 ± 9.7% and females represented 39.7 ± 10.2% of the number of individuals at count (n = 68). There was no significant difference (Wilcoxon test: W=1369.5, p-value=0.912). However, 19.7 ± 18.1% of other individuals remained sex-undetermined, but mainly during the last hours of the rising tide when new individuals joined the area in high number.

Captures and marking

Between the year 2007 and 2014, 62 godwits were caught and colour-marked on Ré Island. Three other individuals were colour-marked on other wintering sites and present on the site during the study period. Twenty-six individuals could be sexed as females, 34 as males and 2 non-sexed, not differing from a balanced sex ratio (NS - Chi-square: $\chi^2 = 0.057$, df = 1, p-value = 0.8). The age-ratio was clearly in favour of juveniles, which represented 71% of the bird caught, with 44 juveniles and 18 adults (Chi-square: $\chi^2 = 10.903$, df = 1, p-value <0.001). Of the 32 individuals color-marked during the winter study, 105 visual observations were done in January and February 2014. Of these 32 godwits, 4 individuals were never resighted on the site.

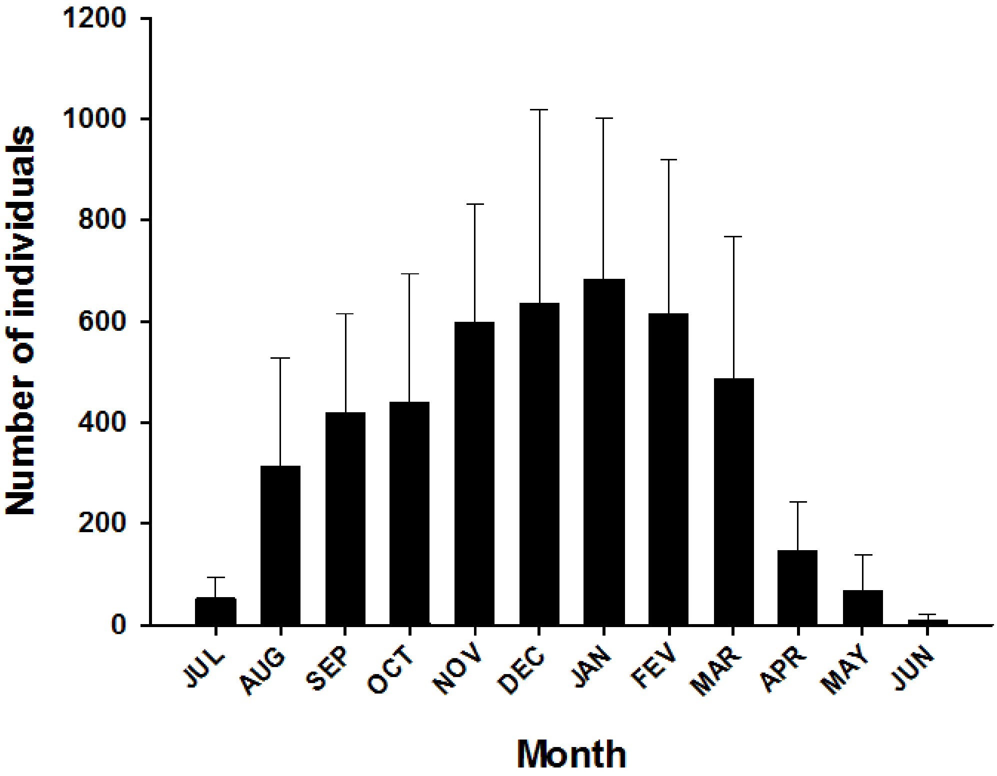

Fig. 2 Monthly mean number (± SD) of bar-tailed godwits on Ré Island (June 2000- July 2016).

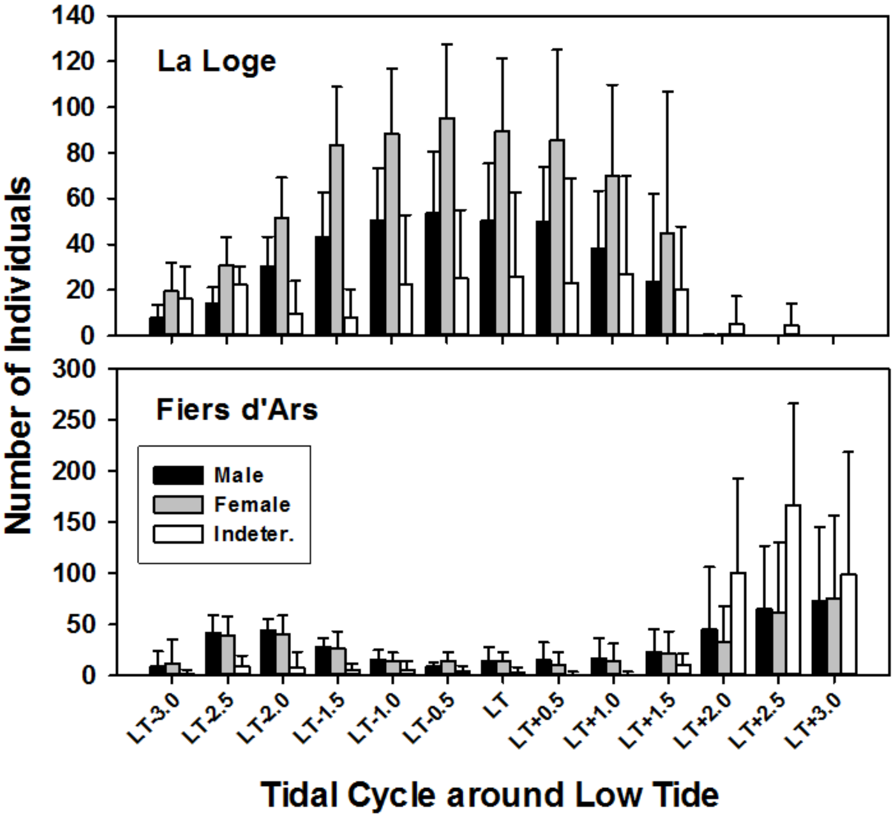

Fig. 3 Variations in numbers of males and females of bar-tailed godwits (mean ± SD) during the tidal cycle on study sites of "La Loge" and "Fier d'Ars" during the winter 2013-2014.

Twenty-two individuals were only recorded on the “La Loge” (11 females, 9 males and 2 non-sexed) and 16 only on “Fier d’Ars” (7 females, 8 males and 1 non-sexed). Ten individuals were seen at the both subsites (4 females and 6 males). Some individuals have been observed up to 8 times, including 7 times on the same site (La Loge). On the “Fier d'Ars”, the maximum of resigthings for an individual was 6 times.

Distribution and availability of trophic resources

For both sub sites, a total of 227 annelids and 367 polychaetes from 30 different taxa were collected at “La Loge” and “Fier d'Ars”, respectively (Table 1). In “La loge”, *Scoloplos armiger*, *Nephtys cirrosa* and *Nephtys hombergii* were the most abundant species in term of density and biomass. In “Fier d’Ars”, *Notomastus latericeus*, *Hediste divsersicolor* and *N. hombergii* occurred with the highest densities, but lugworm *Arenicola marina* was the species with highest biomass abundance (Table 1).

The “Fier d'Ars” presented a higher density of polycheats (Fig. 4 and 5), with a total mean density of 305 ± 372 ind./m² versus 181 ± 182 ind./m² for “La Loge” (Wilcoxon: W = 2731 – p-value = 0.304). In terms of biomass (AFDM), the potential total trophic resource was higher on the “Fier d'Ars” (0.62 ± 1.13 g/m²) compared to “La Loge” (0.54 ± 0.89 g/m²), but was not significantly different (Wilcoxon: W = 2341 - p-value = 0.4659). If we consider the mean biomass accessible only to females (0.49 ± 0.80 g/m²) on “La Loge” compared with “Fier d’Ars” (0.46 ± 0.68 g/m²), or the accessible mean biomass to both sexes (0.32 ± 0.72 g/m²) on “La Loge” versus “Fier d’Ars” (0.25 ± 0.38 g/m²), “La Loge” offered highest food resource available for godwits but without significant differences (Wilcoxon: W = 2214 - p-value = 0.2611 and W = 2365.5, p-value = 0.618, respectively) (Fig. 4). The mean biomass per annelid individual at “La Loge” was higher (0,02 ± 0,1 g AFDM/ind) than at “Fier d'Ars” (0,001 ± 0,018 gAFDM/ind) (W = 1184.5, p-value = 0.1798). In terms of depth distribution, 85% of the biomass was in the depth compartment 0-8 cm on “La Loge”, 12% in the 8-15 cm compartment and 3% below 15 cm. On “Fier d'Ars”, 54% of the biomass was located between 0 and 8 cm depth, 26% at 8 -15 cm depth and 20% beyond 15 cm.

Feeding behaviour

On both feeding sites, males and females spent about 75% of scanned time to food foraging. (Fig. 6). Handling time for females at “La Loge” (12.3 ± 5.5 %) was not significantly different than for those at “Fier d’Ars” (8.0 ± 10.2 %) (NS - kw = 0.7; p-value = 0.4). Handling

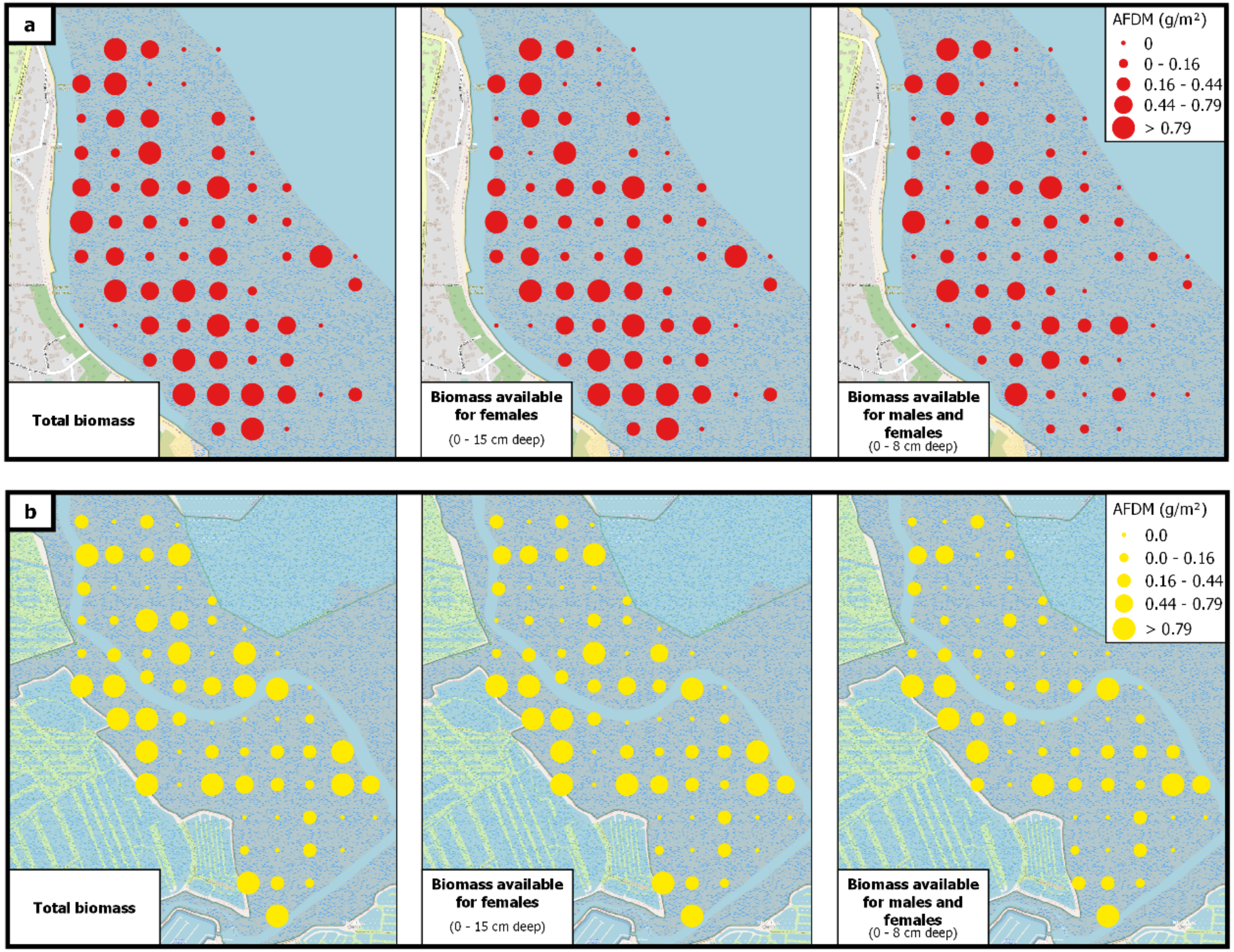

Fig. 4 Distribution of the annelid's biomass (mean AFDMg/m^2) on "La Loge" **(a)** and the "Fier d'Ars" **(b)** according to their total presence and accessibilities for females and males of bar-tailed godwit.

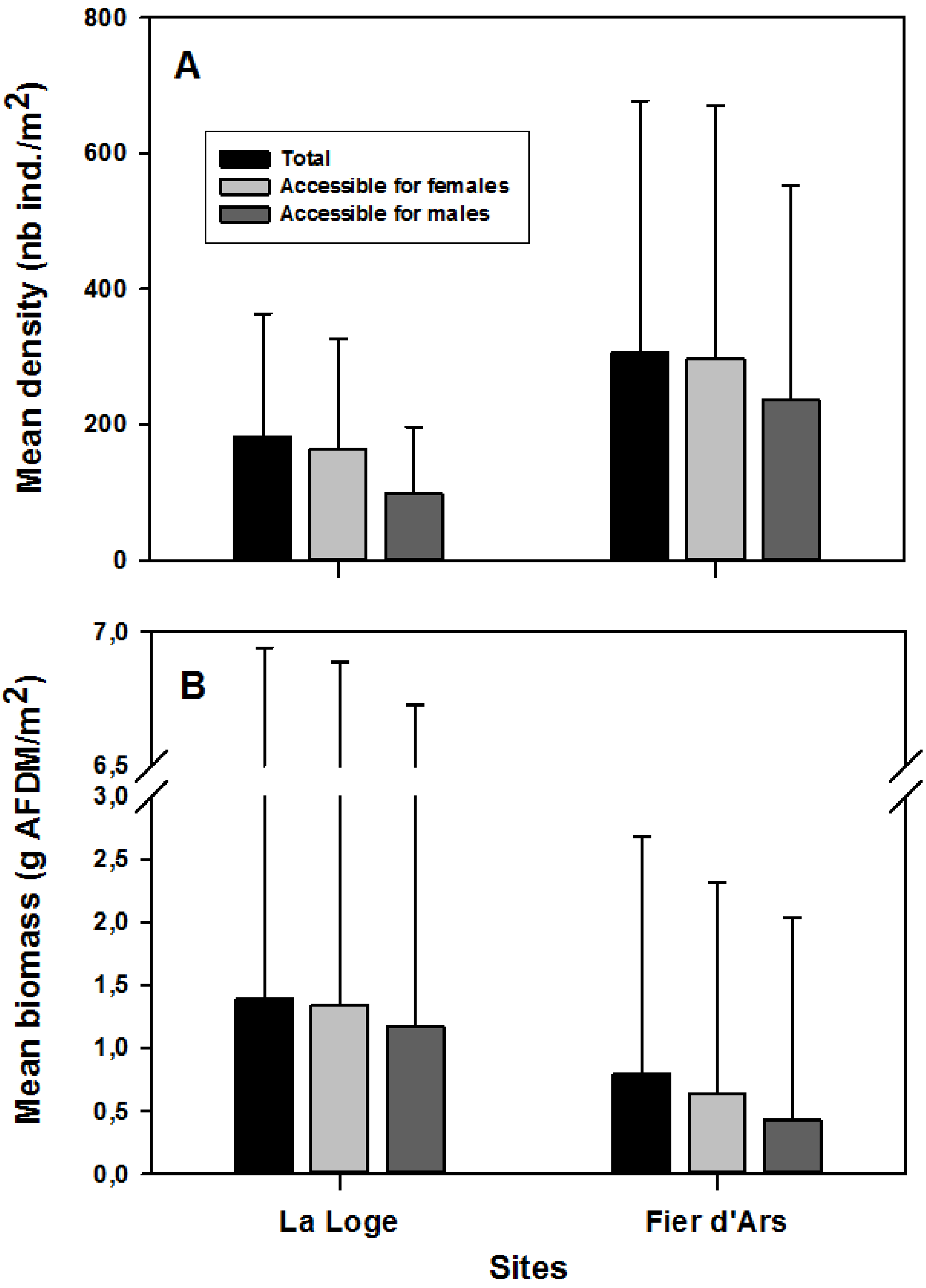

Fig. 5 Mean annelid's densities **(a)** and biomasses **(b)** (± SD) on "La Loge" and "Fier d'Ars" according to the total presence and accessibility for females and males of bar-tailed godwit.

time for males at “La Loge” (14.1 ± 7.9 %) was not significantly different than for those at “Fier d’Ars” (9.4 ± 6.8 %) (NS - kw = 0.7; p-value = 0.4). The time dedicated to preening on feeding sites was low but reached a maximum of 5.6 ± 14.4 % of the total time in “Fier d’Ars” for females. Interferences were more frequent (1.5 ± 2.1 interferences/min) for females than for males (0.7 ± 1.6) on “La Loge” (NS - kw = 2.6; p –value = 0.1), but less frequent on the “Fier d'Ars” for females (0.7 ± 1.4 interferences/ min) than males (1.4 ± 2.1) (NS - kw = 1, 1; p –value = 0.3).

The two foraging methods did not appear at the same frequency, the pecking occurred c.3.6 times greater than probing for all individuals. The frequency of probing was significantly higher on “La Loge” (28,6%) than on “Fier d'Ars” (10,1%) for all individuals (kw = 42.5 - p-value = 6.95e-^{11}). On “La Loge”, the males probed more than the females but without significant differences between both methods (NS - kw = 0.3; p –value = 0.6) (Fig. 6). Males ingested 1.3 ± 1.0 prey/min in “La Loge” and 1.8 ± 1.4 prey/min in “Fier d’Ars” while females ingested 1.4 ± 0.9 prey/min at “La Loge” and 1.6 ± 1.2 prey/min at “Fier d’Ars”. Considering biomass ingested over time, both males and females, the biomass ingested per minute, as well as the biomass ingested by swallowing action were on “La Loge” 0.04 ± 0.03 gAFDM/min and 0.0006 ± 0.0005 gAFDM/probe for males, and 0.03 ± 0.03 gAFDM/min and 0.001 ± 0.002 gAFDM/probe for females. The intake rates were lower on “Fier d'Ars” with 0.009 ± 0.009 gAFDM/min and 0.0004 ± 0.0005 gAFDM/probe for males and 0.004 ± 0.006 gAFDM/min and 0.0004 ± 0.0004gAFDM /probe for females (kw = 41.5 - p-value = 1.16e-10).

Diet

Thirty-three and 31 faeces were collected and sorted for “La Loge” and “Fier d’Ars”, respectively (Table 2). No indication of polychaetes remains was detected in the sediment control samples, the worms remains found in the faeces therefore came from ingested prey. From the jaws remains in faeces, we were able to identify three families of polychaetes among prey: the Glyceridae, the Nephtydae and the Nereididae, which occurred at 16%, 13% and 7%, respectively in “La Loge”, and 55%, 18% and 21% in “Fier d'Ars”. However, on the “Fier d’Ars”, jaws not belonging to these families could not be identified. The silks remains revealed the presence of 11 families of polychaetes on “La Loge” (including the 3 species previously mentioned), potentially representing 21 species, with occurrences for the Glyceridae (80%), Orbiniidae (80%) and Nephtydae (87%) which represented more than twice that of other families. On “Fier d'Ars”, Pectinariidae (87%), Nephtydae (73%), Capitellidae (73%),

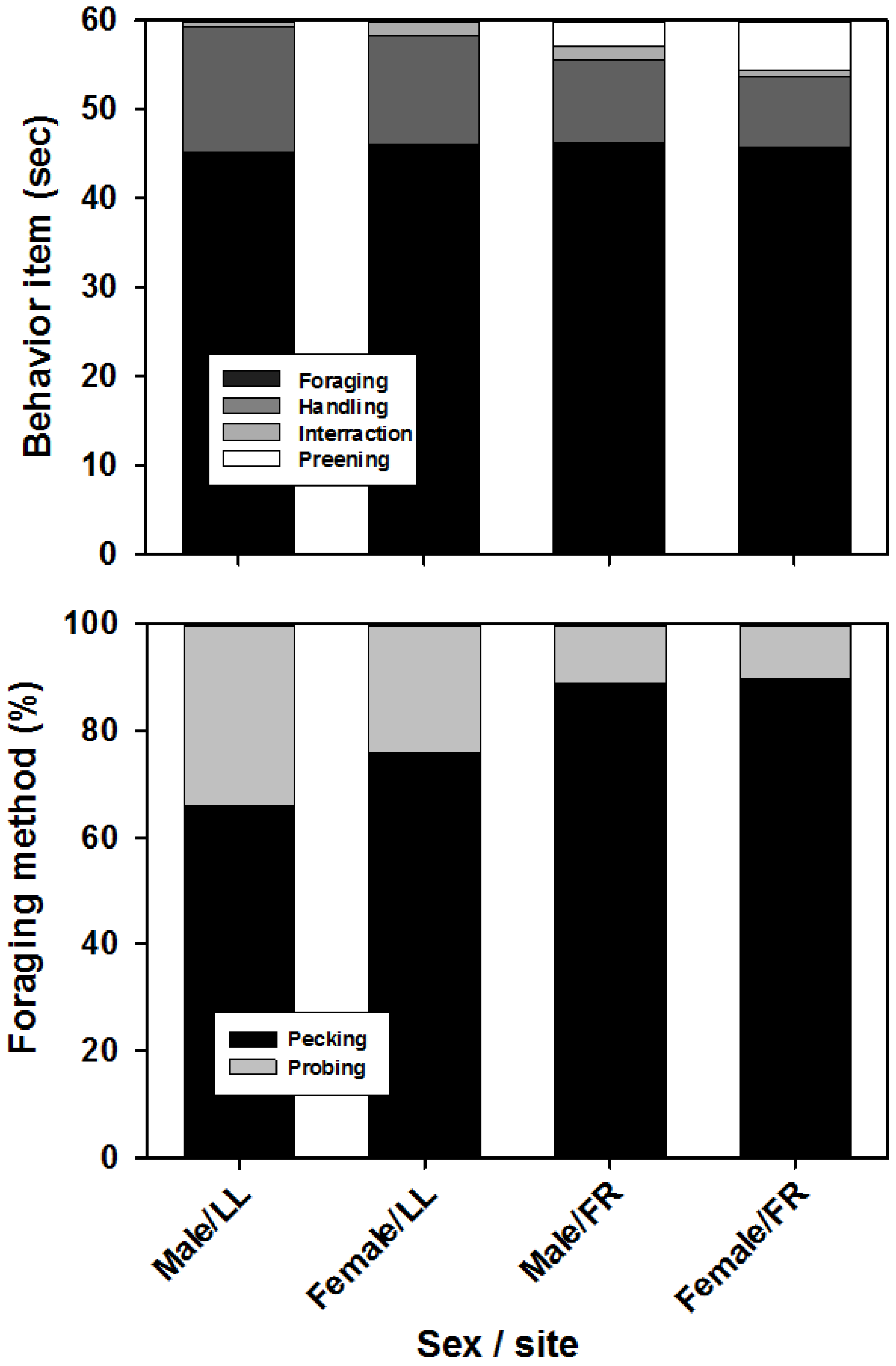

Fig. 6 Mean time of behaviour item (number of sec/min) and percentage of pecking and probing actions for male and female on “La Loge” (LL) and “Fier d’Ars” (FR).

Table 2 Frequency of occurrence (Occ.), mean number of individuals per faeces (Dens.) and total percentage of biomass per taxa (in Ash Free Dry Mass) of annelids in faeces.

Species	**La Loge**			**Fier d'Ars**		
	Occ. (%)	**N ind./faeces**	**AFDM (%)**	**Occ. (%)**	**N ind./faeces**	**AFDM (%)**
Orbiniidae						
Scoloplos armiger	80.0	3.9	46.5	-	-	-
Capitellidae						
Capitellidae ind.	33.3	0.4	1.5	73.3	0.7	5.1
Notomastus latericeus	20.0	0.2	0.9	-	-	-
Arenicolidae						
Arenicola marina	6.7	0.1	6.5	20.0	0.2	30.5
Phyllodocidae						
Phyllodocidae ind.	26.7	0.7	4.4	20.0	0.4	4.1
Sigalionidae						
Sigalion mathildae	6.7	0.1	3.2	-	-	-
Nereididae						
Hediste diversicolor	13.3	0.1	1.4	60.0	1.0	16.3
Glyceridae						
Glycera tridactyla	80.0	1.0	10.1	53.3	0.6	10.1
Nephtyidae						
Nephtys sp.	86.7	1.1	17.1	73.3	0.9	25.3
Oweniidae						
Owenia fusiformis	40.0	0.4	6.8	13.3	0.1	3.6
Pectinariidae						
Lagis koreni	33.3	0.4	1.3	86.7	0.9	5.1

Nereididae (60%) and *Glyceridae* (53%) prevailed among the 9 families represented. At the two subsites, several types of silks remained unidentified (Table 2). The results on the distribution and availability of the polychaetes on both feeding areas (Table 1), allow us to be more precise with regard to the taxa ingested. Indeed, on the studied areas, *Glycera tridactyla* was the only species of Glyceridae found, as well as *Lagis Koreni* (Pectinariidae), *Owenia fusiformis* (Oweniidae), *Arenicola marina* (Arenicolidae) and *Sigalion mathildae* (Sigalionidae) were the only representative species of their family. We can therefore admit that the silks corresponding to these families belonged to these species. The species *Scoloplos armiger* (Orbiniidae), *Hediste diversicolor* (Nereididae) and *Notomastus latericeus* (Capitellidae), which were by far the most dominant species within their families in these areas, could be considered in the same way (Table 1).

Food spectrum from stable isotopes

The isotopic signatures of the males and females, or of juveniles and adults, did not marked segregations between sexes or ages (Fig. 7). The value for ∂15N ranged between 12.1 and 16.6, while value for ∂13C where located between -17.7 and -12.8. Consequently, the birds did not feed on the same prey or they fed on different pools of prey species through the period of three-four weeks preceding of claw sampling.

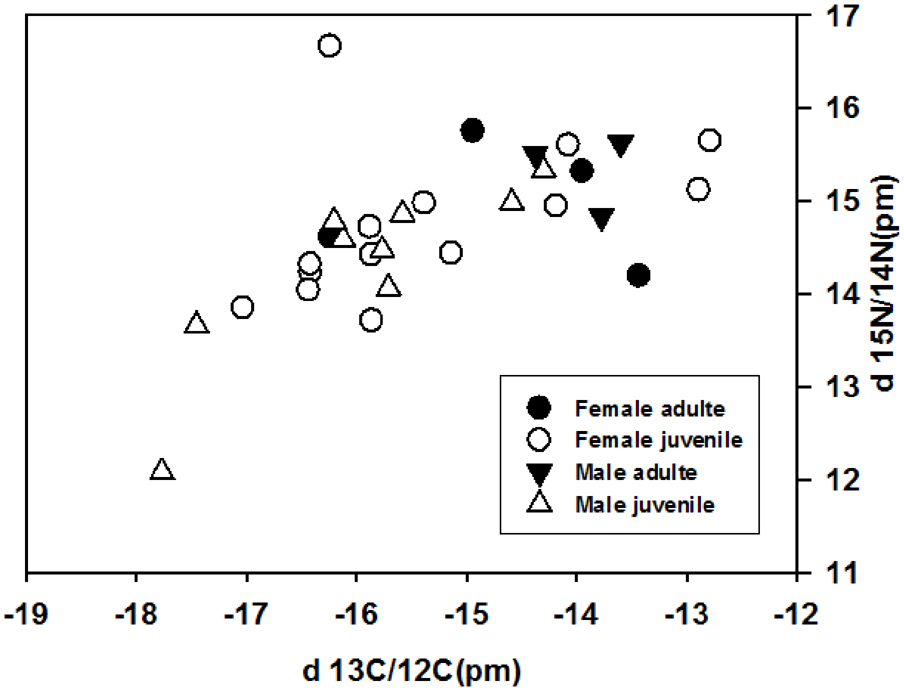

Fig. 7 Isotopic signature of claw tips of the bar-tailed godwit *Limosa lapponica* on Ré Island in winter 2013-2014.

Discussion

On Ré Island, the bar-tailed godwits numbers were highest and stable between November and February, which could be the consequence of the faithfulness of a majority of individuals to its wintering sites. Marked birds resighting have also confirmed this faithfulness, since 28 individuals out of 32 banded during winter on Ré were seen on same winter period or following winters. The use of the two subsites by godwits, with their very distinct feeding habitats, appeared to be different between males and females. The sandflat of “La Loge” was accessible c. 2 hours less than the “Fier d’Ars” and had a lower mean polychaet’s density. Nevertheless, the species richness, mean biomass and mean size of polychaets were higher at “La Loge”. Females outnumbered males at “La Loge” and individuals tended to forage in flock along the waterline, exhibiting a higher number of interactions, including kleptoparasitism. On the mudflat of “Fier d'Ars”, males and females were evenly numerous with lower densities in terms of foraging individuals per hectare but with the benefit of a longer access time to the feeding area. The individuals prospected alone and practised less probing and more pecking actions compared to the individuals at “La Loge". Consequently, the highest quality feeding area is predominantly selected by females while we could not distinguish differences between males and females in the poorest quality site.

If we consider both sites together, the sex-ratio was unbalanced in favour of females. The total number of individuals for both feeding areas at low tide was c. 200 individuals representing around one third of the total number of bar-tailed godwits on Ré Island at the peak abundance in January. Nevertheless, the difference between numbers of males and females was not significantly different during catches on roost. In previous studies, spatial segregation between the sexes has been observed within the European wintering range of the population. Males occur predominantly in climatically mild areas such as cost of the British Isles (Atkinson 1996; Summers et al. 2013), while most females winter in the North European and colder areas as the Wadden Sea (Smith 1975; Scheiffarth 2001b). In a study comparing sexes distribution at the scale of winter distribution area, Djuins *et al*. (2104) described a higher number of males in The Wash, while in Dublin bay, Sylt-Rømø, Wadden Sea and the Western Wadden Sea, a higher proportion of females was present. The percentage of females between sites was not correlated with the cost of wintering, but was positively correlated with the biomass in the bottom layer and negatively with the biomass in the top layer (Djuins et al. 2014). Our results confirm the higher number of females on the site where annelids biomass was higher in bottom layer and where individuals have a higher rate of probing when foraging. If the subsite of "La Loge" with one third of the local wintering birds can be considered as the main feeding area on Ré Island, then the site of Ré island is probably male skewed at the level of the entire winter area distribution.

The sex segregation at the scale of wintering site was documented for coastal Guinea-Bissau (Zwarts 1988), in British Isles (Smith and Evans 1973; Summers et al. 2013), the Wadden Sea (Both et al. 2003, Djuins and Piersma 2014). Nevertheless, Scheiffart (2001a) did not found diet segregation between sexes in winter in Wadden sea but in spring when birds refuel for migration to join breeding area. For shorebirds that feed in soft substrates on mud- or sandflat, shorter-billed individuals may depend on more on shallowly buried prey from the sediment surface compared to longer billed ones, which are able to extract more deeply buried prey (Finn et al. 2008, Djuins et al. 2015). Benthic polychaets are distributed in depth with larger and more profitable prey (e.g. Zwarts and Wanink 1993; Duijns and Piersma 2014) found deeper while closer to the surface occur smaller and less profitable annelids (Zwarts and Wanink 1991). In our study, males and females' diets differed at first by site selection rather by prey species selection. Although we were not able to describe the diet per sex at the scale of the feeding area, we assume that shorter-billed males fed on the smaller and shallowly buried prey, and the longer-billed females predominantly fed on the larger and more deeply buried prey as *Arenicola marina* in "Fier d'Ars" or *Nepthys cirrosa* or *N. hombergii* in "La Loge". Intake rates were higher in term of biomass ingested in "La Loge" for both sexes but females seemed more efficient in term of mean biomass ingested per probes. These differences confirmed the better quality of the sandflat, especially for females, compare to the mudflat, although attenuated by the time of availability of the area. The prey, then larger on "La Loge", could require a longer handling to be swallowed by godwits. The difference in prey size could possibly be the cause of the difference in prey handling time by the godwits (higher on "La Loge"). We also confirm that females are more numerous in sandy habitats, where their longer and stronger bill allows them to penetrate deeper into the sediment compare to males (Djuins et al. 2015). Nevertheless, foraging in flock on the sandy site of "La Loge" lead to more interferences including kleptoparasitism, which the males are less able to cope, due to their smaller size (Both et al. 2003, Edelaar et al. 2003).

Faeces analysis did not show any other prey than polychaets except anecdotal remains of molluscs or crustaceans. We therefore confirm the worm's diet specialisation of the species in wintering period. Up to at least 11 and 8 different species of worms have been recorded in faeces of “La Loge” and “Fier d’Ars”, respectively. Eight species where common to both study sites. The two study sites showed a high diversity of worm species, much greater than those described for the bare mudflats of the Pertuis Charentais, such as the sites in the Aiguillon Bay or Marennes-Oléron Bay (Robin et al. 2015). As a result, godwits on Ré Island, can benefit of a wide choice of prey species distributed in a rich mosaic of habitats (Jourdan et al. 2021). If we consider the diversity of worms as well as the birds' fidelity to restricted feeding areas throughout the winter, it is very likely that the diversity of isotope signatures is explained by the birds' specialisation on certain species of prey within the habitats favoured inside their feeding home ranges (Jourdan et al.2021).

During winters 2015-16 and 2016-17, six females were tracked using GPS loggers on Ré Island (Jourdan et al. 2021, Jourdan et al. *submitted*). The six 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. Of these six females, four were feeding on precise and regular feeding areas inside the “Fier d’Ars” and two were regularly feeding in “la Loge” but also keeping a regular feeding area in the “Fier d'Ars”. It therefore appears that the site of “La Loge”, although being a site of better quality, is possibly not sufficient to meet the energy requirement of the individuals during the winter period. As a consequence, this site appears to be a supplementary feeding area, probably not sufficiently available due to the shorter immersion time of the sandflat compared to mudflat in the “Fier d'Ars”.

This study has shown that the sexual dimorphism in bar-tailed godwit has consequences for its distribution at a local scale and probably on its winter survival strategies. It has been shown that the feeding area of “La Loge” is an integral part of the functional site of the local population. This study thus confirms the importance of maintaining a good quality of wintering habitats, especially on intertidal habitats facing high human pressures such as professional or recreative on-foot fishing, roost-disturbing hunting activities, nautical activities and tourism.

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Chapter 6

High rate of fusion-fission events in foraging flocks of gregarious black-tailed godwit

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Abstract

Social animals generally gather together (fusion) when the benefits of association exceed the competitive and parasitism costs of staying close to other individuals. When this consensus is no longer reached, individuals can leave a group or groups can divide into subgroups (fission). Studying fusion–fission process and their dynamics is required for the comprehension of the social and environmental factors that influence social groups. In birds, individuals feeding in flocks will divide their time between prospecting for food, moving to other places on the patch or stealing prey from other individuals. Social foragers can also collect information about the quality of food patches by observing their companions, and may adjust their prospecting in the patch or decide to leave the group. Environmental factors, such as tidal cycles in shorebirds foraging on intertidal areas, may drive the group decisions and fusion-fission dynamic of birds. The black-tailed godwit (*Limosa limosa islandica*) winters along the coasts of Western Europe, including in France where they mainly forage in intertidal mudflats. Individuals forage in small to dense flocks on exposed mudflats according to tidal rhythm, either by day or by night, and consistently use a limited number of high tide roosts. Beyond the fluid character of godwits, which regularly alternate, in groups, between intertidal feeding areas and specific roost sites, we could investigate if birds of feeding flocks are simply anonymous crowds aggregating at a same food patch, or if social layers with affinities and related individuals exist. In this study, we monitored in total 10 black-tailed godwits (GPS telemetry) at two distinct sites during autumnal wintering days, and explored the bird associations, two by two, also considering environmental factors (day/night, tide table and sea levels). Although differences existed between birds combinations in terms of time spent in the same flock, no particular closely-related individuals appeared on feeding areas. The comparison of fusion-fission events within roosting and feeding periods highlighted different results between the two study sites (which differed by their number of roosts available). Finally, during feeding, the time of day influenced the degree of movement of godwits with more fusion-fission occurrences during the day than at night.

Keywords: Group foraging, Intertidal mudflats, GPS telemetry, Fusion-fission, *Limosa limosa*

In prep.

Introduction

Fusion–fission dynamics are widespread in social animals, including in birds (Krause et al. 2002). Animals generally gather together (fusion) when the benefits of association exceed the competitive and parasitism costs of staying close to other individuals (Krause et al. 2002). Individuals forming a group must be able to achieve a consensus decision to maintain group cohesion (Conradt and Roper 2005). Fission appears when this consensus is not reached and then individuals decide to leave groups separately (Conradt and Roper 2005) or the group will divide into smaller subgroups (Couzin 2006). Costs and benefits of living in group are highly dependent on social and environmental factors (e.g. weather conditions, prey availabilities, mobile predators) as well as on the condition of a given individual (Fortin and Fortin 2009). Changes in group cohesion and composition is thus highly dynamic in space and time (Lehmann et al. 2007; Sueur et al. 2011). Studying fusion–fission systems and their dynamics is required for the comprehension of the social and environmental factors that cause social groups. Fusion–fission dynamics was mainly studied in mammals and fishes (e.g. guppies *Poecilia reticulata*: Croft et al. 2003; bats: Kerth et al. 2006; American bison *Bison bison*: Fortin et al. 2009) and to a lesser extent in birds (Silk et al. 2014; Loretto et al. 2017).

When social foragers exploit a food patch, they continuously adjust their behaviour to the immediate conditions including their own internal state, their feeding success (Lendvai et al. 2006) and the behaviour of their congeners (McCormack 2007). For birds feeding in dense flocks, they will divide their time between prospecting for food, moving to other places on the patch or stealing prey from other individuals (Garrido et al. 2002; Mónus and Barta 2008). Furthermore, social foragers can collect information about the quality of food patches by observing their companions (public information) and then may adjust their behaviour to improve their intake rate or decide to leave the group (Fernández-Juricic and Kacelnik 2004). Nevertheless, flexibility in forming groups does not mean that flocks are simply anonymous crowds that aggregate at a same food patch. These flocks may involve different social layers, like familiar and/or related individuals forming sub-groups (e.g., greylag geese *Anser anser*: Frigerio et al. 2005) or briefly stable units, such as groups with different foraging modes (e.g. ravens: Loretto et al. 2017).

The fusion–fission dynamics of many shorebirds and wildfowl species may be driven by tidal cycles when they exploit resources on intertidal areas. The group decision can be influenced by the decrease or increase in feeding areas according to tidal fluctuation and thus reduce or increase flock size (Fleischer 1983). During tide rise, birds are also forced to forage closer to terrestrial habitats and subsequent increase in predation risk can also impact grouping decisions (van den Hout et al. 2008; Beauchamp 2010; van den Hout et al. 2010). As a consequence, light-bellied brent geese (*Branta bernicla hrota)* were showed to distribute in larger flocks during high tide (Inger et al. 2006). Nevertheless, the stability of social groups relying on intertidal areas should also vary with interspecific differences in non-breeding social structure. For instance, dominance hierarchies in ruddy turnstones (*Arenaria interpres)* led to constant non-random associations among individuals throughout the wintering period (Metcalfe 1986). By contrast, the composition of sanderling (*Calidris alba*) and dunlin (*Calidris alpina*) flocks appeared to be fluid from one low tide to the other (Myers 1983; Roberts and Evans 1993; Conklin and Colwell 2007). Dunlin flock composition was nonetheless fluctuating, and individuals were associated by chance according to shared attraction to common roosts. Red knots (*Calidris canutus*) in the Wadden Sea in Europe wandered on mudflats in high aggregation without site fidelity (i.e. grouping nomads), while in Banc d'Arguin in West Africa they showed less aggregation but were strongly site-faithful (i.e. solitary residents; Oudman et al. 2018).

The black-tailed godwit (*Limosa limosa islandica)* breeds almost exclusively in Iceland and winters along the coast of Western Europe between Scotland and Northern Morocco (Gill et al. 2007). During their wintering in France, they mainly forage on intertidal mudflats in estuarine bays where they feed on bivalves or seagrass roots (Robin et al. 2013; Robin et al. 2015). Individuals forage in small to dense flocks (10s-1,000s individuals; Gill et al. 2001; Alves et al. 2010; Sirot et al. 2012) on exposed mudflats twice a day according to tidal rhythm, either by day or by night (Lourenço et al. 2008). At high tide they can roost on free upper mudflats or on safe nearby wetland in mainland during neap tide (Domínguez and Vidal 2007). Along the Western coasts of France, in the Pertuis Charentais area, birds arrive from July and leave from February to late April for pre-breeding migration (Bocher et al. 2013). Individuals are present all the winter but can move between sites and forage in different habitats. Nevertheless, during the first part of the wintering period, they faithfully feed on mudflat during low tide and consistently used a limited number of roosts close to the feeding area (Bocher et al. 2013). In this study, beyond the fluid character of godwits which seem to regularly alternate between their feeding mudflats and roosting areas in consistent groups, we explored the bird associations over time. To this end, we investigated the relationship in individual combinations during autumnal wintering days, also testing the influence of day/night, tide table and sea levels.

Methods

Study site

The study was carried out in the Pertuis Charentais, on the central French Atlantic coast, a region with large intertidal areas available to wintering shorebirds (Fig. 1). In the southern part of Pertuis Charentais, Yves Bay (46°02'N, 01°03'W) and Marennes-Oléron Bay (46°55'N, 01˚10'W) are two major wintering areas for shorebirds. Part of the bays or adjacent marshes are located in National Nature Reserves (RNN du Marais d'Yves and RNN de Moëze-Oléron) including high tide roosts of quality for shorebirds and other waterbirds. In the present study, the Yves site included the close-by Charente Estuary (45°57'N, 01°05'W), a foraging area used by birds roosting in marshes and supratidal lagoons of the RNN du Marais d'Yves.

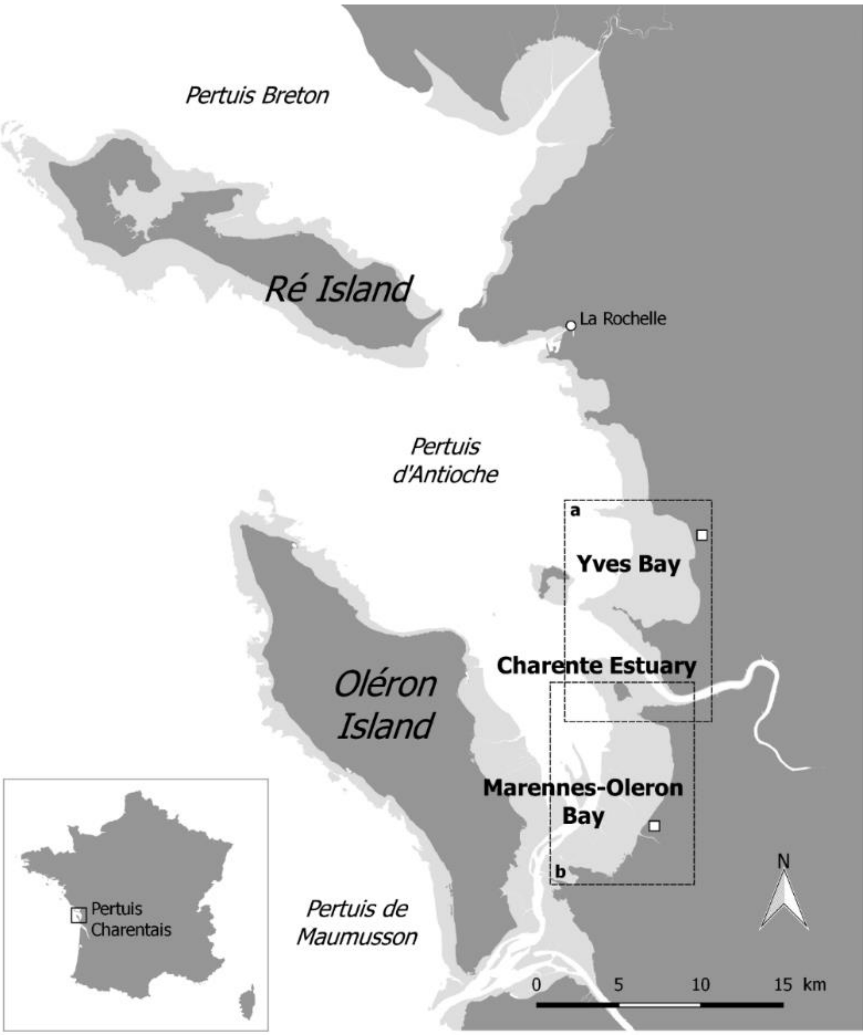

Fig. 1 Map of the Pertuis Charentais (Central French Atlantic coast) and location of the study sites. **(a)** Yves site corresponds to Yves Bay and Charente Estuary, and **(b)** Moëze site corresponds to the eastern side of Marennes-Oléron Bay. Dark grey corresponds to the mainland and light grey to the intertidal areas.

Godwits capture and tracking

Between late-September and late-November 2017, we equipped a total of 12 black-tailed godwits on Yves site and Moëze sites, using the technology of Global Positioning System (GPS) loggers. Godwits were caught by mist nets on their high tide roosts inside Nature Reserves by night during the new moon phase. Birds were individually marked with a metal ring and a unique color rings combination. The biometry (flattened wing, tarsus and bill lengths) and body mass of each bird was measured to the nearest mm or g. Some individuals, preferentially adults and randomly selected, were equipped with a GPS-VHF loggers (STERNA VHF-SRD with solar charger, Ecotone, Gdánsk, Poland; 35 x 16 x 10 mm, 7.5g), attached on the lower part of the back (2 mm Teflon thigh harness) according to the 'leg-loop' method (Mallory and Gilbert 2008). The combined mass of the transmitter and harness did not exceed 3% of the bird body mass. Four individuals were fitted during the same capture session on Yves site, on 22nd September 2017, and eight additional birds were fitted on Moëze site during a second capture session, on 19th October 2017. The GPS loggers were set-up to acquire one location every 30 min, with a tested mean accuracy of ±10m. The tracking duration depends on daily sunshine and efficiency of each logger to recharge its battery. In order to analyze and compare the behaviour of the different birds, we retained study periods when a maximum of birds provided the most complete and synchronous dataset. Thus, among the 12 godwits equipped, only 10 birds were considered for analyses since two individuals monitored on Moëze site did not provided a full month of data. The final dataset consist of four individuals (two males, two females) monitored during 1 month (from 22nd Sept. to 22th Oct. 2017) on Yves, and seven individuals (five males, two females; one bird coming from those equipped on Yves site) monitored during 1 month (from 19th Oct. to 19th Nov. 2017) on Moëze. Data were analyzed and compared at the site level.

Fusion-fission definition

Fusion and fission behaviours were estimated through the spatial association of individuals over time. To qualify the association or non-association of birds, we assessed when birds where considered in the same flock and when they were not. Then, fusion and fission events can respectively be defined when two birds from distinct groups merge between t and $t+1$, and when two individuals found in the same group at time t are then found in two different groups at time $t+1$. GPS locations were assigned to the nearest hour or hour and half, and the distance between simultaneous locations of bird pairs was calculated. Missing time steps for one

Link to animations

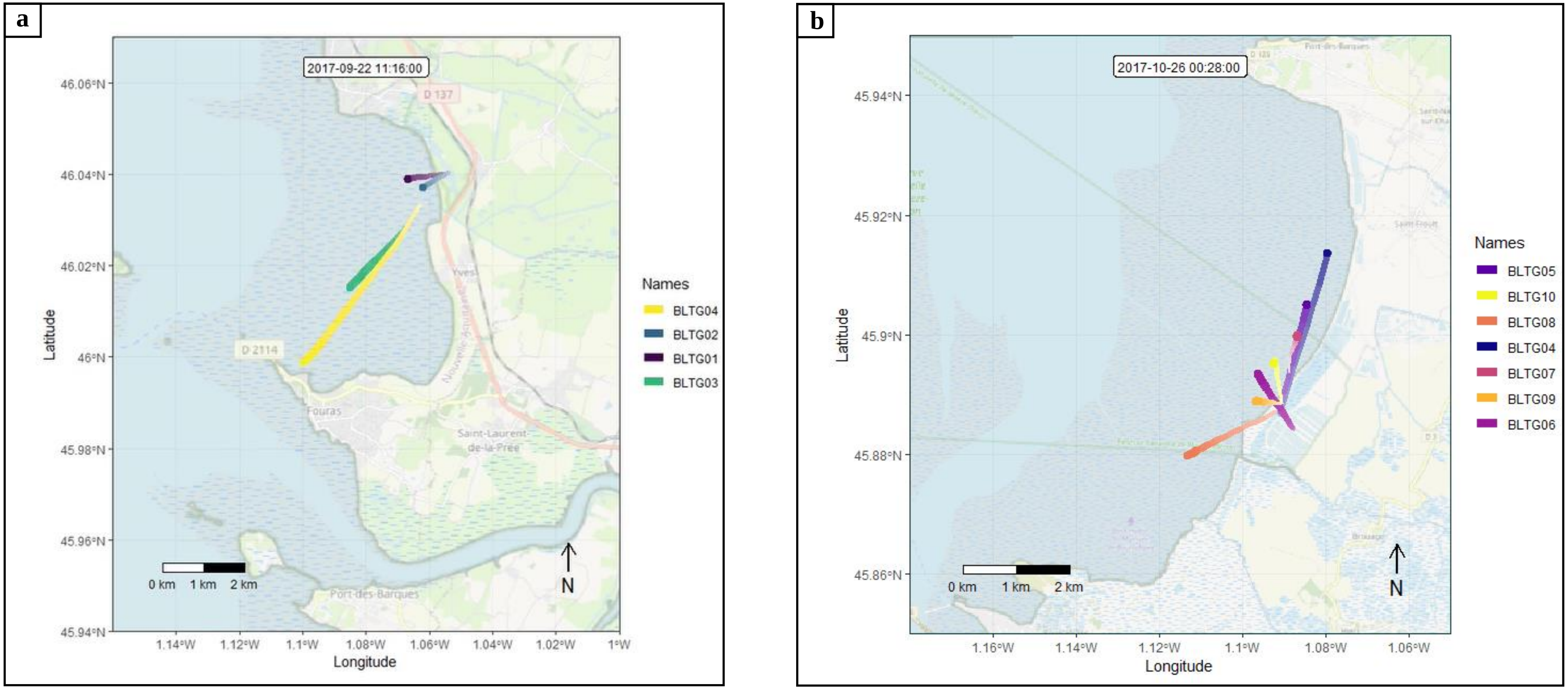

Fig. 2 Animation of spatio-temporal movements of godwits over the entire study period, on **(a)** Yves site and **(b)** Moëze site.

individual of a dyadic combination (i.e. combination of two individuals) were not considered in analysis. Godwits are less mobile on roots and restricted to bordered areas where it is easier to estimate the maximum diameter of a flock. Thus, and based on roosting locations, birds at a distance < 300 m were considered to belong to the same flock, both while feeding and roosting.

Characterization of associations during the wintering

For each study site, associations of godwits over the entire study period were analyzed through the total percentage of time spent by each individual with other monitored birds, two by two, distinguishing feeding from roosting. We also represented the daily pattern of godwits association, over all dyadic combinations, through the average percentage of time spent in the same group per day and per dyad, still distinguishing feeding from roosting as well as day from night. To analyze the fusion-fission dynamics, we explored, for each combination of two individuals and throughout the study period, the association of birds over time, also considering the tidal cycle to illustrate some possible impact of high tide and low tides. We finally estimated the average daily number of fusion-fission events (by adding fusion and fission events) per dyadic combination in order to visualize the general pattern. Fusion-fission dynamics and amount of time spent in the same group per day per dyad have been explored in the two sites throughout autumnal wintering days including day/night, tide table and sea levels events. Statistical analyses (Student t-test, Wilcoxon test) were performed under the statistical software R (3.6.1, R Core Team 2020). Sunrise and sunset data from the R package “GeoLight” were used to distinguish the day and night locations of godwits. Spatial mapping was produced using the software QGIS (2.18, Las Palmas - QGIS Development Team 2016).

Results

Spatio-temporal dynamics of fusion-fission events

At both study sites, spatio-temporal movements of godwits were extremely dynamic along the entire study period (Fig. 2). The general pattern showed an alternating use of intertidal feeding areas and coastal roosting places over time, corresponding to the well-known tidal rhythm in these habitats. Global fusion events occurred recurrently at high tides, when all godwits merge on roosting areas. Conversely, at low tide, individuals mainly showed fission events by joining distinct feeding areas or due to asynchronous departure from roosts. Highly dynamic association of godwits also appeared within feeding and roosting periods. Indeed, several fusion-fission events were observed on feeding areas, reflecting inter-group exchanges. Although less marked, fusion-fission events occurred on roosts at Moëze site (Fig 2b), where

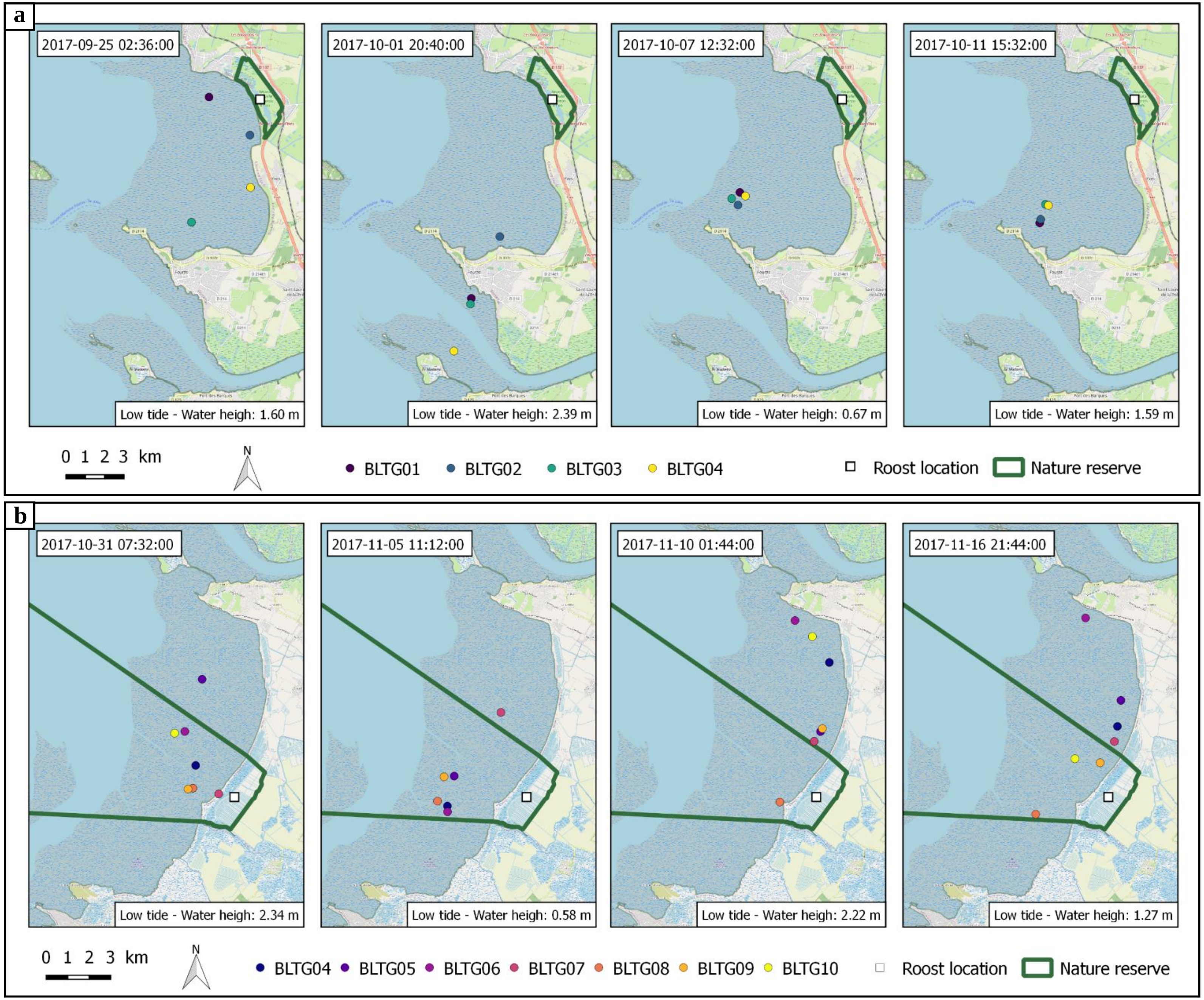

Fig. 3 Examples of black-tailed godwit locations at four different times during low tide at **(a)** Yves and **(b)** Moëze sites, ranked from less to more aggregated situations

birds moved between the three main roosts available. The unique main roost identified at Yves site limited inter-groups exchanges (Fig. 2a). Individual associations at both study sites were not constant but varied along time. Hence, individuals being part of a same feeding flock during one day could forage in different flocks during other days (Fig. 3). With only four and 10 godwits monitored, respectively for Yves and Moëze, individuals found to feed alone (>300m from others equipped birds) were likely within groups of non-monitored birds.

Time spent in same group per individual combination

Considering that almost a single main roost is used in Yves, no large variation of time spent in the same group was expected between dyadic combinations during roosting. Results confirmed this hypothesis with the four monitored godwits which spend from 82% to 97% of their roosting time in the same group (average: 88±5%). Conversely, they spent in average much less time together (two by two) during the feeding period (Wilcoxon signed rank test: V = 21, p-value = 0.031). Indeed, the dyadic combinations spent in average 18±7% of the feeding time in the same group (range: 10-27%; Fig. 4a, Table 1). At Moëze site, the monitored godwits showed the same pattern, with more time spent in the same group per dyad on roosts compared to during feeding (Wilcoxon signed rank test: V = 231, p-value < 0.001). Out of the 36 individual combinations, the average percentage of feeding time spent in the same group was 11±8% (ranging from 17% to 63%), against 47±13% (ranging from 17% to 63%) during roosting (Fig. 4b, Table 2). On Moëze site, at least three main roosts, distant from 1 to 1.5 km, were identified inside coastal marshes of the National Nature Reserve of Moëze-Oléron.

At Yves site, no significant difference was observed in the percentage of dyad association time between day and night during roosting (NS - Paired t-test: t = 0.14, df = 11, p-value = 0.890). During feeding periods, the dyadic combinations showed a significant difference between diurnal and nocturnal percentage of time in the same group (Paired t-test: t = 3.20, df = 11, p-value = 0.009) with 20±9% and 14±4%, respectively (Fig. 5a). At Moëze, the time spent by individuals' combinations in the same roosting group did not underlined a significant difference between day and night, with an average value of 40±15% for both (day = 39.57±15.09%, night = 39.75±15.37%; Wilcoxon signed rank test: V = 418, p-value = 0.6829; Fig. 5b). Conversely, the daily analyse highlighted that dyadic combinations spent significantly less time in the same group during nocturnal feeding (4±4%), than during diurnal feeding (14±11%) (Wilcoxon signed rank test: V = 870, p-value < 0.001).

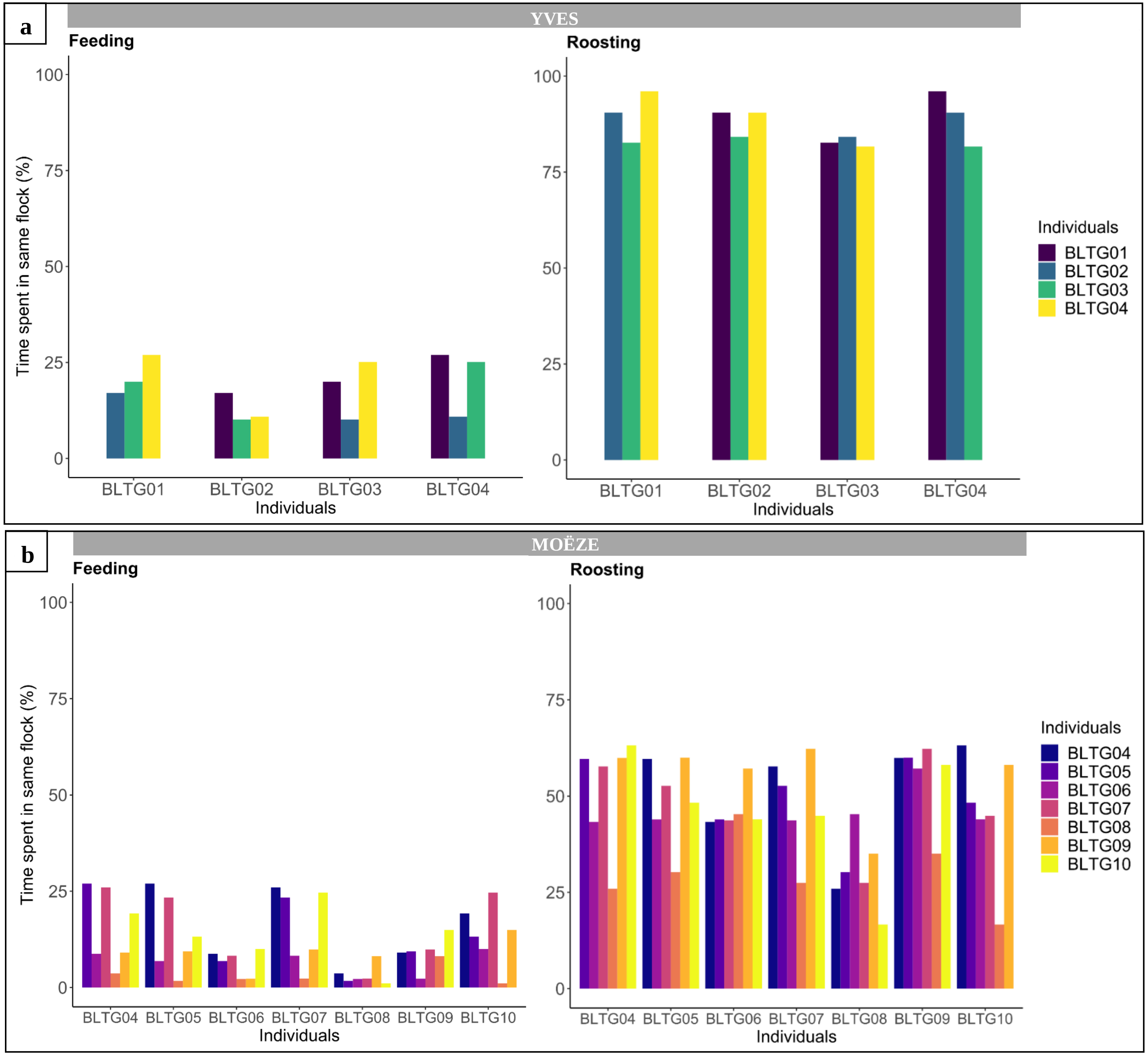

Fig. 4 Proportion of total time spent by birds, two by two, in the same feeding and roosting flocks on **(a)** Yves and **(b)** Moëze study sites.

Table 2 Median distance (+/- SD) between monitored black-tailed godwits (on Yves site), two by two, during feeding and roosting, and proportion of distance values less than 300m.

		BLTG01		**BLTG02**		**BLTG03**		**BLTG04**	
	Activity	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**
BLTG01	Feeding	-	-	17%	2015 ± 2345	20%	2807 ± 2699	17%	1938 ± 2014
	Roosting	-	-	90%	674 ± 2741	83%	387 ± 1081	96%	173 ± 857
BLTG02	Feeding	17%	2015 ± 2345	-	-	10%	2865 ± 2087	11%	2791 ± 2404
	Roosting	90%	674 ± 2741	-	-	84%	711 ± 2428	90%	335 ± 1466
BLTG03	Feeding	20%	2807 ± 2699	10%	2865 ± 2087	-	-	25%	2861 ± 2972
	Roosting	83%	387 ± 1081	84%	711 ± 2428	-	-	82%	409 ± 1078
BLTG04	Feeding	17%	1938 ± 2014	11%	2791 ± 2404	25%	2861 ± 2972	-	-
	Roosting	96%	173 ± 857	90%	335 ± 1466	82%	409 ± 1078	-	-

Fusion-fission events and effect of co-variables

Representations of when birds, considered two by two, are found in the same group over time illustrates the differences in co-occurrence of individuals between high tide (on roosts) and low tide (on feeding areas; Fig. 6a and b). The alternation of high water peak and low water peak coincided with the alternation of a stronger and lower association of individuals, both on Yves and Moëze sites. Most of the dyadic association periods thus occurs during high tide, i.e. when birds are in roosts, while much less co-occurrence events occurs at low tide, during feeding. High tides thus represent recurrent 'fusion' events in godwits organization, where birds coming from distinct feeding areas gather in common roosts, and low tides recurrent 'fission' events by reverse pattern (Fig. 6a and b). Beyond the great variations of individual associations over time, mainly linked to the tide cycle, variations on a finer temporal scale appeared within the same high tide or low tide, giving rise to new fusion-fission events. Indeed, periods of individual co-occurrence are interspersed by several events (>300m), illustrating that birds are successively in the same group and then in a different one, both during feeding and roosting (Fig. 6a and b). At Yves site (Fig. 6a), the close association between BLG01 and BLTG04 during several consecutive high tides and low tides over the period from 08th October to 13th October 2017 underlines the higher proportion of time spent in the same group for this dyad, both during roosting and feeding (Fig. 4a). In the same way, at Moëze site, the individuals of dyads BLTG04-BLTG05 and BLTG04-BLTG07 showed several co-occurrence events over the period from 23th October to 28th October 2017 (Fig. 6b), highlighting their high time spent in the same group compared to others dyads (Fig. 4b).

Table 2 Median distance (+/- SD) between monitored black-tailed godwits (on Moëze site), two by two, during feeding and roosting (resp. F. and R. in Activity column), and proportion of distance values less than 300m.

		BLTG04		**BLTG05**		**BLTG06**		**BLTG07**		**BLTG08**		**BLTG09**		**BLTG10**	
	Activity	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**	**<300m**	**Median±SD (m)**
BLTG04	F.	-	-	27%	931 ± 4526	9%	2402 ± 2593	26%	703 ± 1239	4%	3005 ± 1543	9%	1954 ± 1763	19%	1568 ± 11885
	R.	-	-	60%	148 ± 5500	43%	533 ± 3934	58%	170 ± 2656	26%	690 ± 1286	60%	155 ± 409	63%	166 ± 16710
BLTG05	F.	27%	931 ± 4526	-	-	7%	2328 ± 3927	23%	994 ± 5300	2%	3595 ± 3546	9%	1909 ± 3871	13%	1813 ± 11438
	R.	60%	148 ± 5500	-	-	44%	556 ± 593	53%	168 ± 7137	30%	649 ± 5707	60%	139 ± 4997	48%	542 ± 15075
BLTG06	F.	9%	2402 ± 2593	7%	2328 ± 3927	-	-	8%	1831 ± 2932	2%	3760 ± 2549	2%	3167 ± 2174	10%	3954 ± 10926
	R.	43%	533 ± 3934	44%	556 ± 5983	-	-	44%	545 ± 5424	45%	448 ± 3112	57%	201 ± 3241	44%	536 ± 15702
BLTG07	F.	26%	70 ± 1239	23%	994 ± 3300	8%	1831 ± 2932	-	-	2%	2333 ± 1305	10%	1517 ± 1610	25%	673 ± 7923
	R.	58%	170 ± 2656	53%	168 ± 7137	44%	545 ± 5424	-	-	27%	618 ± 3211	62%	152 ± 2196	45%	444 ± 7209
BLTG08	F.	4%	3005 ± 1543	2%	3595 ± 3546	2%	3760 ± 2549	2%	2333 ± 1305	-	-	8%	1361 ± 1597	1%	2390 ± 11154
	R.	26%	390 ± 1286	30%	649 ± 5707	45%	448 ± 3112	27%	618 ± 3211	-	-	35%	569 ± 1988	17%	914 ± 15868
BLTG09	F.	9%	1957 ± 1763	9%	1909 ± 3871	2%	3167 ± 2174	10%	1517 ± 1610	8%	1361 ± 1361	-	-	15%	1424 ± 10453
	R.	60%	155 ± 409	60%	139 ± 4997	57%	201 ± 3241	62%	152 ± 2196	35%	569 ± 1988	-	-	58%	183 ± 13349
BLTG10	F.	19%	1568 ± 11885	13%	1813 ± 11438	10%	3954 ± 10926	25%	673 ± 7923	1%	2390 ± 11154	15%	1424 ± 10453	-	-
	R.	63%	166 ± 16710	48%	542 ± 15075	44%	536 ± 15702	45%	444 ± 7209	17%	914 ± 15869	58%	183 ± 13349	-	-

Bird association dynamics showed a significant difference in the number of fusion-fission events per day between feeding and roosting periods on Yves site (Wilcoxon signed rank test: V = 300, p-value < 0.001), with an average of 2.4±0.7 and 1.4±0.1 events, respectively (Fig. 7a). On Moëze site, fusion-fission events averaged 1.7±0.6 during feeding, and 1.5±0.2 on roosts, with no significant difference (Wilcoxon signed rank test: V = 2164.5, p-value = 0.091; Fig. 7b). However, the mean numbers of diurnal and nocturnal fusion-fission events during feeding periods were on average 2.9±0.5 and 1.8±0.2 per day at Yves, and 2.0±0.6 and 1.3±0.3 at Moëze. Diurnal and nocturnal differences during feeding period revealed significantly higher fusion-fission events by day than by nigh (Yves – Wilcoxon signed rank test: V = 77, p-value <0.001; Moëze - V = 871.5, p-value <0.001). On roosts, the differences between diurnal and nocturnal fusion-fission occurrences were not significant, both at Yves (Day: 1.4±0.1, Night: 1.3±0.1; Paired t-test: t = 2.17, df = 11, p-value = 0.053) and Moëze (Day: 1.5±0.2, Night: 1.5±0.3; Wilcoxon signed rank test: V = 565, p-value = 0.158).

Discussion

The analysis of individual associations in Icelandic black-tailed godwit at their non-breeding site revealed different patterns depending on bird activities. At high tide, during roosting, birds spent more time in the same large flocks compared to the feeding period when they divided in smaller flocks. Although differences exist in the time spent in the same flocks between individual combinations, no particular closely-related dyad appeared on feeding areas. Indeed, the dynamic of individual association over time highlighted frequent fusion pattern at high tide, followed by a period of greater co-occurrence of birds around the high tide peak (i.e. on roosts), and recurrent fission events during ebbing and rising tides, leading to a feeding period during which monitored individuals were mainly located >300m away from each other. The comparison of fusion-fission events occurring within roosting and feeding periods at Yves site underlined higher dynamics of birds during feeding, with regular movement between flocks given the absence of persistent associations. At Moëze site, which differed from Yves by higher number of roosts, no significant difference appeared in the number of fusion-fission events between feeding and roosting periods. Finally, the analyse of individual associations showed that the time of day influenced the degree of movement of godwits during feeding periods, with more fusion-fission occurrences during the day than at night.

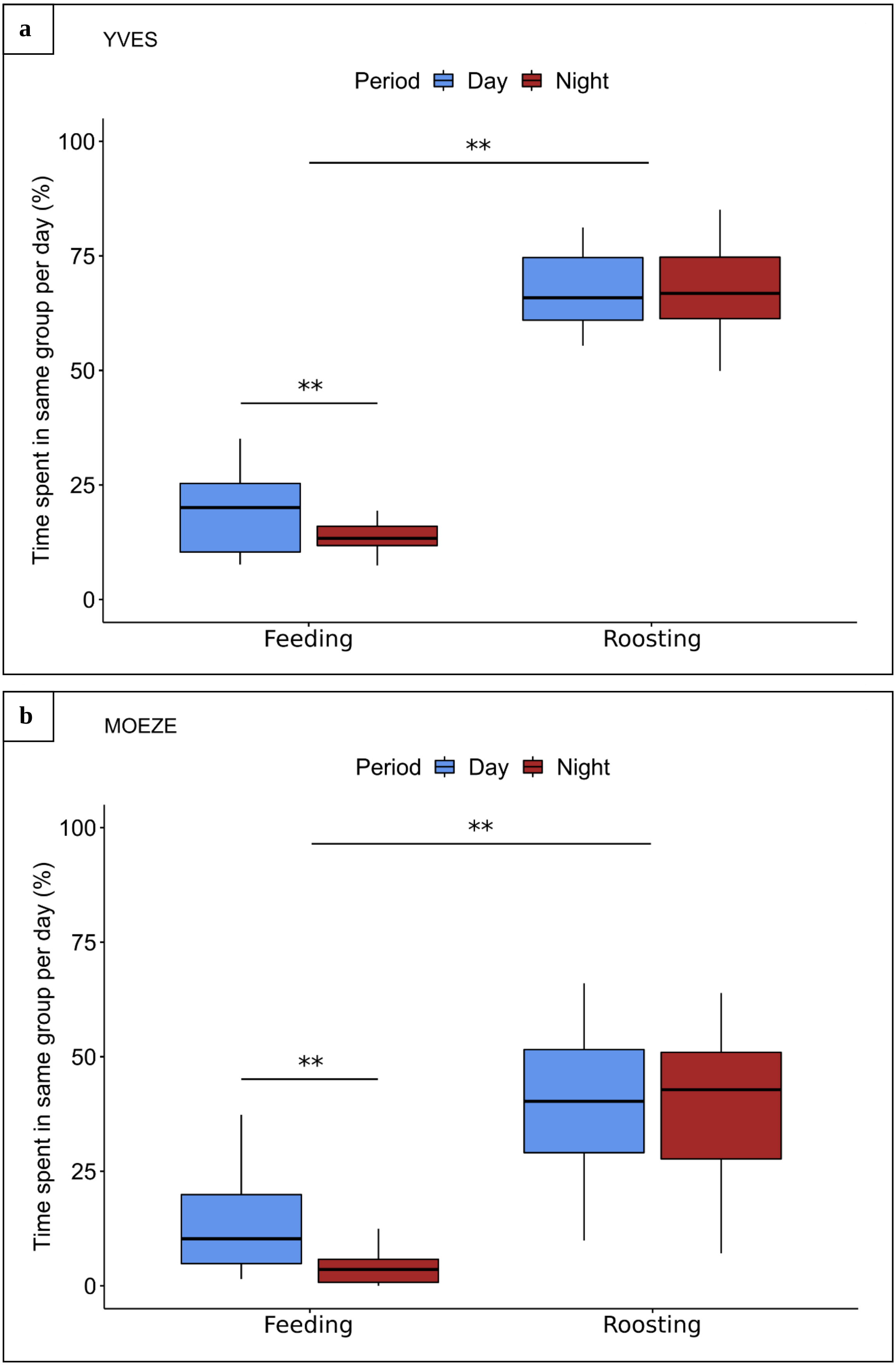

Fig. 5 Pourcent of time spent in same flock per day, per individual combination, on **(a)** Yves and **(b)** Moëze sites according to activity (feeding or roosting) and daytime period (day or night).

At Yves site, the recurring and persistent high associations at high tide suggest that godwits are limited by roost choices, while the many opportunities on feeding grounds encourage them to disperse at low tide. When more roosts are available, as in Moëze, where at least three close roosts were identified, associations appear less consistent from a high tide period to another. At both sites, the high level of bird associations observed during high tides, but no longer valid at low tide on feeding areas, suggests a common roost choice rather than a persistent association of individuals, as previously observed in dunlins (Conklin and Colwell 2007). Although associations beyond the roosting periods exist for some dyadic combinations, sometimes over several successive tidal cycles, no stable social flocks appeared in the long term inside the same site. In shorebirds, the need for high quality roosts, insuring a low exposure to predation risk (Rogers et al. 2006), human disturbance (Kirby et al. 1993) and adverse weather conditions (e.g. wind speed. McConkey and Bell 2005; Peters and Otis 2006) in order to minimize the energy expenditure (Rogers et al. 2006), limits opportunities of suitable sites. Thus, black-tailed godwits gathered by thousands on the rare suitable sites, and in this case almost exclusively located inside both Nature Reserves (Robin 2011).

The costs and benefits of living in groups are highly dependent on the environment and the condition of a given individual in animals (Conradt and Roper 2000; Fortin et al. 2009). Shorebirds could thus gather or separate according to opportunities and the interest to do so. As gregarious species, godwits forage in flocks during feeding, which densities depend on the resource quality of habitats allowing to satisfy daily energy requirements (Gill et al. 2001; Alves et al. 2010; Sirot et al. 2012). Individuals must take advantage of the group, including benefits of cooperation, safety and public information (Bijleveld et al. 2015), while limiting the risks of competition for resources (Beauchamp 2013). Therefore, higher conspecific density in large flocks could decrease the individual intake rate, by increasing interference (conflicts, avoidance movements, etc…; Gils et al. 2015; Yu et al. 2019) and locally decreasing prey density. Hence, the large roosting groups of godwits divide into smaller feeding sub-groups to reduce intraspecific competition. The low, but not null, percentage of time spent in same group by individuals with each other suggests that feeding sub-groups formed at the roost departure are not consistent from tide to tide and within a feeding period. Indeed, even if monitored birds could each belong to a different sub-group, then masking persistent individual associations, the average feeding time spent in the same group (11% and 18%, respectively for Yves and Moëze sites) rather highlights a strong dynamism of birds, with several inter-group exchanges. Previous studies already highlighted the influence of the bird mobility on the co-occurrence

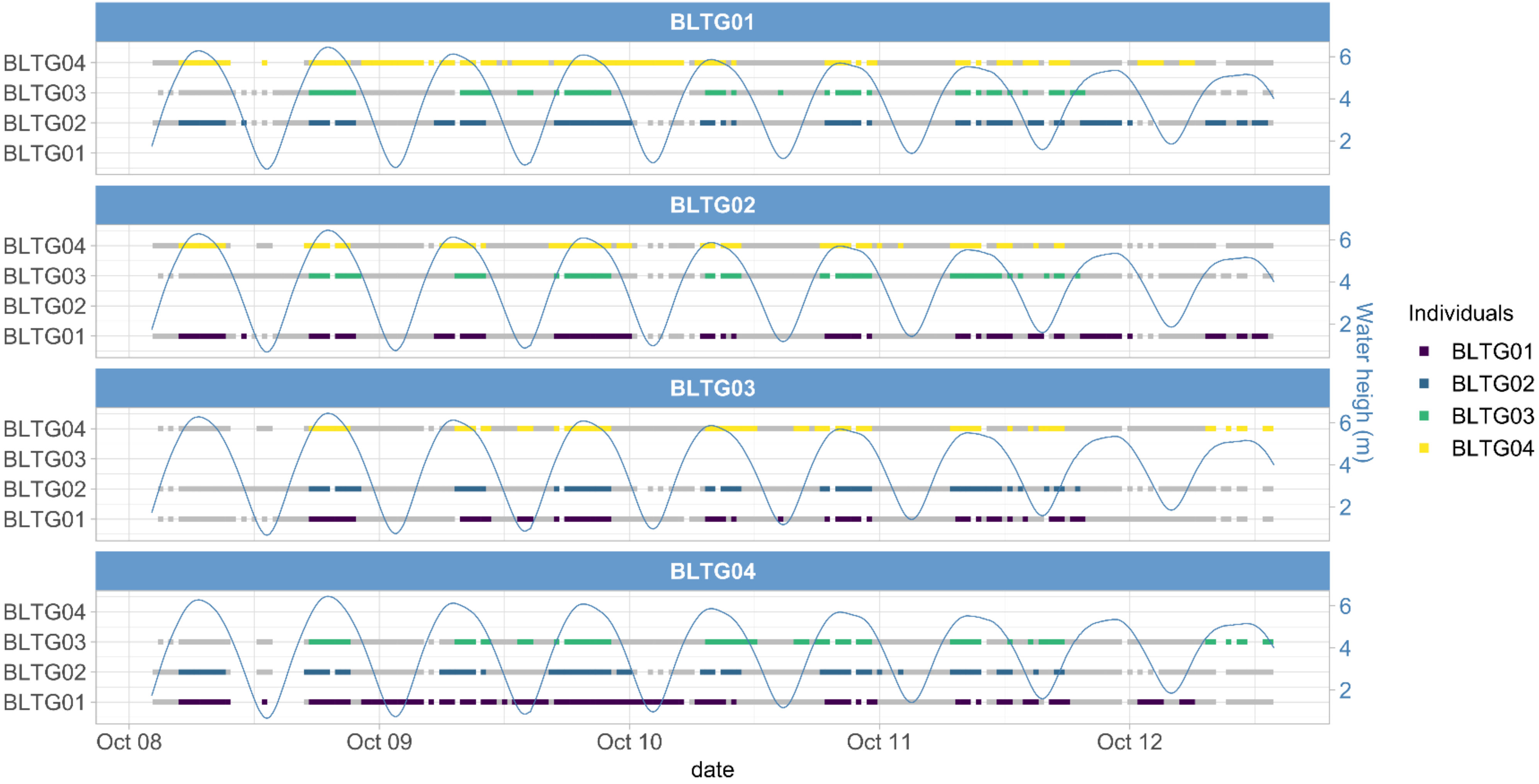

Fig. 6a Representation of the association of each individual with other birds equipped over time, on Yves study site. For each time *t*, a point is represented in grey (>300m) or in colour (<300m) depending on the distance to the reference individual (blue band); no point means that no valid location was recorded by the GPS logger.

(Metcalfe 1986) so that, despite the lack of stable association, more mobile birds could came into contact with more individuals and increase their overall co-occurrence rate (Roberts and Evans 1993; Conklin and Colwell 2007). The continuous observation of spatial distribution of godwits over time shows the erratic movements of birds during feeding, and several fusion-fission events with other tagged individuals. This fusion-fission dynamics throughout multiple feeding groups underlines the large spread-out characteristics of black-tailed godwits at their non-breeding grounds.

Group cohesion and composition is often highly spatio-temporally dynamic in animals (Lehmann et al. 2007; Sueur et al. 2011). In shorebirds, flocks can redistribute according to disturbances, predator attacks or individual decisions (Myers 1984; Conklin and Colwell 2008). These events occurring both during high and low tide periods can explain the absence of difference in fusion-fission dynamics between feeding and roosting at Moëze. Given that only one main roost is available at Yves site, the lack of opportunities to leave the group to join another when facing a disturbance or predator may explain the lower number of fusion-fission events observed. However, at both study sites the fusion-fission occurrence differed between diurnal and nocturnal feeding periods. By day, godwits appeared to more often change groups, while they were more faithful to their feeding flock at night. These results are coherent with previous studies that highlighted larger feeding areas in black-tailed godwits by day (Jourdan et al. *under revision*), likely due to the visual feeding method, which involves higher step rates and movements (Lourenço et al. 2008). Conversely, nocturnal feeding behaviour revealed less movement (Lourenço et al. 2008) and more restricted prospecting areas (Jourdan et al. *under revision*), likely linked with tactile feeding searches and/or higher prey activity by night (Pienkowski 1983). The time of the day also showed an effect on the time spent in the same flock by each dyad combination, so that individuals spent less time with each other during nocturnal feeding periods. This observation is opposed to what we expected, since nocturnal shorebird organisation is supposed to favour large flock formation as antipredator strategy (van den Hout et al. 2008; van den Hout et al. 2010), then involving higher time spent together. However, similar observations have already be mentioned in dunlins, with different nocturnal anti-predator strategies consisting on smaller and motionless flocks, and resulting in both a lower overall co-occurrence and greater persistence of association at night (Conklin and Colwell 2007; Conklin and Colwell 2008). Consistently with these observations, feeding godwits exhibit a less dynamic behaviour and a lower overall association with each other by night, suggesting a feeding in subgroups, as during the day, but with less inter-group exchanges.

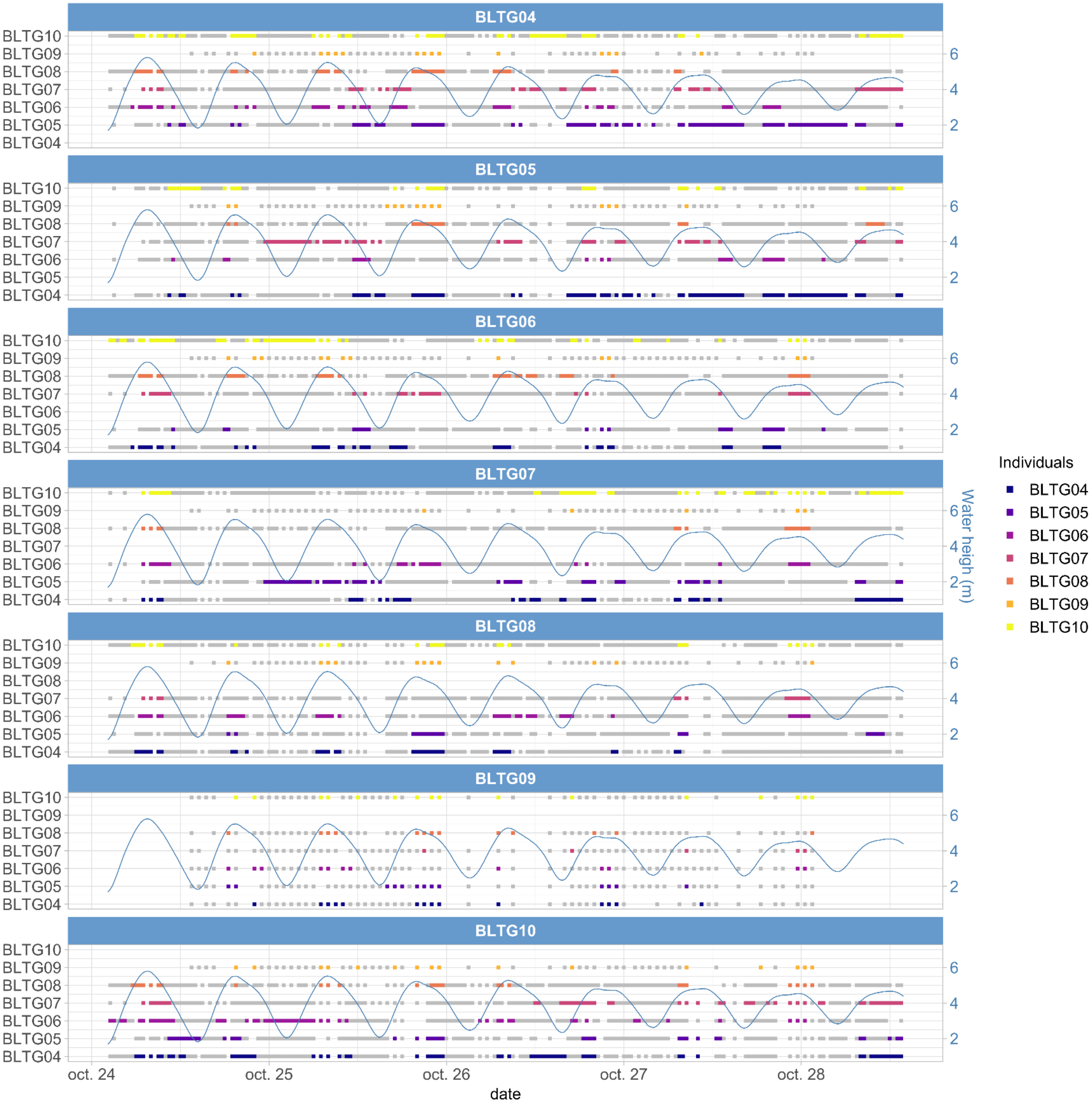

Fig. 6b Representation of the association of each individual with other birds equipped over time, on Moëze study site. For each time *t*, a point is represented in grey (>300m) or in colour (<300m) depending on the distance to the reference individual (blue band); no point means that no valid location was recorded by the GPS logger.

Finally, the fusion-fission dynamics observed in the present study highlighted a very high individual versatility in the choice of feeding group in black-tailed godwits, underlying that birds do not have 'friends' despite the need to prospect in group. Yet, further studies are needed to understand what factors can cause a bird to leave a group. As observed in other animals, body condition could affect these association patterns (Wielgus et al. 2020). Could the bird individual efficiency to feed under prey availability conditions encountered by the group, lead it to join another feeding group? Or, does a less competitive bird, and therefore more subject to interference, have more interest in leaving the group? In these cases, we can also wonder if birds leave a group alone, or with other individuals. In terms of conservation, our results underlined that black-tailed godwits require large intertidal mudflats areas in order to constantly prospect, in flocks, for new feeding areas, although often spatially restricted (Jourdan et al. *under revision*).

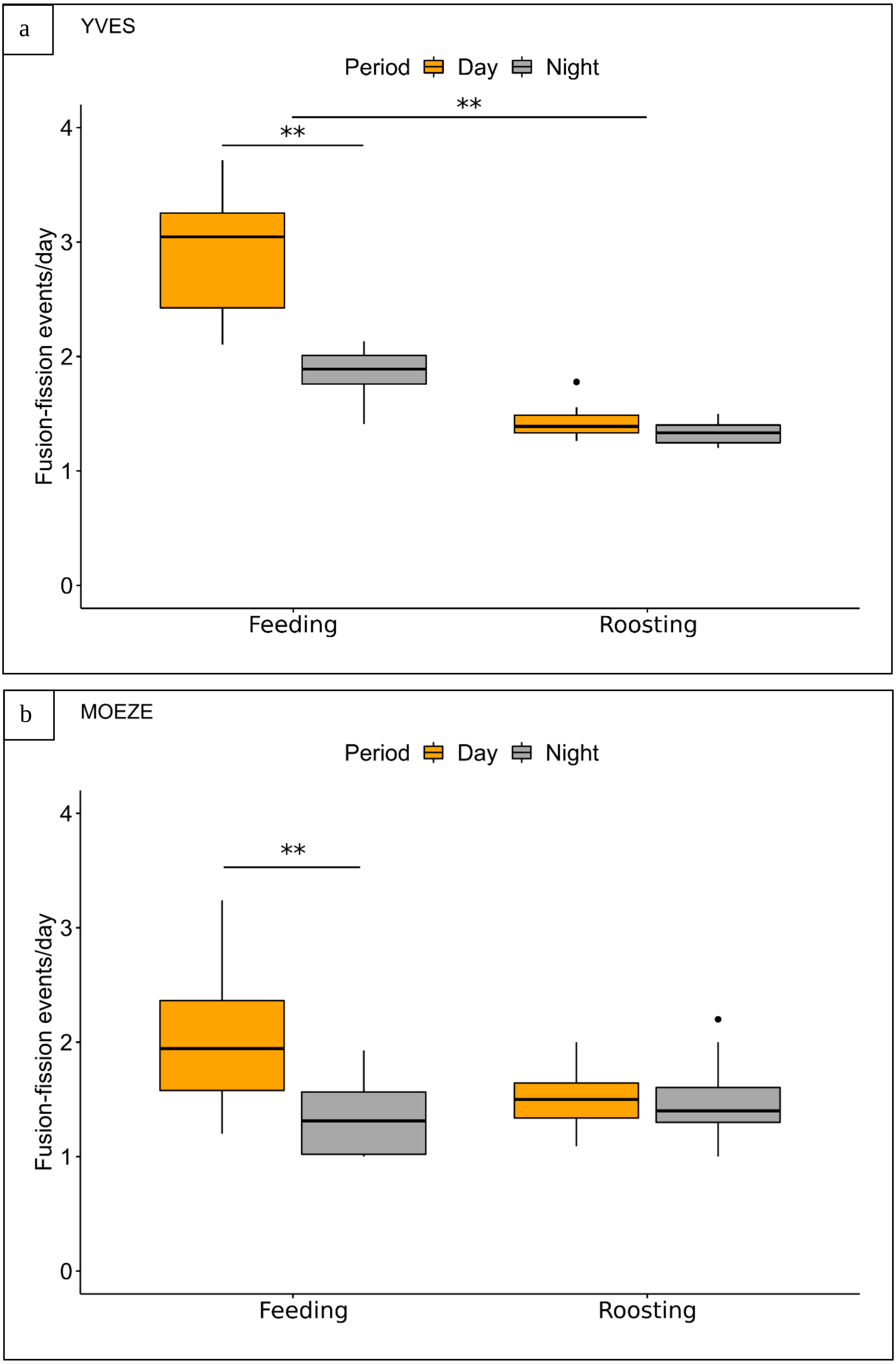

Fig. 7 Mean number (± SD) of fusion-fission events per day over the study periods according to activity (feeding or roosting) and daytime period (day or night) on **(a)** Yves and **(b)** Moëze sites.

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General discussion

Main results of the study

The main objective of this research work was to study habitat use and selection, and its spatio-temporal variations in non-breeding bar-tailed *(L. l. lapponica)* and black-tailed godwits *(L. l. limosa)* during their wintering period, and to explore the role of protected areas in their conservation. The monitoring of these two "medium size" species on a same wintering area, and with such a fine scale survey (GPS technology, with a 30min time step) and large dataset, is new in shorebirds. Although our studies, based on relatively small samples of monitored birds, not allow to generalize the results, we can still describe some characteristics of the fine scale habitat selection in individuals of these two species. Since bar-tailed and black-tailed godwits were not monitored during the same periods and at the same sites, direct comparisons could not be made. However, it is possible to compare their winter habits, in terms of spatial and temporal use of resources and habitats, on related wintering sites of the Pertuis Charentais.

For instance, we highlighted that bar-tailed godwits can use restricted individual foraging patches over the wintering period on Ré Island, a relatively small wintering site. The birds, equipped during a same capture session on the same roosts, showed individual home ranges spatially distinct from each other, and composed of a specific combination of intertidal habitat types among all suitable ones present on site. These results highlight that bar-tailed godwits can be very faithful to their feeding areas during winter, and specialized on their habitat selection (Catry et al. 2014; Ceia and Ramos 2015). Individuals wintering on Ré Island two consecutive years even showed a high repeatability in location of their foraging home ranges (Conklin and Battley 2011; Coleman and Milton 2012). Beyond the predominant selection of marine worms by bar-tailed godwits in their diet, as previously demonstrated along the European coasts by several studies (Scheiffarth 2001; Duijns et al. 2013; Bocher et al. 2014), our observations support the idea of individual specialization (Sutherland et al. 1996; Durell 2000) on particular species of annelids (Chapter 1). On the other hand, the black tailed godwits monitored in the Pertuis Charentais showed a more dynamical use of their wintering grounds, moving between several sites during their monitoring period. These site changes seem to occur both at small and larger spatial scales along the Atlantic French coasts, and probably at country-scales with exchanges with UK, Ireland, Portugal and Spain (F. Robin, *Pers. Com.*). Such a combination of several distant sites, and more particularly the different roosting areas they constitute, illustrate the level of 'landscape complementation' for godwits, defined as the distance between two non-substitutable resources such as roosts. Black-tailed godwits also showed a spread out distribution within a wintering site, with various areas prospected around their main roosts.

These large distribution extents of birds during winter, as well on a local as on a large scale, imply a great variety in the foraging areas and habitats used. Therefore, unlike bar-tailed godwits, individuals of black-tailed godwit do not use feeding areas with a strong fidelity but rather show a high plasticity in their habitat use. These findings highlight the capacities of 'landscape supplementation' at the regional scale for black-tailed godwits, consisting in the use of resources from different landscape elements, including different habitats types, in order to supplement their limited food intake rate in some habitats. Indeed, the species can feed as well on marine as freshwater preys by prospecting on both intertidal and inland wetlands, with shifts from natural to artificial habitats such as seawater reservoirs for saltpans (Gill et al. 2001; Masero 2003; Gill et al. 2007) or hunting ponds. Although such habitat changes were known to seasonally occur during the pre-breeding and post-breeding periods, the monitored black-tailed godwits also prospected in multiple habitat types during the winter season, as well within a day for some individuals. Such different habitats used subject godwits to various environmental constraints, to which they are able to easily adapt by adjusting, for instance, their activity rhythm. Thus, while the species follows a tidal rhythm, when it exploit marine habitats, birds seems to adopt a nycthemeral rhythm when shifting to inland habitats (Chapter 2).

When birds depend on the tidal cycle of intertidal habitats, both for bar-tailed and black-tailed godwit, they usually feed as well at day as at night. However, as mentioned in previous studies (Burton and Armitage 2005; Piersma et al. 2006) the time of the day influence the foraging activities and birds' spatial distribution. For instance, monitored individuals of the two species used distinct diurnal and nocturnal feeding areas, with less movements when prospecting at night (Lourenço et al. 2008; Jourdan et al. 2021), resulting in smaller nocturnal feeding home ranges (Chapter 3 and 4). While in black-tailed godwit these distinct day and night foraging areas did not revealed significant habitat changes, bar-tailed godwits showed some clear differences such as seagrass beds strongly selected during the day and much less used at night. Such a time of day dependent habitat use can result from differences in predation risk, disturbance or density/activity of preys (Burton and Armitage 2005; Piersma et al. 2006). As observed in bar-tailed godwits monitored on Ré Island, habitats subject to human activities during the day (e.g. sandy habitats and oyster parks) were preferentially selected at night, when the disturbances decrease or were null (Chapter 3). Similarly, black-tailed godwits at Moëze and Yves sites explored diurnal feeding areas far from the disturbed coastline, while they prospected closer during nocturnal foraging. Moreover, the protection status of feeding areas also appeared conditioning the temporal pattern of their use by black-tailed godwits. At Moëze site, where both ‘protected’ and ‘unprotected’ intertidal mudflats exist, birds widely selected nature reserve areas to feed at daylight and explored ‘outside the nature reserve’ in a greater extent at night (Chapter 4). For both bar-tailed and black-tailed godwits, we observed a significant inter-individual variability in the size of feeding areas, which could illustrate differences in competitiveness. Indeed, we can hypothesize that some birds can be satisfied with a small home range of high quality by outcompeting other birds. For instance, in black-tailed godwits, results highlighted that birds with smallest foraging areas mainly foraged, both day and night, inside the nature reserve, while birds with larger ones more strongly used outside-reserve areas. Although distinct individual foraging areas appeared in both species, this pattern involved significant interindividual differences in habitat selection only for bar-tailed godwits. These results highlight distinct habitat use strategies and social organization between the two species wintering on the French coasts.

Without generalizing the results, the bar-tailed godwits monitored on Ré Island showed the use of restricted and distinct individual feeding areas with a strong fidelity during the winter, and possibly from year to year. These characteristics support a more individualized feeding behaviour than black-tailed godwits, well known to be gregarious (Goss-Custard 1970; Greenhalgh 1975). Beyond the individual differences in habitat selection in bar-tailed godwits, there could be large differences in the pattern of space use and diet between males and females. Our monitoring study by GPS telemetry, only relied on female bar-tailed godwits. However, another approach allowed to identify a different use of the two Ré Island sub sites, made of different feeding habitats, by males and females. Females outnumbered males on La Loge, the sub site with higher species richness, mean biomass and mean size of polychaets, and individuals tended to forage in flock along the waterline exhibiting a higher number of interactions such as kleptoparasitism. On Fier d’Ars, sub site on which mean polychaetes biomass was lower but with a longer time access to feeding areas, there were as many males and females and in lower bird density per hectare. Compared to La Loge, the individuals practised more probing than pecking actions on Fier d’Ars and prospected alone, as assumed by the GPS tracking. Finally, females outcompeted males in the highest feeding quality site, while no difference could be notice between the sexes in the poorest quality site (Chapter 5). On the other hand, the black-tailed godwits showed interindividual differences in home ranges size, with more diffused feeding areas compared to bar-tailed godwits, and partly common to several individuals. Moreover, although our habitat selection analysis relied only on few birds, including males and females, results showed no significant interindividual difference in preferential habitats selected. These different results highlight that individuals of black tailed godwits were looking for the same resources or even the same feeding areas, assuming feeding in dynamic flocks as generally observed in the field. The exploration of bird associations confirmed a high dynamism of individuals during feeding activities. Large flocks formed in supratidal roosts, through fusion events at high tide, divide into smaller flocks on intertidal areas, with regular inter-group movements through fusion-fission events during feeding. Consequently, black-tailed godwits exhibited a gregarious behaviour during feeding, but the composition of the groups of individuals are dynamic and not consistent over time, with no socially and closely connected individuals. However, the spatial dynamic of bird association seems to depend on the time of the day, so that fewer fusion-fission events occur at night implying less inter-flocks exchanges. At high tide, birds generally aggregate at one to few roost sites and thus spend more time in a same group. However, black-tailed-godwits can remain dynamic and fusion-fission events still occur, probably due to danger of predation or disturbance, mainly leading to a reorganization of birds on the roost (Chapter 6).

Specialist or generalist? Solitary or gregarious?

On intertidal areas, both bar-tailed and black-tailed godwits showed a significant selection of preferential feeding habitats among all available ones. As predicted by the optimal foraging theory, this selection aims to optimize the energy intake rate (Evans 1976). However, the two species highlighted differences in their feeding strategies during the winter. The bar-tailed godwits appeared mostly individually specialized in their site and habitat use on Ré Island, and supposedly on specific polychaete prey species (Duijns et al. 2013), while individuals of black-tailed godwit are likely more generalist on related sites in the Pertuis Charentais. Such a specialization in bar-tailed godwit restrict birds to specific feeding core areas, and could be advantageous by reducing the intraspecific competition through less interindividual overlap (Kouba et al. 2017). Conversely, a more generalist strategy in black tailed godwit, in addition to a gregarious behaviour, leads to increase interferences between feeding individuals (Gils et al. 2015; Yu et al. 2019). This intraspecific competition can explain a part of the highly mobile use of habitats by individuals, with several fusion-fission events in feeding flocks. However, the generalist pattern of black-tailed godwits illustrates a huge plasticity of birds in the use of habitats, and allow them to easily respond to environmental changes such as depletion of food resources (Gill et al. 2001). The species can thus benefit from its generalist pattern, through possibilities offered in landscape ‘complementation’ and landscape ‘supplementation’ of resources, in both marine (intertidal mudflats) and inland habitats (inland marshes and artificial wetlands). Despite their highly gregarious behaviour, both during feeding and roosting, and according to the analysis of bird associations over time, black-tailed godwits did not seem to have 'friends'. Hence, the species favours a group feeding, more clearly than bar-tailed godwits, probably for more energy efficiency through cooperation and not because of benefits linked to social affinities, given the great versatility in the choice of feeding groups.

Exploit mudflats as much as possible

Whatever their feeding strategy, the two godwit species appeared to devote almost all of their time for foraging during the periods of complete access to mudflats. These results support the idea that birds require all the time of feeding area availability to achieve a sufficient net energy intake, and have to optimize their prey collection to fulfil their daily energetic requirements. As previously observed in shorebirds including bar-tailed godwit (McNeil and Rodriguez 1996; Dodd and Colwell 1998), this strong dependence on the availability of emerged mudflats occurred both at day and night. However, Lourenco et al (2008) reported a greater importance of diurnal feeding in black-tailed godwit in the Tagus Estuary (Portugal), with nocturnal feeding observed only during coldest temperatures. The similar importance of diurnal and nocturnal feeding activities in our study can be explained by site-specific conditions to which godwits can adjust, such as lower temperatures in higher latitudes requiring higher energy needs (Wiersma and Piersma 1994). Although diurnal and nocturnal feeding appear as much important in bar-tailed as in black-tailed godwits, some clear differences in space and habitat use exist according to the time of the day in both species.

Foraging methods according to nycthemeral rhythm

To take advantage of both day and night feeding activities, shorebird are thus assumed to have developed physiological adaptations, such as higher tactile sensitivity which facilitate the nocturnal foraging in godwits (Cunningham et al. 2013). The various feeding behavior resulting from these adaptations can partly explain the differences in size, location and habitat types of the prospecting areas between day and night in both species (Lourenço et al. 2008; Dias et al. 2009; Jourdan et al. 2021). Some behavioral adaptations are also assumed to optimize the day and night habitat use in godwits, and the level of disturbance on feeding areas seems to be an important factor. Indeed, while recreational and harvesting activities which occur on oyster parks, beaches and along the coast keep birds away during the day, these areas can be interesting for individuals at night, when disturbances decrease. Moreover, at Möeze site, black-tailed godwits seemed to favor diurnal feeding areas located inside the protected perimeter of the nature reserve, where hunting and recreational activities are prohibited. Not-protected mudflats, more selected at night, are probably too much disturbed during the day to be profitable for godwits (Thomas et al. 2003; Navedo and Masero 2007; Burger and Niles 2013). In addition, human settlements seem to influence the godwits habitat use beyond simple disturbance. For instance, the preferential use of upper foreshores at night by bar tailed and black tailed godwits at different wintering sites could be explained by anthropogenic illuminations along the coast, artificially recreating full-moon visual conditions (Santos et al. 2010; Dwyer et al. 2013). Finally, black-tailed godwits show another important adaptation of their rhythm of activity when they seasonality shift from intertidal to terrestrial habitats. Indeed, their great plasticity allows them to quickly switch from a tidal (mudflats) to a nycthemeral rhythm (inland marshes, saltmarshes and hunting ponds) to optimize the use of each habitat type.

Importance of roosts

The analysis of bird movements and habitat use confirmed the crucial role of roost sites in the functional areas of wintering godwits (Kirby et al. 1993; Rogers et al. 2006). At high tide, after feeding activities on intertidal areas, bar-tailed and black-tailed godwits will reach supratidal areas to roost. In the different wintering sites of the Pertuis Charentais, the main roost sites are located inside Nature Reserves of the region, and hold most of the wintering individuals of both species. Godwits have to minimize their energy expenditure during roosting period, and to this end a low exposure to predation risk, adverse weather conditions and various human disturbance is sought (Kirby et al. 1993; McConkey and Bell 2005; Peters and Otis 2006; Rogers et al. 2006). These specific conditions required are exclusively found in protected areas in our study area except in Guérande saltpans, and explain that most of individuals co-occur on the same roosts. However, even if more quality sites are available, bar-tailed and black-tailed godwits still tend to roost in groups as antipredator strategy or to better face bad weather conditions. In both godwits species, alternative roost sites, located on the upper foreshore, can be used depending on their availability (Piersma et al. 2006). Such roosts can be preferentially chosen for their proximity to the feeding areas (Morrison and Harrington 1979), inducing less energy costs during travelling (Si et al. 2011; Novaes and Cintra 2013). However, the use of these upper mudflats roosts by bar-tailed godwits also seems to depend on the time of the day and related factors, on Ré Island. Less raptors activity over mudflats and a better visibility of approaching predator (Rosa et al. 2006), compared to saltpans, could decide bird to favour upper foreshore during diurnal roosting. At night, saltpans could constitute water barrier against terrestrial predators (Cramp et al. 1983; Sitters et al. 2001). Black-tailed godwits did not appear to have a similar use of upper foreshore at Moëze and Yves sites, since during their neap tide availability birds seemed to regularly use them as roosts, both day and night.

Segregation of the two species prospecting the same feeding areas

Although bar-tailed and black-tailed godwits overlap on their wintering sites, using the same intertidal habitats, they appear to segregate on their diet. Indeed, the bar-tailed godwit is known to almost exclusively feed on polychaete worms during the winter (Duijns et al. 2013), and appear to specialize at individual scale on specific feeding areas and habitats, and probably on particular worms species. Conversely, the black-tailed godwit appears to be generalist, with an omnivorous diet including for instance molluscs and rhizomes of *Zostera noltei* (Robin et al. 2013; Bocher et al. 2014), and exploits widely dispersed feeding areas in dynamic flocks. Therefore, the interspecific competition between the two species could be limited to the grabbing of certain feeding areas by the black-tailed godwits, because of their number when feeding in large flocks. Such a hypothesis could be test in further studies investigating the social interactions during feeding between some individuals of bar-tailed and black-tailed godwits flocks monitored at the same sites. Indeed, in a small site as the Fier d'Ars of Ré Island, more than 4,000 black-tailed godwits can forage on seagrass bed in the center of the bay, while only 600 bar-tailed godwit winter on the Island.

Contributions for conservation

The knowledge of intra and interspecific variations in the wintering habitat use and selection by shorebirds are of major importance to develop conservation actions suitable for as many species as possible. Our results show that bar-tailed and black-tailed godwits have many similarities in their use of space and habitats during the wintering period on the French Atlantic coast, but also highlight noticeable differences. In bar-tailed godwits, the high specialization on particular preys and habitats could make it more vulnerable to important changes in the distribution and quality of food resources. Indeed, huge degradations or disturbances limiting food access, and resulting in increased competition on remaining resources, could especially affect birds having specialized diet or feeding methods. Black-tailed godwits, although less individually specialized and seemingly more able to adapt, also depend on intertidal habitats in early winter facing high anthropogenic disturbances. We thus support the importance of maintaining a good quality of intertidal habitats, especially those concerned by various human pressures (on-foot fishing, hunting, tourism or nautical activities). In addition, the sex-specific spatial distribution of bar-tailed godwits observed on Ré Island remind us of the importance of adapting management measures in order to not favour a part of a population, for instance one sex, in conservation actions. In the same way, although black-tailed godwits mainly use intertidal habitats during their wintering, alternative habitats, such as hunting ponds and saltpans, can be used by a part of the population, seasonally or more extensively. To ensure a management of these artificial habitats, in addition to the protection of key intertidal habitats, seems essential for the wintering of the fragment of the population, and the subsequent migration and reproduction. Finally, both bar-tailed and black-tailed godwits exhibited differences in the feeding areas prospected between day and night. Generally, in both godwits species, these differences highlighted a preferential nocturnal use of specific areas particularly concerned by human activities (hunting, shellfish farming or recreational walking). Hence, the night distribution of birds, still rarely evaluated, should be greatly considered to identify key areas and habitats in the definition of management measures. More generally, beyond the bar-tailed and black-tailed godwits, our results show that even in species that seem very similar, there may be marked differences that conservation measures must take into account. Therefore, more broadly multi-specific studies are needed for the conservation of the biodiversity, to not draw hasty or general conclusions from one or a few species.

Contributions, limits and perspectives

Finally, in view of the previous studies on shorebirds, which already explored the use of space and habitats, this thesis work constitute a new approach on very fine spatial and temporal scales. The monitoring of both bar-tailed and black-tailed godwits during the wintering period, and with a high number of positions recorded each day per bird over several months, is new for such species to which the GPS technology has recently adapted. Bird location data recorded with a fine time step (30 min.), and the high-precision mapping of habitats produced from complementary surveys (benthic macrofauna, sediment granulometry and habitat facies), allowed us to perform a fine-scale habitat selection analysis. Such accuracy of data, enabled by the biologging, allowed us to highlight the importance of nycthemeral cycles and nocturnal ecology in conservation approaches of godwits, but also in general. However, there are limits in our study that should be considered for future researches. As main objective, this monitoring program based on a biologging approach firstly aimed to compare habitat selection in bar-tailed and black-tailed godwits during their overlap on common wintering sites of the Pertuis Charentais. Although individuals of the two species were equipped on the same sites, the sample size and the quality of data collected for some individuals did not allow us to conduct direct comparisons in same site and for the two species. This present study is therefore based on individuals of the two species, but surveyed over different temporal periods as well distinct sites, although strongly connected. Future approaches are needed, focusing on individuals of bar-tailed and black-tailed godwits monitored over the same sites and temporal periods, to limit seasonal and site-specifics bias, and more robustly compare the two species in term of habitat use. In general, the capture and equipment of a larger number of birds would better describe the space and habitat use at the population scale. However, the limited number of individuals equipped also reflects the difficulties for capturing black-tailed godwits, and even more bar-tailed godwits. In addition, in order to more precisely explore the sex-specific distribution and habitat preferences in both species, including different stages, further studies should be conducted when lighter GPS loggers (adapted for males and juveniles) will be able to record the positions with a fine time step and over several winter months. Such increased and diversified bird samples are crucial to have a comprehensive understanding of wintering strategies, including to further investigate bird associations in black-tailed godwits and factors causing an individual to leave a group to prospect new feeding areas. Beyond improvements in bird survey, monitoring of environmental factors should also be improved. For instance, to precisely estimate the impact of human activities (hunting pressure, recreational walkers, shellfish farmers, spotlight intensity along the coast, etc.) on the spatio-temporal use of habitats by godwits, and their ability to meet their energy needs, it appears important to quantify them more precisely.

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Sélection des habitats chez deux espèces d'oiseaux limicoles très appariés hivernants sur la côte Atlantique Française

Résumé :

La barge rousse (*Limosa lapponica*) et la barge à queue noire (*Limosa limosa*) sont deux espèces d'oiseaux limicoles migrateurs, hivernants sur la côte Atlantique Française et se reproduisant dans des régions plus au Nord. Ces deux espèces partagent une grande proximité phylogénétique, et de grande similarités morphologiques héritées d'un ancêtre commun dont elles ont récemment divergé. Chez de telles espèces dites « jumelles », bien que l'on observe généralement des réponses identiques face aux même conditions environnementales, l'existence de propriétés de niche uniques et de besoins écologiques spécifiques a déjà été décrite. C'est le cas chez la barge rousse et la barge à queue noire qui partagent les mêmes zones d'hivernage, mais qui ont une distribution distincte pendant la saison estivale, respectivement dans le Nord de l'Eurasie et l'Alaska, et depuis l'Islande jusqu'à l'Est de la Sibérie. En France, on observe principalement la sous-espèce *L. lapponica lapponica* de barge rousse, et la sous-espèce *L. limosa islandica* de barge à queue noire, toutes deux présentes pendant toute la période d'hivernage (Août-Avril). Les sous-espèces *L. l. taymyrensis* et *L. l. limosa* ne sont, elles, présentes que pendant les périodes de migrations (Février-Mars et Août-Octobre). En hiver, *L. l. lapponica* et *L. l. islandica* utilisent principalement les écosystèmes de vasières dont elles dépendent pour leur alimentation, ainsi que les marais maritimes et littoraux pour leurs périodes de repos. Ainsi, dans les Pertuis Charentais, elles fréquentent les mêmes sites d'hivernage et utilisent les mêmes zones fonctionnelles, mais ont des préférences alimentaires bien distinctes avec un régime principalement composé de vers marins pour la barge rousse, et de bivalves *(e.g. Macoma balthica)* et rhizomes de zostères (*Zostera noltei*) pour la barge à queue noire. Au-delà de ces connaissances, ce travail de thèse vise à décrire et comparer les stratégies de survie hivernale de ces deux espèces et notamment leur utilisation spatio-temporelle des habitats. La miniaturisation récente des balises GPS a permis d'équiper des individus de ces deux espèces afin de suivre leur mouvements journaliers et saisonniers. Une telle approche peut significativement améliorer nos connaissances sur la biologie de ces oiseaux, leur dépendance aux habitats côtiers et leur lien avec les aires protégées. Plus précisément, on cherche à explorer la sélection des ressources (proies et habitats) des deux espèces de barges, en relation avec l'utilisation des rares reposoirs principalement localisés dans les réserves naturelles. L'identification des zones d'alimentation précises des oiseaux, grâce aux données de position GPS, permet d'échantillonner les proies potentielles de macrofaune benthique afin d'estimer la qualité énergétique des patchs d'alimentation et de décrire les habitats disponibles. Par ailleurs, l'analyse de l'activité des oiseaux à fine échelle spatio-temporelle permet d'explorer leur adaptation au rythme Jour/Nuit, croisé avec l'utilisation de zones protégées et non-protégées. Enfin, puisque ces oiseaux présentent un fort dimorphisme sexuel, il apparait intéressant d'explorer l'existence d'une ségrégation sexuelle en terme de stratégie de survie hivernale. Plus généralement, il est possible d'explorer les différences entre individus ou encore leurs interactions pendant l'alimentation, afin de tester l'association étroite d'individus chez une espèce grégaire comme la barge à queue noire. Ce travail apporte ainsi de nouvelles connaissances clés sur les stratégies de survie hivernales de la barge rousse et de la barge à queue noire, et plus spécifiquement sur leur utilisation, dans l'espace et dans le temps, des différents habitats. Les résultats obtenus soulignent que des différences intra-spécifiques mais aussi interspécifiques existent chez ces deux espèces d'apparences très similaires, dont devraient tenir compte les futures mesures de gestion et de conservation.

Mots clés : Oiseaux limicoles, Vasière intertidales, Stratégie hivernale, Sélection d'habitats, Télémétrie GPS

Selection of habitats by two closely-related shorebird species wintering on the French Atlantic coast

Summary:

The bar-tailed godwit (*Limosa lapponica*) and the black-tailed godwit (*Limosa limosa*) are two migratory shorebird species that spend the winter on the French Atlantic coast, before to reach regions further north for breeding. These two species share great phylogenetic proximity, and great morphological similarities inherited from a common ancestor from which they recently diverged. In such “closely-related” species, although identical responses are generally observed facing the same environmental conditions, the existence of unique niche properties and specific ecological needs have already been described. It is the case in bar-tailed and black-tailed godwits, which share the same wintering areas, but have a distinct reproduction distribution, breeding respectively in northern Eurasia and Alaska, and from Iceland to eastern Siberia. In France, we mainly observe the subspecies *L. lapponica lapponica* for bar-tailed godwit, and the subspecies *L. limosa islandica* for black-tailed godwit, which are present throughout the wintering period (August-April). The subspecies *L. lapponica taymyrensis* and *L. limosa limosa* are only present during the migration periods (February-March and August-October). In winter, *L. l. lapponica* and *L. l. islandica* mainly use mudflat ecosystems, on which they depend for feeding, as well as marine and coastal marshes, for roosting. Thus, in the Pertuis Charentais (France), they use the same wintering sites and the same functional areas, but exhibit distinct food preferences with a diet dominated by polychaetes worms for the bar-tailed godwit, and bivalves (eg *Macoma balthica*) and seagrass rhizomes (Zostera noltei) for the black-tailed godwit. Beyond this knowledge, this thesis aims to describe and compare the winter survival strategies of these two species, and especially their spatio-temporal use of habitats. The recent miniaturization of GPS tracking loggers has enabled us to equip individuals of both species to access to their daily and seasonal movements. Such an approach can significantly help to improve our knowledge on the biology of these birds, their dependence on coastal habitats and their link with protected areas / nature reserves. More specifically, we aim to explore the resources selection (prey and habitats) of the two godwit species, in relation to the use of rare roost sites mainly located in nature reserves. Precisely identify birds feeding areas, using GPS position data, allows sampling of potential benthic macrofauna prey, in order to estimate the energy quality of feeding patches and to describe available habitats. In addition, the analysis of bird’s activity on a fine spatial and temporal scale also allows exploring their adaptation to the nycthemeral periodicities, crossed with the use of protected and unprotected areas. Finally, since these birds exhibit a strong sexual dimorphism, it appears interesting to explore the existence of sexual segregation in terms of winter survival strategy. More generally, it is possible to investigate the differences between individuals, or their interactions during feeding in order to test affinities between birds in a gregarious species such as the black-tailed godwit. This work thus provides new key knowledge on the wintering survival strategies of the bar-tailed and the black-tailed godwits, and particularly on their use, in space and time, of different habitats. The results obtained underline both intraspecific and interspecific differences may exist in these two very similar species, which should be considered in future management and conservation measures.

Keywords : Shorebirds, Intertidal mudflats, Wintering strategy, Habitat selection, GPS tracking

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