Wilson Bull., 106(2), 1994, pp. 299–310

DAY/NIGHT VARIATION IN HABITAT USE BY WILSON'S PLOVERS IN NORTHEASTERN VENEZUELA

MICHEL THIBAULT AND RAYMOND MCNEIL

ABSTRACT.—We quantify the temporal variation in day and night habitat use by Wilson's Plovers (*Charadrius wilsonia cinnamominus*) in the Chacopata lagoon complex, in northeastern Venezuela, during the non-breeding season. The overall (day + night) time spent by plovers on foraging habitats did not vary seasonally. However, the duration of their presence on foraging sites during daylight was very short from November to January, but was compensated by an increase during nighttime. The day and night distribution of plovers over the lagoon complex differed substantially. Wilson's Plovers were gregarious and roosted most of the time during daylight. After dusk, they left their diurnal roosts and repositioned themselves solitarily throughout the lagoon mudflats, or flew to their nocturnal individual roosts close to mangroves. They foraged during low tides, but never during the entire low-tide periods, neither during daytime nor during nighttime. The plovers spent more time on foraging sites during the first part of the night than thereafter, and on moonlit nights, although they often occurred on feeding habitats during moonless nights. This appears to be correlated with the observation that *Uca cumulanta,* their main prey, is active during this portion of the night and on moonlit nights. The main reason why Wilson's Plovers are largely nocturnal appears to be the avoidance of diurnal predators. *Received 14 May 1993, accepted 10 Sept. 1993.*

Morrier and McNeil (1991) documented seasonal variation in daily activity of a permanent resident race of the Wilson's Plovers (*Charadrius wilsonia cinnamominus*) which breeds on the coast of northern South America, including the coastal lagoons of Venezuela (Hayman et al. 1986, McNeil et al. 1990). Assuming that Wilson's Plovers were resting from dusk to dawn, daylight feeding alone seemed insufficient from November to March to counterbalance energy expenditure, suggesting that Wilson's Plovers foraged substantially during nighttime (Morrier and McNeil 1991).

In many colonial waterbirds and various waterfowl species, including shorebirds, foraging may take place partly or entirely at night (see McNeil 1991; McNeil et al. 1992, 1993). In shorebirds, most studies concern the temperate zone. Although data are scarce, there are indications that nocturnal foraging also occurs in tropical environments (see McNeil 1991, McNeil et al. 1992). There are two main hypotheses to explain why shorebirds forage at night: (1) the "supplementary hypothesis" which postulates that night feeding occurs when daytime feeding has been inadequate

Dépt. de sciences biologiques, Univ. de Montréal, C.P. 6128, Succ. centre-ville, Montréal (Québec), Canada H3C 3J7.

to meet the birds' energy requirements, and (2) the "preference hypothesis" which postulates that the birds prefer to feed at night because it provides the most profitable, or the safest, feeding opportunities (see review by McNeil 1991, McNeil et al. 1992).

The need for nocturnal foraging presumably varies seasonally with the seasonal variation of energetic requirements for molting and pre-migratory or pre-reproductive fattening. The only available data for tropical areas were provided for migratory species in southern Portugal (Batty 1991) and Mauritania (Zwarts et al. 1990). In addition, it is unknown whether shorebirds forage throughout the night, during the entire duration of the low-tide period, or during part of each? The only available data so far were provided by Zwarts (1990) for Mauritania. Some predominantly visual feeders such as plovers take advantage of moonlight to feed at night (see McNeil 1991, McNeil et al. 1992). However, there are indications that some plover species use sight as the major method for prey detection, even on dark nights (McNeil 1991, McNeil et al. 1992, Turpie and Hockey 1993), and have comparable feeding success (Turpie and Hockey 1993), while other species of plovers and other daylight sight feeders switch to tactile feeding or stop foraging when light intensity is very low and the visual detection of prey is impaired (McNeil and Robert 1988, 1992; Robert and McNeil 1989; McNeil et al. 1992).

In this paper, we quantify the seasonal variation during the non-breeding season in diurnal and nocturnal habitat use by Wilson's Plovers that reside and breed in northeastern Venezuela. We also examine the hourly variation in the time they spend on nocturnal foraging areas. Finally, we discuss the effects of moonlight and tidal cycle on the plovers' use of nocturnal foraging habitats.

STUDY AREA AND METHODS

We conducted this study from October 1991 to March 1992 in the Chacopata lagoon complex (10°41′N, 63°46′W) on the north side of the Araya Peninsula, State of Sucre, in northeastern Venezuela (Fig. 1). Most observations took place in a 2 km^2 area surrounding the Bocaripo lagoon (Fig. 1). We mist-netted plovers monthly at four sites on the Bocaripo study area (Fig. 1). Radio transmitters (BD-2G, Holohil Systems Ltd, Woodlawn, Ontario), weighing 2.8 g and having an individual frequency, were glued to the back of 15 birds, using cyanoacrylate Krazy Glue (Borden Company Ltd, Willowdale, Ontario) according to the method used by Perry et al. (1981). Transmitter mass represented roughly 5% of the birds mass (54.4 g; Morrier 1990). Transmitters had a potential field life of at least 50 days, and their minimal detection range exceeded 2 km in optimal conditions, with the use of portable receivers (TRX-1000S, Wildlife Materials Inc., Carbondale, Illinois) and three element miniature folding antennas. We concentrated on locating daytime roosts within the main study area of the Bocaripo lagoon, but also located daytime roosts elsewhere in the Chacopata lagoon complex (Fig. 1).

Each month, on an hourly basis, we registered the position of radio-tagged plovers by

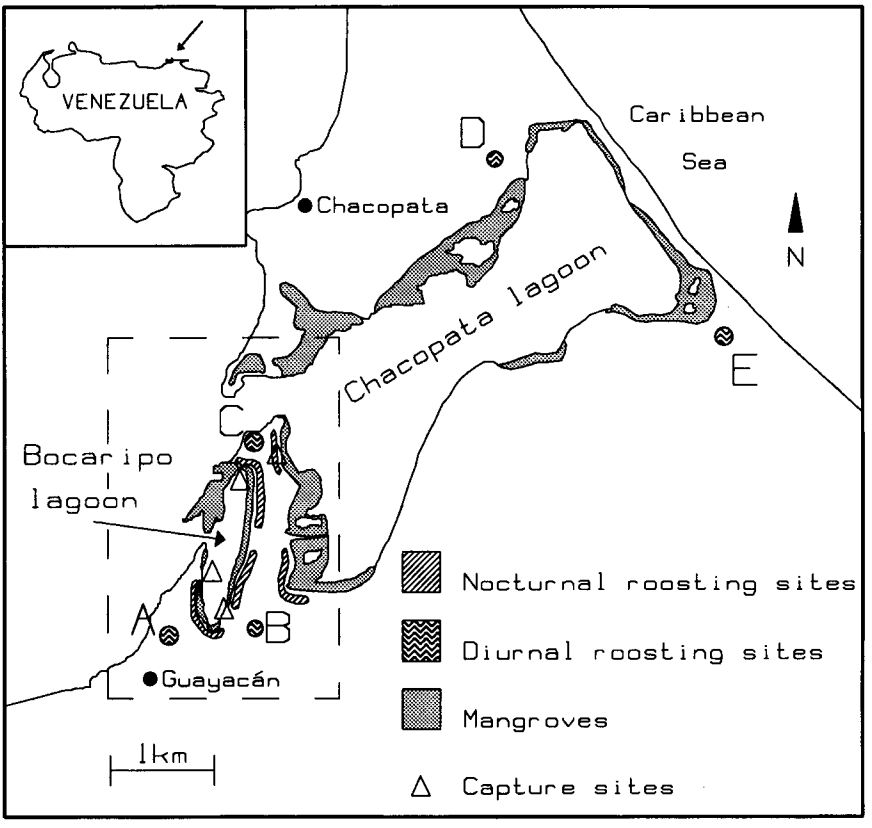

FIG 1. Map of the Chacopata lagoon complex in northeastern Venezuela. The main study area is delimited by a broken line.

using the triangulation method (see Heezen and Tester 1967) during at least five nocturnal and three diurnal periods, each lasting between 11 and 13 h, for a total of approximately 700 h of sampling. At night, we noted the relative size of the moon disc (moonless, quarter, half, or full moon); tide fluctuations were also noted on all occasions.

G-tests (Sokal and Rohlf 1981) were used to compare the percent of time spent by plovers on feeding habitats during daytime and nighttime, and to test the significance of seasonal variation in their hourly pattern of use of foraging areas during nighttime. A *G*-test for goodness of fit to a uniform distribution (Sokal and Rohlf 1981) was also computed to test the significance of the seasonal variation in the number of plovers observed at roost sites during daytime. The same test was also used to verify the significance of hourly variation in the presence of plovers on foraging habitats throughout the night and their relationship with the presence of moonlight and the tidal cycle. Finally, the presence of plovers on foraging sites during moonlit and moonless nights was compared with the Student *t*-test (Sokal and Rohlf 1981).

RESULTS

Diurnal and nocturnal distribution of plovers.—During daytime, from the end of October to March, Wilson's Plovers roosted on three sites (A, B, and C), 0.5 to 1.5 km apart, on the study area of the Bocaripo lagoon (Fig. 1). Site A, located near the village of Guayacán, was a rocky jetty, one meter in height, protecting the village from spring-tides. Site B was situated on the mudflat, beyond the maximum high tide limit on the mudflat, close to xeric vegetation. Site C was a shell (oysters and clams) heap exceeding in height the high tide level. Two other roosting sites were found outside the Bocaripo study area (Fig. 1), one near mangroves (site D), the other on the mudflat (site E), north and south-east of the Chacopata lagoon, respectively. From November to January, the plovers of sites D and E progressively decreased in number and disappeared. The number of Wilson's Plovers observed on sites A, B, and C varied significantly ($G = 20.44$, df = 5, $P < 0.01$) (numbers = 61, Oct. 1991; 101, Nov. 1991; 113, Dec. 1991; 91, Jan. 1992; 86, Feb. 1992; 71, March 1992).

The nocturnal and diurnal distribution of individual Wilson's Plovers differed substantially (Fig. 1). Telemetry revealed that the birds moved more at night than during daylight. For example, starting in November, one individual began to use site B during daytime and regularly moved at night to foraging sites by the Chacopata lagoon where it had previously been captured and radio-tagged. After the end of the transmitter field life, it was frequently observed roosting during daytime at the same site until the end of March, just before the beginning of breeding activities, when the daytime roosting groups broke apart. In addition, during nighttime, none of the 15 radio-tagged birds was gregarious as was observed during daytime. Between 20 to 30 min after dusk, plovers left diurnal roosting sites and distributed themselves on the foraging mudflats all over the lagoon complex, or flew to their nighttime roosting places located close to mangroves. Some 20 to 30 min before sunrise, plovers moved to foraging sites or diurnal roosts.

Monthly variation in the use of diurnal and nocturnal feeding sites.—Wilson's Plovers showed no seasonal variation in the overall percentage of time (i.e., between 25% and 45% of day + night) spent on feeding sites ($G = 10.65$, df = 5, $P > 0.05$; Fig. 2A). However, the duration of their presence on foraging sites from November through January (Fig. 2B) was significantly longer at night than in daytime ($G = 4.20$, df = 1, $P < 0.05$; $G = 23.49$, df = 1, $P < 0.001$; and $G = 8.99$, df = 1, $P < 0.01$, for November, December, and January, respectively). The percentage of time spent at night on foraging sites increased from October to

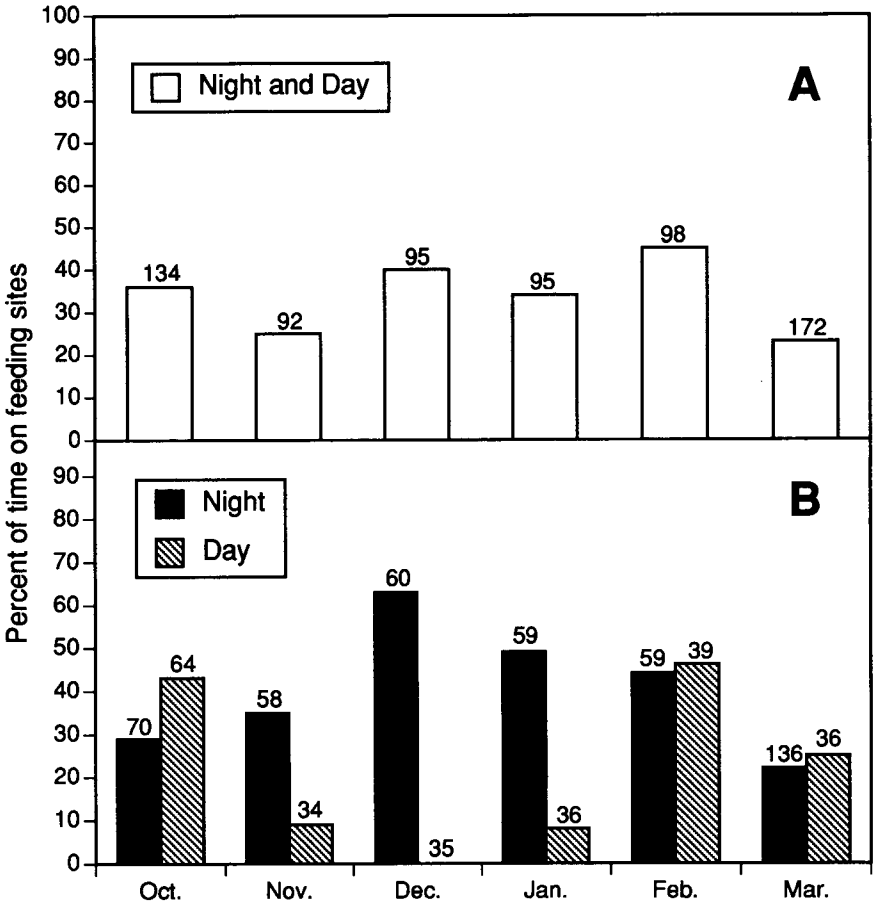

FIG. 2. Seasonal variation in the relative importance of time spent on foraging sites by Wilson's Plovers during daytime and nighttime, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

December and progressively decreased thereafter ($G = 5.17$, df = 1, $P < 0.05$; Fig. 2B). Plovers remained most of the day on their diurnal roosting sites during November, December, and January. In December, they foraged only at night.

Hourly variation in the use of nocturnal foraging areas.—The presence of Wilson's Plovers on their nocturnal foraging areas did not vary significantly among months ($G = 33.33$, df = 55, $P > 0.05$). However, significant hourly differences were observed ($G = 32.04$, df = 11, $P < 0.001$), with the duration of time spent on feeding areas being longer after

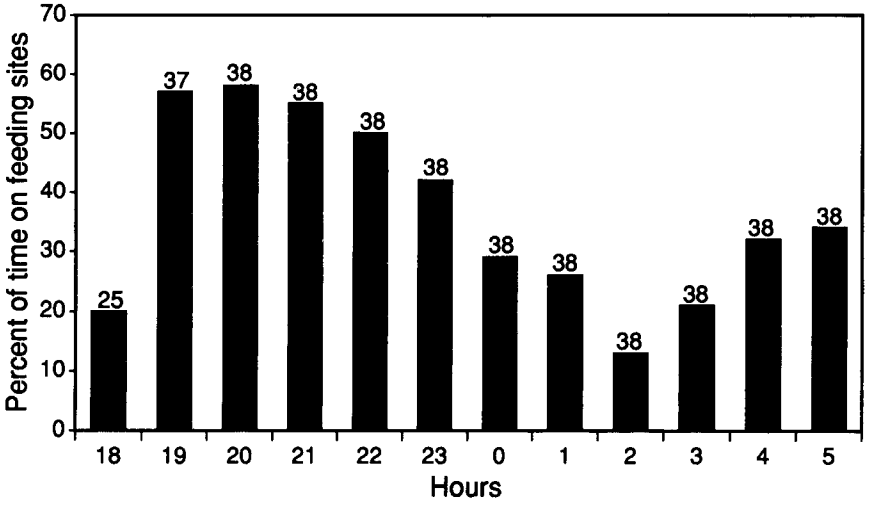

FIG. 3. Hourly variation in the relative importance of the time spent on foraging sites by Wilson's Plovers during nighttime, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

sunset between 19:00 and 20:00 h, progressively decreasing thereafter, and increasing slightly before sunrise (Fig. 3).

Presence on feeding areas in relation to moonlight.—Plovers used nocturnal foraging sites mainly on moonlit nights, regardless of the size of the moon disc, except in December (Fig. 4). The duration of their presence on foraging areas during moonlit nights was longer than on moonless nights during all non-breeding months combined ($t = 2.88$, df = 10, $P < 0.05$). The seasonal pattern of the use of foraging mudflats on moonlit nights tended to increase from October to January and to decrease thereafter, but monthly variation was not significant ($G = 5.13$, df = 5, $P > 0.05$). The percent of time spent on feeding habitats on moonless nights varied seasonally, but essentially because of December data ($G = 22.30$, df = 5, $P < 0.001$).

Presence on feeding areas during low tide periods.—During low tide, the presence of Wilson's Plovers on feeding habitats was generally low during daytime, except in October and February (Fig. 5). The relative importance of diurnal *versus* nocturnal presence of plovers on foraging sites did not differ significantly from one month to another between November and January ($G = 5.06$, df = 2, $P > 0.5$). Nevertheless, during all months combined, the presence of plovers on foraging mudflats was significantly longer during nighttime than during the day ($G = 73.95$, df

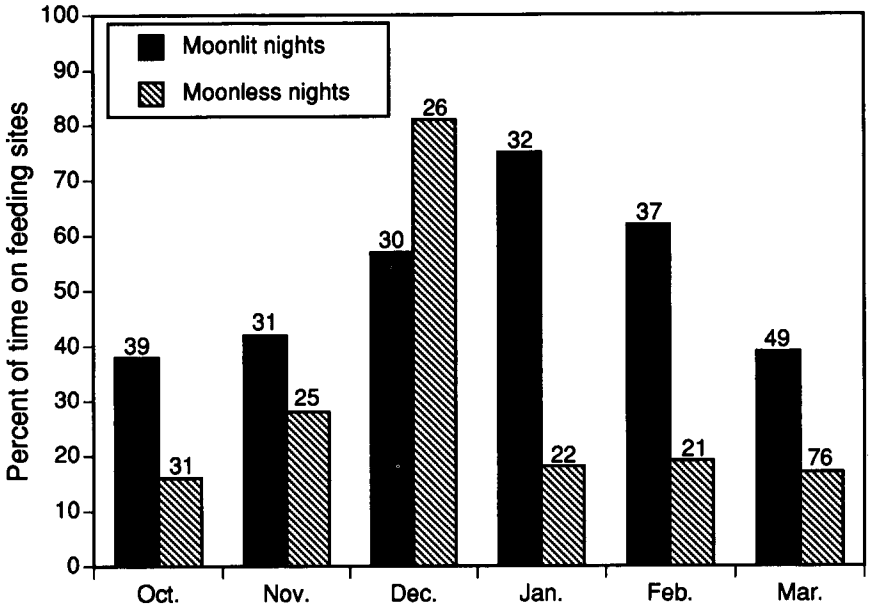

FIG. 4. Seasonal variation in the relative importance of the time spent on foraging sites by Wilson's Plovers during nighttime, as a function of the presence and absence of moonlight, during the non-breeding season. Figures above columns represent the number of radio-tracking hours.

= 3, $P < 0.001$). During the December low tides, they foraged only at night (Fig. 5).

DISCUSSION

Morrier and McNeil (1991) reported that, from November to March, daylight feeding alone was insufficient to counterbalance the energy expenditure of Wilson's Plovers at the Chacopata lagoon complex, indicating that foraging occurred primarily during nighttime. This study shows that, during the same period, the overall (i.e., day + night) time spent on foraging habitats by Wilson's Plovers did not vary seasonally. There absence on foraging sites during daylight was compensated by an increase in their presence at night. However, their diurnal presence on foraging habitats was generally low in November, December, and January but increased considerably in February. As a consequence, the overall time spent on feeding sites tended to be higher in February, but the variation was not significant. The proportion of time spent foraging is likely to vary seasonally with energetic needs. For the Wilson's Plovers of north-

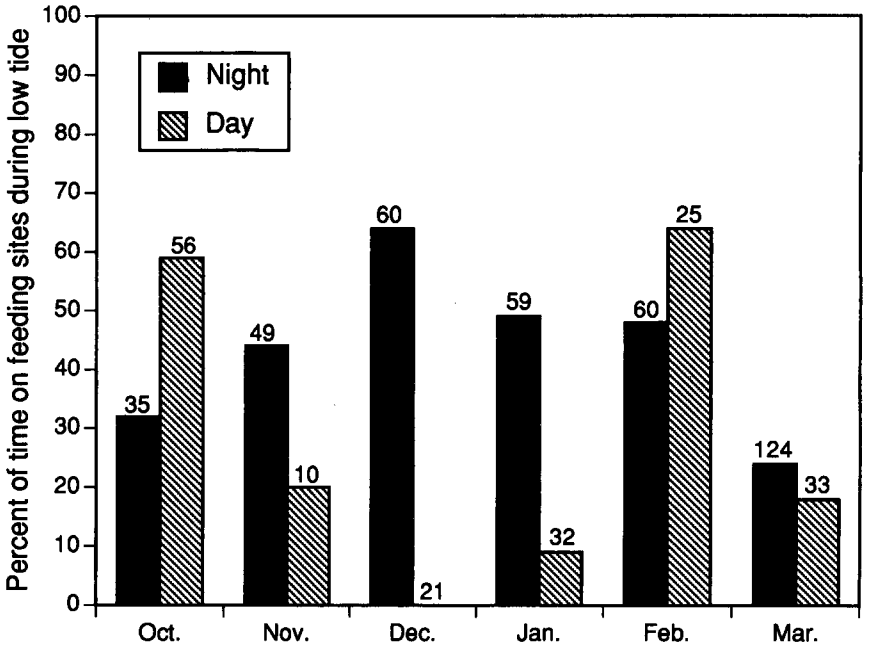

FIG. 5. Seasonal variation in the relative importance of time spent on foraging sites by Wilson's Plovers during daytime and nighttime low-tide periods, throughout the non-breeding season. Figures above columns represent the number of radio-tracking hours.

eastern Venezuela, energetic requirements are likely to be higher during the beginning of the breeding season, which starts in March–April (McNeil 1970; B. Limoges, pers. comm.; Thibault and McNeil, unpubl. data), and during the pre-alternate molt which ends in March–April (F. Mercier, pers. comm.). McNeil (1970) has shown that Wilson's Plovers of northeastern Venezuela accumulate fat reserves between mid-February and April.

The seasonal variation in the number of Wilson's Plovers on the study area during daylight suggest changes in the attachment of birds to the different roosting sites on the lagoon complex. Indeed, the plovers that roosted on sites D and E decreased progressively in number from November to January and disappeared thereafter, while the numbers on sites A, B, and C increased. It thus appears that the Bocaripo roosting sites were preferred during the period of high-water which occurs in the Chacopata lagoon complex from September to the end of January. In addition, Wilson's Plovers were present on foraging areas during nighttime throughout the study period, and from November to January, their pres-

ence at those areas was longer in duration during nighttime than during daylight. On the other hand, plovers were generally solitary during the night and gregarious during the day.

Three factors might be responsible for these differences (1) the water level, (2) the need for protection against aerial predators, and (3) the tide cycle.

The three Bocaripo sites (A, B, and C) had the following features in common: all were located on dry substrata protected from high tides. On the contrary, the wide mudflats of the lagoon complex, including the two daytime roosts (sites D and E) located north and south-east of the Chacopata lagoon, were submerged daily during the period of high waters and were wet all the time, thus not permitting the plovers to roost there.

In addition, the time when the number of Wilson's Plovers started decreasing on the roosting sites D and E and started increasing on sites A, B, and C corresponds to the time when Peregrine Falcons (*Falco peregrinus*) arrive over the Chacopata lagoon complex (Limoges 1987). Limoges (1987) also observed that many of the foraging smaller shorebirds group together more when Peregrine Falcons start chasing them over the Chacopata lagoon. Wilson's Plovers, in contrast with Semipalmated Plovers (*C. semipalmatus*), are solitary foragers (Morrier and McNeil 1991) and thus, while feeding during daylight, suffer higher individual risks of being captured by aerial predators. Being gregarious (see Vines 1971, Page and Whitacre 1975) and motionless on the Bocaripo roosts where the substrata apparently offer better daytime concealing than the wide mudflats, the Wilson's Plovers would be less exposed to predation from Peregrine Falcons or other aerial predators.

Finally, according to Strauch and Abele (1979), Wilson's Plovers forage only during low tides (Panama). On the Chacopata lagoon complex, both during nighttime and daytime, they foraged only occasionally during high tides (Robert et al. 1989, Robert and McNeil 1992, this study). The particular tide cycle of the Chacopata lagoon complex (high tides occur more frequently during daytime) could result in the need for the plovers to forage more at night and to roost during the day because the foraging habitats are submerged more frequently during daytime. Nevertheless, Wilson's Plovers never foraged during the entire low-tide periods, neither during daytime nor during nighttime.

In conclusion, as the high-tide grouping of Wilson's Plovers was observed only during the day, but never at night, and as plovers did not use the entire diurnal low-tide period for foraging, the tidal cycle cannot be invoked as the major factor responsible for their nocturnal foraging. Consequently, the main reason why Wilson's Plovers feed at night appears to be the avoidance of diurnal predators, and thus conforms to the pref-

erence hypothesis of McNeil (1991) and McNeil et al. (1992) which postulates that birds prefer to feed at night because it provides the safest feeding opportunities. Furthermore, in the Chacopata lagoon complex, Wilson's Plovers forage almost exclusively on small fiddler crabs (*Uca cumulanta,* not *U. thayeri* as mentioned by Morrier and McNeil [1991]). The Chacopata mudflats are swarming with millions of these crabs, both during day and night, and it seems quite easy for Wilson's Plovers and other shorebirds to catch them by a wait technique during the night (see Morrier and McNeil 1991). However, due to the fact that fiddler crabs, although active during the first part of the night, are principally active during daylight (Díaz D. 1993, Thibault, unpubl.), we believe that the nocturnal activity of Wilson's Plovers is not due to a daylight food shortage or higher availability of prey during the night.

Wilson's Plovers spent more time on foraging sites during the first part of the night than thereafter (Fig. 3), and on moonlit nights, although they were regularly present on feeding habitats during moonless nights as well (Fig. 4). This appears to be correlated with the activity pattern of the fiddler crabs, which are active only in this portion of the night (see above) and on moonlit nights, and practically are inactive on moonless nights (Díaz D. 1993). Nocturnal foraging, regardless of the presence or absence of moonlight, was previously reported for Wilson's Plovers by Robert et al. (1989) and Robert and McNeil (1992) and also for other shorebird species such as Grey Plovers (*Pluvialis squatarola*) (Turpie and Hockey 1993).

This study shows that the Wilson's Plover is mainly a nocturnal feeding species, and previous studies have shown that it forages visually both during moonlit and moonless nights (McNeil and Robert 1988, 1992; Robert and McNeil 1989, 1992; Robert et al. 1989). The retinal visual receptors of birds, as of all vertebrates, are rods and cones (Meyer 1977, Tansley and Erichsen 1985). Nocturnal birds have a great preponderance of rods in their retinas (Tansley and Erichsen 1985). Rojas de Azuaje et al. (1993) compared the rod/cone ratio of the Grey Plover (1.1:1.0), a visual day and night forager, with that of the Greater Yellowlegs [(*Tringa melanoleuca*) 0.7:1.0], a daylight visual feeder that switches to tactile foraging at night. However, recent results show a ratio of 1.4:1.0 for the Wilson's Plover (Rojas de Azuaje and McNeil, unpubl. data), suggesting that it is better adapted for nocturnal vision than the other species studied thus far.

ACKNOWLEDGMENTS

The Natural Sciences and Engineering Research Council of Canada and the Univ. de Montréal supported this study. We thank G. Rompré for assistance during the field work,

and B. Poulin, Gaëtan LeFebvre, and two anonymous referees for improving a former version of the manuscript. We are also indebted to colleagues of the Univ. de Oriente and, in particular, J. R. Rodríguez S., co-responsible with R. McNeil for the collaboration agreement between that university in Venezuela and the Univ. de Montréal.

LITERATURE CITED

BATTY, L. 1991. Aspects of the phenology of waders (Charadrii) on the Ria Formosa, Portugal. Ph.M. diss., Univ. of Wales, Cardiff, United Kingdom.

DIAZ 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, Univ. de Oriente, Cumaná, Venezuela.

HAYMAN, P., J. MARCHANT, AND T. PRATER. 1986. Shorebirds: an identification guide to the waders of the world. Houghton Mifflin, Boston, Massachusetts.

HEEZEN, K. L. AND J. R. TESTER. 1967. Evaluation of radio tracking by triangulation with special reference to deer movements. J. Wildl. Manage. 31:124–141.

LIMOGES, B. 1987. Dynamique spatio-temporelle des oiseaux aquatiques des lagunes de Chacopata au nord-est du Venezuela. Mémoire de maîtrise, Univ. de Montréal, Montréal, Québec.

MCNEIL, R. 1970. Condicionamiento fisiológico pre y post-reproductivo de *Charadrius wilsonia* (Ridway) y de *Himantopus mexicanus* (Müller) en el noreste de Venezuela. Acta IV Congr. Latin. Zool. Vol. II:749–760.

———. 1991. Nocturnality in shorebirds. Acta XX Int. Ornithol. Congr.:1098–1104.

———, P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. Biol. Rev. 67:381–419.

———, ———, AND R. PIEROTTI. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations, and suspected benefits. Pp. 187–246 *in* Current ornithology, Vol 10 (D. M. Power, ed.). Plenum Press, New York, New York.

———, B. LIMOGES AND J. R. RODRIGUEZ S. 1990. Corocoro Colorado (*Eudocimus ruber*) y otras aves acuáticas coloniales de las lagunas y salinas de la costa centro-oriental de Venezuela. IWRB Spec. Publ. 11:28–45.

——— AND M. ROBERT. 1988. Nocturnal feeding strategies of some shorebird species in a tropical environment. Acta Congr. Intern. Ornithol. 19:2328–2336.

——— AND ———. 1992. Comportamiento alimenticio diurno y nocturno de aves limícolas en ambientes tropicales. Pp. 61–67 *in* Memorias III Congreso Ornitología Neotropical (H. Alvarez L., G. Kattán, and C. Murcia, eds.). Sociedad Vallecaucana de Ornitología, Univ. del Valle, Cali, Colombia.

MEYER, D. B. 1977. The avian eye and its adaptations. Pp. 549–611 *in* The visual system in vertebrates, Vol. VII/5 (F. Crestitelli, ed.). Springer Verlag, Berlin.

MORRIER, A. 1990. Activités diurnes du Pluvier de Wilson (*Charadrius wilsonia*) et du Pluvier semipalmé (*Charadrius semipalmatus*) dans les lagunes de Chacopata, Venezuela. Mémoire de maîtrise, Dépt. de sciences biologiques, Univ. de Montréal, Montréal, Québec.

——— AND R. MCNEIL. 1991. Time-activity budget of Wilson's and Semipalmated plovers in a tropical environment. Wilson Bull. 103:598–620.

PAGE, G. AND D. F. WHITACRE. 1975. Raptor predation on wintering shorebirds. Condor 77:73–83.

PERRY, M. C., G. H. HAAS, AND J. W. CARPENTER. 1981. Radio transmitters for Mourning Doves: a comparison of attachment techniques. J. Wildl. Manage. 45:524–527.

ROBERT, M. AND R. MCNEIL. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. Ibis 131:69–79.

——— AND ———. 1992. Importancia y condiciones de la alimentación nocturna de aves limícolas y otras aves acuaticas en una laguna tropical. Pp. 53–60 *in* Memorias III Congreso de Ornitología Neotropical (H. Alvarez L., G. Kattán and C. Murcia, eds.). Sociedad Vallecaucana de Ornitología, Univ. del Valle, Cali, Colombia.

———, ———, AND A. LEDUC. 1989. Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. Auk 106:94–101.

ROJAS DE AZUAJE, L. M., S. TAI, AND R. MCNEIL. 1993. A comparison of the rod-cone ratio in three species of shorebirds having different nocturnal foraging strategies. Auk 110:141–145.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry. W. H. Freeman and Company, New York, New York.

STRAUCH, J. G. AND L. G. ABELE. 1979. Feeding ecology of three species of plovers wintering on the Bay of Panama, Central America. Stud. Avian Biol. 2:217–230.

TANSLEY, K. AND J. T. ERICHSEN. 1985. Vision. Pp. 623–629 *in* A dictionary of birds (B. Campbell and E. Lack, eds.). Poyser, Calton, United Kingdom.

TURPIE, J. K. AND A. R. HOCKEY. 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.

VINES, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behavior. J. Theor. Biol. 30:405–422.

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.

———, A.-M. BLOMERT, AND R. KUPKES. 1990. Increase of feeding time in waders preparing for spring migration from the Banc d'Arguin, Mauritania. Ardea 78:237–256.