CONDITIONS AND SIGNIFICANCE OF NIGHT FEEDING IN SHOREBIRDS AND OTHER WATER BIRDS IN A TROPICAL LAGOON

MICHEL ROBERT, RAYMOND MCNEIL,[1] AND ALAIN LEDUC

Département de Sciences biologiques and Centre de recherches écologiques de Montréal, Université de Montréal, C. P. 6128, Succ. "A," Montréal, Québec H3C 3J7, Canada

ABSTRACT.—On a small bay of the Chacopata lagoon complex in northeastern Venezuela, we analyzed the temporal feeding activity patterns of shorebirds and other water birds, and we determined the factors or conditions related to these patterns. During daytime and nighttime observations, we measured the abundance of each species as well as environmental factors (time, wind velocity, cloudiness, tide level, presence of moonlight and bioluminescence). A night vision module (light intensifier) was used during nighttime observations. Samples × species matrices were summarized by reciprocal averaging (RA) analysis, and the information was related to environmental factors. Feeding activity patterns were related most significantly to time of day, i.e. daytime and nighttime. Some species like "egrets," the Whimbrel (*Numenius phaeopus*), and the Black-bellied Plover (*Pluvialis squatarola*) fed principally during daylight, but most other species (including a majority of shorebird species) fed more regularly and in higher numbers at night. Lesser and Greater yellowlegs (*Tringa flavipes* and *T. melanoleuca*, respectively) and Willets (*Catoptrophorus semipalmatus*) foraged with comparable frequency during the day and the night. Daytime and nighttime data were analyzed separately, and tide level best explained both the variations of nocturnal and diurnal abundance of foraging birds. Nocturnal feeding may be a natural habit in response to regularly limited feeding space and time mainly induced by tide. *Received 4 January 1988, accepted 24 August 1988.*

FEEDING in shorebirds has been studied, for the most part, in daylight. For several shorebirds and other waders (see Bent 1926, Palmer 1962, Krebs 1974, Black and Collopy 1982, Burger 1984, Goss-Custard 1984, Wood 1986, Powell 1987), the relative importance of night feeding is largely unknown, except in night-herons (*Nycticorax;* see Watmough 1978) and Great Blue Herons (*Ardea herodias;* see Powell 1987).

In addition, daytime and nighttime feedings have been observed almost exclusively in birds that winter in temperate latitudes. At these latitudes, night feeding has been related to high energy requirements under severe winter conditions. Thus, shorebirds presumably feed at night because they cannot obtain enough food during the shortened daylight periods (Goss-Custard 1969; Heppleston 1971; Goss-Custard et al. 1977; Pienkowski 1981, 1982; Puttick 1984). It is also believed that some shorebird species that forage at night (e.g. the Black-bellied Plover wintering in England) may take advantage of increased availability and activity of prey at night (Dugan 1981).

There are indications that night feeding also occurs in tropical latitudes (Engelmoer et al. 1984, Schneider 1985, McNeil and Robert in press, Robert and McNeil in press), where temperatures are higher and daylight longer than in temperate latitudes. We attempted to analyze the temporal feeding activity patterns of shorebirds and other water birds in a tropical habitat and to determine the factors or conditions related to these patterns.

STUDY AREA AND METHODS

The study was carried out at 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 extends over 830 ha and comprises several areas where feeding birds congregate (Limoges 1987). Tidal amplitude is low (30 cm). Because of a very gentle slope, low tide expanse on the mudflats often ranges from 80–100 m.

We scored a total of 156 observation periods (54 by day and 102 by night) in a small bay (2.0 ha) surrounded by mangroves from 12 October to 8 December 1985. Each observation period lasted the time necessary to count all birds. In addition to the abundance of each species, we noted wind velocity (according

[1] To whom reprint requests should be sent.

TABLE 1. Relative abundance of species constituting each group in the Chacopata lagoon complex.

Groups of species	Species	Relative abundance (%)
Small sandpipers[a]	Semipalmated Sandpiper (*Calidris pusilla*)	60
	Western Sandpiper (*C. mauri*)	35
	Least Sandpiper (*C. minutilla*)	5
Small plovers[b]	Wilson's Plover (*Charadrius wilsonia*)	60
	Semipalmated Plover (*C. semipalmatus*)	40
Medium-sized shorebirds[c]	Short-billed Dowitcher (*Limnodromus griseus*)	60
	Stilt Sandpiper (*Calidris himantopus*)	35
	Red Knot (*C. canutus*)	5
Yellowlegs and Willet[c]	Willet (*Catoptrophorus semipalmatus*)	80
	Lesser Yellowlegs (*Tringa flavipes*)	15
	Greater Yellowlegs (*T. melanoleuca*)	5
Egrets[c]	Tricolored Heron (*Egretta tricolor*)	55
	Snowy Egret (*E. thula*)	35
	Reddish Egret (*E. rufescens*)	10
Night-Herons[c]	Yellow-crowned Night-Heron (*Nycticorax violaceus*)	55
	Black-crowned Night-Heron (*N. nycticorax*)	45

[a] Relative abundance according to nocturnal mist-net captures from the beginning of October to mid-December (Francine Mercier unpubl. data).
[b] Relative abundance according to diurnal censuses from the beginning of October to mid-December (F. Mercier unpubl. data).
[c] Relative abundance according to diurnal censuses from the beginning of October to mid-December (Benoît Limoges unpubl. data).

to Beaufort's scale), percentage of cloud cover, and tide level. At night we also noted the relative size of the moon disc (moonless, quarter, half, or full moon), and the presence or absence of bioluminescence.

Daytime observations were made with a 20× telescope. At night, birds were observed at closer range (4–60 m) from a blind through a Litton night vision module or light intensifier (model M911) equipped with a 100–300 mm zoom camera objective lens. Because of the limited light intensifying capacity of the equipment, it was necessary to use distant auxiliary lighting during dark nights (except during full moon periods). We installed 1–4 light bulbs (40 W), driven by 12-V car batteries, near the blind. All data on birds observed close to the light sources (i.e. visible to the naked eye of the observer) were rejected.

Whimbrels, Black-necked Stilts (*Himantopus mexicanus*), Black-bellied Plovers, and Greater Flamingos (*Phoenicopterus ruber*) were identified. With the night-vision equipment, it was generally very difficult to distinguish among Greater and Lesser yellowlegs and Willets, between Semipalmated and Wilson's plovers (*Charadrius semipalmatus* and *C. wilsonia*, respectively), among the small sandpipers (*Calidris pusilla, C. mauri, C. minutilla*), among Red Knots (*Calidris canutus*), Stilt Sandpipers (*C. himantopus*) and Short-billed Dowitchers (*Limnodromus griseus*), among egret species (*Egretta tricolor, E. thula*, and *E. rufescens*), and between night-heron species (*Nycticorax violaceus* and *N. nycticorax*). Consequently, these species were identified as "yellowlegs and Willets," "small plovers," "small sandpipers," "medium-sized shorebirds," "egrets," and "night-herons," respectively. The relative abundance of each species in these groups was obtained through nighttime mist-netting and daytime censuses in the lagoon complex (Table 1).

The data (number of birds of each species per observation period) were submitted to a reciprocal averaging (RA) analysis (Hill 1973, 1974) using the ACOR program (Université de Montréal). This is an ordination technique which represents sample (in this study, observation periods) and species relationships on a two-dimensional graph. Similar samples or species or both are near each other, and dissimilar entities are far apart (Gauch 1982). The method was chosen because of its capability of analyzing samples × species data matrices which include a generally large number of zero (0) values (Gauch 1982, Legendre and Legendre 1984).

This approach ("indirect gradient analysis") organizes data on species abundance exclusively, apart from environmental data, and leaves environmental interpretation to a subsequent and independent step (Gauch 1982). Consequently, we interpreted the variations in the occurrence of species foraging on the study site, a posteriori, by a rank correlation coefficient (Kendall's tau) calculated between the RA analysis component scores and the environmental factors. These analyses used the NONPARR CORR program of SPSS packages (Nie et al. 1975). This procedure comprises a number of steps. Each step provided groups of observation periods that can be used for further analysis. The analysis involved a "successive refinement" (Gauch 1982), i.e. a successive use of various methods (factor analysis and cluster analysis) to discriminate the factors explaining the species occur-

TABLE 2. Correlation coefficients (Kendall's tau) between variables and component scores of the first two axes in the ordination the 156 diurnal and nocturnal observation periods.[a]

Variables	Axis 1	Axis 2	Period[b]
Period	−0.66***	−0.53***	1.00
Moonlight	0.59***	0.38***	−0.78***
Bioluminescence	0.57***	0.46***	−0.82***
Wind	0.35***	0.28***	−0.48***
Tide	0.22***	0.35***	−0.35***
Cloudiness	0.15**	0.14**	−0.21**

[a] ** = $P < 0.01$; *** = $P < 0.001$.
[b] Correlation coefficient between the period and different variables.

rence variations on our study site. The first step was to analyze all observation periods.

RESULTS

Between 12 October and 8 December 1985, the numbers and species composition of birds that occurred on the study site did not vary appreciably. Because of the limits of nocturnal observation equipment, we could not be sure that all birds on the site at night used it only for feeding as did daytime birds; but the majority of nighttime birds (75–80%) actually foraged.

Overall patterns.—Species and numbers of individuals foraging on the study site were correlated with light and darkness (Table 2). Egrets, Whimbrels, and Black-bellied Plovers were observed foraging mainly during daylight periods (Fig. 1). On the other hand, Greater Flamingos, night-herons, Black Skimmers, Black-necked Stilts, medium-sized shorebirds, small sandpipers, and small plovers foraged mainly at night. The position of yellowlegs and Willets in the middle of the ordination figure (Fig. 1) suggested these birds foraged as much during the day as during the night (Table 3). Moonlight, bioluminescence, wind velocity, and tide level were highly correlated with light or darkness (Table 2), and the influence of these variables was uncertain. The influence of cloudiness was negligible.

Diurnal patterns.—The diurnal variations were correlated with tide level (Kendall's tau for axis 1 = −0.30, $P < 0.001$; axis 2 = −0.50, $P < 0.001$). The relative positions of species in the ordination of the diurnal observation periods (Fig. 2) showed that Whimbrels were high-tide feeders contrary to night-herons, and yellowlegs and Willets were low-tide feeders. Other species or groups (Black-bellied Plovers, egrets, small plovers and medium-sized shorebirds) appeared to feed at intermediate tide levels (Table 4). The influence of wind velocity and cloud cover was insignificant ($P > 0.05$ for axis 1 and axis 2).

Nocturnal patterns.—Of all variables studied, none were significantly correlated with the first 2 axes in the ordination of nighttime observation periods (Table 5), except for the occurrence of bioluminescence which was highly correlated with the second axis. The relative positions of species in the ordination of the nocturnal observation periods (Fig. 3) showed night-herons and Black-necked Stilts as species feeding

TABLE 3. Percentage frequency of occurrence of species or groups of species, and frequency of occurrence in relation to class abundance per diurnal or nocturnal observation period.

Species or groups of species[a]	Frequency of occurrence[b]		Frequency of occurrence in relation to class abundance[c]					
			Day			Night		
	Day	Night	1–5	6–10	>10	1–5	6–10	>10
Small sandpipers	3.7	71.6	100.0	0.0	0.0	8.1	8.1	83.8
Small plovers	9.3	74.5	80.0	20.0	0.0	37.7	41.6	20.7
Black-necked Stilt	1.9	66.7	100.0	0.0	0.0	76.8	15.9	7.3
Medium-sized shorebirds	22.2	79.4	81.3	0.0	18.7	21.9	11.0	67.1
Night-Herons	9.3	38.2	100.0	0.0	0.0	95.2	2.4	2.4
Black Skimmer	1.9	21.6	100.0	0.0	0.0	100.0	0.0	0.0
Greater Flamingo	0.0	16.7	0.0	0.0	0.0	52.9	35.3	11.8
Yellowlegs and Willet	85.1	78.4	60.9	10.9	28.2	43.9	23.2	32.9
Whimbrel	81.5	17.7	100.0	0.0	0.0	100.0	0.0	0.0
Egrets	64.8	7.8	82.4	2.9	14.7	100.0	0.0	0.0
Black-bellied Plover	24.1	3.9	100.0	0.0	0.0	100.0	0.0	0.0

[a] See Table 1 for the species in each group.
[b] Percentage of observation periods during which species or group of species was present.
[c] Percentage of the observation periods during which species or group of species was present, in relation to class abundance.

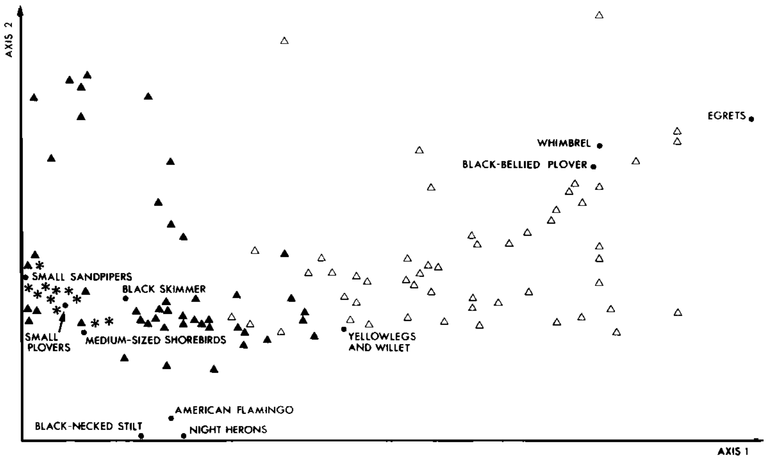

Fig. 1. Ordination of species or groups of species and observation periods in the space of the first 2 principal axes. Open triangles represent diurnal observation periods; closed triangles, nocturnal observation periods; asterisks, an overlapping of ≥5 nocturnal observation periods; closed circles, species or groups of species.

when bioluminescence was present (i.e. during 50 of 102 nocturnal observation periods).

The nocturnal variations were not easily understood with the use of correlation coefficients. To maximize the contrast of these variations, a flexible clustering (intermediate linkage; $\beta = -0.25$) (Lance and Williams 1966) of all nocturnal observation periods was done using the R package (Centre de Calcul, Université de Montréal). In addition, the species, groups of species, or both, responsible for the structure that emerged from this cluster analysis were identified through a contingency analysis using the PARTI program of the R package. These were the small sandpipers, the small plovers, and the medium-sized shorebirds. Among all measured environmental variables, tide level best explained the nocturnal variations of these species. Even if these birds regularly fed in small numbers during very high and high tides, they were rarely observed in large numbers under such tidal conditions (Table 6).

There was a relationship between moonlight and small plovers (two-way contingency table: $\chi^2 = 4.79$, df = 1, $P < 0.05$). In fact, small plovers foraged during 62.1% of the 58 moonless nocturnal periods as compared to 88.5% of the 26 nocturnal periods under a full moon.

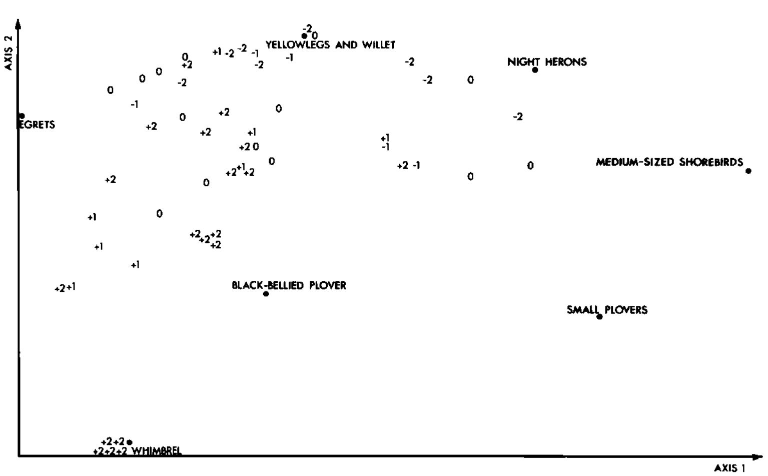

Fig. 2. Ordination of species or groups of species and diurnal observation periods in the space of the first 2 principal axes, as a function of tide levels: very high (+2), high (+1), medium (0), low (−1), very low (−2). Closed circles represent species or groups of species.

TABLE 4. Percentage frequency of diurnal occurrence of species or groups of species, and mean number of individuals (n) counted per observation period as a function of tide levels.

Species or groups of species[a]	Tide level: Very high (17)[b]		High (10)		Medium (14)		Low (5)		Very low (8)	
	%[c]	n	%	n	%	n	%	n	%	n
Whimbrel	38.6	1.2	20.5	1.3	15.9	1.3	15.9	1.6	9.1	1.0
Medium-sized shorebirds	18.7	2.3	25.0	2.8	31.3	6.8	18.7	18.7	6.3	15.0
Small plovers	0.0	0.0	0.0	0.0	60.0	1.7	40.0	6.0	0.0	0.0
Egrets	18.2	1.7	21.2	1.7	33.3	3.4	15.2	6.2	12.1	15.0
Black-bellied Plover	0.0	0.0	15.4	1.6	53.8	1.0	23.1	1.0	7.7	2.0
Night-Herons	0.0	0.0	0.0	0.0	0.0	0.0	50.0	1.0	50.0	1.3
Yellowlegs and Willet	26.2	1.8	15.2	2.6	30.4	14.3	15.2	30.3	13.0	43.7

[a] See Table 1 for the species pertaining to each group.
[b] Numbers of observation periods referring to each of the 5 stages of tide level.
[c] Percentage of the observation periods during which the species or the group of species was present.

DISCUSSION

Nocturnal feeding is important in several shorebird and water bird species, but the study area was much less frequently used by day than by night. Although some species like the Whimbrel, "egrets," and the Black-bellied Plover fed principally during daytime, most other species fed more regularly and in higher numbers at night. The site, one of three in the Chacopata lagoon complex, had the highest density of prey organisms and the least number of birds by day during our study period. When Peregrine Falcons (*Falco peregrinus*) were present over the lagoon complex (Limoges 1987), shorebirds fed on vast, open mudflats more frequently than on small expanses surrounded by mangroves similar to our study area (see also Metcalfe 1984, Townshend 1984). It is possible that shorebirds did not congregate consistently in high numbers on the study area by day, in spite of its richness in prey organisms, because of possible predation. Such a local and temporary factor could have influenced the numbers of shorebirds feeding by day and thereby inflated the relative importance of periods (daylight or darkness) in the analysis of overall patterns (Table 2). However, most species (except night-herons and Black Skimmers) regularly fed by day in several nearby areas of the Chacopata

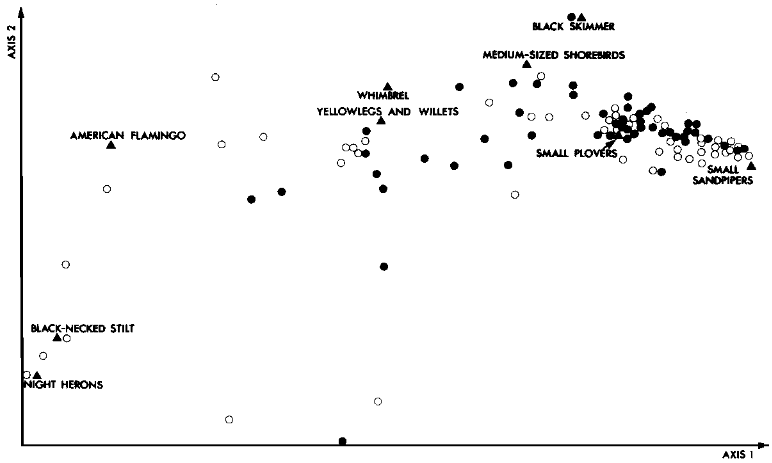

Fig. 3. Ordination of species or groups of species and the nocturnal observation periods in the space of the first 2 principal axes, as a function of the occurrence of bioluminescence. Open circles represent observation periods with presence of bioluminescence; closed circles, observation periods without presence of bioluminescence; closed triangles, species or groups of species.

TABLE 5. Correlation coefficients (Kendall's tau) between different variables and component scores of the first 2 axes in the ordination of the 102 nocturnal observation periods.[a,b]

Variables	Axis 1	Axis 2	Bioluminescence[c]
Bioluminescence	0.02	0.30***	1.00
Moonlight	−0.09	0.17*	0.46***
Wind	−0.03	0.15*	0.003
Cloudiness	0.02	0.13*	−0.04
Tide	0.09	−0.12*	0.25**

[a] Values are given only for the variables which are significantly correlated (i.e. $P < 0.05$) with components scores of at least one axis.
[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.
[c] Correlation coefficient between bioluminescence and different variables.

TABLE 6. Percentage frequency of nocturnal occurrence of small sandpipers, small plovers, and medium-sized shorebirds as a function of tide levels and classes of relative abundance.[a]

	Classes of relative abundance[c]					
	Small sandpipers[b]		Small plovers[b]		Medium-sized shorebirds[b]	
Tide level	≤35	≥36	≤2	≥3	≤4	≥5
Very high	5.9	0.0	28.9	2.9	39.0	0.0
High	10.3	7.3	13.3	5.9	17.1	4.2
Medium	19.0	25.4	11.1	29.4	14.6	25.0
Low	12.1	21.8	4.5	25.0	9.8	20.8
Very low	32.7	45.5	42.2	36.8	19.5	50.0

[a] See Table 1 for the species in each group.
[b] Percentage of observation periods during which the group of species was present.
[c] The mean number of individuals per observation period corresponds to the first 2 partitions obtained by using the PARTI package (R software, Centre de Calcul, Université de Montréal).

lagoon complex. Hence, it should not be concluded that birds fed by night because they were prevented from doing so during the day.

Tide level best explained the variations of both nocturnal and diurnal abundance of birds. Tidal changes may affect feeding times, space, and prey availability (Evans 1976, Burger et al. 1977, Whitfield 1978, Black and Collopy 1982, Puttick 1984, Powell 1987). Tidal effects varied among species and among feeding sites. At Chacopata, Whimbrels (which feed mainly on small crabs) foraged by day in the upper part of the intertidal zone during high and low tides, and they were conspicuous high-tide feeders (Fig. 2). On the other hand, medium-sized shorebirds, yellowlegs, and Willets foraged by day mainly on intermediate and low intertidal zones, and they were conspicuous medium- or low-tide feeders (Fig. 2). These groups appeared more dependent on tide level than Whimbrels. Small sandpipers, small plovers, and medium-sized shorebirds fed more frequently in large numbers at low tide during the night (Table 6). These groups, and especially small sandpipers and medium-sized shorebirds, foraged mainly in the intertidal zones which are exposed only during the periods of low and intermediate tide levels.

Other conditions or factors are related to night feeding. Predominantly sight-feeding species such as the small plovers will take advantage of the moonlight to feed at night. This is in agreement with the observations of Spencer (1953), Swinebroad (1964), Pienkowski (1982), Milsom (1984), McNeil and Robert (in press), and Robert and McNeil (in press). The influence of bioluminescence is less clear. The relationship would be indirect at best if it were demonstrated that prey (e.g. fishes), on which night-herons and Black-necked Stilts feed (Palmer 1962, Robert and McNeil in press), are attracted by luminescent organisms. The regular occurrence of high numbers of shorebirds on the study area at night could have been related to a higher prey abundance than during the day (McNeil and Robert in press, Robert and McNeil in press; see also Dugan 1981, Pienkowski 1983a, b). Comprehensive data that show shorebird prey are more abundant by night than by day in tropical latitudes are still lacking. However, tides periodically limit access to feeding sites regardless of prey abundance. This is especially true for shorebirds that feed mainly at the intermediate and low intertidal zones.

Compared to visual "sandpiper strategists," shorebirds that feed by touch should be relatively unaffected by darkness (Dugan 1981, Pienkowski 1981, Goss-Custard 1983). We expected birds that foraged principally at night to be largely touch-feeding species. However, among the species that fed predominantly during nighttime, only the medium-sized shorebirds, the Black Skimmers, and Greater Flamingos can be considered touch-foragers (Bent 1927, Davis 1951, Allen 1956, Schneider 1983, Hayman et al. 1986). All other species (i.e. small plovers, small sandpipers, night-herons and Black-necked Stilts) forage visually or both by sight and by touch (Palmer 1962, Schneider 1983 McNeil and Robert in press, Robert and McNeil in press). Consequently, we believe that foraging methods, in general, do not limit nocturnal feeding in these birds. Other daytime sight-feeders forage at night, either visually (e.g. *Pluvialis* and *Charadrius*) or tactilely (e.g. *Tringa*) (Evans 1976; Pienkowski 1981, 1982, 1983a; Wood 1983; McNeil and Robert in press; Robert and McNeil in press).

In temperate latitudes, cold temperatures and short daylight periods have been often invoked to explain the fact that wintering shorebirds feed at night (Goss-Custard 1969, Heppleston 1971, Pienkowski 1982, Puttick 1984). We found that several shorebirds and other water birds fed regularly and in high numbers at night in the tropics. Because both visual and tactile shorebirds and waders are influenced by tidal conditions and both feed regularly in darkness, it is compelling to think that nocturnal feeding constitutes a natural habit in response to regularly limited feeding space and time mainly induced by tide.

ACKNOWLEDGMENTS

This study was supported by the Natural Sciences and Engineering Research Council of Canada, Fonds F.C.A.R. (Gouvernement du Québec), and the Université de Montréal. We thank Anne Lasalle for help during the fieldwork, Claudette Blanchard for preparation of figures, and Pierre Drapeau for helpful comments on the manuscript. We also thank Benoît Limoges and Francine Mercier for access to their unpublished data. The manuscript benefited from the criticism and suggestions of Normand David. We are also indebted to colleagues of the Universidad de Oriente, in particular, José Ramón Rodríguez Silva, who was co-responsible with McNeil for the collaboration agreement between the two universities.

LITERATURE CITED

ALLEN, R. P. 1956. The flamingos: their life history and survival. Natl. Audubon Soc. Res. Rep. 5. New York, Natl. Audubon Soc.

BENT, A. C. 1926. Life histories of North American marsh birds. U.S. Natl. Mus. Bull. 135.

———. 1927. Life histories of North American shore birds, part 1. U.S. Natl. Mus. Bull. 142.

BLACK, B. B., & M. W. COLLOPY. 1982. Nocturnal activity of Great Blue Herons in a north Florida salt marsh. J. Field Ornithol. 53: 403-406.

BURGER, J. 1984. Abiotic factors affecting migrant shorebirds. Pp. 1-72 *in* Behavior of marine animals, vol. 6 (J. Burger and B. Olla, Eds.). New York and London, Plenum Press.

———, M. A. HOWE, D. C. HAHN, & J. CHASE. 1977. Effects of tide cycles on habitat selection and habitat partitioning by migrating shorebirds. Auk 94: 743-758.

DAVIS, L. I. 1951. Fishing efficiency of the Black Skimmer. Condor 53: 259.

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 (N. V. Jones and W. J. Wolff, Eds.). New York, Plenum Press.

ENGELMOER, M., T. PIERSMA, W. ALTENBURG, & R. MES. 1984. The Banc d'Arguin (Mauritania). Pp. 293-310 *in* Coastal waders and wildfowl in winter (P. R. Evans, J. D. Goss-Custard, and W. G. Hale, Eds.). London and New York, Cambridge Univ. Press.

EVANS, P. R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distribution and movement in the non-breeding season. Ardea 64: 117-139.

GAUCH, J. G. 1982. Multivariate analysis in community ecology. London and New York, Cambridge Univ. Press.

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

———. 1983. Spatial and seasonal variations in the food supply of waders Charadrii wintering in the British Isles. Proc. Third Nordic Congr. Ornithol. 1981: 85-96.

———. 1984. Intake rates and food supply in migrating and wintering shorebirds. Pp. 233-270 *in* Behavior of marine animals, vol. 6 (J. Burger and B. Olla, Eds.). New York and London, Plenum Press.

———, R. A. JENYON, R. E. JONES, P. E. NEWBERY, & R. L. WILLIAMS. 1977. The ecology of the Wash: II. Seasonal variation in the feeding conditions of wading birds (Charadrii). J. Appl. Ecol. 14: 701-719.

HAYMAN, P., J. MARCHANT, & T. PRATER. 1986. Shorebirds: an identification guide. Boston, Houghton Mifflin.

HEPPLESTON, P. B. 1971. The feeding ecology of oystercatchers *Haematopus ostralegus* L. in winter in northern Scotland. J. Anim. Ecol. 41: 651-672.

HILL, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. J. Ecol. 61: 237-249.

———. 1974. Correspondence analysis: a neglected multivariate method. Appl. Statist. 23: 340-354.

KREBS, J. R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the Great Blue Heron (*Ardea herodias*). Behaviour 51: 99-134.

LANCE, G. N., & W. T. WILLIAMS. 1966. A generalized sorting strategy for computer classifications. Nature (London) 212: 218.

LEGENDRE, L., & P. LEGENDRE. 1984. Ecologie numérique. Tome 1: le traitement multiple des données écologiques. Collection d'écologie 13. Paris, Masson.

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

MCNEIL, R., & M. ROBERT. In press. Nocturnal feeding strategies of some shorebird species in a tropical environment. Proc. 19th Congr. Int. Ornithol., Ottawa.

METCALFE, N. B. 1984. The effects of habitat on the vigilance of shorebirds: is visibility important? Anim. Behav. 32: 981-985.

MILSOM, T. P. 1984. Diurnal behaviour of Lapwings in relation to moon phase during winter. Bird Study 31: 117-120.

NIE, N. H., C. H. HULL, J. G. JENKINS, K. STEINBRENNER, & D. H. BENT. 1975. SPSS statistical package for the social sciences. New York, McGraw-Hill.

PALMER, R. S. 1962. Handbook of North American birds, vol. 1. New Haven and London, Yale Univ. Press.

PIENKOWSKI, M. W. 1981. Differences in habitat requirements and distribution patterns of plovers and sandpipers as investigated by studies of feeding behaviour. Verh. Ornithol. Ges. Bayern 23: 105-124.

———. 1982. Diet and energy intake of Grey and Ringed plovers, *Pluvialis squatarola* and *Charadrius hiaticula*, in the non-breeding season. J. Zool. 197: 511-549.

———. 1983a. Changes in the foraging pattern of plovers in relation to environmental factors. Anim. Behav. 31: 244-264.

———. 1983b. Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. Mar. Ecol. Prog. Ser. 11: 141-150.

POWELL, G. V. N. 1987. Habitat use by wading birds in a subtropical estuary: implications of hydrography. Auk 104: 740-749.

PUTTICK, G. M. 1984. Foraging and activity patterns in wintering shorebirds. Pp. 203-231 *in* Behavior of marine animals, vol. 6 (J. Burger and B. Olla, Eds.). New York and London, Plenum Press.

ROBERT, M., & R. MCNEIL. In press. Comparative day and night feeding strategies of shorebird species in a tropical environment. Ibis.

SCHNEIDER, D. 1983. The food and feeding of migratory shorebirds. Oceanus 26: 38-43.

———. 1985. Predation on the urchin *Echinometra lucunter* (Linnaeus) by migratory shorebirds on a tropical reef flat. J. Exp. Mar. Biol. Ecol. 92: 19-27.

SPENCER, K. G. 1953. The Lapwing in Britain. Hull and London, A. Brown & Sons.

SWINEBROAD, J. 1964. Nocturnal roost of migrating shorebirds. Wilson Bull. 76: 155-159.

TOWNSHEND, D. J. 1984. The effects of predator upon shorebird populations in the non-breeding season. Wader Study Group Bull. 40: 51-54.

WATMOUGH, B. R. 1978. Observations on nocturnal feeding by night herons *Nycticorax nycticorax*. Ibis 120: 356-358.

WHITFIELD, A. K. 1978. The importance of the tidal cycle to wading birds on mudflats. Bokmakierie 30: 24-25.

WOOD, A. G. 1983. Grey Plover time budgets: a hard days night. Wader Study Group Bull. 39: 51 (Abstract).

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