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Letter

Individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding

Shou-Dong Zhang, Zhijun Ma, Chen-Chen Feng, David S. Melville, Jan A. van Gils and Theunis Piersma

S.-D. Zhang (<https://orcid.org/0000-0003-3600-0195>), Z. Ma (<https://orcid.org/0000-0001-7459-9448>) ✉ (zhijunm@fudan.edu.cn) and C.-C. Feng, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Coastal Ecosystems Research Station of the Yangtze River Estuary, Shanghai Inst. of Eco-Chongming (SIEC), Fudan Univ., Shanghai, P. R. China. – S.-DZ, J. A. van Gils (<https://orcid.org/0000-0002-4132-8243>) and T. Piersma (<https://orcid.org/0000-0001-9668-466X>), NIOZ Royal Netherlands Inst. for Sea Research, Dept of Coastal Systems and Utrecht Univ., Texel, The Netherlands. TP also at: Conservation Ecology Group, Groningen Inst. for Evolutionary Life Sciences (GELIFES), Univ. of Groningen, Groningen, The Netherlands. – D. S. Melville, Global Flyway Network, Nelson, New Zealand.

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Especially in birds, it is widely found that the size of individual prey items follows the size of the instruments of prey capture, handling and processing, i.e. bill size. In fact, this is the natural history basis of major discoveries on adaptive evolution in the face of changing food resources. In some birds, e.g. the molluscivore shorebirds ingesting hard-shelled prey, most of the prey processing takes place within the digestive tract. This study of a salvaged sample of actively feeding great knots *Calidris tenuirostris* accidentally drowned in fishing nets in northern China, is the first documentation of diet selection at the level of the individual in previously well-studied molluscivore shorebirds. Diet composition was not associated with the length of the bill, but with the mass of the muscular gizzard. Gizzard mass, which unlike bill length is a phenotypically flexible trait, enables great knots to adjust to changing food resources as an individual, i.e. instantly responding to the food on offer. For migratory species like great knots which rely on seasonal sequences of interdistant feeding areas offering prey with a variety of characteristics, the capacity to individually adjust appears a key adaptation.

Keywords: adaptation, break force, *Calidris tenuirostris*, diet selection, flexible trait, great knot, inflexible trait

Introduction

Morphology reflects the relationship between organisms and their environment (Ricklefs and Miles 1994). In a few cases, morphological diversity among individuals or among species have been causally linked to differences in performance and ultimately to differences in fitness (Grant and Grant 1980, 1996, Wainwright 1994, Young et al. 2010). Understanding the relationships between morphology and organismal performance contributes to a deeper understanding of the phenotype–environment interaction (Schluter and Grant 1984a, b, Wainwright 1994). The phenotype may constrain and modify variations in performance (Lauder 1981, Ricklefs and Miles 1994, Wainwright 1994, Grant 2006). Notably, the ‘classic’ story of adaption in real



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time refers to the selection of bill size in Darwin's Finches (*Geospiza fortis*, *G. scandens* and *G. fuliginosa*) in response to drought and the loss of small seeds (Grant and Grant 1980, 1996, 2017, Schluter 1982, Grant 2002, 2006).

However, in some bird taxa, the processing after capture of refractory prey takes place within the body, i.e. in the digestive tract (Piersma et al. 2003, van Gils et al. 2003, Yang et al. 2013). The 'classic' example here is the red knot *Calidris canutus*, a trophic specialist of hard-shelled molluscs, in which the size of prey that can be crushed is a function of the break force generated by the muscular gizzard (Dietz et al. 1999, Yang et al. 2013, Mathot et al. 2017). Despite several decades of study on food, foraging and digestive tract morphology in red knots (Piersma et al. 1993, 1999, 2003, van Gils et al. 2005a, Yang et al. 2013, Bijleveld et al. 2016, Mathot et al. 2017), the relationship between the size of this processing machinery and prey selection still remains to be established at the individual level.

The present study capitalizes on the, otherwise rather unfortunate, availability of a large sample of drowning victims of great knots *Calidris tenuirostris*, the sister species of red knot (Gibson and Baker 2012), and a similarly specialized molluscivore (Tulp and de Goeij 1994, Choi et al. 2017, Zhang et al. 2018). In the course of the nonbreeding season, great knots predictably use sequences of intertidal mudflat habitats where they encounter prey with a wide range of characteristics, each of which may also change between repeated encounters in different years (Zhang et al. 2019a). We predict that in the present sample of great knots which were experiencing a single 'food environment', prey characteristics should be associated with the internal processing machinery (i.e. gizzard mass) rather than the machinery of food capture and handling (i.e. bill size); individuals with larger gizzards should capture prey which are harder to crush.

Methods

Study area and food situation

This study was carried out during April–May 2018 at the Yalu Jiang coastal wetland (39°40'–39°58'N, 123°34'–124°07'E), Liaoning, China (Zhang et al. 2018, 2019a). About 44 000 great knots (Zhang et al. 2018) stage here for nearly two months during northward migration (Ma et al. 2013, Choi et al. 2015, Tan et al. 2018). From the end of March, local fishermen set up many kilometers of very fine, almost invisible, monofilament nets to catch Mantis shrimp *Oratosquilla oratoria* in the lower intertidal zone. It is estimated that at low tide thousands of waterbirds are accidentally caught and then drown each spring (S. D. Zhang, unpubl.). In view of the fact that the year to year differences in the benthic food situation for great knots have been much larger than the degree of food depletion within a single spring (Zhang et al. 2018, 2019a), the great knots sampled here over a two-month period can nevertheless be considered to have experienced a single food environment.

Gizzard size

In April–May 2018 a total of 118 dead great knots were collected. The carcasses were stored individually in airtight plastic bags at -20°C . In the laboratory, the carcasses were weighed and the bill length (exposed culmen) measured after the feathers were dried with a hair dryer. Carcasses were dissected following the procedures of Piersma et al. (1999). The fresh mass of the gizzard (without contents) was weighed to the nearest 0.1 g.

Diet composition

The contents of each gizzard were washed separately through a 0.3 mm sieve, and then dried at 60°C for 72 h. Dry mass of the shells from gizzards was weighed to the nearest 0.1 mg. The shell fragments were sorted to species, and measured to the nearest 0.1 mm using an Olympus SZX7 dissecting microscope: the height of unbroken hinges for bivalve species, the width of the last whorl of the columella for the gastropod *Umbonium thomasi*, and the shell length for undigested individuals (Zhang et al. 2019a). We also measured the height of the left hinge for different shell lengths of all the bivalve species (Dekinga and Piersma 1993, Yang et al. 2013), and the width of the last whorl of the columella for different sizes of *U. thomasi* (Zhang et al. 2019a). The species-specific functions between size (the longest measurement) and height of left hinge or the width of the last whorl of the columella were established using regression analysis (polynomial, e-exponential, logarithmic and power regression) for each mollusk group (Zhang et al. 2019a). Models with the largest correlation coefficient were selected ($R^2 > 0.85$, $p < 0.05$ for all) (Zhang et al. 2019a). To determine the size composition of ingested organisms contained in the gizzard, we used the regression of left hinge height against shell length for bivalve species, and the regression between columella width and total width in *U. thomasi* (Zhang et al. 2019a).

Break force

Based on freshly collected mollusk samples, we measured the break force (N) of different sizes of mollusks with a fixed digital force gauge (HP-20 and HP-300, Yueqing Ai Li Instrument, China) (Bom et al. 2018, Zhang et al. 2019a). We regressed break force on prey size, trying polynomial, e-exponential, logarithmic and power regression. Models with the largest correlation coefficient were selected ($R^2 > 0.83$, $p < 0.05$ for all, Supplementary material Appendix 1 Table A1). To determine the break force of ingested organisms contained in the gizzard, we used the regression of shell length against break force for bivalve species, and the regression between width in *U. thomasi* and break force (Zhang et al. 2019a).

Data analysis

We analyzed the relationships between the size of body parts and diet by assigning birds to one of the eight strata with bill lengths of 40–41, 41–42, 42–43, 43–44, 44–45, 45–46,

46–47 and 47–48 mm, and to gizzard masses of 6–8, 8–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22 g. The size of *U. thomasi*, the most common prey item, was split in four groups: 5–8, 8–11, 11–14, 14–18 mm (the last category is broader and includes the few largest snails). Pearson correlation tests were used to analyze the relationships between bill length or gizzard mass and prey species number, percentage of different prey species in gizzards, percentage of different size of *U. thomasi*; and the relationship between gizzard mass and bill length. Logarithmic transformation was used when the data were not normally distributed. Spearman's rank correlation tests were used to analyze the relationships between bill length (mm) or gizzard mass (g) and shell dry mass in gizzard or the average break force (N) of prey consumed by per individual. We used regression analyses (polynomial, e-exponential, logarithmic and power regression) to establish the relationship and models with the largest correlation coefficient were selected. The significance level was set at 0.05. All statistical analyses were carried out in SPSS 20.0.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.8pp2rt0>> (Zhang et al. 2019b).

Results

A total of 3150 recognizable prey items of 15 species were identified in the gizzards of 118 dead great knots. *U. thomasi* (94%) was dominant, followed by *Ruditapes philippinarum* (2.5%), *Potamocorbula laevis* (1%) and *Lingula anatina* (1%). The remaining 11 species contributed 1.5% of the total number of prey items (Fig. 1A–B). Bill length was not correlated with gizzard mass ($r=0.14$, $p=0.13$), and there was no correlation between bill length and the numerical percentage of each prey species either ($|r|<0.51$, $p>0.20$ for all, Fig. 1A). However, gizzard mass was significantly correlated with the numerical percentages of *U. thomasi* ($r=0.83$, $p=0.01$) and *R. philippinarum* ($r=-0.83$, $p=0.01$), with the larger gizzard mass containing more *U. thomasi* but less *R. philippinarum*. No significant correlations were detected between gizzard mass and the numerical percentages of other prey species ($|r|<0.66$, $p>0.05$ for all, Fig. 1B).

The most common prey item, the snail *U. thomasi*, is particularly hard to crush (Zhang et al. 2018). There were no consistent correlations between bill length and the numerical percentages of various size groups of *U. thomasi* (5–8 mm: $r=-0.93$, $p=0.001$, 11–14 mm: $r=0.79$, $p=0.02$, 8–11 mm: $r=-0.03$, $p=0.94$, 14–18 mm: $r=-0.06$, $p=0.88$) (Fig. 1C). In contrast, there were consistent and significant correlations between gizzard mass and the numerical percentages of various size groups. Generally, gizzard mass was negatively correlated with the numerical percentages of the small-sized *Umbonium* snails (5–8 mm and 8–11 mm: $r<0.83$, $p<0.01$ for both, Fig. 1D), whilst positively correlated with the large-sized classes (11–14 mm and 14–18 mm, $r>0.88$, $p<0.004$ for both, Fig. 1D).

The dry mass of shell fragments in each gizzard did not significantly correlate with bill length ($r=0.25$, $p=0.34$, Fig. 1E), but exhibited a positive correlation with gizzard mass ($r=0.66$, $p<0.001$, Fig. 1F). Bill length was not correlated with average break force of the prey ($r=0.11$, $p=0.27$, Fig. 1G), but gizzard mass was ($r=0.70$, $p<0.001$, Fig. 1H).

Discussion

During three decades of research it became well established that gizzard mass of red (rather than great) knots is associated with diet and the other way around (Dekinga and Piersma 1993, Piersma et al 1993, 1999, 2003, van Gils et al. 2005b, Yang et al. 2013, Mathot et al. 2017). Yet, in none of these studies such associations could be established at the individual level. Thus, the present study on great knots still fills a gap. Perhaps more importantly, for the first time it enabled us to assess whether the usual phenotypic trait that correlates with diet in birds, i.e. bill size (Grant and Grant 1980, 1996), has equal or better explanatory power as gizzard mass. It did not.

Difference in diet compositions lead to difference in break force (of the ingested prey items in individuals; shown here in Fig. 1), with the shell-crushing power of the muscular gizzard being a (proven) function of gizzard mass (van Gils et al. 2003). Larger gizzards not only can break stronger shells, but can also process more shell material at a given moment. The latter was already known for red knots, but it is exciting to note that the exponent of 2.00 found in the current study (Fig. 1F) exactly matches the exponent found in two red knot studies (van Gils et al. 2003, Oudman et al. 2015).

Just as the Darwin's finches that experienced dramatic inter-annual changes in the size and hardness of seed food (Grant and Grant 1980, 1996, Grant 2002), the great knots in this study experienced stark changes in the composition and hardness of their shellfish food between years (Zhang et al. 2018, 2019a). To adapt to the changed food, in the recent spring seasons when hard-shelled snails *U. thomasi* were the major prey, great knots responded by showing larger gizzards (Zhang et al. 2019a). In the course of these few years, however, there was no significant change in the bill length of salvaged great knots (one-way ANOVA, $F_{4,144}=0.98$, $p=0.42$).

In contrast, red knots *Calidris canutus canutus* on the sea-grass-covered mudflats of the Banc d'Arguin in Mauritania demonstrated that individuals with longer bills ingested more deeply burrowed bivalve prey (van Gils et al. 2016). In fact, during a series of years with a change towards deeper living prey at Banc d'Arguin, longer bills seemed selected for. As on the mudflats at Yalu Jiang the *U. thomasi* snails live on the surface of mudflats, they can easily be found by eye and do not need any probing to be retrieved. Clearly, under these conditions we do not expect a correlation between bill length and diet. Gape width (probably a component of bill size) may constrain the size of prey that can be swallowed (Sherry and McDade 1982, Wheelwright 1985, Zwarts and Blomert 1992). Great knots can ingest 23 mm length of

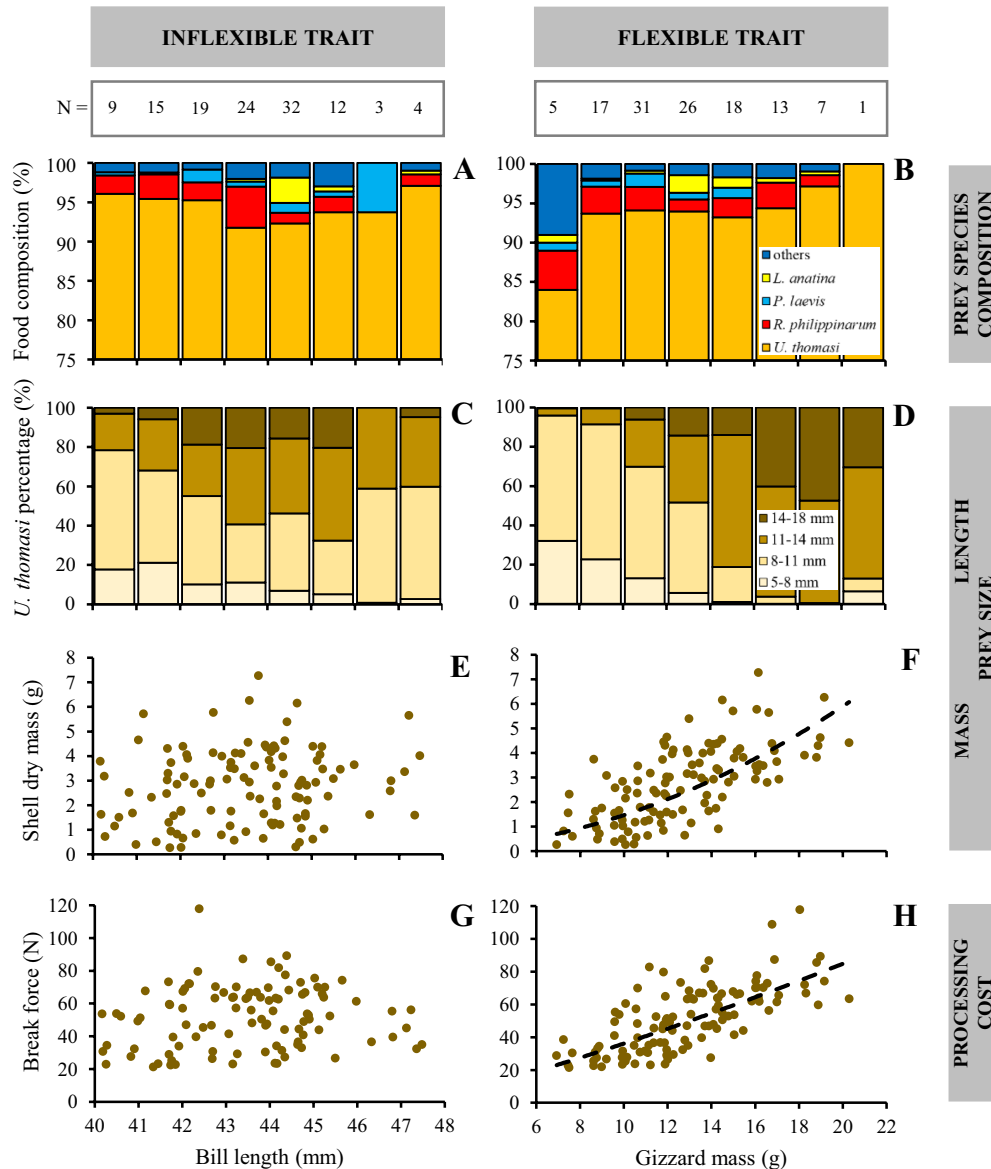


Figure 1. Food composition, numerical percentage of the snail *Umbo thomasi*, shell dry mass in the gizzard and break force of prey in gizzard of great knots as a function of bill length and gizzard mass. (A) Diet composition for great knots with different bill lengths and (B) different gizzard mass; (C) numerical percentages of *U. thomasi* of different sizes in relation to bill length and (D) gizzard mass; (E) shell dry mass in the gizzard as a function of bill length and (F) gizzard mass (equation: shell dry mass = $0.015 \times \text{gizzard mass}^{2.00}$, broken line); (G) break force as a function of bill length and (H) gizzard mass (equation: break force of prey = $2.13 \times \text{gizzard mass}^{1.23}$, broken line). N = individual number per interval.

Mactra veneriformis (Zhang et al. 2019a), 23.1 mm of *R. philippinarum* and 23.8 mm of *P. laevis*, values which are much larger than the 18 mm for *U. thomasi* (the largest one found in gizzards). This indicates once again that the size of *U. thomasi* ingested would not be expected to show a correlation with bill size.

Now, what would happen if the diet of great knots were a function of bill size, as in Darwin's finches? And, what would have happened to the finches of Isla Daphne Major, Galapagos if bill lengths were as flexible as gizzards? The answer to both questions is that flexibility gives animals the

capacity for adjustments on the short term (Dekinga 2001, Piersma and Drent 2003, Piersma and van Gils 2011). The evolutionary question that follows is whether this prevention of deaths, and therefore the decrease in the strength of natural selection (with the benefit of reducing the risk of extinction), also leads to an absence of directional change on gizzard mass per se, or on a possible 'reaction norm' mediating an adaptive phenotypic response of gizzard mass on prey characteristics? Or is the capacity to ontogenetically develop an appropriately sized gizzard (and reversibly alter it in response to later experiences) simply reflecting the ways that organisms, in this case

molluscivore shorebirds, are built? In the words of Turner (2007): ‘organisms are designed not so much because natural selection of particular genes has made them that way, but because agents of homeostasis build them that way.’ And yet, can such dispositions nevertheless be precursors of eventually inherited individual differences in the flexibility of traits, i.e. the reaction norms (West-Eberhard 2003)?

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Author contributions – Z.J.M., T.P. and S.D.Z. conceived the idea; S.D.Z., C.C.F. and D.S.M. collected the data in the field; S.D.Z. processed the samples and analysed the data; S.D.Z., T.P. and Z.J.M. led the writing of the manuscript. All authors contributed to the drafts and approved the final version.

References

- Bijleveld, A. I., MacCurdy, R. B., Chan, Y. C., Penning, E., Gabrielson, R. M., Cluderay, J., Spaulding, E., Dekinga, A., Holthuis, S., ten Horn, J., Brugge, M., van Gils, J. A., Winkler, D. W. and Piersma, T. 2016. Understanding spatial distributions: negative density dependence in prey causes predators to trade-off prey quantity with quality. – *Proc. R. Soc. B* 283: 20151557.
- Bom, R. A., de Fouw, J., Klaassen, R. H. G., Piersma, T., Lavaleye, M. S. S., Ens, B. J., Oudman, T. and van Gils, J. A. 2018. Food web consequences of an evolutionary arms race: molluscs subject to crab predation on intertidal mudflats in Oman are unavailable to shorebirds. – *J. Biogeogr.* 45: 342–354.
- Choi, C. Y., Battley, P. F., Potter, M. A., Rogers, K. G. and Ma, Z. J. 2015. The importance of Yalu Jiang coastal wetland in the north Yellow Sea to bar-tailed godwits *Limosa lapponica* and great knots *Calidris tenuirostris* during northward migration. – *Bird Conserv. Int.* 25: 53–70.
- Choi, C. Y., Battley, P. F., Potter, M. A., Ma, Z. J., Melville, D. S. and Sukkaewmanee, P. 2017. How migratory shorebirds selectively exploit prey at a staging site dominated by a single prey species. – *Auk* 134: 76–91.
- Dekinga, A. and Piersma, T. 1993. Reconstructing diet composition on the basis of faeces in a mollusc-eating wader, the knot *Calidris canutus*. – *Bird Study* 40: 144–156.
- Dekinga, A., Dietz, M. W., Koolhaas, A. and Piersma, T. 2001. Time course and reversibility of changes in the gizzards of red knots alternately eating hard and soft food. – *J. Exp. Biol.* 204: 2167–2173.
- Dietz, M. W., Dekinga, A., Piersma, T. and Verhulst, S. 1999. Estimating organ size in small migrating shorebirds with ultrasonography: an intercalibration exercise. – *Physiol. Biochem. Zool.* 72: 28–37.
- Gibson, R. and Baker, A. 2012. Multiple gene sequences resolve phylogenetic relationships in the shorebird suborder Scolopaci (Aves: Charadriiformes). – *Mol. Phylogenet. Evol.* 64: 66–72.
- Grant, P. R. 2002. Unpredictable evolution in a 30-year study of Darwin’s Finches. – *Science* 296: 707–711.
- Grant, P. R. 2006. Evolution of character displacement in Darwin’s Finches. – *Science* 313: 224–226.
- Grant, P. R. and Grant, B. R. 1980. Annual variation in finch numbers, foraging and food supply on Isla Daphne Major, Galápagos. – *Oecologia* 46: 55–62.
- Grant, B. R. and Grant, P. R. 1996. High survival of Darwin’s Finch hybrids: effects of beak morphology and diets. – *Ecology* 77: 500–509.
- Grant, B. R. and Grant, P. R. 2017. Watching speciation in action. – *Science* 355: 910–911.
- Lauder, G. V. 1981. Form and function: structural analysis in evolutionary morphology. – *Paleobiology* 7: 430–442.
- Ma, Z. J., Hua, N., Peng, H. B., Choi, C., Battley, P. F., Zhou, Q. Y., Chen, Y., Ma, Q., Jia, N., Xue, W. J., Bai, Q., Wu, W., Feng, X. and Tang, C. 2013. Differentiating between stopover and staging sites: functions of the southern and northern Yellow Sea for long-distance migratory shorebirds. – *J. Avian Biol.* 44: 504–512.
- Mathot, K. J., Dekinga, A. and Piersma, T. 2017. An experimental test of state-behaviour feedbacks: gizzard mass and foraging behaviour in red knots. – *Funct. Ecol.* 31: 1111–1121.
- Oudman, T., Hin, V., Dekinga, A. and van Gils, J. A. 2015. The effect of digestive capacity on the intake rate of toxic and non-toxic prey in an ecological context. – *PLoS One* 10: e0136144.
- Piersma, T. and Drent, J. 2003. Phenotypic flexibility and the evolution of organismal design. – *Trends Ecol. Evol.* 18: 228–233.
- Piersma, T. and van Gils, J. A. 2011. The flexible phenotype. a body-centred integration of ecology, physiology and behaviour. – Oxford Univ. Press.
- Piersma, T., Koolhaas, A. and Dekinga, A. 1993. Interactions between stomach structure and diet choice in shorebirds. – *Auk* 110: 552–564.
- Piersma, T., Gudmundsson, G. A. and Lilliendahl, K. 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long distance migrating shorebird. – *Physiol. Biochem. Zool.* 72: 405–415.
- Piersma, T., Dekinga, A., van Gils, J. A., Achterkamp, B. and Visser, G. H. 2003. Cost-benefit analysis of mollusc eating in a shorebird I. Foraging and processing costs estimated by the doubly labelled water method. – *J. Exp. Biol.* 206: 3361–3368.
- Ricklefs, R. E. and Miles, D. B. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. – In: Wainwright, P. C. and Reilly, S. M. (eds), *Ecological morphology – integrative organismal biology*. – Chicago Univ. Press, pp. 13–41.
- Schluter, D. 1982. Seed and patch selection by Galapagos ground finches: relation to foraging efficiency and food supply. – *Ecology* 63: 1106–1120.
- Schluter, D. and Grant, P. R. 1984a. Determinants of morphological patterns in communities of Darwin’s finches. – *Am. Nat.* 123: 175–196.
- Schluter, D. and Grant, P. R. 1984b. Ecological correlates of morphological evolution in a Darwin’s finch, *Geospiza difficilis*. – *Evolution* 38: 856–869.
- Sherry, T. W. and McDade, L. A. 1982. Prey selection and handling in two Neotropical hover-gleaning birds. – *Ecology* 63: 1016–1028.
- Tan, K., Choi, C. Y., Peng, H. B., Melville, D. S. and Ma, Z. J. 2018. Migration departure strategies of shorebirds at a final pre-breeding stopover site. – *Avian Res.* 9: 15.

- Tulp, I. and de Goeij, P. 1994. Evaluating wader habitats in Roebuck Bay (North-western Australia) as a springboard for northbound migration in waders, with a focus on great knots. – *Emu* 94: 78–95.
- Turner, J. S. 2007. The Tinkerer's accomplice: how design emerges from life itself. – Harvard Univ. Press.
- van Gils, J. A., Piersma, T., Dekinga, A. and Dietz, M. W. 2003. Cost–benefit analysis of mollusc–eating in a shorebird. II. Optimizing gizzard size in the face of seasonal demands. – *J. Exp. Biol.* 206: 3369–3380.
- van Gils, J. A., Battley, P. F., Piersma, T. and Drent, R. 2005a. Reinterpretation of gizzard sizes of red knots world–wide emphasises overriding importance of prey quality at migratory stopover sites. – *Proc. R. Soc. B* 272: 2609–2618.
- van Gils, J. A., Dekinga, A., Spaans, B., Vahl, W. K. and Piersma, T. 2005b. Digestive bottleneck affects foraging decisions in red knots *Calidris canutus*. II. Patch choice and length of working day. – *J. Anim. Ecol.* 74: 120–130.
- van Gils, J. A., Lisovski, S., Lok, T., Meissner, W., Ożarowska, A., de Fouw, J., Rakhimberdiev, E., Soloviev, M. Y., Piersma, T. and Klaassen, M. 2016. Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. – *Science* 352: 819–821.
- Wainwright, P. C. 1994. Functional morphology as a tool in ecological research. – In: Wainwright, P. C. and Reilly, S. M. (eds), *Ecological morphology – integrative organismal biology*. Chicago Univ. Press, pp. 42–59.
- West-Eberhard, M. J. 2003. *Developmental plasticity and evolution*. – Oxford Univ. Press.
- Wheelwright, N. T. 1985. Fruit-size, gape width and the diets of fruit-eating birds. – *Ecology* 66: 808–818.
- Yang, H. Y., Chen, B., Ma, Z. J., Hua, N., van Gils, J. A., Zhang, Z. W. and Piersma, T. 2013. Economic design in a long-distance migrating molluscivore: how fast-fuelling red knots in Bohai Bay, China, get away with small gizzards. – *J. Exp. Biol.* 216: 3627–3636.
- Young, R. L., Sweeney, M. J. and Badyaev, A. V. 2010. Morphological diversity and ecological similarity: versatility of muscular and skeletal morphologies enables ecological convergence in shrews. – *Funct. Ecol.* 24: 556–565.
- Zhang, S. D., Ma, Z., Choi, C. Y., Peng, H. B., Bai, Q. Q., Liu, W. L., Tan, K., Melville, D. S., He, P., Chan, Y. C., van Gils, J. A. and Piersma, T. 2018. Persistent use of a staging site in the Yellow Sea by shorebirds despite severe declines in food resources implies a lack of alternative habitats. – *Bird Conserv. Int.* 28: 534–548.
- Zhang, S. D., Ma, Z., Choi, C. Y., Peng, H. B., Melville, D. S., Zhao, T. T., Bai, Q. Q., Liu, W. L., Chan, Y. C., van Gils, J. A. and Piersma, T. 2019a. Morphological and digestive adjustments buffer performance: how staging shorebirds cope with severe food declines. – *Ecol. Evol.* 9: 3868–3878.
- Zhang, S.-D., Ma, Z., Feng, C.-C., Melville, D. S., van Gils, J. A. and Piersma, T. 2019b. Data from: individual diet differences in a molluscivore shorebird are associated with the size of body instruments for internal processing rather than for feeding. – Dryad Digital Repository, <<http://dx.doi.org/10.5061/dryad.8pp2rt0>>.
- Zwarts, L. and Blomert, A.-M. 1992. Why knot *Calidris canutus* take medium-sized *Macoma balthica* when six prey species are available. – *Mar. Ecol. Progr. Ser.* 83: 113–128.

Supplementary material (available online as Appendix jav-02255 at <www.avianbiology.org/appendix/jav-02255>). Appendix 1.