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Assessing alternative anthropogenic habitats for conserving waterbirds: salinas as buffer areas against the impact of natural habitat loss for shorebirds

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Abstract. Because many natural waterbird habitats are threatened by human disturbance and sea level rise, it is vitally important to identify alternative wetlands that may supplement declining natural habitats. Coastal salinas are anthropogenic habitats used for obtaining salt by evaporation of sea water. These habitats support important numbers of waterbirds around the world, but their importance as feeding habitats is poorly understood. I evaluated salinas as feeding habitats relative to natural intertidal habitats by comparing time spent foraging, prey-size selection, and net energy intake rate of four overwintering small-sized shorebird species on intertidal mudflats and on adjacent salinas. In winter, Dunlin *Calidris alpina*, Curlew Sandpiper *C. ferruginea* and Sanderling *C. alba* predominantly used the mudflats, whereas Little Stint *C. minuta* fed mainly on the salina. In the pre-migration fattening period, all species preferred to feed on the salina, significantly increasing the time they spent feeding in the supratidal pans. Net energy intake rates (kJ min^{-1}) were significantly higher on the salina than on the intertidal mudflats in 60% of all comparisons. On average, salina contributed 25.2 ± 24.2% (range: 4–54%) of the daily consumption in winter and 78.7 ± 16.4% (range: 63–100%) of the daily consumption in the pre-migration period. I recommend that modern active salinas maintain flooding conditions in the evaporation pans throughout winter, thus increasing the available surface for foraging waterbirds. I conclude that the conservation of salinas at coastal wetlands is a viable approach for shorebird conservation.

Introduction

Intertidal habitats are among the most productive in the world. They are also among the most threatened, with destruction by coastal development, land reclamation, fisheries, sea-level rise and by disturbance through tourism (Weber et al. 1999). The loss of these habitats could have major implications for many waterbirds that largely rely on intertidal habitats when on passage or wintering (Howe et al. 1989; Goss-Custard et al. 1994; Weber et al. 1999). The extent to which a population declines following habitat loss depends on the efficiency with which it alters its space use strategies (Dolman and Sutherland 1995; Goss-Custard and Sutherland 1997). The effects of habitat loss have resulted in increasing demands on ecologists to inform managers and conservation policy makers of likely responses of populations to new circumstances (Pettiford et al. 2000). In this sense, it has been shown on a worldwide scale that several anthropogenic habitats can provide alternative or complementary feeding habitats for waterbirds, such as rice fields (Fasola and Ruiz 1996; Elphick and Oring 1998; Elphick 2000), coastal grazing marshes (Williams and Hall 1987; Milsom et al. 2000), fish ponds (Young and Chan 1997; Young 1998) or salinas (Britton and Johnson 1987; Collazo et al. 1995; Warnock and Takekawa 1995, 1996; Masero et al. 2000). Within this framework, evaluating the potential role of the anthropogenic habitats relative to more natural habitats is a key issue in conservation biology (Elphick 2000).

Coastal salinas (also called saltworks, saltpans or salt ponds) are anthropogenic habitats used for obtaining salt by evaporation of sea water. They occur in large expanses in several geographical regions, extending, for example, over 100 000 ha in the Mediterranean basin (Sadoul et al. 1998). Salinas are often classified as functional wetlands with a high biological richness, supporting important numbers of waterbirds around the world (Britton and Johnson 1987; Martin and Randall 1987; Myers et al. 1987; Collazo et al. 1995; Warnock and Takekawa 1995; Carmona and Danemann 1998; Sadoul et al. 1998). Despite this, the importance of salinas as feeding habitats relative to natural habitats is poorly understood. Although many shorebird species feed on intertidal mudflats and adjacent salinas (e.g., Velasquez et al. 1991; Velasquez and Hockey 1992; Warnock and Takekawa 1995, 1996; Masero et al. 2000), few studies have compared the feeding ecology of shorebirds using both habitats. Masero and Pérez-Hurtado (2001) showed that food consumption in salinas by Common Redshank *Tringa totanus* contributed significantly to their total daily energy requirement (DER) prior to spring migration, suggesting that salinas act as an important buffer area. However, the value of salinas is being threatened by loss due to changing economics driven by world trade and competing land-uses (Rufino and Neves 1992; Sadoul et al. 1998). There is, therefore, an urgent need to evaluate the ecological value of salinas and to provide a base of information for site-managers of coastal areas.

The quality of different feeding habitats for waterbirds can be directly measured in studies on food selection and intake rate, and the distribution patterns of species can be explained accordingly (Piersma et al. 1993b; Goss-Custard et al. 1995). This approach is more appropriate to evaluate different feeding habitats than studies of food abundance, since it is not total food abundance that affects the suitability of an area, but rather the potential food-intake rate (Piersma et al. 1993a). In this paper, I evaluate salinas as feeding habitats relative to natural intertidal habitats by comparing time spent foraging, prey-size selection, and net energy intake rate of overwintering small-sized calidrid sandpipers on intertidal mudflats and on adjacent salinas. As large numbers of small-sized calidrids feed at low tide in coastal salinas (Velasquez and Hockey 1992; Warnock and Takekawa 1995; Masero et al. 2000), I predict that the potential energy intake rate does not differ between the two habitats. Additionally, data are provided on foraging behaviour and factors that influence the time spent feeding in salinas.

Methods

I studied four long-distance migrating shorebirds: Sanderling *Calidris alba*, Little

Stint *C. minuta*, Curlew Sandpiper *C. ferruginea* and Dunlin *C. alpina*. I chose these species because (1) long-distance migrating shorebirds in particular have life history characteristics that make them rather susceptible to changes in their natural habitats (Piersma et al. 1996), and therefore, to identify valuable habitats for these species is an international conservation challenge (Myers et al. 1987); and (2) salinas are anthropogenic habitats thought to be very important for small-sized calidrid sandpipers (Warnock and Takekawa 1995; Masero et al. 2000).

Study area

Fieldwork was carried out on the intertidal mudflats of the Guadalete River (20–30 ha) and on the adjacent salina named La Tapa (400 ha), at Cádiz Bay (36°23′ N, 6°8′ W), SW Spain (see Figure 1 in Masero et al. 2000). Simultaneous counts on the mudflats and salina showed that populations of shorebirds remain in the study area at low tide and that there are very few shorebird movements between this area and the rest of the bay (Hortas 1997). The count at high tide in the salina is considered to represent the total number of shorebirds present in the study area, while the difference between the total counted at high and low tide in the salina is considered to be the part of the population of shorebirds which goes to the mudflat to feed (Masero and Pérez-Hurtado 2001). About 3,000 shorebirds overwinter in the study area. Compared with other European intertidal areas, the intertidal mudflats support high shorebird densities during winter (98 birds ha^{-1} on average; Masero et al. 2000). Winter extends from late November until late March, although the last month can be considered to be a pre-migration period for small-sized calidrids, since the majority of the populations leave the study area in April (Masero et al. 2000).

The salt extraction in the salina involves three different types of pans at slightly different levels: storage, evaporation and crystallization pans (135, 179 and 41 ha, respectively). Seawater is pumped into the storage pan and is circulated through a number of evaporation pans. As water flows, the salt concentration increases by evaporation to near saturation point and the brine is pumped to the crystallization pans, which produce a salinity gradient ranging from 30 to 60‰ in the storage pan to >200‰ in the crystallizers. The majority of the evaporation pans, as well as the storage pan, are bounded by gently sloping mud dikes, and a large proportion of the perimeter of each is composed of the former lagoon shoreline. The bottoms of these pans are not level and the water depths range from a few centimeters to 80 cm and 30 cm in the storage and evaporations pans, respectively. The crystallizers are bounded by steep-side dikes and their bottoms have a flat topography (water depth: 15–20 cm). Emergent aquatic vegetation is absent from the salina. Between 40 and 53% of the evaporation pans are emptied every winter between late November and mid-March, remaining usually dry during this period. The storage pan is emptied from late October to early April. During spring and summer the water level in each pan is maintained at one level. For more details on the study area see Masero et al. (1999).

Feeding time allocation

The daily time spent feeding on the salina and on the intertidal mudflats was calculated from late January to mid-April 1995. Except in April, the daily time spent feeding in each habitat was derived from time-activity budgets obtained by Masero et al. (2000). Methods for calculating the daily time spent feeding are described in detail in that study and in Masero and Pérez-Hurtado (2001), so only a brief description is given here.

The daily time spent feeding was derived using the proportions of feeding calidrids in each habitat relative to their total populations, number of minutes that habitat was available, and proportion time calidrids spent feeding. For this calculation, the duration of the low-tide period in the salina was considered the same as the emersion period on the mudflats; the rest, up to the completion of the tidal cycle, was considered to be high tide (Masero and Pérez-Hurtado 2001).

During the censuses I noted for each pan the percentage of flooded surface. Subsequently the basin surface for each pan was calculated from an aerial photograph and the total surface of flooded pans was calculated for each census. I also noted the total number of shellfishers on the intertidal mudflats and raptors in both habitats.

(i) Diurnal feeding activity: in order to determine the number of feeding and non-feeding birds in the salina during daylight hours, I conducted weekly surveys of the whole salina at both high and low tide (one high tide count and one low tide count). I began each census 2 h before high or low tide, and each census lasted approximately 4 h. Calidrids were counted from the edge of each pan using a car as a blind.

The day following a census of salina, the number of feeding and non-feeding birds was counted every 60 min throughout the low-tide period (7–9 h) on the adjacent mudflats. Feeding activity on the mudflats, expressed as the percentage of birds feeding, was calculated for each count, and these percentages were later averaged for the whole low-tide period (Zwarts et al. 1990b).

(ii) Nocturnal feeding activity: nocturnal numbers of feeding and non-feeding calidrids were counted in the salina (high and low tide) and on the mudflats. Calidrids were observed at 10–50 m using a 6× light intensifier (70,000×). Artificial illumination from a nearby town helped us to identify calidrids and their activity. A total of 11 counts were performed in each area from the end of January to mid-April 1997, with consecutive counts at least a week apart. During this period, the number of individuals of each species present in the area was very similar to that in 1995, and the environmental conditions in the salina and on the intertidal area did not noticeably change in these 2 years (Masero and Pérez-Hurtado 2001). The feeding activity at night on the mudflats was calculated as described above for diurnal feeding activity.

Foraging behaviour and prey-size selection

Data were collected from late January to early February, and again in late March 1995 prior to spring migration. These two periods are considered separately because the latter coincides with the demanding and critical pre-migration fattening period

(Pfister et al. 1998). All species were observed at distances < 30 m. Individual calidrids were selected at random and observed for 1-min periods through a 25×60 telescope during daylight, usually from inside a car. To minimise the risk of pseudo-replication (Hulbert 1984), each new bird selected for observation was at least 10–20 m from the previous one.

The following information was recorded during the focal observations: number of successful prey captures, and type and size of prey caught. The size of each prey was estimated by comparing it with the birds' bill length (calidrids swallowed prey with the bill out of the sediment). Bill length was 33, 37, 25 and 19 mm for Dunlin, Curlew Sandpiper, Sanderling, and Little Stint, respectively (means for birds captured at Cadiz Bay). Prey identification was confirmed by analysis of prey remains in faeces.

Masero et al. (1999) provide information about the species composition, size distribution, and biomass of available prey items for overwintering shorebirds in the study area.

(i) Intertidal mudflats: data were collected for all four species during winter. However, in the pre-migration period, because of the low number of foraging Sanderling, Little Stint and Curlew Sandpiper on the intertidal area (see Results), data were collected only for Dunlin. Foraging calidrids were watched throughout the low-tide period (7 h on average). Some food items recorded were too small to be visually identified in the field. Analysis of faeces collected in roosting areas at high tide ($n = 83$) and available prey indicated that all small items were mudsnails *Hydrobia ulvae* (no pellets were found in the study area).

Worms taken by Sanderling (range: 1/4–1/2 bill length) and Little Stint (range: 1/3–2/3 bill length) were small and their length was difficult to assess. For worm length estimates, the size frequency distribution of ragworm *Nereis diversicolor* in the faeces of Sanderling and Little Stint was used as an estimate of the sizes taken by both species (*Nereis* lengths were estimated from mandible lengths; see equation in Appendix 1). The absence of mandibles of *Nereis* larger than 12 mm in these provides confidence in the reliability of the estimates (see Results).

Correction for possible bias in the field estimates of captured *Nereis diversicolor* by Curlew Sandpiper and Dunlin was made using the function given in Masero and Pérez-Hurtado (2001) for Common Redshank (note that the bill length is similar in these species). The shell length of intact *Hydrobia* in faeces was measured. The length of broken shells, for which the width at the base could be measured, was estimated using the equation shown in Appendix 1. The average ingested size of *Hydrobia* was estimated using the log-linear model of Dekinga and Piersma (1993).

(ii) Salina: prey items taken by calidrids in the salina were too small to be visually identified. Prey identification was determined by analysis of prey remains in faeces collected in the pans ($n = 58$) and knowledge of the prey available (Masero et al. 1999). Both studies confirmed that the small items were the crustacean *Artemia*. Data were collected during both low and high tide periods (±2 h of each tide period). All four species used a visual foraging technique to feed on *Artemia*. After observing the calidrids at close range (<15 m) I assumed each peck to be an individual capture, because each was followed by swallowing movements.

Energy intake rate, daily consumption and theoretical DER

On the mudflats, biomass intake rate was calculated by multiplying the number of a size class taken per minute by the ash free dry mass (AFDM) of that size class in the mud, and summing the values for all size classes (Goss-Custard 1977). In the salina, the AFDM of the mean *Artemia* size in the pans was calculated and multiplied by the numbers taken per minute to give estimates of the biomass of this prey per unit time. In some small evaporation pans the mean *Artemia* size was lower than in the other pans. In order to control this variation among pans, I considered the numbers of feeding calidrids in each type of pan. *Artemia* had a relatively small variability in biomass in each pan (<0.00003 g AFDM), thus making estimations of energy intake rates more precise. The equations used to predict prey biomass from prey size are shown in Appendix 1. I used length–weight regression equations obtained during winter, as there is seasonal variation in the body condition of the macroinvertebrates eaten by shorebirds feeding on the intertidal areas (Zwarts and Wanink 1993).

The biomass intake rates were converted to energy intake rates using the following energy values: 22.2, 22.8, and 20.9 kJ g^{-1} AFDM for *Nereis*, *Artemia*, and *Hydrobia*, respectively (see Masero and Pérez-Hurtado 2001). An assimilation efficiency of 80% for *Nereis* (Zwarts et al. 1990a), 76% for *Hydrobia* (Zwarts and Blomert 1990), and 70% for *Artemia* was assumed to calculate the net energy intake rates. This value of 70% was assumed by Turpie and Hockey (1993) for shorebirds feeding on prawns. As the assimilation efficiency is strongly determined by food type rather than bird type (Castro et al. 1989), I assumed this value of 70% for shorebirds feeding on the crustacean *Artemia*.

Daily consumption (kJ bird^{-1} day^{-1}) was estimated assuming that nocturnal and diurnal intake rates on the mudflats were equal, and that Curlew Sandpiper and Sanderling in late March obtained at least the same intake rate on the mudflats as in winter. I calculated the field metabolic rate (FMR) according to Nagy's (1987) equation. In winter the theoretical daily energy requirement (DER) was considered to be equal to the FMR, and in the pre-migration period DER was FMR plus DER of fat-protein deposition (see details in Masero and Pérez-Hurtado 2001). In order to calculate FMR I used lean mass (from Zwarts et al. 1990c) and expected body mass in winter and pre-migration period, respectively. I calculated expected body mass for each calidrid for the day I recorded feeding (late March), assuming calidrids start to gain mass at the beginning of the pre-migration period (March 1) (Masero and Pérez-Hurtado 2001). The mass gain per day during the pre-migration period is about 1% of winter lean mass (Zwarts et al. 1990c).

Data analysis

A forward stepwise regression was performed to determine the best model explaining daily feeding time in the salina as a function of independent variables (Bart et al. 2000). The initial exploratory analysis included the following variables: exposure time of the intertidal mudflats (minutes), daily average windspeed (km h^{-1}), number of shellfishers on the mudflats, number of raptors, and total surface of flooded pans (ha). I examined multicollinearity by regressing each independent variable on all of the others and evaluating the coefficient of determination (Hamilton 1990). As the variables exhibited low intercorrelations ($R^2 < 0.40$), I did not exclude any variables from the analysis. Windspeed data were obtained from a meteorological station located at Cadiz Bay. All variables were log-transformed to avoid violating assumptions of the analysis.

I compared feeding rates on the salina and daily feeding time between periods by means of t-tests. Prey length and feeding rate on the mudflats were analysed with the Mann–Whitney U-test, because these data were not normally distributed. To test whether feeding and intake rate changed over the low-tide period, the observations were grouped into seven periods of one hour each (Ens and Goss-Custard 1984). Differences between periods in both rates were tested by the Kruskal–Wallis test. Values are given as mean ± SD. Significance was set at $P \leq 0.05$.

Results

Feeding time allocation

In Dunlin, Curlew Sandpiper and Sanderling, the daily time spent feeding in each habitat showed significant seasonal variations (Table 1). In winter, these species fed mainly on the mudflats (55–94% of the total daily feeding time), whereas in the pre-migration period they spent more time feeding on the salina (57–79% of the total daily feeding time). The salina was particularly important for Little Stints, which feed mainly in the pans during both periods (Table 1). In order to increase body mass during the period prior to spring migration, Little Stint significantly increased the time they spent feeding in the salina, but the total daily feeding time decreased significantly in this period (Table 1). Dunlin and Curlew Sandpiper increased both feeding time in the salina and total daily feeding time, whereas Sanderling only significantly increased the feeding time in the salina (Table 1).

Calidrids were not seen feeding in the salina at night, and there was no evidence that they flew to other sites to feed at night: the total number of calidrids on the mudflats at night, plus the number of calidrids resting in the salina at night, did not differ from the total number of calidrids at high tide during daylight (t-test; Dunlin: $t_{18} = -1.3$, Curlew Sandpiper: $t_{18} = 1.2$; Sanderling: $t_{18} = 0.9$; Little Stint: $t_{18} = -1.6$; $P > 0.12$ for all species).

Feeding time in the salina increased as the surface of flooded pans increased, and the model explained 44% of the variation in the time spent feeding in the salina (all species: $F_{1,46} = 36.2$; intercept $= -2.5 \pm 0.8$; $\beta = 0.6 \pm 0.1$; $R^2 = 0.44$; $P < 0.0001$). No other variables significantly improved the model.

Foraging behaviour and prey-size selection

For all four species the feeding and net energy intake rates did not change through

Table 1. Mean number of minutes per day that calidrids spend feeding in each habitat during both winter and pre-migration period (data are shown without transformation: $\log_{10} x$). S = salina, M = intertidal mudflats, T = total daily feeding time.

Species		Winter	Pre-migration	t_{10}	*P*
	S	39.7 ± 6.3	450.8 ± 51.9	−28.2	**
Dunlin	M	652.6 ± 14.8	325.6 ± 11.1	41.5	**
(719–690)[a]	T	692.3 ± 19.9 (36)[b]	776.5 ± 43.4 (24)[b]	−3.2	***
	S	29.8 ± 3.5	448.6 ± 11.5	−47.7	**
Curlew Sandpiper	M	418.6 ± 11.7	203.1 ± 14.9	37.9	**
(61–72)[a]	T	448.5 ± 12.5 (0)[b]	651.8 ± 10.2 (0)[b]	17.1	**
	S	281.1 ± 7.5	500.8 ± 17.1	−32.7	**
Sanderling	M	339.8 ± 19.3	135.6 ± 11.4	22.2	**
(104–135)[a]	T	621.0 ± 19.5 (4)[b]	636.5 ± 15.9 (0)[b]	−1.5	NS
	S	394.8 ± 13.5	561.2 ± 10.6	−21.9	**
Little Stint	M	376.0 ± 7.3	0	–	–
(90–105)[a]	T	770.8 ± 16.1 (24)[b]	561.2 ± 10.6 (0)[b]	27.4	**

**$P < 0.01$; ***$P < 0.0001$; NS = not significant; [a] Total number of calidrids at high tide (winter−premigration). [b] Percentage of nocturnal feeding on the mudflats with respect to total daily feeding time (calidrids were not seen feeding in the salina at night).

the exposure period of the intertidal area (feeding rate, Dunlin: $\chi^2_6 = 8.6$; Curlew Sandpiper: $\chi^2_6 = 6.6$; Sanderling: $\chi^2_6 = 4.8$; Little Stint: $\chi^2_6 = 4.5$; Dunlin-premigration: $\chi^2_6 = 5.1$; $P > 0.19$ for all species; net energy intake rate, Dunlin: $\chi^2_6 = 5.2$; Curlew Sandpiper: $\chi^2_6 = 4.3$; Little Stint: $\chi^2_6 = 5.5$; Sanderling: $\chi^2_6 = 6.1$; Dunlin-premigration: $\chi^2_6 = 4.9$; $P > 0.38$ for all species).

On the mudflats calidrids preyed mainly on polychaetes. Overall, feeding rates were significantly lower in this habitat than on the salina (Dunlin: $Z = -8.5$; Curlew Sandpiper: $Z = -8.0$; Sanderling: $Z = -7.2$; Little Stint: $Z = -8.3$; Dunlin-premigration: $Z = -8.4$; $P < 0.0001$ for all species) (Figure 1). For Dunlin, the mudflat feeding rate was significantly lower in the pre-migration period than in winter ($Z = -8.2$, $P < 0.01$) (Figure 1). In winter *Nereis diversicolor* contributed ca. 100% to the total biomass ingested by Curlew Sandpiper and Dunlin. The estimated average length of *Nereis* eaten during the daylight period was similar in both species (see statistical comparisons in Table 2). *Nereis* also was the main prey of Dunlin in the pre-migration period, with the average length taken similar to that in winter (Table 2). The difference between the sizes of *Nereis* estimated in the field and found in faeces was not significant (Table 2). Little Stint and Sanderling preyed on small polychaetes (Little Stint: 8.9 ± 0.9 mm, range: 7.1–10.8 mm, $n = 19$; Sanderling: 9.0 ± 1.1 mm, range: 7.5–10.7 mm, $n = 14$; mean size of *Nereis* in faeces), contributing ca. 100% to the total biomass ingested. Despite the high density of small bivalves and *Hydrobia*, calidrids ignored them almost completely. *Hydrobia* were not taken at all by Curlew Sandpiper and only rarely by the other species.

On the salina, calidrids fed mainly in the evaporation pans (82% of all individuals). The mean feeding rate in this habitat (high and low tide periods combined) was significantly higher in the pre-migration period than in winter for

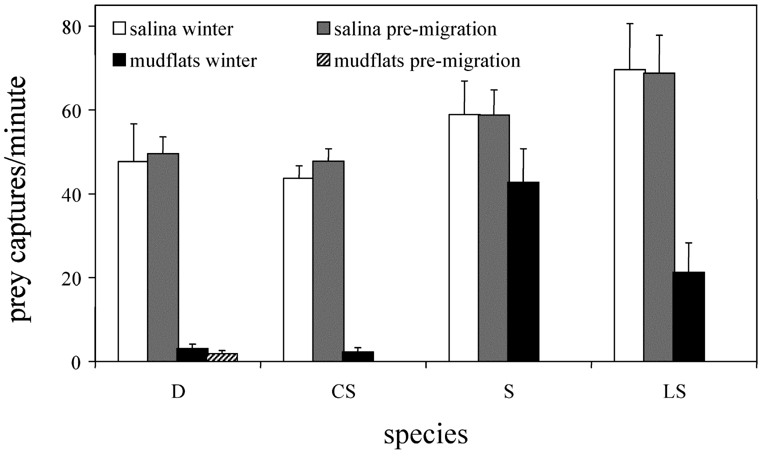

Figure 1. Mean prey captures per minute (±SD) on the salina and on the intertidal mudflats in both winter and pre-migration period. D = Dunlin, CS = Curlew Sandpiper, S = Sanderling, LS = Little Stint. Sample sizes: D, winter–mudflats, $n = 49$, winter–salina, $n = 55$, premigration–mudflats, $n = 51$, premigration–salina, $n = 80$; CS, winter–mudflats, $n = 65$, winter–salina, $n = 52$, premigration–salina, $n = 58$; S, winter–mudflats, $n = 49$, winter–salina, $n = 38$, premigration–salina, $n = 55$; LS, winter–mudflats, $n = 37$, winter–salina, $n = 59$, premigration–salina, $n = 52$. See text for statistical comparisons.

Table 2. Mean length (±SD) of *Nereis diversicolor* estimated in the field and found in faeces.

Species	Field	*n*	Faeces	*n*	*Z*	*P*
Dunlin						
Winter	26.3 ± 6.1[a,b]	97	25.3 ± 3.2[c,d]	52	−0.4	NS
Pre-migration	28.5 ± 4.9[a]	81	27.2 ± 5.2[c]	41	−0.5	NS
Curlew Sandpiper						
Winter	28.0 ± 4.8[b]	82	27.1 ±2.4[d]	48	−0.5	NS

NS = not significant; n = sample size. Statistical comparisons: [a]$Z = -0.4$; [b]$Z = -0.5$; [c]$Z = -0.6$; [d]$Z = -0.4$; $P > 0.27$ for all species.

Dunlin ($t_{133} = -2.5$, $P < 0.05$) and Curlew Sandpiper ($t_{108} = -6.9$, $P < 0.01$), but was similar in both periods for Sanderling ($t_{102} = 0.09$, $P = 0.12$) and Little Stint ($t_{109} = 0.3$, $P = 0.27$) (Figure 1). In the salina, 100% of the ingested biomass was the crustacean *Artemia*. It was not possible to estimate the size of ingested *Artemia* from calidrids faeces collected in pans. Thus, the mean body length of *Artemia* in the pans (see below) was used as the best estimate of the sizes ingested by calidrids (Masero and Pérez-Hurtado 2001; Masero 2002). In this calculation I discarded naupliar stages (<1 mm), since they are too small to be visible in the water column (at least to the human observer) and were not found in the faeces.

Energy intake rates and daily consumption

In winter, net energy intake rates were significantly higher on the salina than on the

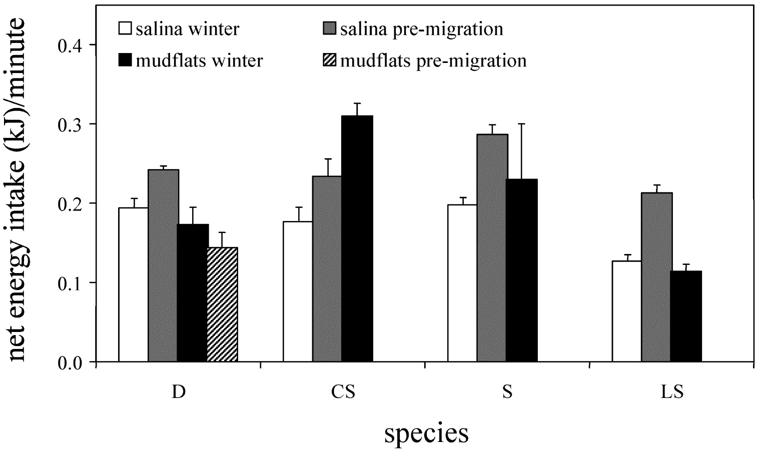

Figure 2. Mean net energy intake per minute (±SD) on the salina and on the intertidal mudflats in both winter and pre-migration period. Sample sizes and species codes are listed in the legend of Figure 1. See text for statistical comparisons.

intertidal mudflats for Dunlin and Little Stint (Dunlin: $Z = -9.5$; Little Stint: $Z = -5.8$; $P < 0.0001$ for both species), but significantly lower for Curlew Sandpiper and Sanderling (Curlew Sandpiper: $Z = -9.2$; Sanderling: $Z = -6$; $P < 0.0001$ for both species) (Figure 2). For Dunlin, the mudflat energy intake rate (Figure 2) was significantly lower in the pre-migration period than in winter ($Z = -7.1$, $P < 0.0001$). For all four species, salina energy intake rates were significantly higher in the pre-migration period than in winter (Dunlin: $Z = -8.7$; Curlew Sandpiper: $Z = -8.2$; Little Stint: $Z = -8.9$; Sanderling: $Z = -9.4$; $P < 0.0001$ for all species), with winter intake rates about 71% of those in pre-migration.

Although Little Stint had a higher feeding rate than the other species (Figure 1), their intake rate was lower (Figure 2), because many Little Stints exploited some small evaporation pans where the average size of *Artemia* (winter: 2.6 ± 0.5 mm; pre-migration: 3.7 ± 0.6 mm) was lower than in the pans used by Dunlin, Curlew Sandpiper and Sanderling (winter: 4.4 ± 0.8 mm; pre-migration: 5.1 ± 1.0 mm).

The estimated energy intake rates were sufficient to fulfil theoretic daily energy requirements, even if the energy requirement in the pre-migration period increases about 22% (Table 3). On average, salina contributed 25.2 ± 24.2% of the daily consumption in winter and 78.7 ± 16.4 of the daily consumption in the pre-migration period (see Table 3).

Discussion

Prey-size selection and feeding-habitat use by overwintering calidrids

Shorebirds are able to increase their intake rate at high prey densities by eating the

Table 3. Theoretical daily energy requirement (DER; kJ bird^{-1} day^{-1}) and daily consumption (DC; kJ bird^{-1} day^{-1}) in both winter (W) and pre-migration period (PM).

Species	Lean mass in winter[a]	Expected body mass[b]	DER[c]		DC[d]	
	(g)	(g)	W	PM	W	PM
Dunlin	42.0	52.9	119	152	121 (6)	156 (70)
Curlew Sandpiper	51.6	61.5	136	169	136 (4)	168 (63)
Sanderling	46.9	60.0	128	165	152 (37)	175 (82)
Little Stint	22.1	28.1	79	99	93 (54)	120 (100)

The percentage (%) of daily energy obtained on the salina with respect to daily consumption is shown in parentheses. [a] From Zwarts et al. (1990c). [b] Assuming that the mass gain per day during the pre-migration period is about 1% of winter lean mass (Zwarts et al. 1990c). [c] In winter DER is considered to be equal to Field Metabolic Rate (FMR; Nagy 1987), and in the pre-migration period DER is FMR plus the daily energy requirement of fat–protein deposition. [d] Assuming that nocturnal and diurnal intake rates on the mudflats are equal, and that Curlew Sandpiper and Sanderling in late March obtained at least the same intake rate on the mudflats as in winter.

most profitable prey, and they only include less profitable prey in their diet as prey density declines (Zwarts and Wanink 1993; Zwarts et al. 1996). Overall, small-sized calidrids prefer soft-bodied polychaetes to hard-shelled species, because of the more favourable rate at which their energy can be processed (Kalejta 1993; Zwarts and Wanink 1993). It has been shown, for example, that Dunlin preyed on mudsnails and bivalves only when the available density of the most preferred prey, the polychaete *Nereis*, decreased (Worrall 1984). On the Cadiz mudflats polychaetes, mudsnails, and small bivalves were abundant (Masero et al. 1999), but calidrids preyed almost exclusively on polychaetes. Accordingly, there was no evidence for decline in intake rate due to the presence of competitors or prey depression, as seems to occur in Common Redshanks at the same intertidal mudflats (Masero and Pérez-Hurtado 2001). The potential intake rate is the main factor that shorebirds take into account to evaluate the suitability of an area for feeding (Piersma et al. 1993a). Thus, the high availability of a soft-bodied prey like *Artemia* in the salina would appear to be the main reason why calidrids preferred to feed in this habitat, since this prey can be taken at high rates with a search time approaching zero (Masero et al. 2000).

From spring to autumn, invertebrate species richness and abundance is higher in the salina (Castro 2000), but in winter usually only *Artemia* remains. Calidrids fed on this prey during several weeks in the salina. In Mono Lake (California), Rubega and Inouye (1994) showed that the Red-necked Phalarope *Phalaropus lobatus* is incapable of surviving on a diet composed solely of *Artemia monica*. However, this seems to be related with the nutritional profile of *Artemia monica* or with a particular physiological limitation of the Red-necked Phalarope, since small-sized calidrids can use *Artemia* as their main food resource (see Britton and Johnson 1987; Verkuil et al. 1993; Tripp and Collazo 1997). For example, Dunlin and Curlew Sandpiper feed exclusively on *Artemia* in hypersaline lagoons during their northward migration through Ukraine (Y. Verkuil, personal communication).

The overall foraging patterns found are consistent in time (see Hortas (1997) for similar foraging patterns through several winters). On the salina, the increase of the prey size was the main factor that contributed to the increase in the estimated energy intake rates in the pre-migration period, since the average size of *Artemia* in the pans increased in this period (Masero et al. 1999), and I assumed this value as the average size ingested by calidrids. Unfortunately, the analysis of factors affecting the daily feeding time in the salina did not include the variables average size and density of *Artemia* in the pans (the salina only was sampled on two occasions, early February and late March). It seems likely that both variables would explain an important percentage of the variation in the time spent feeding in the salina.

On the mudflats, I estimated the size of prey items in relation to the bird's bill length. Although this method has several potential errors associated with it, the estimates were performed under conditions where the method is reliable: flat environments, field observations in conjunction with faeces analysis, and prey biomass was calculated controlling the seasonal variation in the body condition of the prey population (Lee and Hockey 2001). On the other hand, on the salina, I assumed 100% successful pecks. Because calidrids are exclusively sight feeders, *Artemia* was available in high densities in the shores of the pans (up to 30000 *Artemia* m^{-2}; Masero et al. 1999), and this crustacean has little apparent behavioural adaptation against predation (Britton and Johnson 1987), it is compelling to think that the number of unsuccessful pecks is negligible. In addition, note that the estimated intake rate for Dunlin and Curlew Sandpiper feeding on *Artemia* in hypersaline lagoons (12–23 mg AFDW min^{-1}; Y. Verkuil, personal communication) is similar to those measured in the salina.

The crude estimate of the energy budget suggests that calidrids meet their DER. In the period prior to spring migration, Little Stint decreased the total daily feeding time, which supports the idea that the increase of diurnal feeding time in the salina is enough to obtain the trophic resources needed for migration. The absence of nocturnal feeding on the intertidal mudflats during the pre-migration period by Curlew Sandpiper, Sanderling and Little Stint also supports this idea (calidrids presumably did not feed at night on the salina because of their reliance on visual searching to capture *Artemia* on the water column).

Conservation value of salinas and management implications

Salinas are thought to be high-quality feeding habitats for many non-breeding shorebird species, merely based on the high number of feeding birds that they support, but it is possible that birds could also be found at high densities in habitats of low quality (Stephens and Krebs 1986). However, the results of this study, together with those obtained for Common Redshank (Masero and Pérez-Hurtado 2001), are an empirical confirmation that salinas are indeed suitable feeding habitats for several migrating shorebird species that rely on intertidal habitats, including species with declining populations such as Sanderling and Dunlin (Piersma et al. 1996).

In a migratory pathway, previously unused sites can act as a buffer area against the impact of natural habitat loss (Weber et al. 1999). This study supports the idea that salinas are valuable buffer wetlands that may supplement declining natural habitat for migrating shorebirds. Salinas will become more critical to shorebirds as natural feeding habitats progressively decrease on coastal wetlands where salinas occur in large expanses, for example on Mediterranean, southern Atlantic European and North American Pacific coasts.

Overall, a threat to the value of the present salinas for shorebirds is the abandonment of the salt production as a consequence of economic constraints (Rufino and Neves 1992). Salina loss has been especially extensive in the Mediterranean. Of 168 known sites of salinas in 18 countries, 45% are inactive or have been transformed into fish-farms (Sadoul et al. 1998). Where salinas are to be found near important wintering and/or staging areas, further salina loss could cause a movement and even an increase in the mortality of the displaced birds through density-dependent forces (Young and Chan 1997). At Cadiz Bay, for example, the coincidence of salina loss and the decline and redistribution of some shorebird species has led to the suggestion of a causal link between the two (Pérez-Hurtado et al. 1993).

The most important conclusion of this study is that the conservation, restoration, or enhancement of salinas at coastal wetlands is a viable approach to the conservation of shorebirds. To date, most efforts for the conservation of the salinas have been focussed on the inclusion of these habitats under some form of legal protection (75% of the Mediterranean salinas are protected; see Sadoul et al. 1998). However, this effort is insufficient, since, even protected, the majority of the salinas are private properties and the salt production has been abandoned. The salinas lose their value for waterbirds in the absence of adequate water management. Therefore, at least in parks and reserves, the site-managers of coastal wetlands should establish agreements with the owners to manage water levels to balance the interest of salt producers and waterbirds (Rufino and Neves 1992).

On the other hand, it must be noted that large evaporation surfaces of modern salinas usually are emptied during winter (Sadoul et al. 1998). Consequently, these surfaces are unsuitable for most shorebirds during a large proportion of winter. I recommend that flooding conditions are maintained in the evaporation pans throughout the winter. This increases the available surface for the waterbirds, and decreases potential density-dependent effects on the feeding distribution of some shorebird species (Masero and Pérez-Hurtado 2001).

Lastly, despite the great value of the salinas as feeding habitat, I do not advocate the building of salinas to replace natural feeding habitats, since the salinas' attractiveness varies between species and this habitat is not suitable for all (Velasquez 1992; Masero 2002). Thus, the recommendations I made are intended for existing salinas.

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Appendix 1

Functions used to calculate prey size from prey remains and prey biomass from prey size. AFDM – ash free dry mass; DM – dry mass; TL – total length; ML – mandible length; WB – width at the base.

Prey	Function	R^2	Source
Nereis diversicolor	TL (mm) = 40.17 ML (mm) − 3.42	0.96	Masero et al. (1999)
	Log DM (g) = 2.53 Log (TL; mm) − 5.94	0.98	Moreira (1994a)
	AFDM = 0.771 DM		
Hydrobia ulvae	TL (mm) = 1.95 WB (mm) − 0.38	0.95	Masero and Pérez-Hurtado (2001)
	Log AFDM (mg) = 2.20 Log (TL; mm) − 1.16	0.94	Moreira (1994b)
Artemia	AFDM (g) = 2.57 10^{-5} TL (mm)$^{1.529}$	0.96	Masero et al. (1999)

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