The Condor 96:734–738

SEASONAL CHANGES IN DAY AND NIGHT FORAGING OF WILLETS IN NORTHEASTERN VENEZUELA[1]

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Abstract. We studied whether or not the proportion of foraging Willets (*Catoptrophorus semipalmatus*), a Nearctic migrant in northeastern Venezuela, varies seasonally on the wintering grounds in tropical environment as a function of energetic requirements. Data on the number of birds feeding and roosting were collected once or twice a week, from 19 October 1991 to 5 May 1992, during diurnal and nocturnal observation periods, each lasting 12 consecutive hours. There was a correlation between the seasonal changes in the proportion of Willets foraging (day + night) and the seasonal variations in the fat content of other individuals collected in the same region. Willets fed as often during nighttime as during daytime, except in autumn when they fed more during darkness. Compared to December and January, the percentage of birds feeding was greater in October and November. In addition, proportionally more birds fed, both during daytime and nighttime, in preparation for spring migration than in October–November.

Key words: Nocturnal foraging; seasonal variation; Willet; Catoptrophorus semipalmatus; *wintering; Venezuela.*

INTRODUCTION

Nocturnal foraging in shorebirds has mainly been reported both during stop-overs at staging areas and when wintering in coastal and estuarine habitats in temperate latitudes (for review, see McNeil 1991, McNeil et al. 1992). However, recent studies in northeastern Venezuela and Africa have shown that some Holarctic winter migrants do feed at night in tropical environments (McNeil and Robert 1988, Robert and McNeil 1989, Robert et al. 1989, Swennen 1990, Zwarts and Dirksen 1990, Zwarts et al. 1990, Morrier and McNeil 1991, Fasola and Canova 1993, Thibault and McNeil 1994).

In northern Europe, nocturnal feeding may be most intense during winters, apparently compensating for shorter daylight periods and for decreased availability of prey and intertidal organisms that are less active or move deeper within the sediment as temperature falls (Goss-Custard 1969, 1983; Heppleston 1971; Smith 1975; Evans 1976, 1987; Goss-Custard et al. 1977; Pienkowski 1981a, 1981b, 1982; Puttick 1984; McNeil et al. 1992). More time should be devoted to nocturnal foraging when energetic requirements are higher, both in tropical and temperate regions. Myers and McCaffery (1984), Morrier and McNeil (1991) and McNeil et al. (1993) suggested that the frequency and duration of food intake in migratory species should vary seasonally. For example, birds must eat more when (1) refueling at a stop-over place after a long, non-stop flight over the ocean, (2) molting, or (3) accumulating fat in preparation for migration. In contrast, seasonal changes in energy intake should be less in allied or congeneric species residing the entire year in tropical regions.

Little is known concerning seasonal variations in the efforts devoted to foraging by shorebirds wintering or residing in tropical environments. Zwarts et al. (1990) showed that the lowest feeding activity in Palearctic shorebirds wintering in Mauritania occurred in February and that the activity was maximum in March–April. Morrier and McNeil (1991) obtained similar results for Semipalmated Plovers (*Charadrius semipalmatus*) wintering in Venezuela. Zwarts et al. (1990) showed that, during the 4–6 weeks before their northward departure from Mauritania, some shorebird species increased the total time spent feeding, in particular by foraging more at night. Batty (1991), on the other hand, found that nocturnal feeding in southern Portugal was the norm during the migration periods, but much less common from November to March.

In this paper, we document the seasonal vari-

[1] Received 18 November 1993. Accepted 3 February 1994.

TABLE 1. Monthly data on the number of observed daytime and nighttime observation hours and cumulative numbers of Willets observed foraging and roosting.

Months	Daytime			Nighttime		
	Number of observation hours	Cumulative number of Willets observed		Number of observation hours	Cumulative number of Willets observed	
		Foraging	Foraging and roosting		Foraging	Foraging and roosting
October	22	430	1,993	23	532	875
November	38	1,677	3,199	47	2,259	3,184
December	44	1,078	3,661	49	237	922
January	30	606	2,408	45	649	1,824
February	42	2,186	3,223	45	1,346	2,249
March	43	1,660	2,030	46	1,098	1,784
April	55	688	1,026	59	576	978
May	10	184	269	11	169	244

ations in the proportion of Willets (*Catoptrophorus semipalmatus*) foraging on their wintering grounds in a tropical environment. Two races (*C. s. semipalmatus* and *C. s. inornatus*) winter in the coastal lagoons of northern Venezuela (McNeil 1970). The number of oversummering birds represent close to 40% of the maximum number observed during the winter (McNeil 1970, McNeil et al. 1990). This species forages both by night and by day (Stenzel et al. 1976, Robert et al. 1989, McNeil et al. 1992) and continues, under certain conditions, to defend during darkness the foraging territories defended during daylight (Rompré 1993, McNeil and Rompré, in press).

STUDY AREA AND METHODS

The study was conducted 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. The lagoon complex (Bocaripo and Chacopata) extends over 830 ha and comprises several areas where foraging shorebirds congregate (Limoges 1987). Observations took place in a 2 km² area, comprising the Bocaripo lagoon and, to the east, the adjacent shallow water area, strewn with sparse dead mangroves, which forms part of the Chacopata lagoon (for a map of the study area, see McNeil and Rompré, in press, Thibault and McNeil 1994).

We censused feeding and roosting Willets on an hourly basis, from 19 October 1991 to 5 May 1992, during diurnal and nocturnal observation periods, each lasting 12 consecutive hours, giving a total of 284 and 325 observation hours during day and darkness, respectively. Observations were made from a pickup truck, during daylight, through a 15–45× spotting scope, and at night, with the use of a 6.8× night-vision module (light intensification = 60,000), model MK-303A (Star-Tron Technology Corporation, Pittsburgh, PA). Because of the limited light intensifying capacity of the equipment, it was necessary to use auxiliary lighting during moonless nights.

Concerning seasonal variations in fat content as percent of the lean body mass, we used data collected in other lagoons (Chiguana and El Peñón; see McNeil 1970) of northeastern Venezuela as by the method of McNeil and Carrera de Itriago (1968), McNeil (1970) and McNeil and Cadieux (1972a, 1972b). Briefly, specimens were weighed (fresh mass) to the nearest 0.1 g. The method involved dehydration for two days in an 80°C oven, storage for two days in cold petroleum ether, boiling for 30 min in a Soxhlet apparatus with petroleum ether, and drying and weighing the fat-free dehydrated residues. Three values were obtained: dry mass, fat-free mass, and by subtraction, fat content.

G-tests (Sokal and Rohlf 1981) were used to test the significance of seasonal changes in the percent of Willets foraging. χ^2-tests were also used to compare the percent of birds foraging during daytime and nighttime.

RESULTS

The first fall-migrating Willets arrived in the study area on 25 July and their number progressively increased to 250 birds by the end of October (Fig. 1A). Numbers slightly decreased by November, varied between 150 and 220 until the beginning of March, and progressively decreased thereafter until mid-April, when the last spring migrants

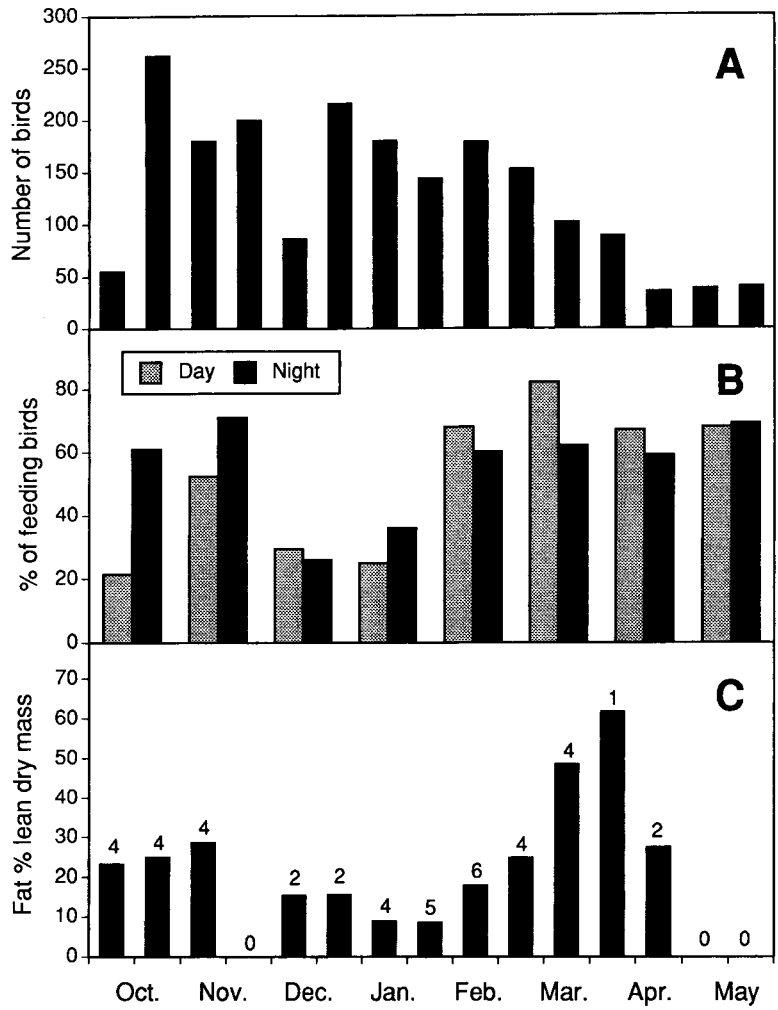

FIGURE 1. Seasonal variations (A) in the number of Willets in the study area, (B) in the percentage of Willets foraging during daytime and nighttime in the study area, and (C) in the fat content, expressed as percent of the lean dry mass, of other Willets collected in the same region in northeastern Venezuela, as by data taken from McNeil (1970). Figures above the columns represent the number of birds.

left the lagoon complex. Some 30 individuals remained during the summer.

Monthly data on cumulative numbers of Willets observed feeding and roosting reveal that, compared to December and January, the overall (i.e., daytime + nighttime) percentage of Willets foraging was greater in October and November ($G = 25.834$, $P < 0.001$, df = 1), then from February to May ($G = 73.406$, $P < 0.001$, df = 1) (Table 1, Fig. 1B). The overall percentages of February–May were higher compared to those of October–November ($G = 12.673$, $P < 0.001$, df = 1). In October and November, the percentage of birds feeding was higher at night (roughly 60–70%) than during daylight (roughly 20–50%) ($\chi^2 = 25.25$, $P < 0.001$, df = 1). However, in December and January, the percentage significantly decreased to about 25–38% at night ($G = 30.141$, $P < 0.001$, df = 1). The nocturnal decrease alone was largely responsible for the decrease in the proportion of birds observed foraging during both months; the diurnal percentage did not decrease significantly ($G = 3.314$, df = 1, ns). The percentages of Willets observed foraging increased significantly in February–March and remained high until the end of the study: roughly 60% dur-

ing darkness ($G = 5.887$, $P < 0.05$, df = 1), and 70–80% during daylight ($G = 14.630$, $P < 0.001$, df = 1). In that period, the proportion of Willets foraging was similar during daytime and nighttime ($\chi^2 = 3.10$, df = 1, ns).

DISCUSSION

There is a positive correlation between the seasonal changes in the overall percentage of Willets foraging (day + night) and the seasonal variations in the fat content of other individuals collected by McNeil (1970) in the same region in northeastern Venezuela ($r = 0.690$, $P < 0.05$, $n = 7$; compare Figs. 1B and 1C). Indeed, Willets have a fat content of about 25 to 31% of lean dry mass from September to November, varying between 9 and 15% from December to February, and then increasing to 50 to 60% (80% in the fattest birds) in April (Fig. 1C; see also McNeil 1970). Furthermore, their energetic demands increase shortly after their fall arrival on the wintering grounds, not only because transient birds rebuild fat reserves to some extent before departing elsewhere, but also because some individuals are still completing prebasic molt (McNeil 1970).

Therefore, as expected, our results indicate a strong association between the seasonal variations in the efforts devoted to foraging by a Nearctic migratory shorebird and those of its energetic needs on the wintering ground in tropical environments. Throughout their stay on the Chacopata Lagoon complex, equal proportions of Willets fed during nighttime and daytime, except during the autumn when more birds foraged during darkness. In addition, proportionately more birds fed, both during daytime and nighttime, when accumulating fat for the spring migration. These results, especially those dealing with diurnal foraging, are similar to those of Morrier and McNeil (1991) for the Semipalmated Plover at the same lagoon complex. In contrast, at Bolinas Lagoon in California, Stenzel et al. (1976) found Willets feeding at night during the winter but not during the fall. This region is 27 degrees of latitude north of Chacopata and has shorter daylight periods and lower night temperatures during the winter.

ACKNOWLEDGMENTS

The Natural Sciences and Engineering Research Council of Canada, the University de Montréal and Universidad de Oriente supported this study. We thank Michel Thibault for assistance during the field work and Nils Warnock for helpful comments on the manuscript. We are also indebted to colleagues of the Universidad 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 Université de Montréal.

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