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Foraging Habitat Use in a Mediterranean Estuary by Dunlin, *Calidris alpina*

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ABSTRACT

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In the Mediterranean sea tides oscillate only a few meters and water displacement is mainly due to the influence of winds and changes in atmospheric pressure. This makes Mediterranean estuaries an unpredictable system for shorebirds. The causal mechanisms on habitat selection of Dunlin was studied in such system at Ebro Delta, where littoral and rice field habitats were available for shorebirds. Dunlins choose to forage littoral habitats where prey are more abundant showing higher intake rate in this habitat, however, this species also uses rice fields. No differences in microhabitat use and foraging technique was found between habitats. Intake rate and searching speed were lower when high bird density was present in littoral but not in rice fields. Therefore, the use of both habitats can be explained by a combination of density-dependent effects following the "ideal free distribution" model and the unpredictability of water movements that reinforce that effect. The study suggests the importance of rice fields as alternative habitats and that the availability of these alternative habitats could contribute significantly to the maintenance of wintering populations of shorebirds in Mediterranean estuaries.
ADDITIONAL INDEX WORDS: *Habitat selection, mud flats, rice fields, shorebirds, Spain.*

INTRODUCTION

Shorebirds usually forage during winter in intertidal habitats. Foraging possibilities of animals living in intertidal areas are further restricted by the tides. The cyclic tidal inundation of mudflats and beaches causes changes both in the available feeding space and in the diversity and availability of prey items (BURGER *et al.*, 1977; PUTTICK, 1980). Usually, the rhythm of tides is highly predictable as exposed areas fluctuate and the timing of tides varies regularly. Birds feeding on tidal flats can foresee at what time the foraging area will be exposed, and learn whether or not there is a daily time shift in the tidal cycle (DAAN and KOENE, 1981). However, there are tidal areas where onset and duration of tides are not regular and tidal cycle can be affected by a combination of unpredictable factors such as wind and atmospheric pressure. The tidal areas may remain submerged for long periods which restricts or makes their foraging impossible, or tidal areas emerged for too long time, causing a decrease in prey availability due to desiccation effects (EVANS, 1976).

Most wader studies have been carried out on Atlantic or North European areas (*e.g.* HARRIS, 1967; GOSS-CUSTARD, 1969; ZWARTS, 1978) where tidal oscillations have great importance for shorebirds. However, studies on shorebirds in the Mediterranean are very scarce. In the Mediterranean, tides oscillate only a few meters and water displacement is mainly due to the influence of winds and changes in the atmospheric pressure (MARTINEZ-VILALTA, 1985). The Ebro Delta is one of the most important wintering areas in the Mediterranean (GRIMMET and JONES, 1989; BARBOSA, 1992), where two main habitats are used by shorebirds, littoral and rice field (BARBOSA, 1994). The homogeneity between these habitats in the absence of tidal oscillations provides an excellent opportunity for a comparative study of habitat exploitation by a common wader species as Dunlin. The causal mechanisms by which Dunlin uses both habitat is discussed comparing the foraging behavior between main and alternative habitats.

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STUDY AREA AND METHODS

The study was conducted at Ebro Delta Natural Park (NE Spain, 40°43′N 00°44′E) which is one of the main wintering areas for *Calidris alpina* in the Mediterranean with an average population around 10,000 individuals (GRIMMET and JONES, 1989; BARBOSA, 1992). It consists of 32,000 ha in total, comprising 15,000 ha of rice fields, 9,500 ha of market gardens, and 7,500 ha of natural wetlands (beaches, saltmarshes, lagoons). The area potentially usable by Dunlin is 14,549 ha, which 12,376 ha (85%) are rice fields and 2,173 (15%) are littoral habitats. These areas are based on the information of Natural Park Service obtained through annual bird censuses and they are measured by means of aerial photography.

There are two areas with distinct water regimen in the Ebro Delta. Littoral habitats, in which water level is mainly determined by winds, and rice fields in which the water level is determined by annual cyclic floodings from April to September. From October to March the irrigation channels are open and water level decreases progressively.

Table 1. *Statistics for variables considered in each habitat. x = mean, se = standard error.*

	Littoral	Rice fields
	x se	x se
Intake rate (residuals)	2.12 ± 1.43	−5.73 ± 1.14
% Time pecking (residuals)	2.16 ± 3.62	−5.88 ± 4.41
% Time probing (residuals)	−1.52 ± 2.48	4.70 ± 3.30

Habitat selection and foraging behavior were studied in Delta's Dunlin population. Observations were made between November and April of 1990–1991 and 1991–1992. Bird counts were carried out during regular surveys on the area potentially usable by Dunlin along the whole study period.

Behavior was recorded using the focal observation method (ALTMANN, 1974). Focal birds were randomly chosen during regular surveys on the study area and their behavior was tape-recorded during a 2 min period on average. All observations were made during daylight with 8×30 binoculars or a 40X-60X spotting scope. To avoid problems of pseudoreplication (HULBERT, 1984), individuals were sampled only once. As birds were not colour-marked, I sampled no more birds in a flock than being sure they were different individuals. In a flock of about 100 individuals, I sampled 5–10 birds from the upper side, 5–10 birds from the lower side, 5–10 birds from the left side, and 5–10 birds from the right side of the flock. Each bird sampled were at least at 20 m from the previous bird sampled. This procedure assures that different individuals were sampled (see BARBOSA, 1995). Pecking and probing rates were recorded as estimates of intake rate (BAKER and BAKER, 1973). Foraging technique (visual or tactile) was assigned by the percentage of time pecking (visual) or probing (tactile). Capture rate has been considered a bad predictor of intake rate, especially when comparing different habitats, and therefore different prey types. Large preys usually produce high handling times and are often taken at a much slower rate than small prey. Therefore, capture rate could actually be an inverse measure of biomass intake rate. However, I have selected this methodology to estimate intake rate, because in my study area, there are no differences in prey size captured by Dunlin (Mann-Whitney U test, U = 1.31 $p > 0.05$ n = 103; rice fields x = 10.00 ± 1.38 n = 27 and littoral x = 8.58 ± 0.41 n = 76). Therefore, size prey did not influence in the estimate of intake rate throughout capture rate. Size of prey taken were estimated visually by comparing total length with bill length, this being approximately 32 mm in Dunlin (CRAMP, 1983). Step rate was recorded as an estimate of searching speed (SPEAKMAN and BRYANT, 1993; BARBOSA, 1994). Flock size was recorded to assess its effect on foraging behavior.

Foraging behavior could be affected by flock size (BARBOSA, 1995). To control for this potential effect each variable was regressed against flock size and the residuals from the regression were use in the statistical analyses. In each observation, habitat (littoral or rice fields) and water depth were also recorded. Water depth were recorded considering shallow water level (below the half of tarsometatarsus) and deep water (above the tarsometatarsus). The frequency of birds using each category was used in the analyses.

Statistics include Student's t, Chi-square, Mann-Whitney U, regressions and ANOVA test. All test are two-tailed. Probability values below 0.05 are termed significant.

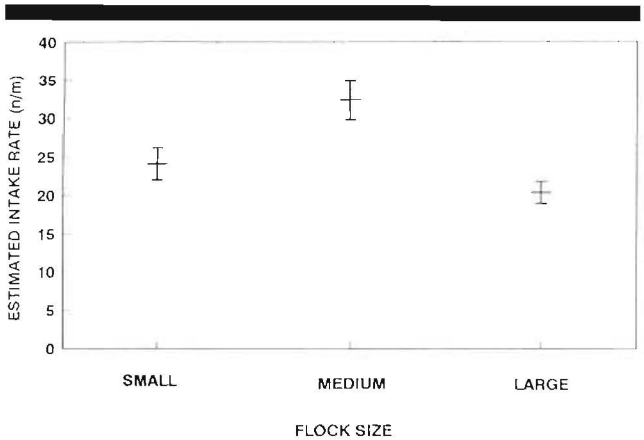

Figure 1. Differences in intake rate related to flock size in littoral habitats.

RESULTS

I have recorded habitat use of 4,904 individuals, which represent about 50% of the Dunlin population in Ebro Delta. Littoral habitats were used by the 76.75% (3,764 birds) of the birds observed, whereas 23.40% (1,140) used rice fields. The availability of littoral habitats is 15% of the potentially usable area by Dunlin, whereas rice fields represent 85% (see Methods section) indicating that Dunlins selected littoral habitats to forage.

Results of foraging technique used in each habitat showed no differences between habitats. Visual technique, characterized by percent time pecking was higher in rice fields than in the littoral habitats. In contrast, tactile technique, characterized by percent time probing, was higher in littoral habitats, but these differences were not significant ($t_{103} = 1.36$ $p > 0.05$ and $t_{103} = -1.52$ $p > 0.05$ respectively; Table 1).

Dunlin forages on areas covered by deep water (above tarsometatarsus) in both habitats (95% and 63.25% of observations in rice fields and littoral, respectively). Analyses on water depth use show differences within habitat (rice fields: $\chi^2_1 = 20.57$ $p < 0.01$ and littoral: $\chi^2_1 = 5.90$ $p < 0.01$) and between habitats ($\chi^2_1 = 8.77$ $p < 0.01$). Differences between habitats could be attributed to differences in the use of shallow water (5% and 36.51% in rice fields and littoral respectively).

Intake rate showed differences between habitats. Dunlins have a greater intake rate ($t_{103} = 3.79$ $p < 0.01$; Table 1) in littoral than in rice field habitats.

The relationships between intake rate and searching speed with flock size were not equal in both habitats. ANOVA results showed no differences in intake rate among small, medium and large flocks in rice fields ($F_{2,25} = 1.60$ $p > 0.05$), however in littoral habitats there were significant differences among flocks categories ($F_{2,73} = 4.05$ $p < 0.05$; Fig. 1). On the other hand, searching speed was not related to flock size in rice fields ($r = -0.14$ $n = 27$ $p > 0.05$) but in littoral habitats an inverse significant relationship was found ($r = -0.22$ $n = 76$ $p < 0.001$).

DISCUSSION

Variation in habitat occupancy by a species can arise from many factors, but the effects of the population density of that species may be especially important (WIENS, 1989). BROWN (1969) proposed that habitats differ in their suitability to a species and that individuals will preferentially select the most suitable habitat. Optimal foraging theory predicts that the foraging distribution of predator that inhabit heterogeneous habitats should be non-random (KREBS *et al.*, 1983). Some models assume a direct relationship between foraging distribution and prey density (MCARTHUR and PIANKA, 1966) which have been supported by empirical results (PRESTON, 1990).

Many shorebirds are known to concentrate their feeding effort in areas which have the highest prey densities to obtain the highest intake rates (BRYANT, 1979). At Ebro Delta Dunlin prefer to forage in littoral habitats showing the highest densities and the highest intake rate. This observation agrees with the greater abundance and diversity of invertebrates potentially preyed upon by Dunlin in littoral habitats relative to rice field (CHINCHILLA and COMIN, 1977; FORTUÑO, 1988; BROS and BECH, 1989).

However, several studies have pointed out that patch selection is not based simply on prey density (KELSEY and HASSALL, 1989) but also on physical characteristics of the habitat. For example, wetness can influence substrate penetrability. Substrate characteristics not only affect patch selection but also the foraging technique used in the patch (GRANT, 1984). Nevertheless, our results indicate no differences between habitats in foraging technique in terms of pecking or probing. On the other hand, Dunlins select water covered areas in both habitats, showing a clear microhabitat preference available in littoral and rice field habitats. These two results indicate that in our study area habitat selection by Dunlin would be affected by prey density more than other factors. However, a question arises about the use of other habitats instead of the optimal one.

Why Dunlin Uses Rice Fields in Ebro Delta?

The use of alternative habitats to forage has been explained as birds cannot satisfy their daily energy intake because either the daily or tidal cycle are too short (DAVIDSON and EVANS, 1986; MARTIN, 1991; VELASQUEZ and HOCKEY, 1992). For the Mediterranean two explanations can be proposed. The unpredictability of tides in the Mediterranean coast implies that during long periods (several days), the intertidal area could be submerged and therefore not available to birds. On the other hand, intertidal habitats could be emerged for several days and prey could be unavailable due to desiccation (EVANS, 1976).

Another explanation to the use of alternative habitats is related to density-dependent effects on habitat occupancy (BROWN, 1969; WIENS, 1989). As population density increases, the available area of this habitat type becomes saturated with individuals, increasing interference and reducing intake rates to the same level as can be achieved on lower quality patches. In these circumstances it will then pay some individuals to leave the better patches to occupy the poorer ones, as predicted by the "ideal free distribution" model (FRETWELL and LUCAS, 1970).

In the study area a combination of these two effects seems to account for the distribution of Dunlins over the different habitats. At the Ebro Delta, littoral feeding areas have limited availability. At the same time, wind effects may submerge certain areas and may emerge others. However, wind effects can reduce the available littoral feeding areas by increasing associated foraging costs and, therefore reinforcing density-dependent effects. Intake rate and searching speed will be lower when high bird density is present indicating associated costs (PUTTICK, 1980; see also GOSS-CUSTARD, 1980). My results show lower intake rates and searching speed while foraging in large flocks at littoral feeding areas, but these results were not found in rice fields. This could be considered as costs associated to forage in large flocks at littoral feeding areas, considering that larger flocks are present in rice fields (Barbosa unpublished). This supports the hypothesis that causal mechanisms on foraging habitat use by Dunlin are a combination of both unavailability of feeding areas and density-dependent effects.

This study suggests the importance of rice fields as alternative habitat in Ebro Delta. It is very likely that the availability of these alternative habitats contributes significantly to the maintenance of wintering populations of shorebirds in Mediterranean estuaries, although more evidence is needed.

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□ RESUMEN □

En el mar Mediterráneo las mareas oscilan escasos metros y los desplazamientos de agua se deben principalmente a la influencia de los vientos y a cambios de la presión atmosferica. Esto hace que los estuarios medierráneos formen un sistema con un gran componente de impredecibilidad para las aves limícolas. En el presente artículo, se estudian los mecanismos cuasales de la selección de hábitat del Correlimos Comùn (*Calidris alpina*) en el Delta del Ebro, donde hábitats litorales y arrozales son utilizados por las aves limícolas. El correlimos Comyun selecciona como zonas de alimentación los ambientes litorales donde las presas son más abundantes, mostrando las tasas de ingestión más altas. Sin embargo, esta especie también utiliza los arrozales para alimentarse, aunque en menor medida. No se han encontrado diferencias en la técnica de obtención de alimento entre hábitats. La tasa de ingestión y la velocidad de búsqueda de presas fueron más bajas cuando la densidad de aves era más alta. Este resultado no se encontró en las aves que se alimentaban en el arrozal. En cuanto al uso de la profundidad a la cual se alimentaban las aves, en ambos hábitats los correlimos utilizaban aguas profundas (por encima del tarsometatarso).

El uso de ambos hábitats por el Correlimos Común, puede explicarse por una combinación de efectos denso-dependientes siguiendo elmodelo de "distribución libre ideal" y por la impredecibilidad de los movimientos de agua que refuerzan dicho efecto. Este estudio sugiere la importancia de los arrozales como hábitats alternativos y su importancia para el mantenimiento de la población invernante de aves limícolas en los estuarios Mediterráneos.