

University of Groningen

Phenotype-limited distributions

Duijns, Sjoerd; van Gils, Jan A; Smart, Jennifer; Piersma, Theunis

Published in:
Royal Society Open Science

DOI:
[10.1098/rsos.150073](https://doi.org/10.1098/rsos.150073)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2015

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Duijns, S., van Gils, J. A., Smart, J., & Piersma, T. (2015). Phenotype-limited distributions: Short-billed birds move away during times that prey bury deeply. *Royal Society Open Science*, 2, [150073].
<https://doi.org/10.1098/rsos.150073>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



Cite this article: Duijns S, van Gils JA, Smart J, Piersma T. 2015 Phenotype-limited distributions: short-billed birds move away during times that prey bury deeply. *R. Soc. open sci.* **2**: 150073.
<http://dx.doi.org/10.1098/rsos.150073>

Received: 13 February 2015

Accepted: 15 May 2015

Subject Category:

Biology (whole organism)

Subject Areas:

ecology/behaviour

Keywords:

body size, distribution, food availability, *Limosa lapponica*, morphology, resource use

Author for correspondence:

Sjoerd Duijns

e-mail: duijns.sjoerd@gmail.com

Phenotype-limited distributions: short-billed birds move away during times that prey bury deeply

Sjoerd Duijns¹, Jan A. van Gils¹, Jennifer Smart² and Theunis Piersma^{1,3}

¹Department of Marine Ecology, NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

²Wash Wader Ringing Group, The Old School House, Rhooon Road, Terrington St Clement, Norfolk PE34 4H, UK

³Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands

In our seasonal world, animals face a variety of environmental conditions in the course of the year. To cope with such seasonality, animals may be phenotypically flexible, but some phenotypic traits are fixed. If fixed phenotypic traits are functionally linked to resource use, then animals should redistribute in response to seasonally changing resources, leading to a ‘phenotype-limited’ distribution. Here, we examine this possibility for a shorebird, the bar-tailed godwit (*Limosa lapponica*; a long-billed and sexually dimorphic shorebird), that has to reach buried prey with a probing bill of fixed length. The main prey of female bar-tailed godwits is buried deeper in winter than in summer. Using sightings of individually marked females, we found that in winter only longer-billed individuals remained in the Dutch Wadden Sea, while the shorter-billed individuals moved away to an estuary with a more benign climate such as the Wash. Although longer-billed individuals have the widest range of options in winter and could therefore be selected for, counterselection may occur during the breeding season on the tundra, where surface-living prey may be captured more easily with shorter bills. Phenotype-limited distributions could be a widespread phenomenon and, when associated with assortative migration and mating, it may act as a precursor of phenotypic evolution.

1. Introduction

Most organisms on the Earth live in seasonal environments with respect to climate and food [1]. The ability of individuals

to reversibly change phenotype in response to a change in environmental conditions is called phenotypic flexibility [2,3]. Animals making adjustments in digestive organ size to cope with different prey types or prey quality represent a well-known example of (often seasonally structured) phenotypic flexibility (e.g. [4–6]). However, some aspects of the phenotype are essentially inflexible. Traits such as bill length in birds that show determined growth are hardly flexible [7,8]. Bill morphology is a strong predictor of foraging niche (e.g. [9–15]), and may lead to phenotype-related differences in diet [16,17]. In addition, in response to environmental change, animals can show behavioural responses such as changes in foraging time (e.g. [18,19]), diet [20,21], or the movement to sites where good food may be more favourable (e.g. [22–24]).

Intra-population variation in dietary optima, and temporal and spatial variation in the abundance or availability of different prey is known for many species of fish, amphibians, insects, mammals and birds [25]. Body size, dominance, prior residency or food availability appear to be responsible for individual differences in migratory tendencies within populations [26]. Food availability is relatively easy to quantify in intertidal areas [27], and non-breeding shorebirds provide a good system for correlating distribution of animals with their food resources (e.g. [28–30]). Non-breeding shorebirds in temperate zones mostly feed on benthic prey that tends to bury deeper in winter than in summer (e.g. [31,32]). Although burying depth may be ultimately determined by climatic factors, the seasonal rhythm of burying depth for a certain location appears a response to changes in day length rather than changes in seawater temperature, at least in the case of polychaetes [32]. With seasonally changing fractions of benthic prey burying beyond the bill lengths of most shorebird species (e.g. [33,34]), the part of the population for which too high a proportion of prey has become inaccessible should move elsewhere. This could lead to ‘phenotype-limited’ forager distributions, a term that was first used to predict spatial distributions of individuals differing in dominance [35].

Bar-tailed godwits (*Limosa lapponica*) are sexually dimorphic migratory shorebirds, with females having 25% longer bills than males and mainly feeding on deep burying lugworms (a polychaete worm, *Arenicola marina*), while the shorter-billed males mainly forage on shallow-buried prey [36,37]. Among the available benthic prey items, seasonal variation in burying depth is largest in lugworms [32], so the potential for a phenotype-limited distribution should be most pronounced in female godwits. In addition, there is considerable variation in bill length within the sexes [38–40]. Although the larger sex (females) should incur lower energetic costs per unit body mass, the differential distribution between the sexes is best explained by sex-specific prey availability [41]. We therefore hypothesized that this differential distribution could be extended to individuals within a sex and tested whether phenotype-limited distributions in female bar-tailed godwits exist. Individuals with shorter bills are predicted [42] to (i) move to more favourable wintering sites (i.e. areas with prey buried less deeply) and/or (ii) switch to prey items that are buried less deeply to sustain their minimum intake requirement.

Females with longer bills would be able to reach a larger fraction of the available biomass compared with shorter-billed individuals. This idea is shown in figure 1. We explored the possibility of a phenotype-limited distribution by analysing the monthly distribution in bill lengths using long-term datasets of measured and marked non-breeding females in the Dutch Wadden Sea and in the Wash, UK. To estimate how intake rates depend on prey burying depth, and to predict the observed seasonal changes in diet composition [37], we used generally applicable functional response parameters [44].

2. Material and methods

2.1. Study species

The bar-tailed godwit is a sexually dimorphic long-distance migratory shorebird, of which two subspecies are identified along the East-Atlantic flyway [45]. The subspecies *L. l. taymyrensis* mainly winters in West Africa, breeds in northern Siberia and uses the Wadden Sea area twice a year as a refuelling site. The *L. l. lapponica* subspecies winters in Northwestern Europe and breeds in northern Scandinavia [40,46]. To explore the possibility of a phenotype-limited distribution, we initially distinguished between the subspecies, as the *taymyrensis* subspecies has on average a shorter bill length than the nominate *lapponica* subspecies [40,45], with considerable overlap in morphometrics. The subspecies occur together in the Dutch Wadden Sea during six months of the year (April–October) [40]. During this period, they would encounter similar environmental conditions in the Dutch Wadden Sea, and therefore all females with known bill lengths from known and unknown sub-specific identity were included in the analyses.

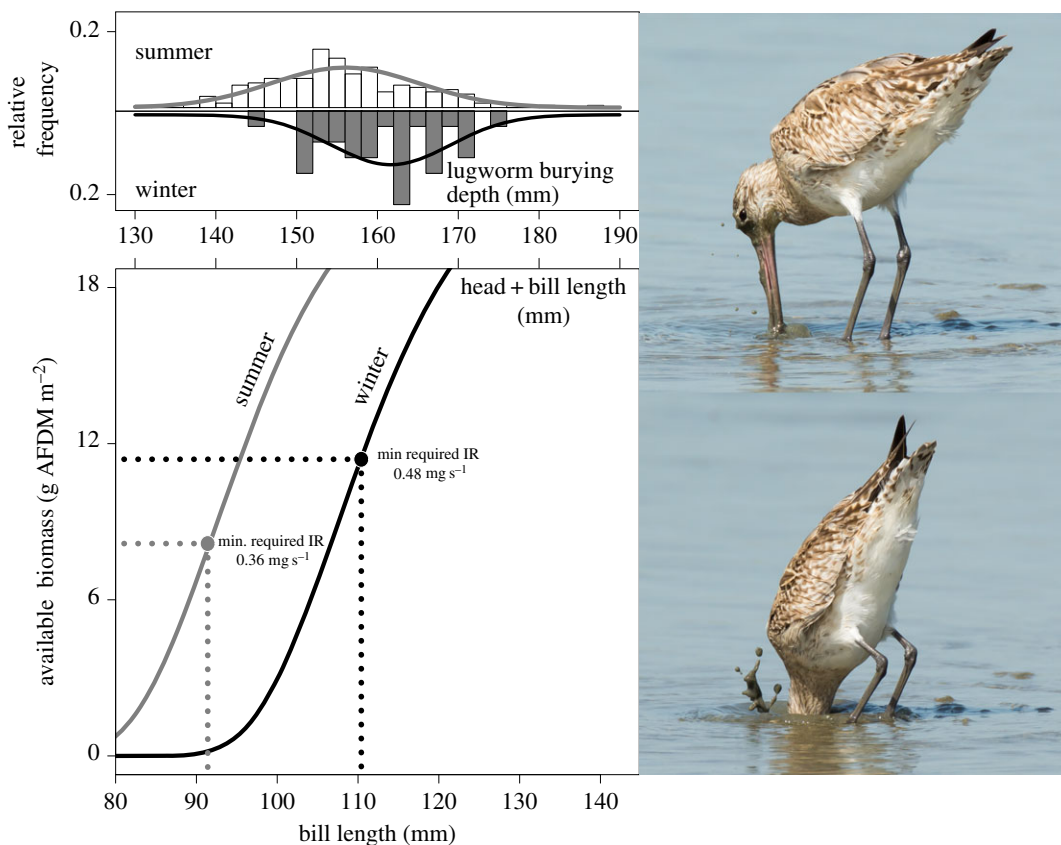


Figure 1. Conceptual model of available lugworm biomass in relation to bill length of female bar-tailed godwits in the Dutch Wadden Sea. Upper panel shows the distribution of individual lugworm burying depths, measured in 1981/1982 (corrected for accessibility; i.e. 40 mm subtracted), and separated for summer (April–September) and winter (October–March). From this, the availability in relation to bill length can be deduced (lower panel, in which upper axis expresses head + bill). In summer, available biomass increases steeply as a function of bill length (due to the shallower burying depth), while minimum required intake rate (IR; $0.36 \text{ mg AFDM s}^{-1}$) is relatively low. Therefore, almost all individuals (more than 92 mm bill) are able to reach their minimum requirement foraging only on lugworms. In winter, available biomass only increases at longer bills and, furthermore, minimum requirement is relatively high (due to higher maintenance costs [43]). Shorter-billed females cannot acquire their minimum requirement and are predicted to leave this wintering site or shift their diet towards more accessible prey. Minimum requirements were calculated as follows: minimum requirement = $(\text{DEE}_{\text{season}}/e)/T_f$, where e is a lugworm's energy content (22 kJ g^{-1} AFDM) [32], the required daily energy expenditure DEE per season was set at $2.4 \times \text{BMR}$ in winter and $1.8 \times \text{BMR}$ in summer [43], daily foraging time T_f was assumed to be 12 h for both seasons (i.e. 50% [43]), assuming an assimilation efficiency of 80% [43]. The photos on the right exemplify the ability of female bar-tailed godwits to reach depths beyond the bill length. Original photos by Dave Montreuil.

2.2. Sightings and catches of marked individuals

Birds were caught with 'wilsternets' [47] or mist nets at various locations throughout the Dutch Wadden Sea area. Before release, length of bill (exposed culmen, from tip of bill to base of feathers), wing (flattened and straightened), tarsus and mass were measured using standard methods [48]. Captures ($n = 2433$) and sightings of marked individual females in the Dutch Wadden Sea ($n = 4069$) were analysed over the period from capture up to May 2014 to assess bill length distributions per month. The 4069 sightings were based on 1541 individuals, of which 864 individuals were sighted multiple times (i.e. different months and/or years). They were all included in the analysis, as the analyses with and without multiple sightings did not differ, while the repeated presence of an individual is considered indicative of a preference to reside at a site. Full details on number of birds caught and sighted per month and year are given in table 1. To compare bill length distributions with another major non-breeding site, biometric data were obtained from the Wash Wader Ringing Group in the UK. Here, bar-tailed godwits have been caught on the Wash with both cannon nets and mist nets [49]. The data for 1693 female bar-tailed godwits were collected in 1994–2011.

Table 1. Overview of numbers of female bar-tailed godwits caught and sighted in the Dutch Wadden Sea, by year and by month. Note that individuals may be sighted more than once in the same month.

year	no. caught	no. sightings	month	no. caught	no. sightings
2001	94	8	Jan	0	9
2002	99	10	Feb	9	28
2003	287	162	Mar	18	122
2004	149	146	Apr	117	237
2005	126	206	May	2057	2504
2006	180	276	June	0	38
2007	133	379	July	39	190
2008	79	172	Aug	90	641
2009	211	360	Sep	60	234
2010	262	425	Oct	38	42
2011	332	658	Nov	5	10
2012	257	588	Dec	0	14
2013	224	486			
2014	0	193			

Although seasonal differences in bill length distributions have been reported in several bird species, differential bill wear was held responsible for this variation (e.g. [50–52]). For shorebirds, it is known that the rhamphotheca, the horny covering of a bird's bill, constantly grows at the base of the bill. Despite this growth, the bill wears and within individual variation appears to be negligible (less than 1 mm; [7]). Indeed, recaptures (more than 1 year interval) of marked bar-tailed godwits show no evidence of intra-individual variation in bill length ($F_{1,12} = 936.5$, $R^2 = 0.99$, $p < 0.001$; slope = 0.95 s.e. 0.03 and intercept = 4.5 s.e. 2.6).

2.3. Prey availability

The burying depth, density and length of lugworms was measured each month in the eastern part of the Dutch Wadden Sea along the mainland coast of the province of Friesland (53°25' N, 6°04' E) during two consecutive years (1980/1981) [32]; the principal investigator (L. Zwarts) ensured that the original raw data became available for later analysis. Burying depth was measured as the distance between the surface and the deepest point of their U-shaped burrow [32]. As lugworms will be captured as their tail resides in one of their vertical shafts, while their body is in the bottom of the U-shaped burrow [53], we subtracted 40 mm (i.e. half of the mean length of lugworms; $n = 205$) from each depth measurement, to represent availability.

2.4. Predicting intake rates

To examine whether the predicted energy intake rate (PEIR) was related to lugworm burying depth, we averaged monthly prey burying depths ($n = 205$) and predicted intake rates throughout the year based on functional response parameters [44]. Note that the bill lengths of the birds used in the published experiment (91.4, 93.7, 94.6, 98.5 and 99.5 mm, respectively) coincided with population averages (mean = 96.2 ± 0.06 s.e., $n = 2433$), and no effects of bill length were detected. For these reasons, PEIR should fairly represent population averages. By using the slope and intercept of a linear model of the searching efficiency on prey burying depth [44], we here estimated depth i specific searching efficiency a_i . Searching efficiency was independent of prey length and density [44]. Handling time T_h was independent of prey burying depth and constant for prey density but increased with prey length [44]. Therefore, we here used the intercept and slope from a linear model of handling time against prey length to estimate length-specific handling times [44]. The month-specific predicted energy intake rate (PEIR_{*m*}) was calculated

using the following equation:

$$\text{PEIR}_m = \sum_{ij} \frac{(a_i N_{ijm} e_j)}{(1 + a_i N_{ijm} T_{hj})} \quad (2.1)$$

where N is the mean density (# m^{-2}) for depth i , prey length j and month m , as measured by Zwarts & Wanink [32], and e the ash-free dry mass (AFDM (mg); i.e. energetic value) per individual prey using the length–AFDM relation (e.g. [36,54]). Next, we evaluated the mean monthly energetic contribution of lugworms to the year-round diet based on field observations ($n = 76$) [36,37,55] and dropping analyses ($n = 240$) [54].

2.5. Statistical analyses

Monthly lugworm burying depth and monthly bill length distributions (with and without subspecies differentiation) were explored using linear and quadratic models. In the linear (null) model, prey burying depth or bill length did not depend on month. The alternative (quadratic) model was evaluated using model selection methods and ranked using Akaike Information Criterion (AIC), and the model was considered to be substantially better when the AIC value was at least two points lower when compared with the other model [56]. To assess the proportion of available prey in relation to bill length, the empirical cumulative distribution function (ECDF [57]) was plotted for females captured or sighted in summer (April–September) and winter (October–March). All analyses were conducted using R v. 3.0.1 [58].

3. Results

Burying depth of lugworms varied predictably throughout the year (figure 2a). Lugworms bury deepest during winter ($F_{2,202} = 5.03$, $R^2 = 0.05$, $p = 0.007$). The bill length distribution of both subspecies showed comparable seasonal trends ($F_{3,1087} = 28.06$, $R^2 = 0.07$, $p < 0.001$; figure 2b). The mean bill length of the *lapponica* subspecies showed a decrease in length from January towards spring and summer, whereas from August onwards bill length increased again. As expected, bill lengths of *taymyrensis* females were shorter than of *lapponica* ($p < 0.001$), though this subspecies showed the same pattern during the seven months they occurred in the Dutch Wadden Sea (figure 2b). Not surprisingly then, the bill length distribution of all sighted individuals with known bill lengths showed a strong seasonal trend ($F_{2,6105} = 95.45$, $R^2 = 0.03$, $p < 0.001$; figure 2c). That shorter-billed females may have moved from the Dutch Wadden Sea towards the Wash was indicated by the inverse relationship of monthly bill length distributions in the course of the non-breeding season ($F_{2,1690} = 11.81$, $R^2 = 0.013$, $p < 0.001$ figure 2d). The disappearance of the shorter-billed females from the Dutch Wadden Sea was also indicated by the negative relationship between the mean bill lengths of the Wash and the Dutch Wadden Sea ($F_{1,7} = 8.53$, $R^2 = 0.49$, $p = 0.020$; figure 3).

In winter, a longer bill is needed to access the same proportion of prey available as in summer (figure 4), which is the likely explanation for the positive correlation between mean monthly burying depth and mean bill length ($F_{1,10} = 15.20$, $R^2 = 0.60$, $p = 0.003$; figure 5a). There was a clear negative correlation between burying depth of lugworms and predicted intake rate (PEIR), suggesting that in winter some bar-tailed godwits would not be able to satisfy their minimum energy requirement by foraging on lugworms only ($F_{1,10} = 12.24$, $R^2 = 0.55$, $p = 0.006$; figure 5b). Indeed, individuals remaining in the Dutch Wadden Sea in winter included prey other than lugworms in their diet; the energetic contribution (% of AFDM) of lugworms was negatively correlated with lugworm burying depth ($F_{1,8} = 6.97$, $R^2 = 0.40$, $p = 0.030$; figure 5c).

4. Discussion

The vast majority of studies of changing resource landscapes and their use by animals has focused on differences between species or sexes (e.g. [16,59–61]). However, it is the variation between individuals that provides the raw material for evolutionary and ecological processes [62–64]. Here, we provide an example of a seasonally changing phenotype-limited distribution in one species and in one sex.

Female bar-tailed godwits redistributed in accordance with the seasonal changes in availability of their dominant prey. In winter, when lugworms are buried more deeply, individually marked shorter-billed individuals were no longer seen in the Dutch Wadden Sea. One of the areas they moved to is

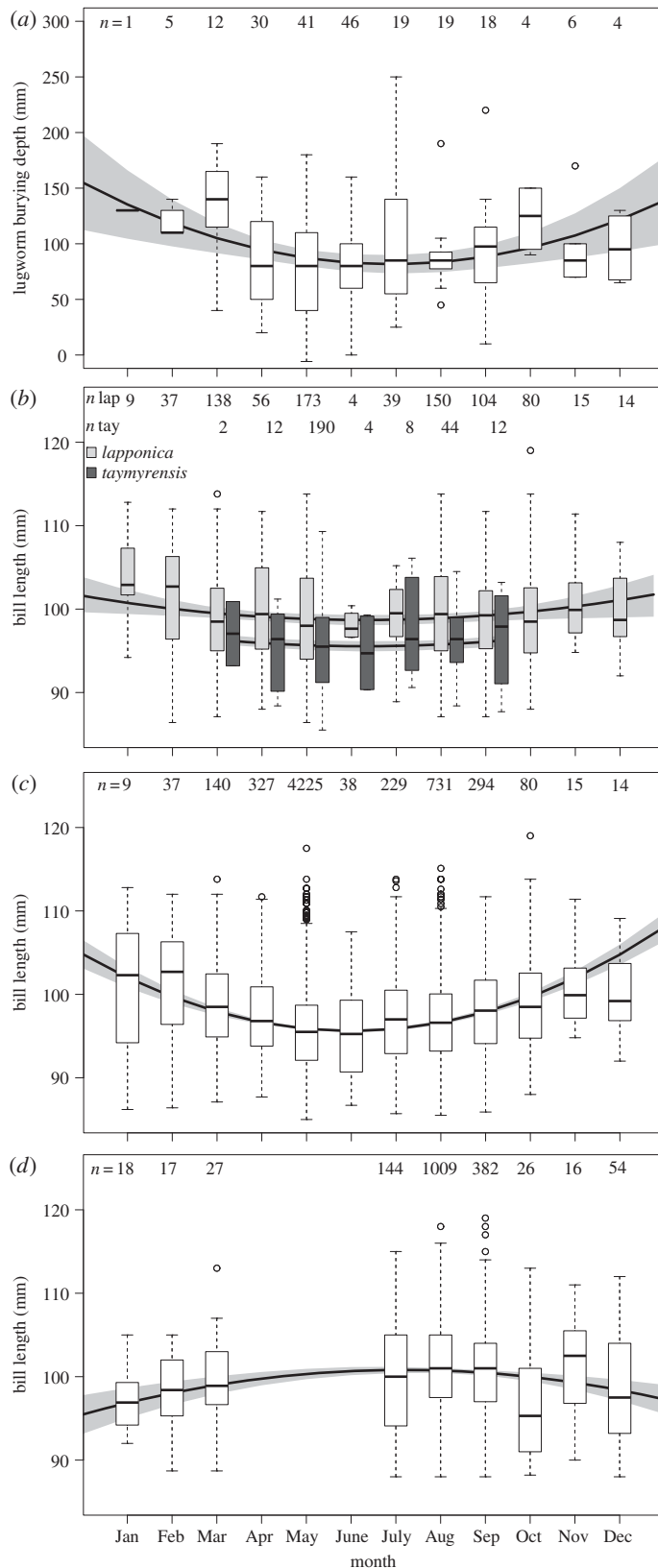


Figure 2. By month, (a) lugworm burying depth in the Dutch Wadden Sea, (b) bill length distributions of female bar-tailed godwits in the Dutch Wadden Sea, separated for both subspecies, (c) as (b) but now subspecies pooled and (d) bill length distributions for female bar-tailed godwits in the Wash, subspecies pooled. Curved lines represent model outputs and grey areas represent 95% confidence intervals (CIs). Box plots show median (line in box), interquartile range (box), 10th and 90th percentiles (bars) and outliers (dots). Sample sizes are shown in all plots.

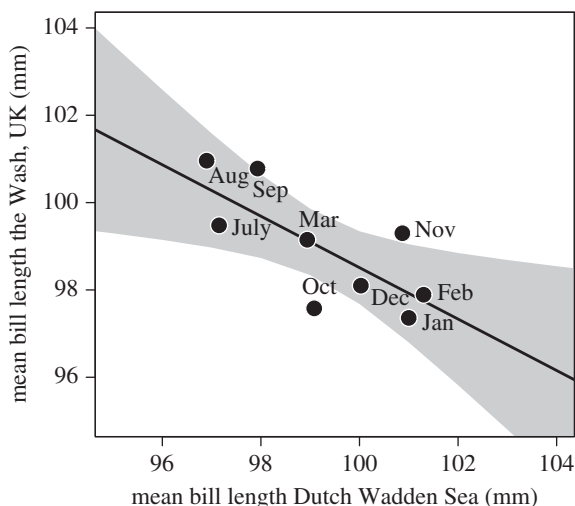


Figure 3. Correlation between monthly mean bill lengths of bar-tailed godwits captured in the Wash and resighted in the Dutch Wadden Sea. Grey shading represents 95% CI level.

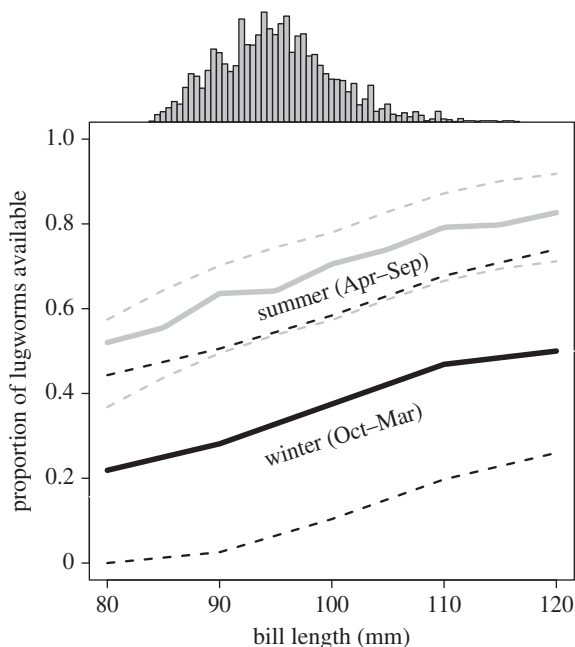


Figure 4. Summer and winter pattern of the (numerical) proportion of accessible lugworms in relation to bill length, based on the year-round depth measurements of lugworms in the Dutch Wadden Sea. Solid lines represent mean summer (grey) and mean winter (black) lugworm availability (dashed lines represent the 95% CI levels). In either season availability increases with an increase in bill length, though in winter overall availability is much lower. Bars on top of the graph denote the frequency distribution of bill length of female bar-tailed godwits captured in the Wadden Sea ($n = 2433$).

probably the Wash, where during the winter months an increase in numbers has been observed [65]. Indeed, while shorter-billed individuals disappeared from the Wadden Sea during winter, there was a build-up of such individuals in the Wash. This pattern is consistent with the finding that in the climatically more benign Wash, benthic prey are buried less deeply than in the Dutch Wadden Sea [41].

The lugworm data were collected long before most of the data on bar-tailed godwits, and mean seawater temperature increased over the last three decades by about 1.2°C [66]. This increase in average seawater temperature is unlikely to have biased our lugworm availability assessment because, in the short term, burying depth appears unrelated to temperature, i.e. it has no effect on depth within months [32].

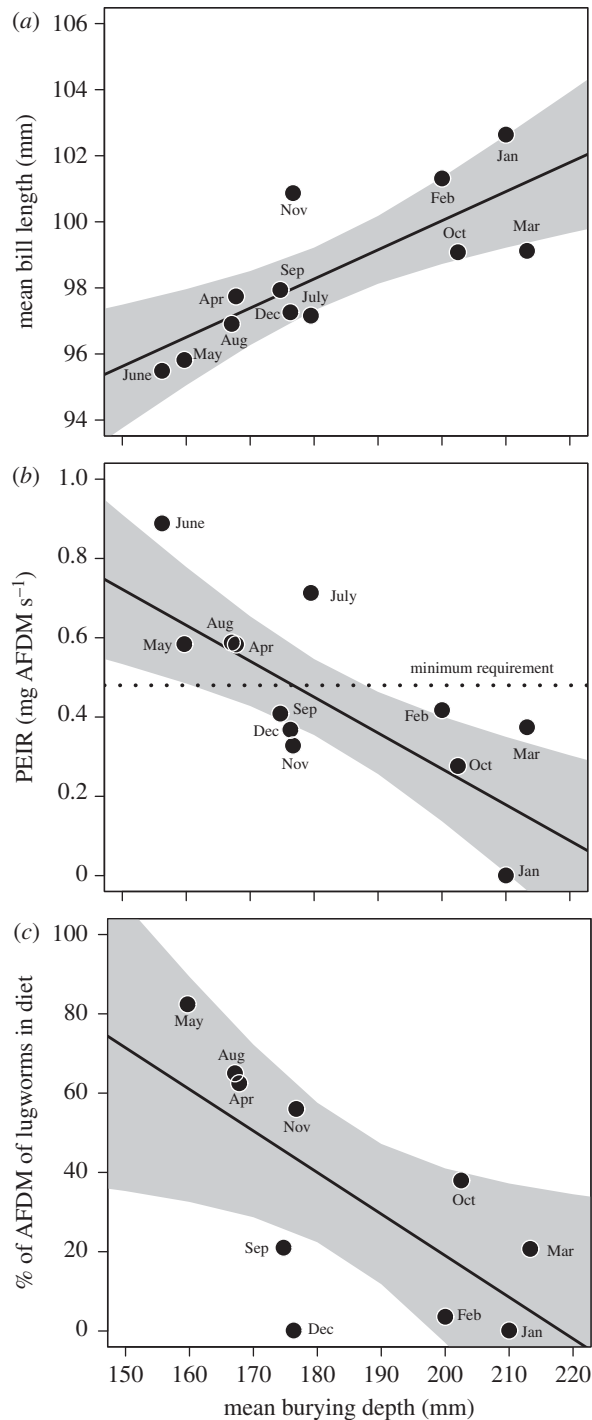


Figure 5. Effect of prey burying depth on bill length, intake rate and diet composition of bar-tailed godwits present in the Dutch Wadden Sea. (a) Mean bill lengths of females are larger in winter, when prey are buried deeper (the grey area represent the 95% CI level). (b) PEIRs, based on parameters from the functional response, correlate negatively with mean burying depth. (c) The mean contribution of lugworms to the diet of female bar-tailed godwits (based on AFDM) increases when lugworms are closer to the surface.

In addition to the increased burying depth of lugworms in the colder winter months, there is an additional reason why lugworms will be more difficult to capture in these months. Bar-tailed godwits rely on cast-formation (defaecation) to detect lugworms and in the colder and thus metabolically more inactive winter months they produce fewer casts [34,53]. Together these two factors could result in bar-tailed godwits failing to achieve their daily required intake when only eating lugworms. Therefore, even the longer-billed individuals are predicted to add smaller, less profitable prey species to their diet.

That a more varied diet was indeed observed in various places across coastal Europe [37,54] emphasizes once more that sex-specific food availability is a main driver of winter distributions [64].

If the intake rate benefits accrued by longer-billed individuals result in long-term fitness benefits, there should be directional selection for a longer bill. However, bar-tailed godwits breed on the tundra where they feed mainly on surface and shallow-buried arthropods, also available to their shorter-billed self-foraging chicks [67,68]. It has been suggested that shorter bill sizes may actually be advantageous when feeding on such prey [69,70], suggesting that there may be selection for longer bills in winter and shorter bills in summer.

After unpredictable extreme conditions such as prolonged drought or cold spells, some phenotypes with particular body size values may die, while other phenotypes survive or even benefit from these events. The available examples (e.g. [71–73]), however, pertain to resident or territorial birds that do not move away. In most birds however, individuals often move, and as most benthic prey show seasonal variations in burying depth [32], phenotype-limited distributions are likely to be found more in species dependent on benthic prey. In fact, we predict that phenotype-limited distributions occur across a range of taxa with reference to a range of traits.

5. Conclusion

By examining a fixed aspect of the phenotype (in our case bill length), we could show that female bar-tailed godwits redistribute themselves across soft-sediment systems along the southern North Sea coast in accordance with the seasonal changes in the availability of their dominant prey. Phenotype-limited distributions could be widespread and, when associated with assortative migration and mating, they may act as precursors of phenotypic evolution.

Ethics. All work adhered to Dutch and UK standard requirements. Birds were ringed and caught using mist nets, ‘wilsternets’ under licences of the Dutch Ringing Centre. The captures in the Wash were performed by the Wash Wader Ringing Group (WWRG) and conducted under BTO licences as part of ongoing research.

Data accessibility. Data used in this study are deposited in Dryad: <http://dx.doi.org/doi:10.5061/dryad.v51t0>.

Authors’ contributions. S.D., J.A.v.G. and T.P. designed the study and drafted the manuscript; S.D. carried out the statistical analyses; J.S. provided field data; S.D. coordinated the study. All authors gave final approval for publication.

Competing interests. None of the authors have any competing interests.

Funding. S.D. was supported by operational funds from NIOZ. T.P. was supported by *Metawad* (WF 209925), a project awarded by Waddenfonds. J.A.v.G. was supported by a VIDI grant (no. 864.09.002) from The Netherlands Organisation for Scientific Research (NWO). J.S. was funded by the Wash Wader Ringing Group.

Acknowledgements. This study builds on research efforts of many people. First of all we thank our dedicated wilsternetters Joop Jukema, Catharinus Monkel, Jaap Strikwerda, the bird-catchers of VRS-Castricum, VRS-Calidris on Schiermonnikoog and the numerous others that have helped with catching and colour ringing. We thank our former colleague Bernard Spaans for running the colour ringing programme. We kindly thank Leo Zwartz for his far-sighted efforts to make his impressive dataset available and accessible for future use. Many thanks also to all ring-readers, professional and amateur, and in particular Harry Horn and Jan de Jong, for their continuous efforts to record individually marked bar-tailed godwits at various locations. We also thank the many volunteers of the Wash Wader Ringing Group for their efforts in collecting long-term wader data on the Wash. Jesse Conklin, Phil Battley and two anonymous referees graciously reviewed earlier versions of this manuscript. We thank Dave Montreuil for making photos available of a female bar-tailed godwit in Gambia.

References

1. Fretwell SD. 1972 *Population in a seasonal environment*. Princeton, NJ: Princeton University Press.
2. Piersma T, Lindström Å. 1997 Rapid reversible changes in organ size as a component of adaptive behaviour. *Trends Ecol. Evol.* **12**, 134–138. (doi:10.1016/S0169-5347(97)01003-3)
3. Piersma T, van Gils JA. 2011 *The flexible phenotype: a body-centred integration of ecology, physiology, and behaviour*. Oxford, UK: Oxford University Press.
4. Zaldúa N, Naya DE. 2014 Digestive flexibility during fasting in fish: a review. *Comp. Biochem. Physiol. A* **169**, 7–14. (doi:10.1016/j.cbpa.2013.12.006)
5. McWilliams SR, Karasov WH. 2014 Spare capacity and phenotypic flexibility in the digestive system of a migratory bird: defining the limits of animal design. *Proc. R. Soc. B* **281**, 20140308. (doi:10.1098/rspb.2014.0308)
6. van Gils JA, Piersma T, Dekinga A, Dietz MW. 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. (doi:10.1242/jeb.00546)
7. Hulscher JB. 1985 Growth and abrasion of the oystercatcher bill in relation to dietary switches. *Neth. J. Zool.* **35**, 124–154. (doi:10.1163/002829685X00109)
8. Lok T, Overdijk O, Piersma T. 2014 Interpreting variation in growth of Eurasian spoonbill chicks: disentangling the effects of age, sex and environment. *Ardea* **102**, 181–194. (doi:10.5253/arde.v102i2.a8)
9. Selander RK. 1966 Sexual dimorphism and differential niche utilization in birds. *Condor* **68**, 113–151. (doi:10.2307/1365712)
10. Abzhanov A, Protas M, Grant BR, Grant PR, Tabin CJ. 2004 Bmp4 and morphological variation of beaks in Darwin’s finches. *Science* **305**, 1462–1465. (doi:10.1126/science.1098095)
11. Nebel S, Jackson DL, Elner RW. 2005 Functional association of bill morphology and foraging

- behaviour in calidrid sandpipers. *Anim. Biol.* **55**, 235–243. (doi:10.1163/1570756054472818)
12. Le V dit Durell, SEA. 2000 Individual feeding specialisation in shorebirds: population consequences and conservation implications. *Biol. Rev.* **75**, 503–518. (doi:10.1111/j.1469-185X.2000.tb00053.x)
 13. Temeles EJ, Miller JS, Rifkin JL. 2010 Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): a role for ecological causation. *Phil. Trans. R. Soc. B* **365**, 1053–1063. (doi:10.1098/rstb.2009.0284)
 14. Schoener TW. 1974 Resource partitioning in ecological communities. *Science* **185**, 27–39. (doi:10.1126/science.185.4145.27)
 15. Gonzalez-Terrazas TP, Medellin RA, Knornschild M, Tschapka M. 2012 Morphological specialization influences nectar extraction efficiency of sympatric nectar-feeding bats. *J. Exp. Biol.* **215**, 3989–3996. (doi:10.1242/jeb.068494)
 16. Mathot KJ, Smith BD, Elner RW. 2007 Latitudinal clines in food distribution correlate with differential migration in the western sandpiper. *Ecology* **88**, 781–791. (doi:10.1890/06-1225)
 17. Alves JA, Gunnarsson TG, Potts PM, Sutherland WJ, Gill JA. 2013 Sex-biases in distribution and resource use at different spatial scales in a migratory shorebird. *Ecol. Evol.* **3**, 1079–1090. (doi:10.1002/ece3.503)
 18. Abrams PA. 1984 Foraging time optimization and interactions in food webs. *Am. Nat.* **124**, 80–96. (doi:10.1086/284253)
 19. Bergman CM, Fryxell JM, Gates CC, Fortin D. 2001 Ungulate foraging strategies: energy maximizing or time minimizing? *J. Anim. Ecol.* **70**, 289–300. (doi:10.1111/j.1365-2656.2001.00496.x)
 20. Peers MJL, Wehtje M, Thornton DH, Murray DL. 2014 Prey switching as a means of enhancing persistence in predators at the trailing southern edge. *Glob. Change Biol.* **20**, 1126–1135. (doi:10.1111/gcb.12469)
 21. Oudman T, Onrust J, de Fouw J, Spaans B, Piersma T, van Gils JA. 2014 Digestive capacity and toxicity cause mixed diets in red knots that maximize energy intake rate. *Am. Nat.* **183**, 650–659. (doi:10.1086/675759)
 22. van der Graaf SAJ, Stahl J, Klimkowska A, Bakker JP, Drent RH. 2006 Surfing on a green wave – how plant growth drives spring migration in the barnacle goose *Branta leucopsis*. *Ardea* **94**, 567–571.
 23. Duriez O, Bauer S, Destin A, Madsen J, Nolet BA, Stillman RA, Klaassen M. 2009 What decision rules might pink-footed geese use to depart on migration? An individual-based model. *Behav. Ecol.* **20**, 560–569. (doi:10.1093/beheco/arp032)
 24. Alerstam T. 1990 *Bird migration*. Cambridge, UK: Cambridge University Press.
 25. Smith TB, Skulason S. 1996 Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* **27**, 111–133. (doi:10.2307/2097231)
 26. Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A. 2011 The ecology and evolution of partial migration. *Oikos* **120**, 1764–1775. (doi:10.1111/j.1600-0706.2011.20131.x)
 27. Compton TJ *et al.* 2013 Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *J. Sea Res.* **82**, 103–116. (doi:10.1016/j.seares.2013.02.002)
 28. Piersma T, Hoekstra R, Dekinga A, Koolhaas A, Wolf P, Battley P, Wiersma P. 1993 Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* **31**, 331–357. (doi:10.1016/0077-7579(93)90052-T)
 29. Goss-Custard JD *et al.* 1991 Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn estuary. *J. Appl. Ecol.* **28**, 1004–1026. (doi:10.2307/2404222)
 30. Gill JA, Sutherland WJ, Norris K. 2001 Depletion models can predict shorebird distribution at different spatial scales. *Proc. R. Soc. Lond. B* **268**, 369–376. (doi:10.1098/rspb.2000.1386)
 31. Zwarts L, Wanink J. 1989 Siphon size and burying depth in deposit-feeding and suspension-feeding benthic bivalves. *Mar. Biol.* **100**, 227–240. (doi:10.1007/bf00391963)
 32. Zwarts L, Wanink JH. 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 behavior of tidal-flat invertebrates. *Neth. J. Sea Res.* **31**, 441–476. (doi:10.1016/0077-7579(93)90059-2)
 33. Esselink P, Zwarts L. 1989 Seasonal trend in burrow depth and tidal variation in feeding activity of *Nereis diversicolor*. *Mar. Ecol. Prog. Ser.* **56**, 243–254. (doi:10.3354/meps056243)
 34. Cadée GC. 1976 Sediment reworking by *Arenicola marina* on tidal flats in Dutch Wadden sea. *Neth. J. Sea Res.* **10**, 440–460. (doi:10.1016/0077-7579(76)90020-X)
 35. Parker GA, Sutherland WJ. 1986 Ideal free distributions when individuals differ in competitive ability: phenotype limited ideal free models. *Anim. Behav.* **34**, 1222–1242. (doi:10.1016/S0003-3472(86)80182-8)
 36. Duijns S, Piersma T. 2014 Interference competition in a sexually dimorphic shorebird: prey behaviour explains intraspecific competition. *Anim. Behav.* **92**, 195–201. (doi:10.1016/j.anbehav.2014.04.007)
 37. Scheiffarth G. 2001 The diet of bar-tailed godwits *Limosa lapponica* in the Wadden Sea: combining visual observations and faeces analyses. *Ardea* **89**, 481–494.
 38. Prokosch P. 1988 The Schleswig-Holstein Wadden Sea as spring staging area for arctic wader populations demonstrated by grey plover *Pluvialis squatarola*, L. 1758, knot *Calidris canutus*, L. 1758 and bar-tailed godwit *Limosa lapponica* L. 1758 [in German with English summary]. *Corax* **12**, 273–442.
 39. Piersma T, Jukema J. 1990 Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of bar-tailed godwits at successive spring staging sites. *Ardea* **78**, 315–337.
 40. Duijns S, Jukema J, Spaans B, van Horssen P, Piersma T. 2012 Revisiting the proposed leap-frog migration of bar-tailed godwits along the East-Atlantic Flyway. *Ardea* **100**, 37–43. (doi:10.5253/078.100.0107)
 41. Duijns S, van Gils JA, Spaans B, ten Horn J, Brugge M, Piersma T. 2014 Sex-specific winter distribution in a sexually dimorphic shorebird is explained by resource partitioning. *Ecol. Evol.* **4**, 4009–4018. (doi:10.1002/ece3.1213)
 42. Scheiffarth G. 2003 Born to fly—migratory strategies and stopover ecology in the European Wadden Sea of a long-distance migrant, the bar-tailed godwit (*Limosa lapponica*). PhD thesis, Universität Oldenburg, Oldenburg, Germany.
 43. Scheiffarth G, Wahls S, Ketzenberg C, Exo KM. 2002 Spring migration strategies of two populations of bar-tailed godwits, *Limosa lapponica*, in the Wadden Sea: time minimizers or energy minimizers? *Oikos* **96**, 346–354. (doi:10.1034/j.1600-0706.2002.960216.x)
 44. Duijns S, Knot IE, Piersma T, van Gils JA. 2015 Field measurements give biased estimates of functional response parameters, but help explain foraging distributions. *J. Anim. Ecol.* **84**, 565–575. (doi:10.1111/1365-2656.12309)
 45. Engelmoer M, Roselaar CS. 1998 *Geographical variation in waders*. Dordrecht, The Netherlands: Kluwer.
 46. Drent R, Piersma T. 1990 An exploration of the energetics of leap-frog migration in arctic breeding waders. In *Bird migration, physiology and ecophysiology* (ed. E Gwinner), pp. 399–412. Berlin, Germany: Springer.
 47. Jukema J, Piersma T, Hulscher JB, Bunschoke EJ, Koolhaas A, Veenstra A. 2001 *Goudpleviereren en wilsterflappers: eeuwenoude fascinatie voor trekvogels*. Leeuwarden, The Netherlands: Fryske Akademy & KNNV Uitgeverij.
 48. Prater AJ, Marchant JH, Vuorinen J. 1977 *Guide to the identification and ageing of holarctic waders*. Tring, UK: British Trust for Ornithology.
 49. Atkinson PW. 1996 The origins, moult, movements and changes in numbers of bar-tailed godwits *Limosa lapponica* on the Wash, England. *Bird Study* **43**, 60–72. (doi:10.1080/00063659609460996)
 50. Davis J. 1954 Seasonal changes in bill length of certain passerine birds. *Condor* **56**, 142–149. (doi:10.2307/1364781)
 51. Morton ML, Morton GA. 1987 Seasonal changes in bill length in summering mountain white-crowned sparrows. *Condor* **89**, 197–200. (doi:10.2307/1368781)
 52. Matthyssen E. 1989 Seasonal variation in bill morphology of nuthatches *Sitta europaea*: dietary adaptations or consequences. *Ardea* **77**, 117–125.
 53. Smith PC. 1975 A study of the winter feeding ecology and behaviour of the bar-tailed godwit (*Limosa lapponica*). PhD thesis, University of Durham, Durham, UK.
 54. Duijns S, Hidayati NA, Piersma T. 2013 Bar-tailed godwits *Limosa L. lapponica* eat polychaete worms wherever they winter in Europe. *Bird Study* **60**, 509–517. (doi:10.1080/00063657.2013.836153)
 55. Duijns S, van Dijk JGB, Spaans B, Jukema J, de Boer WF, Piersma T. 2009 Foraging site selection of two subspecies of bar-tailed godwit *Limosa lapponica*: time minimizers accept greater predation danger than energy minimizers. *Ardea* **97**, 51–59. (doi:10.5253/078.097.0107)
 56. Burnham KP, Anderson DR. 2002 *Model selection and multi-model inference: a practical information-theoretic approach*. New York, NY: Springer.
 57. Forbes C, Evans M, Hastings N, Peacock B. 2011 *Statistical distributions*. Hoboken, NJ: John Wiley & Sons.
 58. R Development Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
 59. Beaulieu M, Sockman K. 2012 One meadow for two sparrows: resource partitioning in a high elevation

- habitat. *Oecologia* **170**, 529–540. (doi:10.1007/s00442-012-2327-7)
60. Griffen BD, Mosblack H. 2011 Predicting diet and consumption rate differences between and within species using gut ecomorphology. *J. Anim. Ecol.* **80**, 854–863. (doi:10.1111/j.1365-2656.2011.01832.x)
61. Duffy JE, MacDonald KS, Rhode JM, Parker JD. 2001 Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* **82**, 2417–2434. (doi:10.2307/2679926)
62. Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28. (doi:10.1086/343878)
63. Gunnarsson TG, Sutherland WJ, Alves JA, Potts PM, Gill JA. 2012 Rapid changes in phenotype distribution during range expansion in a migratory bird. *Proc. R. Soc. B* **279**, 411–416. (doi:10.1098/rspb.2011.0939)
64. Piersma T. 2012 What is habitat quality? Dissecting a research portfolio on shorebirds. In *Birds and habitat: relationships in changing landscapes series: ecological reviews* (ed. RJ Fuller), pp. 383–407. Cambridge, UK: Cambridge University Press.
65. Holt CA, Austin GE, Calbrade NA, Mellan HJ, Hearn RD, Stroud DA, Wotton SR, Musgrove AJ. 2012 Waterbirds in the UK 2010/11: The Wetland Bird Survey. Thetford, UK: BTO/RSPB/JNCC.
66. van Aken HM. 2008 Variability of the water temperature in the western Wadden Sea on tidal to centennial time scales. *J. Sea Res.* **60**, 227–234. (doi:10.1016/j.seares.2008.09.001)
67. Cramp S, Simmons KEL. 1983 *Handbook of the birds of Europe, the Middle East, and North Africa*, vol. 3. Oxford, UK: Oxford University Press.
68. Piersma T, van Gils J, Wiersma P. 1996 Family Scolopacidae (snipes, sandpipers and phalaropes). In *Handbook of birds of the world*, vol. 3. *Hoatzins to Auks* (eds J Hoyo, A Elliot, J Sargital), pp. 444–533. Barcelona, Spain: Lynx Editions.
69. Jönsson PE. 1987 Sexual size dimorphism and disassortative mating in the dunlin *Calidris alpina schinzii* in southern Sweden. *Ornis Scand.* **18**, 257–264. (doi:10.2307/3676893).
70. Jönsson PE, Alerstam T. 1990 The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biol. J. Linn. Soc.* **41**, 301–314. (doi:10.1111/j.1095-8312.1990.tb00838.x)
71. Clark JA. 2009 Selective mortality of waders during severe weather. *Bird Study* **56**, 96–102. (doi:10.1080/00063650802648465)
72. Boag PT, Grant PR. 1981 Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* **214**, 82–85. (doi:10.1126/science.214.4516.82)
73. van de Pol M, Brouwer L, Ens BJ, Oosterbeek K, Tinbergen JM. 2010 Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution* **64**, 836–851. (doi:10.1111/j.1558-5646.2009.00859.x)