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Authors: Estrella, Sora M., and Masero, José A.

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Sora M. Estrella[1,2,*] and José A. Masero [3]

[1]Centro Andaluz de Ciencias y Tecnologías Marinas, Universidad de Cádiz, E-11510 Puerto Real, Spain

[2]Current address: School of Animal Biology (M092), University of Western Australia, 35 Stirling Highway, Crawley, 6009, W.A. Australia

[3]Conservation Biology Research Group, Área de Zoología, Universidad de Extremadura, Avenida de Elvas s/n, E-06071 Badajoz, Spain

[*]Corresponding author; E-mail: sora.marin@uca.es

Abstract.—Near-threatened Black-tailed Godwits *Limosa limosa* and other shorebirds rely on non-tidal areas during their annual migration but understanding of stopover ecology in these areas is lacking. Here, field observations, analysis of droppings and prey abundance were combined to investigate diet and prey-size selection by Black-tailed Godwits during fall migration in salinas (also called salt works or salt ponds) of southern Europe. Although several potential macroinvertebrate prey species were available and abundant, godwits positively selected the chironomid *Chironomus salinarius*. The larvae and pupae of this prey represented >95% of the total number of items present in droppings during migration (July-September). Consumption of prey of a given size class was not dependent on its abundance. Thus, although larger size-classes of chironomid larvae were not necessarily the most abundant for some months (mean size of available larvae: 8.2 ± 0.2 mm, 6.4 ± 0.2 mm and 8.4 ± 0.2 mm in July, August and September, respectively), they were the ones most frequently consumed by the godwit (mean size of larvae predated: 9.9 ± 0.8 mm, 9.2 ± 1.7 mm, and 9.4 ± 1.3 mm in July, August and September, respectively). The role salinas play as stopover foraging areas for godwits appears dependant not only on the abundance of *C. salinarius* but also on the abundance of large size-classes of this soft-bodied prey. Conservation and management of salinas that allows the production of high densities of chironomids during the peak of Black-tailed Godwit migration would assist the conservation of this species. *Received 22 December 2009, accepted 30 April 2010.*

Key words.—Black-tailed Godwit, chironomid, diet, migration, prey-size selection, Salinas, shorebirds, waders.

Annually, many shorebird species make long distance migrations between their breeding and wintering grounds. These long distance migrations are energetically costly and shorebirds concentrate in specific stopover sites where physical and biological conditions, such as prey abundance, allow them to replenish their energy reserves (Myers *et al.* 1987; Davies and Smith 2001; Skagen 2006).

Due to a strong decline in numbers, the Black-tailed Godwit *Limosa limosa* was recently classified as 'Near Threatened' by the IUCN Red List of Threatened Species (IUCN 2008). In some regions of the East Atlantic Flyway, the nominate species of Black-tailed Godwit uses mainly anthropogenic habitats such as salinas and rice fields as stopover feeding grounds (Masero *et al.* 2000; Sánchez *et al.* 2006a; Lourenço and Piersma 2008). Although the importance of such anthropogenic habitats for migrating shorebirds has been documented (Elphick and Oring 1998, Masero 2003; Sánchez-Guzman *et al.* 2007), there is still a lack of information relating to these habitats' use as foraging sites and the diet of Black-tailed Godwits (and other declining shorebirds) which employ these habitats during migration.

A few studies have either directly or indirectly demonstrated the diet of Black-tailed Godwits foraging in salinas (also called salt works or salt ponds) during migration (Green and Sánchez 2006; Sánchez *et al.* 2006b; Sánchez *et al.* 2007). However, to the best of our knowledge, there is no quantitative information on prey-size selection by Black-tailed Godwits during migration in anthropogenic habitats. As the nominate subspecies of Black-tailed Godwit is suffering rapid population decline (Stroud *et al.* 2004; Gill *et al.* 2007), research into the not-so-well-known feeding ecology of this shorebird at stopover sites in Europe and Africa is impor-

tant (Gill *et al.* 2007; Jensen and Perennou 2007). Such research could prove invaluable in the design and implementation of future conservation strategies. Here, we studied prey and prey-size selection by Black-tailed Godwits during post-breeding migration in salinas of southern Europe. Information gathered may provide essential input on key prey species with respect to habitat management of migratory shorebird species such as Black-tailed Godwit (e.g. Masero 2003; Sánchez *et al.* 2006a).

METHODS

Study Area

The study was carried out in the "La Tapa" salina (314 ha), Cádiz Bay Natural Park (southwest Spain) (Fig. 1). Cadiz Bay is a Ramsar site of International Importance for several shorebird species and each year several hundred Black-tailed Godwits stopover en route to Africa during July-September (Masero *et al.* 2000; Estrella 2001). The salina consists of shallow, interconnected pans of varying surface area and salinity: storage, evaporation and crystallization pans (135, 179 and 41 ha, respectively; Fig. 1). A detailed description of the area is given in Masero (2003). A few Black-tailed Godwits were normally found foraging at low tide in an adjacent intertidal mudflat on the north side of the salina (overall, <5% of the total godwits present in the salina at high tide; Masero *et al.* 2000).

Observations and Droppings

During studies of the use of this salina by shorebirds (Masero *et al.* 2000; Estrella 2001; Masero 2003), we noted that most Black-tailed Godwits foraged consistently on the benthos of storage and evaporations pans, with only a few birds (<2%) foraging in the crystallization pans. To determine prey and prey-size selection by Black-tailed Godwits foraging in the storage and evaporation pans during post-breeding migration (July-September), we combined field observations of birds

Figure 1. Map indicating the location of the study area Cádiz Bay, the Salina 'La Tapa', southwest Spain.

foraging actively, analysis of droppings and prey abundance (see below) (Dekinga and Piersma 1993; Mouritsen 1994; Gillings and Sutherland 2007). Droppings (n_{July} = 15; n_{August} = 14; $n_{September}$ = 13) were collected in monospecific resting areas located on the shores of the pans. Only fresh droppings were collected, and to avoid pseudo-replication (collection of droppings from the same individual), each was at least 50 cm from the previous one (Sánchez *et al.* 2005). Complete droppings were carefully scraped from the soil with the help of tweezers and stored at -10°C. Subsequently, the dropping was thawed and disaggregated in a Petri dish for analysis. The dropping was sieved with a 200 μm mesh with the aid of a continuous stream of seawater and a brush. Droppings were analyzed using the same stereomicroscope used in the benthos samples analysis (see below).

All representative hard prey remains were counted and identified at least to genus level in each dropping. The relative abundance of the prey items was calculated for each month. The original prey length was estimated by using regression equations relating hard prey remains measurements and body length. We measured maximum head width, left mandible length (distance from the base of the proximal 'tooth' to the distal end 'tip' of the mandible), shell base maximum width (width of the last whorl) for chironomid, *Chironomus salinarius*, larvae, ragworms, *Nereis diversicolor*, and mud snails, *Hydrobia ulvae*, respectively. We used equations from literature for prey species other than *C. salinarius* (Dekinga and Piersma 1993; Masero *et al.* 1999; Masero and Pérez-Hurtado 2001). In the latter case, we constructed a body length (L) - maximum head width (W) regression equation to estimate the original size taken by Godwits: L (mm) = 19.145 × W (mm) + 0.835 (r = 0.83, P < 0.05, n = 38).

In addition, observations of actively foraging Black-tailed Godwits chosen randomly were made, by following each individual during a one-minute period through a 25 × 60 telescope (n_{July} = 318; n_{August} = 231; $n_{September}$ = 147). During these observations, prey type was determined visually. Most prey items captured by godwits were small relative to bill size, making it impractical to estimate prey size by comparing prey size with bill size. Data were taken throughout the day light period (5-19 GMT). To avoid pseudo-replication (Hulbert 1984), each new bird selected for observation was at least 10-20 m from the previous one.

Prey Abundance

To determine potential prey items and prey sizes available in the pans, reference benthos sampling was carried out every month (July-September) in the foraging pans (storage and evaporation pans). At each pan a benthos sample was obtained immediately following foraging observations, consisting of five replicate sediment cores pooled together in order to account for intra-pan variability. The samples were taken using a sediment core of 78.5 cm² to maximum depth (2-5 cm in the sampled pans). The samples were frozen at -10°C until their analysis in the laboratory. They were defrosted at air temperature, and then washed with seawater and sieved through a 0.5 mm mesh with the aid of a brush.

All samples were analyzed through a stereomicroscope (10 × 21) provided with a micrometer, taking note of the species or genus, number and sizes. Invertebrates
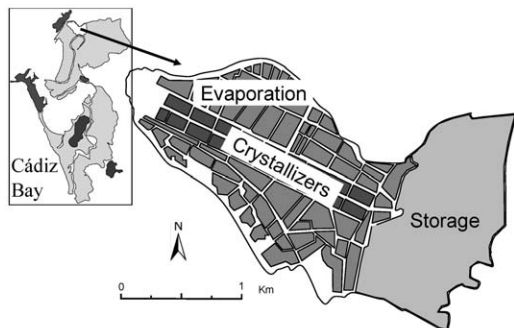
that were too large for the micrometer scale were measured with a digital caliper (to the nearest 0.01 mm).

Statistical Analysis

Normality and homoscedasticity were tested for each variable. When normality of the data was not achieved using transformations, non-parametric statistics were used (Sokal and Rohlf 1995). Differences in the mean prey size captured by Black-tailed Godwits during each month were evaluated using a Kruskall-Wallis Test in the case of *C. salinarius*, and one-way ANOVA in the case of ragworm. When analyses showed significant differences, post-hoc tests (Multiple Comparisons or Tukey's test) were used to determine amongst which months differences existed. Ivlev's electivity Index (Jacobs 1974) was used to evaluate prey size selection. Ivlev's Index is defined by the formula $E = (r - p) / (r + p)$ where r is the fraction of a certain prey size class taken by Black-tailed Godwits and p is the fraction of this size class in the population. E ranges from -1 to +1, where -1 to 0 stands for negative selection, while values > 0 to +1 can be interpreted as positive selection of that size class. Significance of prey size classes' preference was evaluated using the Mann-Whitney U test.

Values are presented as means ± SD, unless stated otherwise. Statistical significance was set at $P \leq 0.05$. All statistical tests were conducted using Statistica 7.0 (StatSoft. Inc. 2004).

RESULTS

Food Abundance

The potential prey items found in the storage pan were mud snails, cockles and the larvae and pupae of *C. salinarius*, while in the evaporation pans the only prey available in the benthos were larvae and pupae of the chironomid. The mean size and densities of these potential prey are shown in Table 1. There were significant differences in the mean size of chironomid larvae over the three month study (Kruskall-Wallis Test, $H_{2, 657} = 112.24$, P < 0.0001; Test for Multiple Comparisons, $Z_{Jul, Aug} = 10$, P < 0.00001; $Z_{Aug, Sep} = 9.08$, P < 0.05; $Z_{Jul, Sep} = 1.29$, n.s.).

Prey and Prey Size Selection

Droppings analysis: *Chironomus salinarius* larvae were the most common prey in Black-tailed Godwit diet over the three months studied. The chironomid larvae represented 89.6%, 72.1% and 96.9% of the total number of captured prey for July, August and September, respectively, while the pupae of this species represented 5.6%, 24.8% and 2.2%

Table 1. Mean size and densities (± SE) of available invertebrates during southward migration for shorebirds at the salina 'La Tapa', Cadiz Bay, southwest Spain.

	July (N = 4)		August (N = 3)		September (N =3)	
	Size (mm)	Density (ind · m⁻²)	Size (mm)	Density (ind · m⁻²)	Size (mm)	Density (ind · m⁻²)
Chironomus salinarius larvae	8.2 ± 0.2	1974.5 ± 463.3	6.4 ± 0.2	2140.1 ± 594.0	8.4 ± 0.2	5753.7 ± 466.8
Chironomus salinarius pupae	6.0 ± 0.6	54.6 ± 37.9	6.2 ± 0.2	50.2 ± 46.7	6.3 ± 0.2	212.3 ± 71.1
Cockles (*Cerastoderma* spp.)	5.8 ± 0.1	3286.6 ± 454.9	—	—	—	—
Mud Snail (*Hydrobia ulvae*)	4.1 ± 0.2	394.9 ± 88.0	—	—	—	—

of the total number of captured prey for the same months. Ragworm represented 4.6%, 2.8% and 0.9% of the total number of captured prey for July, August and September, respectively. The remaining prey items (<0.4% of the total) were mud snails (July and August) and brine fly larvae, *Ephidra* spp. (August).

The mean size of chironomid larvae taken by Black-tailed Godwit differed significantly over the three months (Kruskall-Wallis Test, $H_{2, 3578}$ = 114.92, P < 0.0001). The mean size of chironomid larvae taken in July was significantly different from those taken in August and September (Test for Multiple Comparisons: $Z_{Jul, Aug}$ = 9.5, P < 0.05; $Z_{Jul, Sep}$ = 9.48, P < 0.05; $Z_{Aug, Sep}$ = 0.30, n.s.). The estimated size of chironomid larvae found in the droppings was significantly greater than sizes found in the pans for the three months studied (Mann-Whitney U Test, Z_{Jul} = -10.27, P < 0.0001; Z_{Aug} = -13.65, P < 0.001; Z_{Sep} = -8.51, P < 0.0001; Fig. 2). Godwits selected *C. salinarius* larvae from 8.5 to 11.5 mm (Fig. 3), with 65% ranging from 9.5 to 11.5 mm (Fig. 2). The mean sizes of chironomid larvae taken by godwits were 9.9 ± 0.8 mm, 9.2 ± 1.7 mm and 9.4 ± 1.3 mm for July, August and September respectively.

The estimated sizes of ragworms taken by Black-tailed Godwit were 76.9 ± 18.2 mm, 69.1 ± 11.7 mm and 70.6 ± 8.8 mm for July, August and September, respectively, with no significant differences in these mean sizes taken by the godwits over the three-month study (ANOVA $F_{2, 85}$ = 2.57, P = 0.08).

In the case of mud snails, it was not feasible to estimate the size of these gastropods taken by godwits in July since the few hard remains found in the droppings were at an advanced stage of digestion. However, in August it was possible to estimate the size of the mud snails corresponding to two hard remains taken by godwits (1.2 mm and 1.3 mm). Estimates for the sizes of brine fly larvae taken by godwits was not possible since there were no measurable hard remains in the droppings.

Direct observations: 99.4% of prey items taken by Black-tailed Godwits (n = 696) were too small to visually determine the prey type.
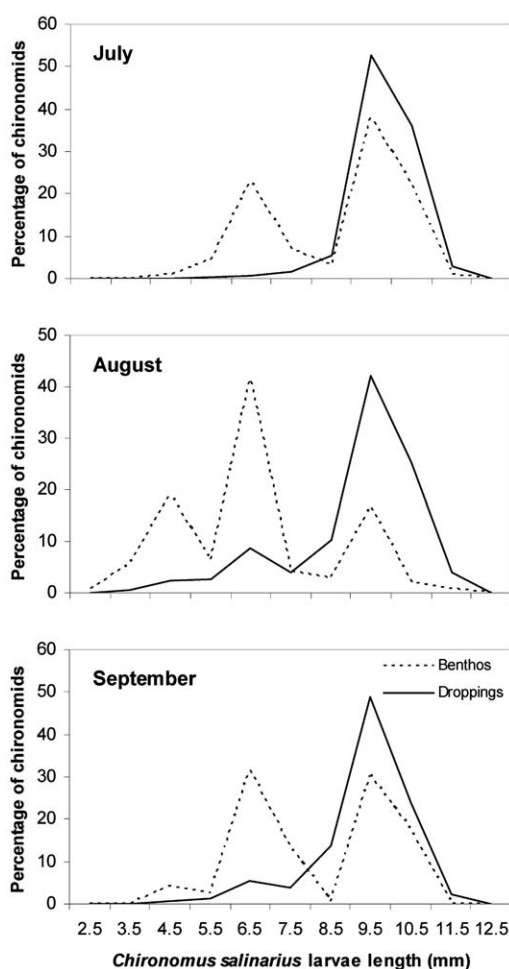

Figure 2. Size frequency distribution of *Chironomus salinarius* larvae available in the benthos (chironomus larvae measured n_{Jul} = 245; n_{Aug} = 142; n_{Sep} = 270) and droppings (chironomus larvae heads' measured n_{Jul} = 938; n_{Aug} = 1233; n_{Sep} = 1407) of Black-tailed Godwits during post-breeding migration (July, August and September) in the Salina 'La Tapa', Cadiz Bay, southwest Spain.

DISCUSSION

The main prey of Black-tailed Godwits in the salina was the dipteran *C. salinarius*. The fact that ragworm jaws and brine fly remains were found in a few droppings indicated that some godwits fed at low tide on the adjacent intertidal mudflat and crystallization pans, respectively. *Chironomus salinarius* was selected among other potential
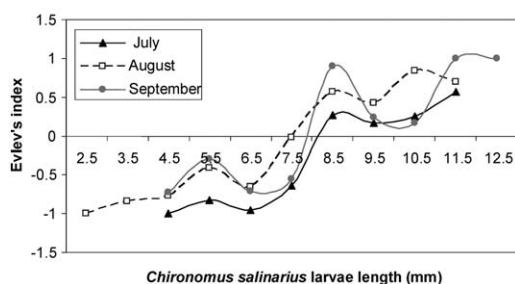
Figure 3. Size selection of *Chironomus salinarius* larvae by Black-tailed Godwits based on consumed and available sizes given in Fig. 2. Prey size selection was assessed using the index of electivity (E), where the zero line denotes no selection, the negative values show negative selection or rejection and positive values indicate positive selection.

prey, which were abundant and readily available, at least in the early migration period. The storage pan was not sampled in August and September, since most (>70%) godwits did not forage in this pan during both months. However, the literature indicates that choronomids are abundant in the storage pans of salinas at Cádiz Bay over the three-month period studied (Drake and Arias 1994; Drake and Arias 1997). Therefore, the positive selection of chironomid by Black-tailed Godwit is probably the case for the entire migration period.

Black-tailed Godwits fed mostly on soft-bodied prey items. Our results suggest that although cockles and mud snails were abundant and available in the salinas, they were rejected by foraging godwits. Rejection could be related to the high shell: flesh ratio of both molluscs. For shorebirds other than mollusc specialists, prey items with shells or exoskeletons are considered unprofitable compared with soft-bodied prey of similar size, since the high content of inorganic matter of these prey items reduces their digestibility (Zwarts and Bloment 1992; Kalejta 1993). In addition, prey items with a high shell: flesh ratio such as cockles and mud snails possibly represent a digestive constraint (bottleneck) for shorebirds relying on benthic macroinvertebrates during periods of high energy requirements (Zwarts and Dirksen 1990; Zharikov and Skilleter 2003; van Gils *et al.* 2005).

Black-tailed Godwits selected the large size classes of the available chironomid larvae even though the large classes were not always the most abundant. Selection of larger chironomid larvae may result from active selection of either energetically more favorable sizes (Zwarts and Wanink 1993) or to limitations in godwit prey handling capacity of smaller chironomid larvae.

Chironomus salinarius is widespread, found, for example, in Europe, America and Asia (Ree and Yum 2006). The species is particularly tolerant of high salinities and often recorded as the only benthic invertebrate species available for small-medium shorebirds in habitats such as salinas (Sánchez *et al.* 2006a). Previous studies have shown that Black-tailed Godwits and other long-distance migratory shorebirds stopping over in salinas rely heavily on this prey (Sánchez *et al.* 2005, 2006a). Here, we showed that Black-tailed Godwit are not only reliant on the abundance of chironomid larvae but probably also on the abundance and availability of the largest size-classes. In Cadiz Bay, and most likely in latitudes with high temperatures such as those of southern Spain, *C. salinarius* is postulated to have five generations a year (see discussion in Sánchez *et al.* 2006a); hence, a prey item which is available throughout the year. Managing salinas and similar habitats in ways that promote the availability of high densities of chironomid larvae during the migration peak of Black-tailed Godwits and other shorebirds appears feasible. For example, it would be possible to reduce the water levels (from 60-40 cm to < 5cm) of some channels and evaporation pans sequentially throughout the post-breeding migration, thereby making available foraging areas with chironomid larvae that otherwise would be not accessible to shorebirds.

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