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

Source: Waterbirds, 33(3): 293-299

Published By: The Waterbird Society

URL: https://doi.org/10.1675/063.033.0304

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Prey and Prey Size Selection by the Near-Threatened Black-tailed Godwit Foraging in Non-Tidal Areas during Migration

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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.
Waterbirds 33(3): 293-299, 2010

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 Blacktailed 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 shore-

birds 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-

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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 interidal 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

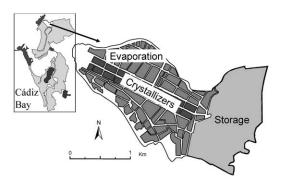


Figure 1. Map indicating the location of the study area Cádiz Bay, the Salina 'La Tapa', southwest Spain.

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

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) = $19.145 \times W$ (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 $(n_{\rm July}=318;\,n_{\rm August}=231;\,n_{\rm September}=147)$. 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 +1can 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 \pm SD, unless stated otherwise. Statistical significance was set at $P \le 0.05$. All statistical tests were conducted using Statistica 7.0 (Stat-Soft. 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 Blacktailed 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%

 5753.7 ± 466.8 Table 1. Mean size and densities (± SE) of available invertebrates during southward migration for shorebirds at the salina 'La Tapa', Cadiz Bay, southwest Spain. Size (mm) 2140.1 ± 594.0 $\operatorname{ind} \cdot \operatorname{m}^{-2}$ 974.5 ± 463.3 54.6 ± 37.9 8.2 ± 0.2 6.0 ± 0.6 Size (mm) Chironomus salinarius pupae Chironomus salinarius larvae

 286.6 ± 454.9

 394.9 ± 88.0

 4.1 ± 0.2

 5.8 ± 0.1

Cockles (*Cerastoderma* spp.) Mud Snail (*Hydrobia ulvae*) 296 Waterbirds

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, $H_{9.3578} = 114.92$, 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: $Z_{Iul, Aug} = 9.5$, 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, $Z_{Iul} = -10.27$, $P < 0.0001; Z_{Aug} = -13.65, P < 0.001; Z_{Sep} = -13.65$ 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 $F_{9.85} = 2.57$, 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.

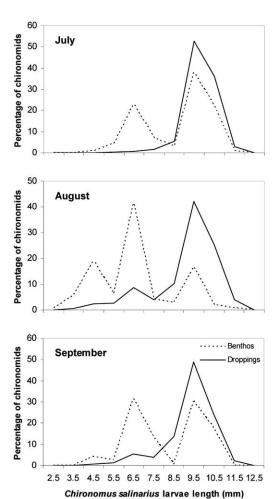


Figure 2. Size frequency distribution of *Chironomus salinarius* larvae available in the benthos (chironomus larvae measured $n_{\rm Jul}=245$; $n_{\rm Aug}=142$; $n_{\rm Sep}=270$) and droppings (chironomus larvae heads' measured $n_{\rm Jul}=938$; $n_{\rm Aug}=1233$; $n_{\rm Sep}=1407$) of Black-tailed 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

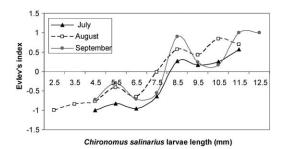


Figure 3. Size selection of *Chironomus salinarius* larvae by Black-tailed Godwits based on consumed and available sizes given in Fig. 2. Prey size selection was assessed using the index of electivity (E), where the zero line denotes no selection, the negative values show negative selection or rejection 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 softbodied 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 sizeclasses. 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 Blacktailed 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.

ACKNOWLEDGMENTS

We thank M. Castro for field assistance. T. Ransome and two anonymous referees commented on the manuscript. We thank the staff of 'Salinas La Tapa' and 'Unión Salinera S.A.' for use of their field installations.

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LITERATURE CITED

- Davis, C. A. and L. M. Smith. 2001. Foraging strategies and niche dynamics of coexisting shorebirds at stopover sites in the Southern Great Plains. Auk 118: 484-495.
- Drake, P. and A. Arias. 1994. Distribution and production of *Chironomus salinarius* (Diptera: *Chironomidae*) in a shallow coastal lagoon in the Bay of Cádiz. Hydrobiologia 299: 195-206.
- Drake, P. and A. Arias. 1997. The effect of aquaculture practices on the benthic macroinvertebrate community of a lagoon system in the Bay of Cadiz (Southwestern Spain). Estuaries 20: 677-688.
- Dekinga, A. and T. Piersma. 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. Bird Study 40: 144-156.
- Elphick, C. S. and L. W. Oring. 1998. Winter management of California rice fields for waterbirds. Journal of Applied Ecology 35: 95-108.
- Estrella, S. M. 2001. Comportamiento alimentario, selección de presa y balance energético de la Aguja Colinegra *Limosa limosa* (Scolopacidae) en hábitats supralitorales de la Bahía de Cádiz. Unpublished M.Sc. Dissertation, University of Cádiz, Cádiz, Spain.
- Gill, J. A., R. H. W. Langston, J. A. Alves, P. W. Atkinson, P. Bocher, N. Cidraes Vieira, N. J. Crockford, G. Gélinaud, N. Groen, T. G. Gunnarsson, B. Hayhow, J. Hooijmeijer, R. Kentie, D. Kleijn, P. M. Lourenço, J. A. Masero, F. Meunier, P. M. Potts, M. Roodbergen, H. Schekkerman, J. Schröder, E. Wymenga and T. Piersma. 2007. Contrasting trends in two Blacktailed Godwit populations: a review of causes and recommendations. Wader Study Group Bulletin 114: 43-50.
- Gillings, S. and W. J. Sutherland. 2007. Comparative diurnal and nocturnal diet and foraging in Eurasian Golden Plovers *Pluvialis apricaria* and Northern Lapwings *Vanellus vanellus* wintering on arable farmland. Ardea 95: 243-257.
- Green, A. J. and M. I. Sánchez. 2006. Passive internal dispersal of insect larvae by migratory birds. Biology Letters 2: 55-57.
- Hulbert S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.
- IUCN. 2008. Red List of Threatened Species. Accessed 6 March 2009 at http://www.iucnredlist.org.
- Jacobs, J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's Electivity Index. Oecologia. 14: 413-417.
- Jensen, F. P. and C. Perennou. 2007 Management plan for Black-tailed Godwit (*Limosa limosa*) 2007-2009. Luxembourg: Office for Official Publications of the European Communities (Technical Report 019-007).
- Kalejta, B. 1993. Diets of shorebirds at the Berg River Estuary, South Africa: spatial and temporal variation. Ostrich 64: 123-133.
- Lourenço, P. M. and T. Piersma. 2008. Stopover ecology of Black-tailed Godwits *Limosa limosa limosa* in Portuguese rice fields: a guide on where to feed in winter. Bird Study 55: 194-202.
- Masero, J. A., M. Pérez-González, M. Basadre and M. Otero-Saavedra. 1999. Food supply for waders (Aves: Charadrii) in an estuarine area of the Bay of Cádiz (SW Iberian Peninsula). Acta Oecologica 20: 429-434.

- Masero, J. A., A. Pérez-Hurtado, M. Castro and G. M. Arroyo. 2000. Complementary use of intertidal mudflats and adjacent Salinas by foraging waders. Ardea 88: 177-191.
- Masero, J. A. and A. Pérez-Hurtado. 2001. Importance of the supratidal habitats for maintaining overwintering shorebird populations: how Redshanks use tidal mudflats and adjacent saltworks in southern Europe. Condor 103: 21-30.
- Masero, J. A. 2003. Assessing alternative anthropogenic habitats for conserving waterbirds: Salinas as buffer areas against the impact of natural habitat loss for shorebirds. Biodiversity and Conservation 12: 1157-1173.
- Mouritsen, K. N. 1994. Day and night feeding in Dunlins *Calidris alpina*: choice of habitat, foraging technique and prey. Journal of Avian Biology 25: 55-62.
- Myers, J. P., R. G. Morrison, P. Z. Antas, B. A. Harrington, T. E. Lovejoy, M. Sallaberry, S. E. Senner and A. Tarax. 1987. Conservation strategy for migratory species. American Scientist 75: 19-26.
- Ree, H. and J. Yum. 2006. Redescription of *Chironomus salinarius* (Diptera: Chironomidae), nuisance midges that emerged in brackish water of Jinhae-man (Bay), Kyongsangnam-do, Korea. Korean Journal of Parasitology 44: 63-66.
- Sánchez, M. I., A. J. Green and E. M. Castellanos. 2005. Seasonal variation in the diet of the Redshank *Tringa totanus* in the Odiel Marshes, south-west Spain: a comparison of faecal and pellet analysis. Bird Study 52: 210-216.
- Sánchez, M. I., A. J. Green and E. M. Castellanos. 2006a. Spatial and temporal fluctuations in use by shorebirds and in availability of chironomid prey in the Odiel saltpans, south-west Spain. Hydrobiologia 567: 329-340.
- Sánchez, M. I., A. J. Green, and E. M. Castellanos. 2006b. Temporal and spatial variation of an aquatic invertebrate community subjected to avian predation at the Odiel salt pans (SW Spain). Archiv für Hydrobiologie 166: 199-223.
- Sánchez, M. I., A. J. Green, F. Amat and E. M. Castellanos. 2007. Transport of Brine Shrimps via the digestive system of migratory waders: dispersal probabilities depend on diet and season. Marine Biology 151: 1407-1415.
- Sánchez-Guzmán, J. M., R. Morán, J. A. Masero, C. Corbacho, E. Costillo, A. Villegas and F. Santiago-Quesada. 2007. Identifying new buffer areas for conserving waterbirds in the Mediterranean basin: the importance of the rice fields in Extremadura, Spain. Biodiversity and Conservation 16: 3333-3344.
- Skagen, S. K. 2006. Migration stopovers and the conservation of Arctic-breeding calidridine sandpipers. Auk 123: 313-322.
- Sokal, R. R. and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co., New York, New York.
- StatSoft, Inc. (2004). STATISTICA (data analysis software system), version 7. www.statsoft.com.
- Stroud, D. A., N. C. Davidson, R. West, D. A. Scott, L. Haanstra, O. Thorup, B. Ganter and S. Delany. 2004. Status of migratory wader populations in Africa and Western Eurasia in the 1990s. International Wader Studies 15: 1-259.
- van Gils, J. A, S. R. De Rooij, J. van Belle, J. van der Meer, A. Dekinga, T. Piersma and R. Drent. 2005. Digestive

- bottleneck affects foraging decisions in Red Knots *Calidris canutus*. I. Prey choice. Journal of Animal Ecology 74: 105-119.
- Zharikov, Y. and G. A. Skilleter. 2003. Nonbreeding Eastern Curlews *Numenius madagascariensis* do not increase the rate of intake or digestive efficiency before long-distance migration because of an apparent digestive constraint. Physiological and Biochemical Zoology 76: 704-715.
- Zwarts, L. and D. Dirkesen. 1990. Digestive bottleneck limits the intake rate food of Whimbrels preparing
- for spring migration from the Banc D'Arguin, Mauritania. Ardea 78: 275-278.
- Zwarts, L. and A. M. Blomert. 1992. Why knots *Calidris* canutus take medium-sized *Macoma balthica* when six prey species are available. Marine Ecology Progress Series 83: 113-128.
- Zwarts, L. and J. H. Wanink. 1993. How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. Netherlands Journal of Sea Research 31: 441-476.