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PREDATOR-PREY RELATIONSHIP BETWEEN WILSON'S PLOVERS AND FIDDLER CRABS IN NORTHEASTERN VENEZUELA

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ABSTRACT.—In coastal lagoons of northeastern Venezuela, resident Wilson's Plovers (*Charadrius wilsonia cinnamominus*) forage almost entirely on fiddler crabs (*Uca cumulanta*). During the non-breeding season, particularly from November to January, plovers are seldom on foraging sites during daylight but forage more during nighttime. Objectives of this study were to document the availability of *Uca cumulanta* and to determine if night foraging by Wilson's Plovers in tropical areas is tied to abundance or activity of fiddler crabs. We used a time-lapse video camera to monitor the number of crabs outside burrows, both during nighttime and daytime. Results show that crab activity was almost exclusively diurnal. Although some crabs were active after sunset, particularly from May to August, diurnal activity of crabs was always 3–10× higher than nocturnal activity. Therefore, Wilson's Plovers feeding patterns are not exclusively a function of the period when their main prey is most active or abundant. Results best support our previous interpretation that nocturnal foraging in Wilson's Plover is a strategy for avoiding diurnal predators. *Received 17 May 1994, accepted 15 Sept. 1994.*

Recent studies on shorebirds in northeastern Venezuela and Mauritania have shown that Holarctic winter migrants and Neotropical resident species regularly feed at night in tropical environments (Robert et al. 1989, Zwarts et al. 1990, 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 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). Direct observations indicate that at night invertebrate prey items are more active or closer to the sediment surface where shorebirds forage (see McNeil et al. 1992). Similarly, the abundance of swimming prey such as fishes and insects appears to be higher at night than during daylight (Robert and McNeil 1989, McNeil and Robert 1992). In some species, individuals apparently forage at night to take advantage of nocturnally active prey and/or to avoid diurnal predation, only feeding in daytime to supplement a nighttime deficit in energy intake (see Batty 1991, McNeil et al. 1992).

In coastal lagoons of northeastern Venezuela, the resident race of the Wilson's Plover (*Charadrius wilsonia cinnamominus*) forages mainly

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(98% of their diet) on the fiddler crab *Uca cumulanta,* as do Willets (*Catoptrophorus semipalmatus*) and Whimbrels (*Numenius phaeopus*) (Morrier and McNeil 1991, McNeil and Rompré 1995). Crabs occupy the intertidal zones year-round. During their non-breeding season, particularly from November to January, the plovers' presence on foraging sites is very short during daylight but is counterbalanced by an increase during nighttime (Thibault and McNeil 1994). Day and night distributions of plovers over lagoon habitats differ substantially. Wilson's Plovers are gregarious and spend most of their time roosting during the day. After dusk, they leave their diurnal roosts and distribute themselves solitarily throughout the lagoon mudflats or fly to nocturnal individual roosts close to mangroves (Thibault and McNeil 1994). They forage during low tides, but never during the entire low-tide period, neither during daytime nor during nighttime. They also spend more time on foraging sites during the first part of the night (19:00–22:00 h) than thereafter. Morrier and McNeil (1991) and Thibault and McNeil (1994) suggested that the main reason why Wilson's Plovers are largely nocturnal is to avoid diurnal predators.

Most *Uca* species are predominantly diurnal (Young and Ambrose 1978, Zucker 1978, Zwarts 1990), but some species are active after sunset, e.g., *U. tangeri* in Mauritania (Zwarts 1990). Predator-prey relationships between shorebirds and fiddler crabs have been investigated mainly by Zwarts (1990) and Zwarts and Dirksen (1990) who considered the dependency of Whimbrels on *U. tangeri* for foraging after sunset when wintering in Mauritania.

Due to the large dependency of Wilson's Plovers on fiddler crabs and their peculiar habit of being active on foraging sites almost exclusively at night during the non-breeding season, the objectives of this study were (1) to document the monthly and diel availability of *U. cumulanta* in coastal Venezuela and (2) to determine whether night foraging in Wilson's Plovers in tropical areas is tied to the nocturnal abundance and/or activity of fiddler crabs. The factors responsible for rhythms of activity and/or abundance of fiddler crabs are not considered in this paper.

STUDY AREA AND METHODS

The study was conducted around the Bocaripo lagoon, part of the Chacopata lagoon complex (10°40'N; 63°48'W) on the north side of the Araya Peninsula, State of Sucre, Venezuela, from January to August 1992. In that region, daytime is roughly 2-h longer in June than in December. Wilson's Plovers and their prey, *U. cumulanta,* are present in the complex year-round (Limoges 1987). We used a time-lapse video camera (Fieldcam WCMS type 6/V801 field television system assembled by Fuhrman Diversified Inc., LaPorte, Texas 77571) to monitor the number of crabs outside their burrows at 10-sec intervals in a 1 × 1 m area. Infrared lamps were used to avoid disturbing crab behavior during nighttime (i.e., between sunset and sunrise). These lamps produced no heat on the plot. More than 530 h

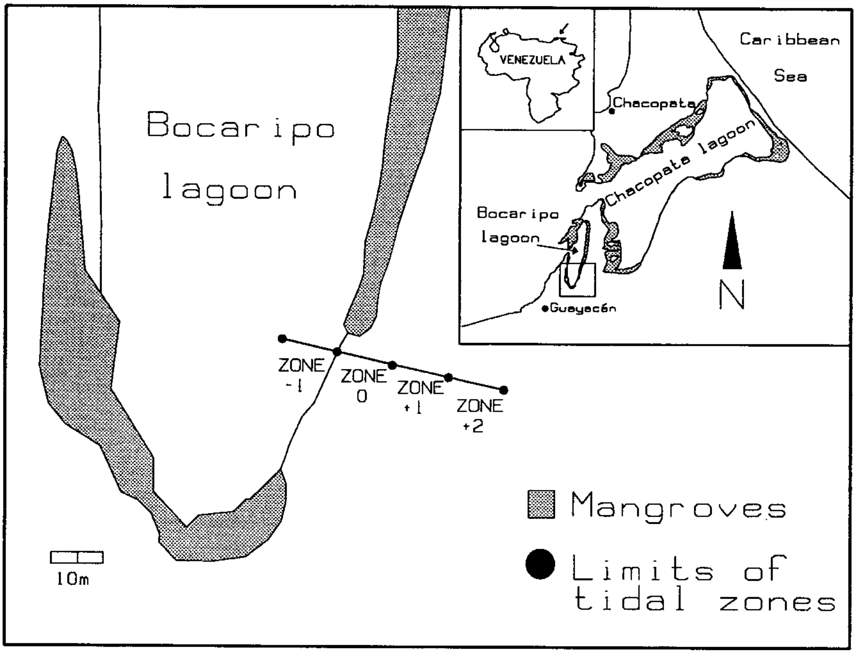

FIG. 1. Location of the transect for counting crab burrows on the shore of the Bocaripo Lagoon, State of Sucre, Venezuela.

were devoted to recording on six sites in turn around Bocaripo lagoon. The total recording time was distributed, as far as possible, equally from month-to-month during 24-h periods from March to July. In January, recording was done during only one 24-h period and, in February and August, data were collected only over one and two nights, respectively, with no recording during the daytime. At the same time that video-recording was being done, Wilson's Plovers feeding during nighttime in the surroundings of the video camera were counted hourly with a 6.8× nightscope (light intensification: ×60,000), model MK-303A (Star-tron Technology Corporation, Pittsburgh, Pennsylvania 15238, USA). In addition, from March to July 1992, we counted crab burrows in five 1 × 1 m plots distributed along a 48-m transect oriented perpendicularly to the tide line. The transect covered the entire intertidal zone (Fig. 1) from the upper tidal zone (zone +2) to the mud inside the lagoon (zone −1).

One-way ANOVA (Sokal and Rohlf 1981) was used to compare crab densities as a function of tide zones and to test the significance of hourly and monthly variation in fiddler crab activity (i.e., number of individuals outside burrows). Bartlett's test (Sokal and Rohlf 1981) was used to evaluate the homogeneity of variance on each data set before using ANOVA. In case of heterogeneity of variance, the nonparametric Kruskal-Wallis test was used (Sokal and Rohlf 1981). *G*-tests for goodness of fit to a uniform distribution (Sokal and Rohlf 1981) were performed to test the significance of hourly variation in crab activity for January (only one 24-h period). Finally, we employed Pearson's correlation coefficient to study the relationship between fiddler crab activity and plover night feeding activity.

RESULTS

Wilson's Plovers frequently were observed feeding on *Uca* crabs, both during daytime and nighttime. Wilson's Plovers are visual feeders and catch fiddler crabs by running after them. Very often, during daylight, when plovers came within a certain distance, fiddler crabs retreated underground into their burrows, preventing plovers from catching them. During nighttime, Wilson's Plovers were also observed catching some small prey, apparently insects, which abound on the mudflat at night.

From January through August, there was significant variation in crab numbers outside burrows. In May, June, and August, the nighttime crab density was significantly higher than during the January–April interval ($F_{1,82} = 30.89$, $P < 0.001$). It was also higher in July, compared to May, June and August ($H = 6.65$, df = 1, $P < 0.001$). Overall, from January through July, the presence of Wilson's Plovers feeding at night varied inversely with crab activity ($r = -0.735$, N = 7, $P < 0.05$; Fig. 2A). During daytime, monthly variation in crab numbers was significant ($F_{5,66} = 27.20$, $P < 0.001$), increasing from January through May and decreasing thereafter (Fig. 2B).

Each month, except February and August (no data for daytime), crabs were outside burrows in significantly higher numbers by day than by night (January: $G = 121.90$, df = 23, $P < 0.001$; March: $F_{19,72} = 11.30$, $P < 0.001$; April: $F_{20,94} = 5.39$, $P < 0.001$; May: $F_{21,34} = 5.16$, $P < 0.001$; June: $F_{23,75} = 10.31$, $P < 0.001$; and July: $F_{23,76} = 1.88$, $P < 0.05$; see Fig. 3). Overall, crab activity tended to be higher just after sunrise, except in April, due to high tide which took place during early morning. Although some activity was observed after sunset, particularly from May to August, the diurnal activity of crabs was always 3–10× higher than their nocturnal activity (Figs. 2 and 3).

Wilson's Plovers were seen feeding in zone 0 and, occasionally, in zone +1 of our transect (Fig. 1). During April and May, the mudflat dried up in zones +1 and +2. In fact, April and May had the lowest tides of the year. Nevertheless, the number of burrows in zones +1 and +2 did not vary during the five months ($F = 4.48$, ns; see Fig. 4). However, mainly due to May data, zone 0 was the one where the number of burrows reached the highest density ($F_{3,16} = 6.44$, $P < 0.01$). Since low tides began in March, the mudflats of zone −1 remained uncovered most of the time, and crabs used that zone more than before. But during other months, the water line remained in zone 0, and zone −1 was covered most of the time. As a consequence, fiddler crabs left this zone.

DISCUSSION

The time-lapse video camera revealed that each burrow was normally occupied by a crab. This indicates that the method used by Zwarts (1985),

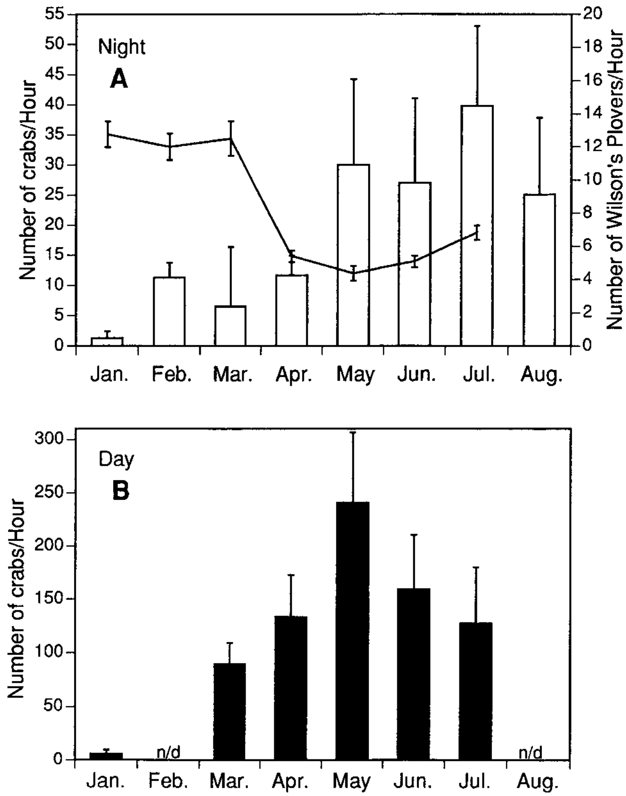

FIG. 2. Seasonal variation in the number of fiddler crabs observed per hour outside burrows (bars) during nighttime (A) and daytime (B). The line in A represents the variation in the number of Wilson's Plovers foraging at night. Vertical lines represent 95% confidence intervals and n/d indicates the absence of data.

i.e., count of burrows, is appropriate to estimate crab density. Our count of burrows revealed that zone 0 of our transect (Fig. 1) had the highest crab density. This zone also supported the majority of Wilson's Plovers feeding on the mudflat.

Zwarts (1990) reported that *U. tangeri* is active during the first part of the night in Mauritania. In Chacopata, *U. cumulanta* remained active after sunset, but their activity was always three to 10 times lower at night than during the day (Figs. 2 and 3). In addition, they showed no preference for any particular part of the night, their activity being low but regular from dusk to dawn, particularly from May to August (Figs. 2 and 3). Taking into account the fact that *U. cumulanta* is considerably less active at night than during the day, the fact that Wilson's Plovers, during the

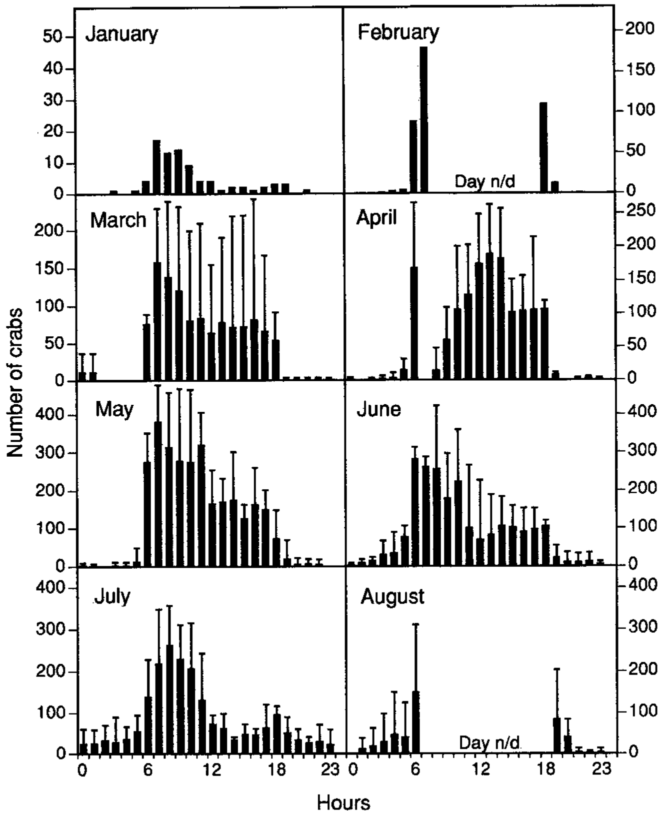

FIG. 3. Diel variation in the number of fiddler crabs recorded outside burrows between January and August. Vertical lines represent 95% confidence intervals and n/d indicates the absence of data.

non-breeding season, rest during daytime and forage almost exclusively during the nighttime cannot be interpreted as a strategy to take advantage of the period when their main prey is most active and/or abundant. This conclusion is reinforced by the fact that, overall, the presence of Wilson's Plovers feeding at night varied inversely with nocturnal crab activity. Morrier and McNeil (1991) suggested that nocturnal foraging by Wilson's Plovers is a strategy for avoiding diurnal aerial predators. This study supports that explanation. In fact, why should the plovers complicate their life by avoiding foraging when their prey are more plentiful and can more easily be detected by sight? Nevertheless, the activity of *Uca* crabs, although much lower at night than during daytime, appeared sufficient for Wilson's Plovers to forage almost exclusively during nighttime.

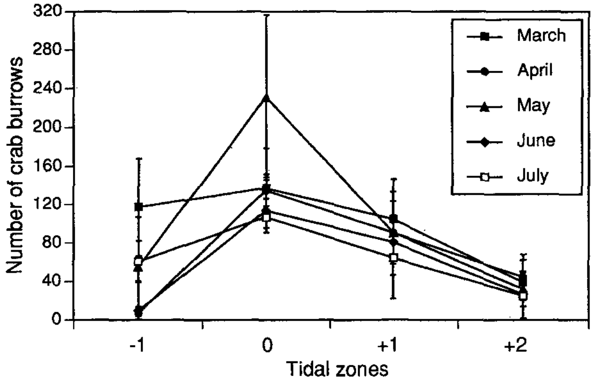

FIG. 4. Monthly variation in the number of burrows of fiddler crabs counted per m² as a function of tidal zones for each month between March and July. Vertical lines represent 95% confidence intervals.

The number of *Uca* crabs per hour outside burrows (Fig. 2B) was highest in May, and the extent of their nighttime activity started increasing in May and was at a maximum in July (Fig. 2A). In the Chacopata Lagoon complex, Wilson's Plovers start egg-laying at the beginning of May and the last eggs hatch around mid-August (Thibault 1993, Thibault and McNeil, unpubl. data). In accordance with the hypothesis that breeding seasons of birds have evolved so that the birds have their young when food is most available (see Lack 1954, Marshall 1961), we suspect that Wilson's Plovers start breeding when food resources become more abundant and, particularly, in such a way that hatching coincides with the time when nocturnal abundance of *Uca* crabs outside burrows is highest, thus ensuring better feeding success for chicks. In addition, during the laying and incubation periods, compared with the non-breeding season, the feeding pattern of Wilson's Plovers changes radically; during nighttime, males incubate most of the time and females forage (Thibault 1993, Thibault and McNeil, unpubl. data). Males and non-breeding individuals forage during the daytime (Thibault 1993); this could explain the decrease in the number of plovers observed feeding at night during April as compared with January–March.

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