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### Sex-specific foraging

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# 8

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

Sjoerd Duijns, Jan A. van Gils, Jennifer Smart & Theunis Piersma

### Abstract

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 so-called 'phenotype-limited' distribution. Here we examine this possibility for a probe-feeding shorebird, the bar-tailed godwit (*Limosa lapponica*; a long-billed and sexually dimorphic shorebird), that has to reach its cryptic prey with their bill of a fixed length. The main prey of female bar-tailed godwits are lugworms (*Arenicola marina*), which are buried deeper in winter than in summer. By analysing 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 estuaries such as the Wash, where prey live closer to the surface. 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 their 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.

## Introduction

Most organisms on Earth live in seasonal environments with respect to climate and food (Fretwell 1972). The ability of individuals to reversibly change phenotype in response to a change in environmental conditions is called phenotypic flexibility (Piersma & Lindström 1997; Piersma & van Gils 2011). 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. van Gils *et al.* 2003a; McWilliams and Karasov 2014; Zaldúa and Naya 2014). However, some aspects of the phenotype are essentially inflexible. Traits such as bill length in birds that show determined growth, are hardly flexible (Hulscher 1985; Lok *et al.* 2014). Bill morphology is a strong predictor of foraging niche (e.g. Selander 1966; Schoener 1974; Durell 2000, Abzhanov *et al.* 2004; Nebel *et al.* 2005; Temeles *et al.* 2010; Gonzalez-Terrazas *et al.* 2012), and may lead to phenotype-related differences in diet (Mathot *et al.* 2007, Alves *et al.* 2013b). In addition, animals can show behavioural responses to environmental change. They can increase foraging time (e.g. Abrams 1984; Bergman *et al.* 2001), select alternative prey (Oudman *et al.* 2014; Peers *et al.* 2014), or move to sites where food is more favourable (e.g. Alerstam 1990; van der Graaf *et al.* 2006; Duriez *et al.* 2009).

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 (Smith & Skulason 1996). Body size, dominance, prior residency or food availability appear to be responsible for individual differences in migratory tendencies within populations (Chapman *et al.* 2011). Food availability is relatively easy to quantify in intertidal areas, and non-breeding shorebirds provide a good system for correlating distribution of animals with their food resources (e.g. Goss-Custard *et al.* 1977b; Mathot *et al.* 2007; Piersma & van Gils 2011). Non-breeding shorebirds in temperate zones mostly feed on benthic prey that tends to bury deeper in winter than in summer (e.g. Zwarts & Wanink 1989; Zwarts & Wanink 1993). The latter being a response to changes in day length rather than changes in seawater temperature, at least in the case of polychaetes (Zwarts & Wanink 1993). With seasonally changing fractions of benthic prey burying beyond the bill lengths of most shorebird species (e.g. Cadée 1976; Esselink & Zwarts 1989), the part of the population for which too many prey have 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 (Parker & Sutherland 1986).

Here we explore phenotype-limited distributions in female bar-tailed godwits (*Limosa lapponica*). Females have 25% longer bills than males and mainly feed on deep burying lugworms (a polychaete worm, *Arenicola marina*), while the shorter-billed males mainly forage on shallow buried prey (Scheiffarth 2001a; Duijns & Piersma 2014). In addition,

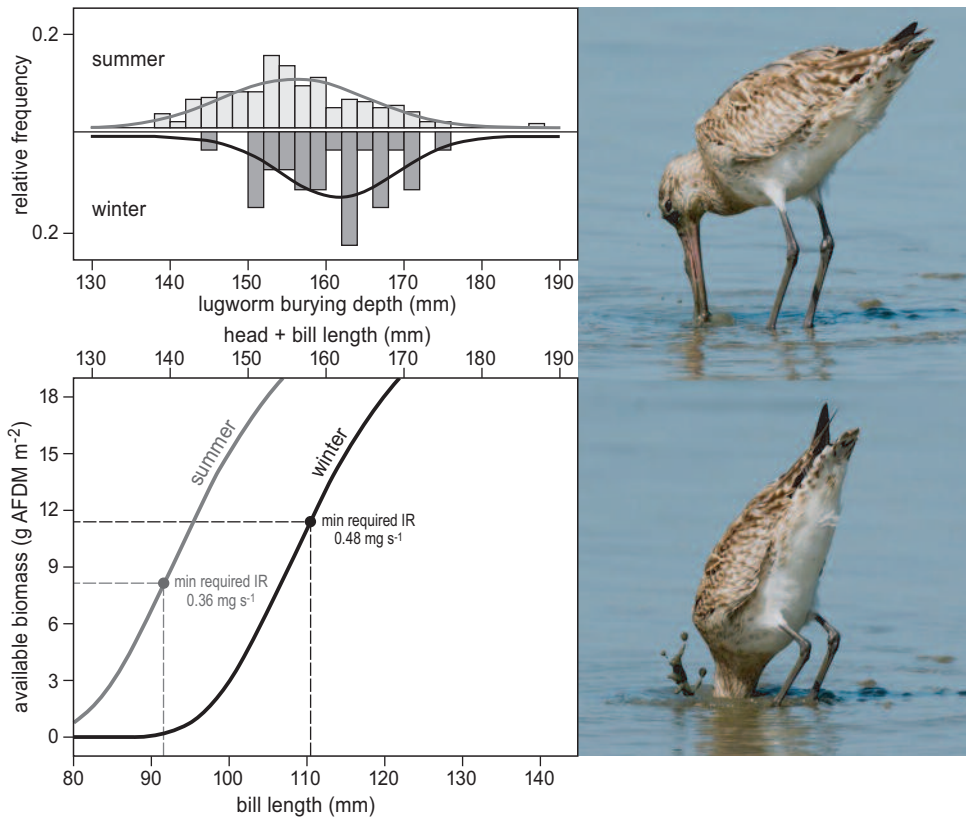
there is considerable variation in bill length within the sexes (Prokosch 1988; Piersma & Jukema 1990; Duijns *et al.* 2012). Among the available benthic prey items, seasonal variation in burying depth is largest in lugworms (Zwarts & Wanink 1993), so the potential for a phenotype-limited distribution should be most pronounced in female godwits. 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 (Duijns *et al.* 2014b). This pattern could extend to individuals within a sex, such that those with shorter bills would be predicted (Scheiffarth 2003) 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 to shorter-billed individuals. This idea is shown in Fig. 8.1. We explored the possibility of 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 (Scheiffarth 2001a), we used generally applicable functional response parameters (Duijns *et al.* 2014a).

## Methods

### *Study species*

Along the East-Atlantic Flyway two subspecies of bar-tailed godwits occur (Engelmoer & Roselaar 1998). 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 North-western Europe and breeds in northern Scandinavia (Drent & Piersma 1990; Duijns *et al.* 2012). To explore the possibility of a phenotype-limited distribution, we first distinguished between the subspecies, as the *taymyrensis* subspecies has on average a shorter bill length than the nominate *lapponica* subspecies (Engelmoer & Roselaar 1998; Duijns *et al.* 2012). Although a considerable proportion of bar-tailed godwits cannot be assigned to either subspecies using morphometrics, they may occur together in the Dutch Wadden Sea during six months of the year (April-October; Duijns *et al.* 2012). During this period they would encounter similar environmental conditions in the Dutch Wadden Sea and therefore we included females with known bill lengths from known and unknown sub-specific identity in the analyses.



**Figure 8.1.** 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. 4 cm subtracted), and separated for summer (Apr – Sep) and winter (Oct – Mar). From this, available biomass in relation to bill length can be deduced (lower panel). In summer, available biomass increases steeply as a function of bill length (due to the shallower burying depth), while minimum required intake rate ( $0.36 \text{ mg AFDM s}^{-1}$ ) is relatively low. Therefore almost all individuals ( $> 92 \text{ mm}$  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; Scheiffarth *et al.* 2002). 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:

$$\text{Minimum requirement} = \frac{\text{DEE}_{\text{season}}}{E} / T_f,$$

where  $E$  is a lugworm's energy content ( $22 \text{ kJ g}^{-1} \text{ AFDM}$ ; Zwarts & Wanink 1993), 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 (Scheiffarth *et al.* 2002), daily foraging time  $T_f$  was assumed to be 12 h for both seasons (i.e. 50%; Scheiffarth *et al.* 2002), assuming an assimilation efficiency of 80% (Scheiffarth *et al.* 2002). 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.

### *Sightings of marked individuals*

Birds were caught with 'wilsternets' (Jukema *et al.* 2001) 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 (Prater *et al.* 1977). Captures ( $n = 2,433$ ) and sightings of marked individual females in the Dutch Wadden Sea ( $n = 4,069$ ) were analysed over the period from capture up to May 2014 to assess bill length distributions per month. The 4,069 sightings were based on 1,541 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 showed no change, 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 8.1. To compare bill length distributions with another major non-breeding site, biometric data was 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 (Atkinson 1996). The data on 1,693 female bar-tailed godwits used were collected in 1994-2011.

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. Davis 1954; Morton & Morton 1987; Matthysen 1989). For shorebirds it is known that the rhamphotheca, the horny covering of a bird's bill, constantly grows at the base of the bill.

**Table 8.1.** Overview of numbers of female bar-tailed godwits caught and sighted in the Dutch Wadden Sea, by year and 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	Jun	0	38
2007	133	379	Jul	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			

Despite this growth, the bill wears and within individual variation appears to be negligible ( $< 1$  mm; Hulscher 1985). Indeed, recaptures ( $> 1$  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).

### **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 ( $53^{\circ}25'$  N,  $6^{\circ}04'$  E) during two consecutive years (1980/1981; Zwarts & Wanink 1993); 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 (Zwarts & Wanink 1993). 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 (Smith 1975), all depths were decreased by 4 cm (i.e. half of the mean length of lugworms;  $n = 205$ ), to represent availability.

Although the lugworm data were collected long before most of the data on bar-tailed godwits, this unlikely to influence our results, as although the mean sea water temperature increase over the last 3 decades is about  $1.2^{\circ}\text{C}$ , the current sea water temperatures are similar to the early 1980's (van Aken 2008); note also that the variation between seasons is much larger than the long-term temperature change of  $1.2^{\circ}\text{C}$ .

### **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 (Duijns *et al.* 2014a). Note that variation of bill lengths of the birds used in the experiment (Duijns *et al.* 2014a) was rather small (95.5 mm, 95% CI (91.33; 99.7),  $n = 5$ ), 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 (Duijns *et al.* 2014a), we here estimated depth  $i$  specific searching efficiency  $a_i$ . Searching efficiency was independent of prey length and density (Duijns *et al.* 2014a). Handling time ( $T_h$ ) was independent of prey burying depth and constant for prey density, but not for prey length. We therefore here used the intercept and slope from a linear model of handling time against prey length to estimate handling time per prey. The month-specific predicted energy intake rate ( $PEIR_m$ ) was calculated using the following equation:

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

For depth  $i$ , prey length  $j$  and month  $m$ , where  $N$  is the mean density ( $\# \text{ m}^{-2}$ ) as measured by Zwarts & Wanink (1993), and  $e$  the ash free dry mass (i.e. energetic value, mg AFDM) per individual prey using the length-AFDM relation (e.g. Duijns *et al.* 2013; Duijns & Piersma 2014). Next, we evaluated the mean monthly energetic contribution of lugworms to the year-round diet based on field observations ( $n = 76$ ; Scheiffarth 2001a, Duijns *et al.* 2009; Duijns & Piersma 2014) and dropping analyses ( $n = 250$ ; Duijns *et al.* 2013).

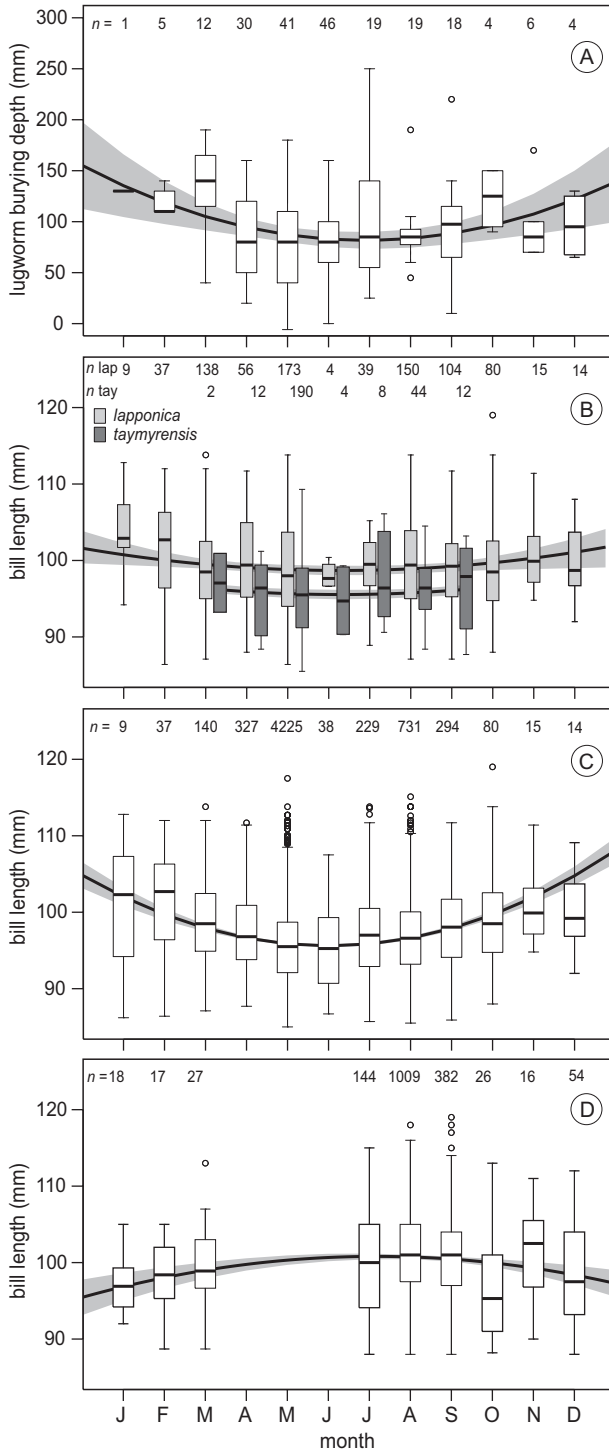
### **Statistical analyses**

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 2 points lower when compared the other model (Burnham & Anderson 2002). To assess the proportion of available prey in relation to bill length, the empirical cumulative distribution function (ECDF; Forbes *et al.* 2011), was plotted for females captured or sighted in summer (Apr–Sep) and winter (Oct–Mar). All analyses were conducted using R 3.0.1 (R Development Core Team 2014).

## **Results**

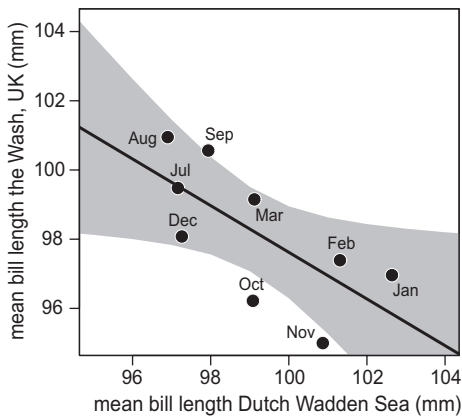
Burying depth of lugworms varied predictably throughout the year (Fig. 8.2A). Lugworms bury deepest during winter ( $F_{2,202} = 5.03$ ,  $R^2 = 0.05$ ,  $P = 0.007$ ). The bill length distribution of both subspecies showed comparable seasonal trends ( $F_{3,1087} = 28.06$ ,  $R^2 = 0.07$ ,  $P < 0.001$ ; Fig. 8.2B). The 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 the 7 months they were sighted in the Dutch Wadden Sea (Fig. 8.2B). Not surprisingly then, the bill length distribution of all sighted individuals with known bill lengths showed a strong seasonal trend ( $F_{2,6105} = 95.45$ ,  $R^2 = 0.03$ ,  $P < 0.001$ ; Fig. 8.2C). 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 nonbreeding season ( $F_{2,1690} = 11.81$ ,  $R^2 = 0.013$ ,  $P < 0.001$  Fig. 8.2D). 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 ( $F_{1,7} = 6.47$ ,  $R^2 = 0.48$ ,  $P = 0.03$ ; Fig. 8.3).



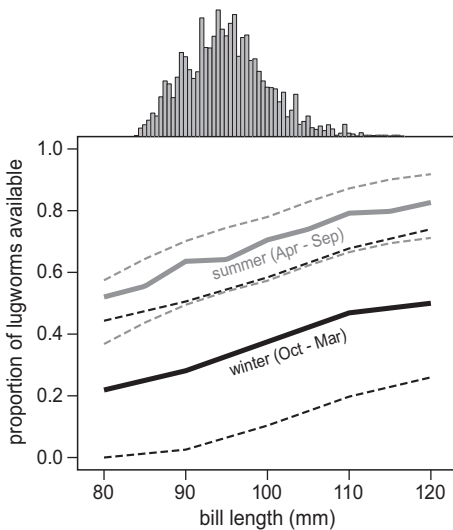


**Figure 8.2.** By month, (A) lugworm burying depth in the Dutch Wadden Sea, (B) bill length distributions of female bar-tailed godwits in the Dutch Wadden Sea, separated for both subspecies, (C) as B but now subspecies pooled, and (D) bill length distributions for female bar-tailed godwits in the Wash, subspecies pooled. Curved lines represent model outputs and grey areas represent 95% confidence intervals. 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.

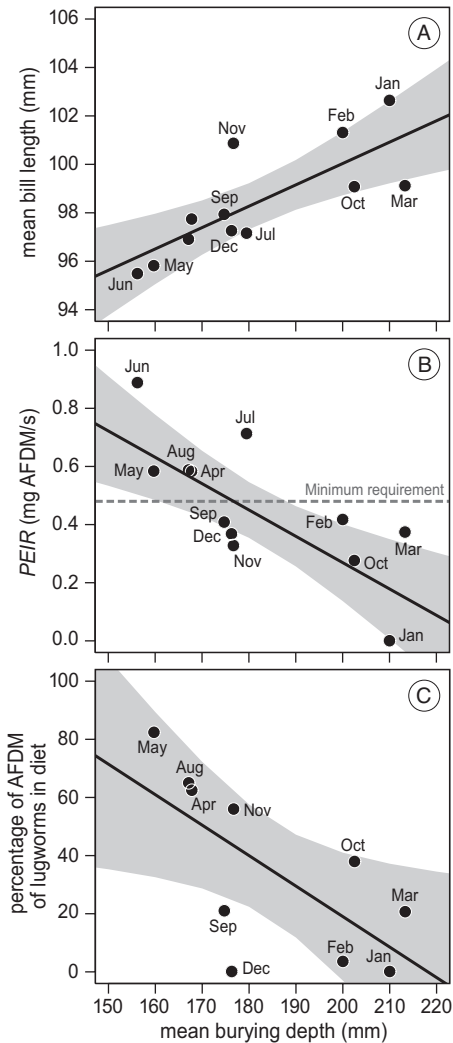
In winter a longer bill is needed to access the same proportion of prey available as in summer (Fig. 8.4), which is the likely explanation for the positive correlation between mean monthly burying depth and mean bill length ( $F_{1,10} = 15.2$ ,  $R^2 = 0.60$ ,  $P = 0.003$ ; Fig. 8.5A). There was a 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 ( $F_{1,10} = 12.24$ ,  $R^2 = 0.55$ ,  $P = 0.006$ ; Fig. 8.5B). 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 ( $F_{1,8} = 6.97$ ,  $R^2 = 0.40$ ,  $P = 0.03$ ; Fig. 8.5C).



**Figure 8.3.** Correlation between monthly mean bill length in the Wash and the Dutch Wadden Sea, where the grey shading represents 95% CI level.



**Figure 8.4.** 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. 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 ( $n = 2,433$ ).



**Figure 8.5.** 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) Predicted energy intake rates (*PEIR*), based on parameters from the functional response, correlates 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.

## 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. Duffy *et al.* 2001; Mathot *et al.* 2007; Griffen & Mosblack 2011; Beaulieu & Sockman 2012). However, the variation between individuals is just as important to understand evolutionary and ecological processes (Bolnick *et al.* 2003; Gunnarsson *et al.* 2012; Piersma 2012). Here we provided an example of seasonally changing phenotype-limited distributions, within one species and even within 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, marked shorter-billed individuals were no longer seen in the Dutch Wadden Sea. One of the areas they moved to is probably the Wash, where during the winter months an increase in numbers has been observed (Holt *et al.* 2012). 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 at the Wash, benthic prey are buried less deeply than in the Dutch Wadden Sea (Duijns *et al.* 2014b).

If bill length is such an important determinant of being able to reach deeply burying prey, and if prey bury deeper during northern winters, northerly wintering godwits are expected to have longer bills. That the European wintering subspecies (*lapponica*) have longer bills than the subspecies (*taymyrensis*) wintering in West-Africa (Prokosch 1988; Engelmoer & Roselaar 1998), is consistent with this prediction. Furthermore, 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 tundra where they feed mainly on surface and shallow-buried arthropods, also available to their shorter-billed self-foraging chicks (Cramp & Simmons 1983; Piersma *et al.* 1996a). It has been suggested that shorter bill sizes may actually be advantageous when feeding on such prey (Jönsson 1987; Jönsson & Alerstam 1990). We propose that there may be balanced selection between 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 appear to benefit from these events (e.g. Boag & Grant 1981; Clark 2009; van de Pol *et al.* 2010). These examples reflect resident or territorial birds that cannot or will not move, but cases where individuals with certain fixed phenotypic traits move away, is likely to be a general pattern. We may thus find phenotype-limited distributions across many traits across a range of taxa. For example, wing morphology is a non-flexible trait where longer and pointier wings may increase flight efficiency for longer migration distances, while shorter and rounder wings may be beneficial for agility in flight during acrobatic aerial displays, aerial feeding of insects, or take-off performance as an anti-predation adaptation (Rayner 1988; Fernandez & Lank 2007; van den Hout *et al.* 2010). At sites where predation danger has increased (Ydenberg *et al.* 2004), phenotypes with shorter and rounder wings would be expected to cope better with this predation danger and the phenotypes with longer and pointier wings would be predicted to leave such a site. Similarly, variation in neck length could lead to phenotype-limited distributions in swans, giraffes and goats for example, as longer necks would allow for a larger proportion of food availability. Phenotype-limited distributions could be widespread and when associated with assortative migration and mating patterns, they may act as precursors of phenotypic evolution.

## Acknowledgements

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