Variability in day and night feeding habitat use in the Willet *Catoptrophorus semipalmatus* during the non-breeding season in northeastern Venezuela

Ghislain Rompré & Raymond McNeil

Rompré, G. & McNeil, R. 1996. Variability in day and night feeding habitat use in the Willet *Catoptrophorus semipalmatus* during the non-breeding season in northeastern Venezuela. *Wader Study Group Bull.* 81: 82-87.

This study, conducted in a coastal lagoon complex located in northeastern Venezuela, was carried out to determine whether feeding habitat use by Willets *Catoptrophorus semipalmatus* in tropical environment varied between day-time and night-time. Birds were colour-marked and radio-tagged. We registered their foraging position in six different micro-habitats, characterized by soft or liquid mud, muddy sand, and harder sand-mud substrata. Habitat use in Willets differed between day-time and night-time and varied with the presence and absence of moonlight, depending on the behavioural status (territorial or non-territorial) of individuals, their foraging strategy (visual or tactile), and types and abundance of available prey. Territorial Willets were visual foragers when feeding on fiddler crabs (*Uca cumulanta*) on sand-mud substrata, both by day and on moonlit nights. Territorial Willets, on moonless nights, and non-territorial ones, during all light conditions, foraged tactilely on soft or liquid mud habitats.

G. Rompré & R. McNeil, Département de sciences biologiques, Université de Montréal, C.P. 6128, Succ. "Centre-ville", Montréal, Québec, Canada H3C 3J7.

INTRODUCTION

Many shorebird species are known to forage both by day and by night during the non-breeding season and the benefits arising from night feeding vary depending on species and conditions (for a review, see McNeil 1991; McNeil *et al.* 1992). Shorebirds use two main foraging strategies, visual or tactile. Some species may specialize in only one technique both by day and by night: *e.g.* visual searching in Grey Plover *Pluvialis squatarola*, Semi-palmated *Charadrius semipalmatus* and Wilson's *C. wilsonia* plovers, and tactile probing in long-billed species such as the Short-billed Dowitcher *Limnodromus griseus* (see McNeil & Robert 1988; Robert & McNeil 1989; McNeil *et al.* 1992). However, other species use both techniques, being visual feeders in some conditions and tactile in others. For example, *Tringa* species feed by sight during daylight, and switch to tactile feeding at night (Goss-Custard 1970; McNeil & Robert 1988; Robert & McNeil 1989).

The abundance of prey for shorebirds usually varies between sites and habitats (see Mercier & McNeil 1994). In addition, direct observation on organisms like fishes, isopods, amphipods, *Penaeus* shrimps, corixids and polychaetes confirm that they may be more abundant and closer to the substratum surface at night than during day-time (see Robert & McNeil 1989; McNeil *et al.* 1992, 1995; Díaz D. 1993). It might be expected that shorebirds that detect such prey by touch and those which can switch to tactile foraging when visual detection of prey is impaired would be able to feed as fast in darkness as they do during daylight, whereas birds that detect prey by sight would feed more slowly (McNeil *et al.* 1992). In such conditions, it may even be advantageous for shorebirds to feed at night at sites and on prey that are not used during the day (Goss-Custard 1969; Evans & Dugan 1984; Townshend *et al.* 1984; Robert & McNeil 1989; Robert *et al.* 1989). Though not tested, it is possible that some shorebirds, when visual detection of prey is impaired, feed at night on sites where tactile feeding on swimming insects, crustacea and fishes during darkness is easier (chances of contact with prey are higher because prey are bigger, more abundant, and/or more active). The use of different day and night prey and feeding habitats was reported for Grey Plovers (Dugan 1981; Wood 1986) and might be an obligatory requirement for the survival of overwintering shorebirds in some regions.

Many shorebird species are known to defend day-time feeding territories on the winter range in the tropics (*e.g.* Myers *et al.* 1979a, 1979b; Mallory 1982; Zwarts 1990). In coastal lagoons of northern Venezuela, some Willets *Catoptrophorus semipalmatus* and Whimbrels *Numenius phaeopus* defend feeding territories on which they forage by sight on fiddler crabs (*Uca* sp.) while others like Black-necked Stilts *Himantopus mexicanus*, in shallow-water muddy areas, are gregarious foragers (Rompré 1993; McNeil & Rompré 1995). Grey Plovers in Europe and South Africa (Townshend *et al.* 1984; Wood 1986; Turpie & Hockey 1993), Eurasian Curlew *Numenius arquata* in Europe (Cramp & Simmons 1983), and Willets and Whimbrels in Venezuela (Rompré 1993; McNeil & Rompré 1995) also use their day-time feeding territory at night.

The purpose of the present study was to determine whether habitat use by Willets in a tropical environment was influenced by temporal factors (day and night, presence or absence of moonlight), and varied with avian

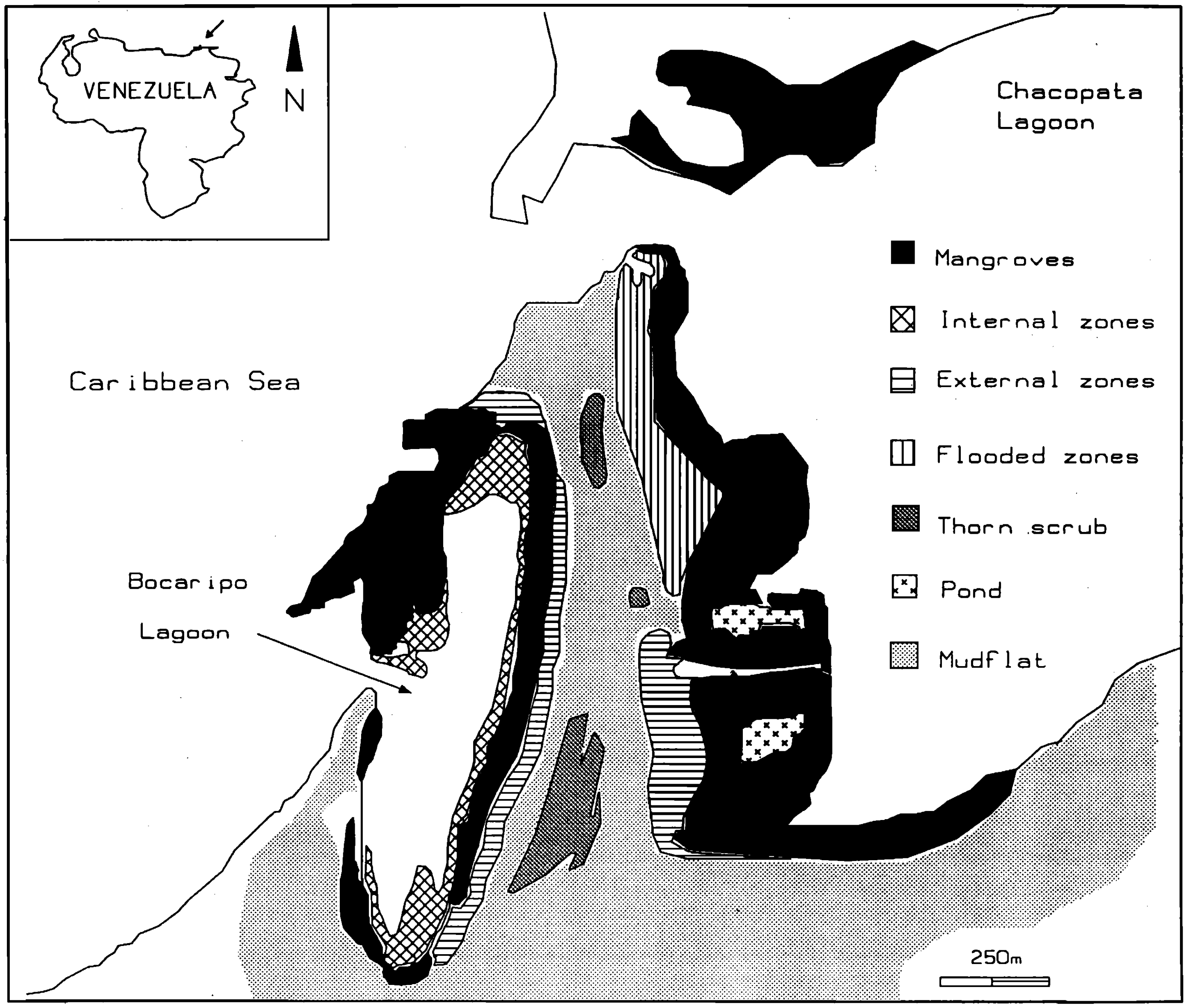

Figure 1. Study area in the Chacopata Lagoon complex in coastal Venezuela.

foraging strategies (visual or tactile), and types and abundance of available prey.

STUDY AREA AND METHODS

The study was carried out in the Chacopata lagoon complex (10°40'N; 63°46'W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela (Figure 1). The complex extends over 830 ha and comprises the Chacopata lagoon and the Bocaripo lagoon, surrounded by mangroves and mudflats. During the period of spring tide flooding, from September to the end of January, the wide mudflats, including the favourite foraging habitats of Willets, are submerged daily, but more frequently during day-time than night-time. Outside the flooding period (especially during February-March), large expanses of mudflats dry out almost completely.

Data were collected in a 2 km^2 area, comprising the Bocaripo lagoon and, to the east, the adjacent part of the Chacopata lagoon (Figure 1). A narrow mangrove fringe divides the eastern shore of Bocaripo lagoon. In the study area, shorebirds used six different micro-habitats as feeding or roosting sites:

(1) internal zones, generally exposed at low tide, except during the period of high waters;

(2) external zones with high level substrata, where there is a high density of fiddler crabs *Uca cumulanta* living in burrows (this area is flooded at times of full moon spring high tides);

Table 1. Contingency analysis of temporal factors influencing the use of feeding habitats by Willets.

Individual birds	Date of capture	Behaviour	Micro-habitat zones	d.f. (χ^2)	Day-time	Night-time	
						Moonless	Moonlit
Willet 46A	23 Dec. 1991	Territorial	Internal	4(15.63)***[a]	2(0.20)*[b]	3(0.30)*	5(0.50)
			External		18(0.56)	0(0.00)*	14(0.44)
			Mangroves		6(0.86)*	1(0.14)	0(0.00)*
Willet 46B	21 March 1992	Non-territorial	Internal	4(22.08)***	17(0.71)	5(0.21)*	2(0.08)*
			Flooded		13(0.72)	0(0.00)*	5(0.28)
			Mangroves		0(0.00)*	0(0.00)	5(1.00)*
Willet 47	17 Jan. 1992	Territorial	Internal	6(14.07)**	0(0.29)*	3(0.21)*	7(0.50)
			External		18(0.47)	3(0.08)	17(0.45)
			Flooded		10(1.00)	0(0.00)	0(0.00)*
			Mangroves		3(0.50)	1(0.17)	2(0.33)
Willet 48	31 Jan. 1992	Non-territorial	Internal	6(8.32)	48(0.70)	13(0.19)	8(0.11)
			External		2(1.00)	0(0.00)	0(0.00)
			Flooded		20(0.57)	13(0.37)*	2(0.06)
			Mangroves		5(1.00)	0(0.00)*	0(0.00)
Willet 53	3 March 1992	Non-territorial	Internal	6(8.74)	15(0.48)	9(0.29)	7(0.23)
			Flooded		26(0.54)	13(0.27)	9(0.19)
			Mangroves		1(1.00)	0(0.00)	0(0.00)
			Mudflat		0(0.00)	2(1.00)*	0(0.00)
Willet 56	21 March 1992	Non-territorial	Internal	8(19.47)***	0(0.00)	1(1.00)*	0(0.00)
			External		2(0.22)*	0(0.00)*	7(0.78)*
			Flooded		14(0.61)	2(0.09)	7(0.30)
			Mangroves		8(0.61)	4(0.31)*	1(0.08)*
			Ponds		11(0.48)	4(0.17)	8(0.35)

*Observed frequencies are different than expected.

[a] Observed frequencies are significantly higher (** $P < 0.005$; *** $P < 0.001$) than expected (based on the null hypothesis of independence).

[b] Number (and percentage) of times the behaviour was observed. The summation of percentage values on each line equals 1.

(3) mudflats flooded only during the highest tides, and thus generally dry, except after rains;

(4) the flooded zone, *i.e.* a shallow-water area strewn with sparse, dead, mangroves that remains flooded after higher tides;

(5) mangrove woodlands; and

(6) small ponds surrounded by mangroves.

All areas, except external zones (muddy sand substrata) and mudflats (harder sand-mud substrata) were covered with soft or liquid mud substrata. The flooded area and mangrove woodlands were only slightly affected by tidal fluctuations and often dried out completely during March, *i.e.* during the dry season and the period of low waters. Ponds were affected by tides but dried out during the period of low waters.

From the end of December 1991 to the end of April 1992, 15 Willets were mist-netted and marked individually with a numbered metal band, coloured plastic rings, and a radio-transmitter. A few of these Willets had been colour-marked by Francine Mercier several months before being radio-tagged. Radio-transmitters (RI-2BA, Holohil Systems Ltd, Woodlawn, Ontario), weighing 5.3 g, were glued to the back of birds using cyanoacrylate (Krazy Glue, Borden Company Ltd, Willowdale, Ontario) (Perry *et al.* 1981). The transmitter mass represented roughly 2.4% of the Willets' mass. Transmitters had a potential field life of at least 30 days (two were still transmitting after 40 days), and their range exceeded 3 km in optimal conditions, when using portable receivers (TRS-1000S, Wildlife Materials Inc., Carbondale, Illinois) and three-element, miniature, folding antennas. Willet-46 was captured twice and radio-tagged with two different transmitters (Table 1). Radio-tracking started at least two days after attachment of transmitters. Once or twice a week, on an hourly basis during 12-h nocturnal and diurnal periods, we registered the position of radio-tagged birds by triangulation (see Heezen & Tester 1967). Transmitters emitted two different built-in signals; one when the bird was standing upright, as when resting, the other when the bird had its head down during foraging. Therefore, in addition to locating the bird's position, it was possible to determine whether a bird was resting or feeding. We noted the stage of the moon (moonless, quarter, half, or full moon). Tide fluctuations were also noted, on a scale varying between -3 to +2, qualifying the water line at the mangrove level with the value of 0.

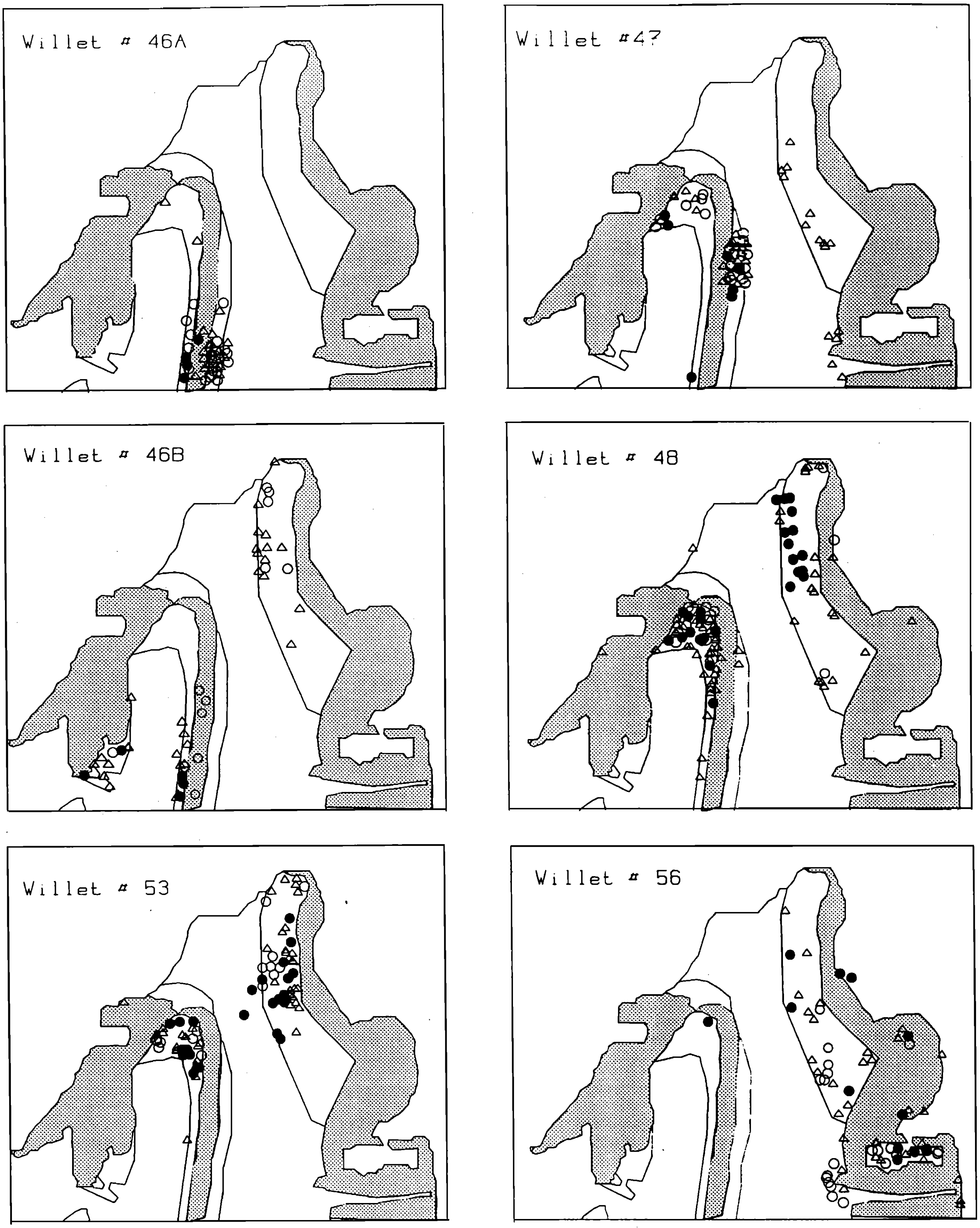

Figure 2. Feeding habitat utilization by five Willets in the Chacopata Lagoon complex during day-time and on moonlit and moonless nights. For more details concerning micro-habitats, see Figure 1. Open triangles represent diurnal observations; open circles, moonlit observations; closed circles, moonless observations.

For the present study, we retained the data of only five Willets. Data for other birds were rejected because either too few observations were obtained, or because transmitters fell off. The behaviour of colour-marked birds that were observed before and after being radio-tagged did not change after the transmitter attachment. Depending on whether or not the birds behave all the time as territorial (based on alert posture, ritualised walk along boundaries, calling, chasing of intruders) or only during part of the observation periods, they were considered as generally territorial, sporadically territorial, or non-territorial (for a detailed description of territorial behaviour in Willets, see Rompré 1993; McNeil & Rompré 1995).

Contingency analysis was used to examine the relationship between the frequencies of different habitat uses as a function of temporal variables (day-time, night-time, moonlit and moonless) (see Legendre & Legendre 1984).

RESULTS

The behavioural status of Willet-46 changed with time (Table 1). It was territorial for three weeks after its first capture in December 1991 but was thereafter only rarely observed on its territory. In March 1992, after being recaptured and equipped with a second transmitter, it was non-territorial. As a consequence, data for both periods are dealt with separately (46A and 46B, Table 1 and Figure 2). Willet 47 used its territory sporadically. Willets (46A and 47) were territorial only until the end of January, when the period of high waters ended and the substrata of their territories dried out.

According to the contingency analysis (Table 1), three Willets (46A, 47 and 56) were influenced by temporal factors (day-time, moonless or moonlit nights) in using foraging habitats. Indeed, territorial Willets (46A and 47) foraged mainly on the muddy sand substrata of external zones both during day-time and during moonlit nights. During moonless nights, they rarely foraged in comparison to daylight and moonlit nights but, when feeding, they foraged almost exclusively outside the external zone where they had their territory (Figure 2). In comparison, during day-time and night-time, when non-territorial, Willet 46 avoided external zones totally and used the internal and flooded areas almost exclusively (see 46B in Table 1 and Figure 2). This individual foraged in mangroves only on moonlit nights. Willet 56 was non-territorial and, during daylight, mainly used the flooded zone and mangrove ponds. In addition, this bird foraged mainly in mangroves and mangrove ponds during moonless nights, and in open habitats (flooded and external zones, mangrove ponds) on moonlit nights (Figure 2). All habitats, except external zones, were more highly used by marked Willets during day-time than at night. At night, all habitats, except mangroves, were more highly used in presence of moonlight.

Finally neither of the two other non-territorial Willets (48 and 53) was significantly influenced by temporal factors. Willet 48 foraged, both by day and by night, almost exclusively in internal (mainly) and flooded zones (Table 1, Figure 2). Willet 53 behaved about the same, except that it used the flooded zone (Figure 2).

DISCUSSION

It is important to recall that this study is based only on five individuals, in which much variability was observed. As a consequence, we need to be careful about extending our results to all Willets.

The absence or end of territoriality in Willets during the low-water period, well illustrated by Willet 46 which was territorial (46A) during the period of high waters and was non-territorial (46B) during the low water period, can be explained by the fact that, during that period, in particular in February and March, large stretches of the Chacopata Lagoon mudflats dry out almost completely. This was the case for the sand-mud substrata of external zones from where fiddler crabs moved to mangrove areas and internal zones.

Studies conducted in the Chacopata Lagoon complex have shown that the abundance of swimming prey (*e.g.* fishes, crustaceans, insects) and that of organisms living at the surface of substrata (insects, polychaetes, isopods, *etc.*) are between 3 and 30 times higher at night than during day-time (McNeil *et al.* 1995). This is the case, in particular, for the soft mud substrata of internal and flooded zones, as well as for mangrove ponds (Robert & McNeil 1989; Díaz D. 1993; McNeil *et al.* 1995). As far as it concerns fiddler crabs, they are more active during the day than at night on the sand-mud substrata of external zones, although they continue to be active in good numbers until past 21:00 (Thibault 1993; Díaz D. 1993; Thibault & McNeil 1995; McNeil *et al.* 1995). According to Zwarts & Dirksen (1990), fiddler crabs such as *Uca tangeri* are sometimes easy to catch at night. Willets are visual feeders, both during night-time and day-time, when catching fiddler crabs on muddy sand substrata but, on soft mud areas, their foraging strategy is different (McNeil & Rodríguez 1990; McNeil *et al.* 1992; R. McNeil, pers. observ.). Although they occasionally forage by sight, most of the time they feed by probing, and sometimes ploughing, through the soft sediments or liquid mud.

Willets in Chacopata Lagoon are both territorial and non-territorial, depending on the state of the tides and time of the year (Rompré 1993; McNeil & Rompré 1995). Territorial Willets foraged on the sand-mud external substrata on moonlit nights, while non-territorial gregarious individuals foraged tactilely in the soft mud or liquid mud internal and flooded zones, as much during moonless as during moonlit nights (Rompré 1993; McNeil & Rompré 1995). Willets 46A and 47, when territorial, were restricted almost exclusively to external zones both during daylight and moonlit nights, where they foraged by sight on fiddler crabs. Willets sometimes left their territory to forage gregariously with non-territorial individuals, in the flooded and internal zones, particularly on moonless nights, when tactile foraging was likely to be more profitable than sight feeding because prey availability or activity is higher at night than during daylight. Habitat use by non-territorial Willets was not influenced by temporal factors (day/night, presence or absence of moonlight).

In conclusion, this study shows that habitat use by Willets in the Chacopata Lagoon complex varies with day and night, but depends on individuals, their behavioural status (gregarious or territorial), their foraging strategy and food regime and, by night, on the presence or absence of moonlight, and types and abundance of available prey.

ACKNOWLEDGEMENTS

This study was financed by the Natural Sciences and Engineering Research Council of Canada, the University of Montréal and Universidad de Oriente through the collaboration agreement between that university and Université de Montréal. We thank Michel Thibault for assistance during the field work. We are also indebted to colleagues of the Universidad de Oriente, in particular to José Ramón Rodríguez S. and Marcos Tulio Díaz.

REFERENCES

Cramp, S. & Simmons, K.E.L. 1983. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palearctic.* Vol. 3. Oxford University Press, Oxford.

Díaz D., O.F. 1993. *Comparación de la Disponibilidad Diurna y Nocturna de Presas para aves Limícolas en el Complejo Lagunar de Chacopata, Edo Sucre.* Tesis de licenciatura, Universidad de Oriente, Cumaná, Venezuela.

Dugan, P.J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. Pp. 251-260. *In: Feeding and Survival Strategies of Estuarine Organisms.* Ed. by N V. Jones & W.J. Wolff. Plenum Press, New York, N.Y.

Evans, P.R. & Dugan, P.J. 1984. Coastal birds: numbers in relation to food resources. Pp. 8-28. *In: Coastal waders and wildfowl in winter.* Ed. by P.R. Evans, J.D. Goss-Custard & W.G. Hale. Cambridge University Press, Cambridge, U.K.

Goss-Custard, J.D. 1969. The winter feeding ecology of the Redshank *Tringa totanus. Ibis* 111: 338-356.

Goss-Custard, J.D. 1970. Feeding dispersion in some overwintering wading birds. Pp. 3-35. *In: Social behaviour in birds and mammals.* Ed. by J.H. Crook. Academic Press, New York, N.Y.

Heezen, K.L. & Tester, J.R. 1967. Evaluation of radio tracking by triangulation with special reference to deer movements. *J. Wildl. Manage.* 31: 124-141.

Legendre, L. & Legendre, P. 1984. *Ecologie Numérique. Tome 1: Le Traitement Multiple des Données Écologiques.* Masson, Paris.

Mallory, E.P. 1982. Territoriality of Whimbrels *Numenius phaeopus* wintering in Panama. *Wader Study Group Bull.* 34: 37-39.

McNeil, R. 1991. Nocturnality in shorebirds. *Acta Congr. Int. Ornithol.* 20: 1098-1104.

McNeil, R. & Robert, M. 1988. Nocturnal feeding strategies of some shorebird species in a tropical environment. *Acta Congr. Int. Ornithol.* 19: 2328-2336.

McNeil, R. & Rodríguez, J.R. 1990. When does the Willet "plough" the water to catch fish? *Wader Study Group Bull.* 58: 50-51.

McNeil, R., & Rompré, G. 1995. Day and night feeding territoriality in Willets *Catoptrophorus semipalmatus* and Whimbrel *Numenius phaeopus* during the non-breeding season in the tropics. *Ibis* 137: 169-176.

McNeil, R., Díaz D., Liñero A., & Rodríguez S. 1995. Day- and night-time prey availability for waterbirds in a tropical lagoon. *Can. J. Zool.* 73: 869-878.

McNeil, R., Drapeau, P. & Goss-Custard, J.D. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biol. Rev.* 67: 381-419.

Mercier, F. & McNeil, R. 1994. Seasonal variations in intertidal density of invertebrate prey in a tropical lagoon and effects of shorebird predation. *Can. J. Zool.* 72: 1755-1763.

Myers, J. P., Connors, P.G. & Pitelka, F.A. 1979a. Territoriality in non-breeding shorebirds. *Stud. Avian Biol.* 2: 231-245.

Myers, J. P., Connors, P.G. & Pitelka, F.A. 1979b. Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk* 96: 551-561.

Perry, M. C., Haas, C.H. & Carpenter, J.W. 1981. Radio transmitters for Mourning Doves: a comparison of attachment techniques. *J. Wildl. Manage.* 45: 524-527.

Robert, M. & McNeil, R. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* 131: 69-79.

Robert, M., McNeil, R. & Leduc, A. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. *Auk* 106: 94-101.

Rompré, G. 1993. Étude du Comportement Diurne et Nocturne du Chevalier Semipalmé (*Catoptrophorus semipalmatus*) et autres Limicoles dans le Nord-Est du Venezuela. Mémoire de maîtrise, Université de Montréal, Montréal, Québec.

Thibault, M. 1993. Etude du Comportement Diurne et Nocturne du Pluvier de Wilson (*Charadrius wilsonia*) dans le Nord-Est du Venezuela. Mémoire de maîtrise, Université de Montréal, Montréal, Québec.

Thibault, M. & McNeil, R. 1995. Predator-prey relationship between Wilson's Plovers and fiddler crabs in northeastern Venezuela. *Wilson Bull.* 107: 73-80.

Townshend, D.J., Dugan, P.J. & Pienkowski, M.W. 1984. The unsociable plover-use of intertidal areas by Grey Plovers. Pp. 140-159. *In: Coastal waders and wildfowl in winter.* Ed. by P.R. Evans, J.D. Goss-Custard & J.D. Hale. Cambridge University Press, Cambridge, U.K.

Turpie, J.K. & Hockey, P.A.R. 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus* in South Africa. *Ibis* 135: 156-165.

Wood, A.G. 1986. Diurnal and nocturnal territoriality in the Grey Plover at Teesmouth, as revealed by radio telemetry. *J. Field Ornithol.* 57: 213-221.

Zwarts, L. 1990. Increased prey availability drives premigration hyperphagia in Whimbrels and allows them to leave the Banc d'Arguin, Mauritania, in time. *Ardea* 78: 279-300.

Zwarts, L. & Dirksen, S. 1990. Digestive bottleneck limits the increase in food intake of Whimbrels preparing for spring migration from the Banc d'Arguin, Mauritania. *Ardea* 78: 257-278.