Horizontal prey distribution determines the foraging performance of short- and long-billed waders in virtual resource landscapes

Journal:	*IBIS*
Manuscript ID	IBIS-2023-OAR-009.R2
Wiley - Manuscript type:	Original Article
Category:	behaviour: feeding, ecology: behavioural, ecology: competition, ecology: habitat, waders
Note: The following files were submitted by the author for peer review, but cannot be converted to PDF. You must view these files (e.g. movies) online.	
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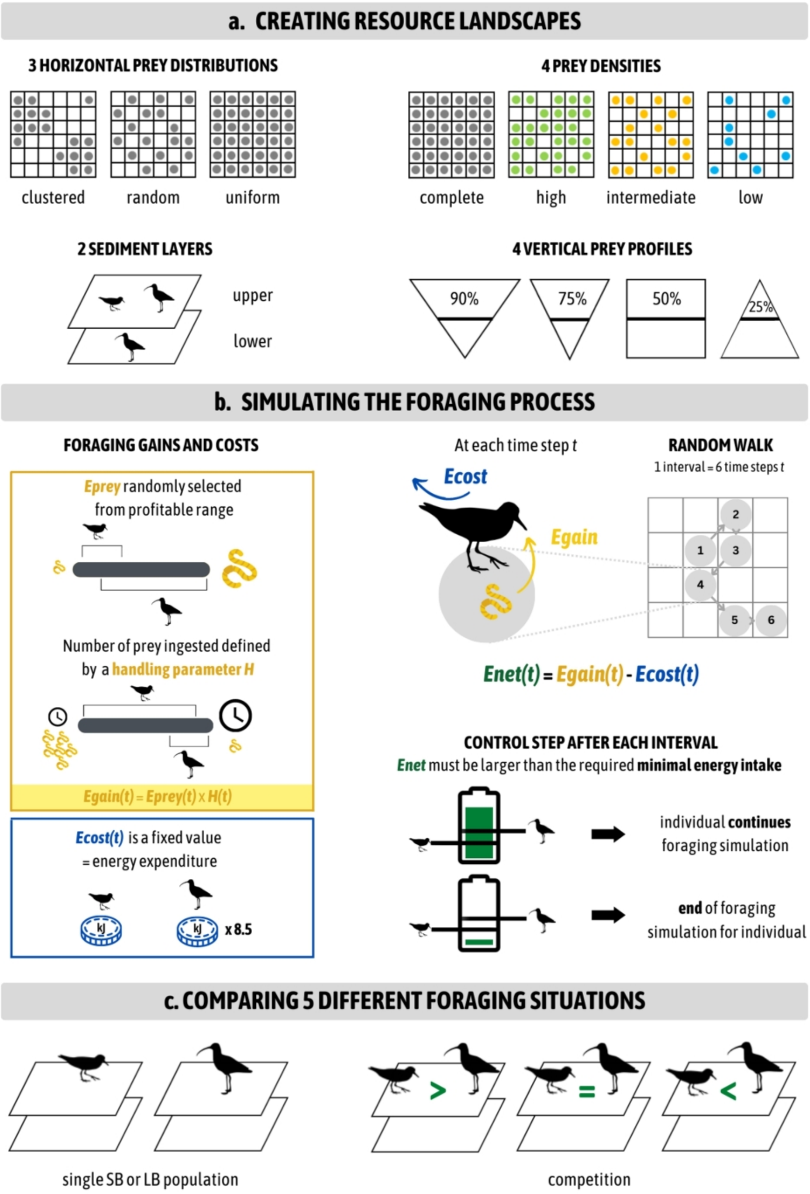

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Table 1 Overview of model parameters, their definition, and selected values for this study. Parameters that are related to the one that is discussed are indicated in bold. Details and calculations can be consulted in **SI.2**.

Parameter	Definition	Values
Area (m^2)	Surface area of the foraging landscape	20 cells × 20 cells = 400 m^2
Time step	Smallest time unit considered for all simulations. Within one time step, all individuals perform a set of activities based on the model's rules defined for foraging and moving through the landscape.	5 seconds
Total simulation time	Duration of the simulation after which foraging performance is evaluated. Here, each simulation consists of 60 time steps.	300 seconds = 5 minutes
Control step	After each set of six time steps, those individuals are removed from the landscape that failed to gain a **minimum amount of energy** from prey.	30 seconds
Minimal energy intake (kJ)	Energy birds must ingest within one time step to remain foraging in the landscape, required for maintaining metabolism and performing activities (foraging).	SB: 0.015 kJ LB: 0.283 kJ
Lean body mass LBM (g)	Average body mass of an individual wader excluding fat reserves. LBM is used to determine the **minimum intake rate** and the **searching cost** of both wader species (Davidson 1983).	LBM_{SB} = 40.07 g LBM_{LB} = 870.98 g
Energy gain from prey E_{gain} (kJ)	The energy acquired by an individual bird when taking prey from the sediment within one time step. The **maximum gross energy intake** is set as the upper limit of consumption by waders (Kersten & Piersma 1987, Zwarts & Wanink 1993, Kvist & Lindstrom 2003).	$E_{gain,SB}$ = 0 to 0.2 kJ $E_{gain,LB}$ = 0 to 3.3 kJ
Prey handling parameter H (number of prey per time step)	Parameter correcting for the time required for a wader to recognise, capture, lift, handle, and swallow a prey, and move its bill downward again to continue foraging. It is equal to the amount of prey that can be caught and ingested by waders within one **time step** (Zwarts & Esselink 1989, Zwarts & Wanink 1993).	$H_{SB, small}$ = 7.5 (prey ≤ 50 mm) $H_{SB, large}$ = 2.5 (prey > 50 mm) $H_{LB, peck}$ = 2.2 $H_{LB, probe}$ = 0.625
Searching cost E_{cost} (kJ)	Energy expenditure of waders when moving from the midpoint of a grid cell to the midpoint of a vacant adjacent grid cell, for one **time step**. Based on the metabolic rate for the general locomotion of birds (Taylor *et al.* 1982), for waders moving through the landscape at a speed of 0.2 $\mathrm{m \cdot s^{-1}}$ (Dias *et al.* 2009).	$E_{cost,SB}$ = 0.00439 kJ $E_{cost,LB}$ = 0.03712 kJ
Peck-to-probe rate	Preference of LBs for pecking, *i.e.* how likely an LB will peck instead of probe (Navedo & Masero 2008)	0.70
Interference	Probability that an LB can chase away an SB from its location when individuals are placed in the landscape, or when they move while foraging. After being chased, an individual can return to the landscape in the next **time step**. Only applies to the competition mode.	0.25, 0.50, 0.75
Population size	Number of individuals of an SB or LB population present in the landscape for a certain time step.	Single-species: 50 SBs or 50 LBs Competition: 25 SBs and 25 LBs

Running head: ***Prey distribution modulates wader foraging performance***

Horizontal prey distribution determines the foraging performance of short- and long-billed waders in virtual resource landscapes

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When waders gather in mixed-species flocks to feed on benthic prey, differences in morphological traits, foraging strategies and prey selection may allow different species to optimise their energy intake while reducing competition. As the effect of the fine-scale spatial distribution of resources on energy intake is unknown, we simulated the foraging performance of two types of waders with contrasting body plans and foraging strategies in a variety of virtual mudflats with different horizontal and vertical prey distribution patterns. Although larger, longer-billed individuals had higher energy intake rates, smaller individuals with shorter bills maintained higher prey capture rates by relocating if prey was insufficiently available. Shorter-billed individuals struggled more to meet their energetic demands because they selected smaller prey items and had a more limited capacity to metabolise energy from food. Being able to catch larger, high-quality prey offered a competitive advantage for longer-billed individuals, which could be a driving force for the evolutionary lengthening of bills in waders. Interestingly, their performance was more affected by the horizontal than the vertical prey distribution. Quantifying prey distributions may help explain how some wader species can co-occur in the field and why some wetland areas are unattractive as foraging areas. The work confirms that the foraging performance of larger, longer-billed birds is not limited by bill size *per se*, but by the energetic trade-offs associated with the ability to catch larger prey items more efficiently, increased handling times and higher absolute energy costs. These trade-offs may become particularly important in landscapes where prey is scarce and spatially patchy.

Keywords: Individual-based model, prey distribution, foraging strategy, morphological adaptations, exploitative competition

Waders, a group of avian families within the order Charadriiformes, congregate *en masse* in wetlands, where birds of different shapes and sizes feed on benthic prey (Bocher *et al.* 2014, Cestari *et al.* 2020). The birds' co-occurrence on intertidal mudflats and marshes may select for broadly similar morphological and physiological adaptations for foraging in these particular habitats. However, competition for resources may stimulate niche differentiation of phenotypic traits or behaviours in different species, thus facilitating local co-occurrence (Kim 2016, Oudman *et al.* 2018). Competition can be reduced by exploiting different types of resources or different parts of a resource space, especially if access to food is limited (Lifjeld 1984, Franks *et al.* 2013). At present, however, we do not know how birds with contrasting body plans and foraging strategies acquire resources when they are placed in environments with similar resource distributions.

Wader bill morphology displays much inter- and intraspecific variation in terms of length, shape and thickness (Swennen *et al.* 1983, Vahl *et al.* 2005). Other body traits and behaviours are often linked with bill length or shape (Moreira 1997, Barbosa & Moreno 1999, Nebel *et al.* 2005; Supporting Information Fig. S1). Shorter-billed waders such as plovers (*Charadrius* spp.) generally weigh less and have shorter legs compared to longer-billed species like curlews (*Numenius* spp.). Because of their longer bill and legs, longer-billed waders can also forage in zones with higher water levels than the maximum water depth tolerated by shorter-billed species (Feare 1966, Finn *et al.* 2007, Mu & Wilcove 2020). While shorter-billed birds mostly rely on visual cues and usually feed by pecking, *i.e.* picking food items from the surface of the sand or mud, longer-billed birds can peck as well as probe by inserting more than a quarter of their bill in the sediment (Barbosa & Moreno 1999). Gaining insight into which characteristics entail the largest energetic costs and benefits for foraging waders would help to better understand the trade-offs of having a certain bill morphology, body plan and foraging technique. Such knowledge can help explain how wader populations with different body plans persist in similar habitats alongside one another.

Although field (Bijleveld *et al.* 2012, Duijns & Piersma 2014, Cestari *et al.* 2020) and modelling (Stillman *et al.* 2002, Goss-Custard *et al.* 2006) studies have yielded insight into the effects of *e.g.* competition or disturbance on the birds' intake rates, in previous research only landscapes with different prey densities were compared, rather than different spatial distribution patterns of prey. Waders mostly feed on macro-invertebrates such as polychaetes, crustaceans and molluscs, which are extracted from the sediment. The spatial distribution of these prey items can be highly variable depending on the local environmental conditions, tidal cycle, geographical location and season (Anderson & Smith 1998, Duijns *et al.* 2015, Zhang *et al.* 2016). Also, the relative abundance, size and energetic content of prey vary throughout different depth layers of the sediment (Zwarts & Blomert 1992, Zwarts & Wanink 1993, Deboelpaep *et al.* 2020). The largest numbers of macroinvertebrates are found at the shallowest depths, but larger and/or higher-quality prey individuals generally reside in deeper sediment layers (Esselink & Zwarts 1989, Zwarts & Wanink 1991, Piersma *et al.* 1993a). Both horizontal and vertical resource availability patterns may thus be important for assessing which prey could be collected by different waders with the highest probability and the lowest effort. Based on such information we could predict which types of waders would maintain the highest foraging performance at a certain foraging site based on observed resource distribution patterns.

In this study, we compared the foraging performance of two hypothetical wader populations with contrasting morphological characteristics and foraging strategies: a group of long-billed, large-bodied waders that both peck and probe (*e.g.* Eurasian Oystercatcher *Haematopus ostralegus*, Eurasian Curlew *Numenius arquata*, Black-tailed Godwit *Limosa limosa*), versus a group of short-billed, small-bodied waders that exclusively forage by pecking (*e.g.* Little Ringed Plover *Charadrius dubius*, Ruddy Turnstone *Arenaria interpres*, Little Stint *Calidris minuta*). We evaluated how easily these two wader types could attain their required energy intake in a set of virtual foraging landscapes with different horizontal and vertical prey distributions. For this, we developed an individual-based model in R. Advantages of this approach are that all individuals can interact with each other and their environment, fixed prey distributions can be simulated, and confounding effects on the waders' foraging performance can be eliminated (*e.g.* weather, predictability of food; Vahl *et al.* 2005). Such models are effective for assessing how individual behavioural processes and decision rules give rise to population-level responses, including the wader population size supported by a site (Stillman *et al.* 2015).

The model incorporates two main trade-offs. First, long-billed birds have access to prey from deeper sediment layers (Nebel *et al.* 2005), but they need more time to handle and ingest prey (Zwarts & Wanink 1993) than shorter-billed birds. The required energy intake and energy expenditure per individual is lower for short-billed than for longer-billed waders (Taylor *et al.* 1982, Kersten & Piersma 1987, Zwarts & Wanink 1993). Second, small birds cannot reach prey from deeper sediment layers, but they are more efficient at handling small prey (Zwarts

& Wanink 1993). We assume that the combined effects of horizontal and vertical prey distribution are crucial determinants of the foraging performance of waders in prey landscapes. As a first hypothesis, we expect that long-billed birds would forage more efficiently in landscapes where prey is clustered, because long-billed birds require more energy during relocation than short-billed birds. In turn, short-billed birds have more modest net energy requirements and a higher prey handling efficiency, which might make them more efficient foragers overall, especially in landscapes where prey is randomly distributed (***hypothesis 1***). Secondly, we challenge the intuitive expectation that long-billed birds benefit when prey is concentrated in deeper sediment layers. Because it takes more time and energy to search for prey in deeper parts of the sediment (Zwarts & Esselink 1989), we hypothesise that long-billed waders would forage more efficiently in landscapes when a higher proportion of the total available energy is located in the upper part of the sediment (***hypothesis 2***).

Overall, our model can provide first insights into the potential relative importance of horizontal and vertical prey distributions for the foraging performance of waders. For this, we integrate known energetic trade-offs and explore different degrees of interference competition during foraging, both in landscapes where prey are abundant and in landscapes where prey are more scarce.

METHODS

To evaluate how the foraging performance of two contrasting wader types is influenced by the spatial distribution of prey, we built an individual-based model in R (version 4.0.2, R Core Team 2020; script available in Supporting Information). Foraging performance was calculated with a high spatiotemporal resolution at both the individual and population level. The term 'population' is here used in a liberal sense to designate all individuals with the same body plan and foraging strategy. Baseline data on benthic macroinvertebrate distribution patterns and wading bird foraging rates were collected from literature, and supplemented with field data from previous work.

Foraging landscapes

The model landscapes represent intertidal mudflats, typical foraging habitats for waders (Zwarts & Wanink 1993, Bocher *et al.* 2014). Different landscape types were simulated to compare how easily waders can exploit food resources with different horizontal and vertical distributions and densities (Sutherland *et al.* 2000, Nebel *et al.* 2005, Henry & Cumming 2017). The virtual foraging landscape is a horizontal 20 × 20 grid of 1 m × 1 m cells (400 m²), which consists of two horizontal layers (Fig. 1a). In these, prey is represented as a certain amount of energy at a grid cell, which is the maximum energy that could be consumed at that location by waders throughout the simulation. Replenishment was not included as this process occurs over longer time scales than the foraging simulations (five minutes). In each sediment layer, grid cells containing (energy from) prey are distributed in a clustered, random or uniform pattern (Fig. 1a; Dierschke *et al.* 1999, Kristensen *et al.* 2013). To assess how varying levels of prey availability affect the waders' foraging performance, we iterated simulations at four different prey densities, where a different proportion of the landscape was occupied by prey (Fig. 1a**,** Supporting Information TableS1). This corresponds to a low (0.25), intermediate (0.50), high (0.75) prey density and complete (1) cover of the landscape with grid cells that contain prey. At the start of each simulation, prey distribution was identical in the upper and lower sediment layer of the same landscape to enable comparison of the different wader populations under identical foraging situations. However, in reality, the relative abundance of benthic prey is often higher at the sediment surface, whereas larger prey items are typically more common in deeper parts of the sediment (Zwarts & Wanink 1991, Zwarts & Blomert 1992, Piersma *et al.* 1993a). To incorporate this level of complexity, foraging simulations were repeated for four different hypothetical vertical prey distributions, where the upper layer contributed to 25, 50, 75 or 90 % of the total energy that could be gained from prey in the foraging landscape.

Two wader species

We defined two model bird species, a short-billed (SB) and a long-billed (LB) wader (Supporting Information Table S2). Here, the term 'species' is used liberally to designate birds with different body plans and associated foraging strategies. Morphological characteristics and foraging strategy of both waders were based on generalised features of short- and long-billed species. The SB has a short bill (length: 18 mm), short legs and a small body mass, similar to the Little Stint, a small wader measuring 15 to 20 cm (Barbosa & Moreno 1999, Lee & Hockey 2001). SBs forage exclusively by pecking if prey is available in the upper layer. The LB is characterised by a relatively long bill (length: 164 mm), long legs and a large body, comparable to the Eurasian Curlew (body size of 60 cm; Ens *et al.* 1990, Moreira 1997, Bocher *et al.* 2014). LBs peck prey from the top part of the sediment as well as probe for more deeply buried prey (Davidson *et al.* 1986, Sutherland *et al.* 2000). Based on pecking and probing rates found for

Eurasian Curlews preying on polychaetes, the probability of an LB pecking prey from the upper layer is 0.70 (Zwarts & Esselink 1989). If there is no prey (left) in the upper layer, LBs automatically probe.

Energetic gains and costs of foraging

At the beginning of each time step, for each individual wader having access to prey, the energy gained from catching a single prey item is randomly drawn from a uniform distribution between an upper and lower limit. The latter prey selection limits were based on Zwarts and Wanink's (1993) formula for minimal profitable prey biomass and the observed mean and maximum size of prey ingested by short- and long-billed waders (Supporting Information Table S3; Zwarts & Esselink 1989, Davis & Smith 2001). The total time invested by waders to search for, locate, recognise, handle and ingest a single prey item is an important cost of foraging (composite handling time, Zwarts & Wanink 1993). Based on this composite handling time required for a single prey item, within each time step of five seconds SBs catch seven smaller or three larger prey items, whereas LBs capture two prey items by pecking and half a prey item by probing (Table 1, Zwarts & Wanink 1993). When calculating the total energy gained from prey per time step, the energetic content of a randomly selected prey item is thus multiplied with the fixed number of prey items that can be caught by a wader within this time frame (Supporting Information Table S2).

Foraging also entails an energetic cost, for sustaining the basal metabolism as well as for walking through the landscape and searching and processing prey. This searching cost is a fixed value that depends on a bird's body mass and walking speed (0.000878 kJ/s for SBs and 0.00742 kJ/s for LBs, Supporting Information Table S2; Taylor *et al.* 1982). Additionally, there is a physiological limit to the amount of food that can be processed and metabolised by waders. Within each time step, birds could not gain more energy than the maximal energy intake observed in migrating waders, *i.e.* 10 times the basal metabolic rate (SB: 0.2 kJ, LB: 3.3 kJ; Supporting Information Table S2; Kersten & Piersma 1987, Kvist & Lindstrom 2003). Note that the required intake and expenditure of energy are higher for individual LBs than SBs, but when scaled for body mass, the energy demands of LBs are smaller than those of SBs (Kersten & Piersma 1987).

Competition between two wader species

Complexity is built up in two versions of the model, which allows us to evaluate how the waders' foraging performance is affected by interspecific competition. In a first set of simulations ('single-species model'), waders forage without competition from the other species (50 SBs or 50 LBs; Fig. 1c). Waders cannot be chased from their location by conspecifics once they occupy a certain grid cell, which aligns with the concept of pre-emption: the advantage of being the one who occupies a resource space, only because it makes resources at that location unavailable to others. In a second set of simulations ('competition model', Fig. 1c), the effect of heterospecific birds removing prey (exploitative competition) and chasing individuals from their foraging location (interference competition) is included (Yates *et al.* 2000). As both wader species are placed in the same landscape (25 SBs and 25 LBs) and there is no distinction between different prey species, SBs and LBs exploit the same food resources and foraging locations (apart from the lower sediment layer which is only accessible to LBs). If at initialisation or while foraging an LB tries to move into a grid cell occupied by an SB, or *vice versa*, one of both is chased away. A user-defined probability for the success of the wader species during such interspecific chases determines whether the SB or LB remains at the contested grid cell. In this case, LBs have a 75, 50 or 25% chance to remain in a grid cell and SBs 25, 50 or 75% (interference, Table 1). The wader that is expelled is not allowed to forage during that time step, but is again placed in the foraging landscape during the following time step according to the same rules defined for the initialisation of the foraging simulation. Here, we assume that conspecifics never chase away each other from a location, as we focus on the effect of interactions between wader species, but not within populations, on foraging performance.

Simulation of the foraging process

Before each simulation the landscape is initialised according to user-defined input values for landscape area, horizontal and vertical prey distribution, and prey density. Waders are randomly assigned a unique starting position, with one grid cell hosting at most one bird. All single-species model runs are repeated in sets of 10 replicates for each landscape type for a total duration of 60 time steps. A selection of runs is also executed for the competition mode (Table 1, Supporting Information Table S4). During each time step, all waders in the landscape first try to take prey. If prey is present in an accessible layer, the foraging attempt of the individual in that grid cell is automatically successful. When there is no prey at the bird's location the energy gain is zero. At each grid location and during each time step, the amount of energy consumed by waders is subtracted from the energy present at that location. Only the remaining energy is available to waders during the following time step(s).

Foraging attempts are followed by randomly moving to a vacant and adjacent grid cell, in which midpoints of cells are connected by straight or diagonal segments (Moore neighbourhood). Birds can only move once between two grid locations per time step. Searching and foraging speeds reported for waders are circa 0.2 m/s (Stillman *et al.* 2002, Dias *et al.* 2009), resulting in a time step duration of five seconds for foraging in one-m² grid cells. Moving straight or diagonally between grid cells is here considered equal in terms of duration, walking speed and the energy required for walking (Supporting Information Table S2). After every six time steps each bird's total energy gain up to the current time step is compared to a threshold that determines whether the individual continues to forage in the landscape or leaves (minimum intake rate, Supporting Information Table S2). Waders are known to abandon habitat patches if their energy intake rates are too low (Duijns *et al.* 2015). This means that, if a bird cannot attain an energy intake of 0.003 kJ/s (SB) or 0.06 kJ/s (LB), it leaves the landscape and does not return for the remainder of the simulation. Individuals that gained more than the minimum intake threshold are allowed to continue the foraging process. The more birds fail to meet their metabolic requirements, the smaller the population that remains in the landscape until the end of the simulation.

Model output

For each scenario, energy gains and searching costs are stored individually for each wader and for each time step. From these values, the net energy gain $\boldsymbol{E_{net}}$ (kJ) for a single-species population of $\boldsymbol{N}$ individual waders $\boldsymbol{i}$ is calculated using Equation 1.

$$E_{net} = \sum_{i=1}^{N} \sum_{t=1}^{T_i} (E_{gain,it} - E_{cost,i} \cdot T_i) \qquad \text{Equation 1}$$

where $\boldsymbol{E_{gain,it}}$ is the energy gained by an individual wader $\boldsymbol{i}$ from consuming prey during time step $\boldsymbol{t}$, and $\boldsymbol{E_{cost,i}}$ is the energy lost while searching for prey and moving through the landscape. $\boldsymbol{T_i}$ marks the end of the simulation ($\boldsymbol{t} = 60$), or the time step $\boldsymbol{t}$ after which wader $\boldsymbol{i}$ left the foraging landscape because it could not reach the minimally required energy intake. $\boldsymbol{E_{gain,it}}$ is equal to the energy gain from a single prey multiplied by the number of prey items that can be handled within a time step $\boldsymbol{t}$ by the individual (Fig. 1b). The total net energy gain $\boldsymbol{E_{net}}$ is calculated by taking the sum of all individual net energy gains $\boldsymbol{E_{net,i}}$ of a population over the entire time spent foraging $\boldsymbol{T_i}$.

The waders' foraging performance is evaluated by means of four different metrics. First and second, the averaged and maximum net energy gain of individuals give a general idea about how much energy from prey can be collected in different landscape settings. Both values are presented as the percentage of the maximum potential net energy intake that can be achieved during the entire simulation, where waders would ingest the upper limit of the energy that they are able to metabolise during each time step (SB 12 kJ and LB 196 kJ per individual; Supporting Information Table S5). Third, the population sizes of SBs and LBs at the end of the foraging simulation provide an indication of how long a population might persist in a certain environment. Fourth, dividing the number of successful foraging attempts (*i.e.* the number of time steps during which prey was caught) by the total number of foraging attempts (*i.e.* the length of the random walks of waders) yields the prey capture rate. This value provides an estimate of how frequently prey items are encountered and caught in the different landscapes. Finally, the influence of different parameter settings on the model outcome was investigated in a sensitivity analysis. While maintaining all parameter values but one constant, the foraging performance was evaluated for different handling parameters, searching costs, metabolic limits and population sizes of waders, prey sizes and longer simulation durations (Supporting Information Table S6).

RESULTS

LBs gain more energy, but SB populations maintain higher prey capture rates

Overall, when waders foraged in absence of heterospecifics, LBs tended to perform better than SBs, with most LBs collecting more energy than SBs. Especially at higher prey densities, the net energy gain of individual waders was larger for LBs than for SBs (23–40 %, Fig. 2a). When prey was present in each cell of landscapes with a complete cover or uniform prey distribution, LBs attained more than 90% of their maximum gross energy intake throughout the simulation period. The net gain of SBs never exceeded 70% of this maximum level. However, when looking at the individuals with the highest net energy gain, SB waders could maximise their energy intake in all types of landscapes to the levels achieved when foraging in landscapes with a complete prey cover (Fig. 2b). The maximum energy gained by LBs, in contrast, was considerably lower in landscapes with a random distribution at low and intermediate prey densities. Similarly, the SBs' prey capture rate was distinctly higher than the LBs' – even though the prey capture rate of individual SBs displayed quite some variation among landscapes with the lowest prey density (Fig. 2c).

Compared to SBs, more LBs could continue foraging at higher prey densities (Fig. 2d), but the spatial distribution of prey was more important for the LBs' persistence than prey density. In landscapes with a random prey distribution, more LB than SB waders remained foraging until the end of the simulation. Even when prey was most scarce, at the lowest prey density, at least a quarter of the SB or LB population was able to gather sufficient prey to continue foraging. When prey was distributed in clusters or uniformly, the difference between the final population sizes of SBs and LBs was smaller than in landscapes with a random prey distribution pattern. In simulations without interspecific competition, all SBs that acquired sufficient energy to continue foraging by the first control step remained in the landscape until the end of the simulation, but the population size of LBs continued to decrease slightly at consecutive control steps. At most four individuals, or up to 30% of those LBs that left the landscape, did so after the sixth time step. When prey density was low, at most eight individuals or up to 50% of all removed LBs additionally departed from the landscape after six time steps (Supporting Information Fig. S2).

Horizontal prey distribution patterns are more important for LBs than for SBs

All waders performed best in foraging landscapes with a complete prey density or in landscapes with a uniform distribution at any prey density. For SBs, the prey density of the landscape appeared to be more important than the actual distribution of prey: there was little difference between different prey distribution patterns at the same prey density when considering the net individual energy gain (Fig. 2a), prey capture rate (Fig. 2c), and the number of SB waders that continued foraging (Fig. 2d). In contrast, the number of LBs that remained foraging was notably higher in landscapes with a random prey distribution than with a clustered pattern, although, overall, in landscapes with a clustered prey distribution, LB waders tended to attain higher maximum energy gains (Fig. 2b) and catch more prey (Fig. 2c).

For LBs horizontal prey distribution is more important than vertical prey distribution

In all landscape types, LBs obtained a largely similar proportion of their energy from prey from the upper layer (70–75 %). Only at the lowest density in random and clustered prey landscapes, LBs pecked with a frequency that diverged a little from the 70% preference for foraging from the upper instead of lower layer defined when setting up the simulation parameters (67–78%; Supporting Information Table S7). This indicates that prey from either sediment layers was not depleted within the timeframe of the simulations, apart from a few situations where all prey was taken from the upper or lower layer in a certain number of cells at low prey density. Overall, the foraging performance of LBs decreased in landscapes with lower prey availability, but was similar in landscapes with different vertical prey distributions. The importance of prey density and horizontal prey distributions varied for different aspects of the waders' foraging performance. The net individual energy gain (Fig. 2a) and prey capture rate (Fig. 2c) showed a clearer influence of prey density, but the maximum individual energy gain (Fig. 2b) and final population size (Fig. 2d) changed more strongly in landscapes with different prey distribution patterns than with different prey densities.

Interspecific competition has a stronger negative effect on SB than on LB

When SBs competed for resources with LB waders in landscapes with a random or clustered prey distribution, the mean net energy gain of SBs slightly decreased (2–10 %) compared to single-species simulations (Fig. 3a). This decrease was larger in landscapes with lower prey densities and occurred regardless of whether SBs could easily chase away LBs from their foraging location or not. Similarly, competition with SBs caused a small decrease in the mean net energy (1–13 %) collected by individual LBs, compared to when LBs foraged alone. In general, however, the decrease in the mean energy gain due to interspecific competition was larger for SBs than for LBs. The negative effect of competition on the LBs mean and maximum net energy gain (Fig. 3a & 3b) and prey capture rate (Fig. 3c) was most pronounced if LBs were more readily displaced by SBs, especially in landscapes with a low density of clustered prey. In other landscape types, there was no clear negative influence of competition from SBs on the maximum energy gain of LB individuals, or on their prey capture rate and the number of waders that could continue foraging until the end of the simulation in all landscapes.

Compared to simulations without competition, for SBs foraging in landscapes with a low prey density, competition with LBs for prey and prey locations led to large decreases of their prey capture rate (Fig. 3c) and the highest energy gain SBs could achieve (Fig. 3b). This reduction was remarkably larger in landscapes with a random (38–57 %) than with a clustered (12–45

%) prey distribution pattern. For both SBs and LBs foraging on clustered prey, interspecific competition resulted in an increase in the variation in the maximum energy gain and prey capture rate.

When SBs could more easily chase LBs from a certain location in clustered landscapes, the maximum net energy gain (Fig. 3b) and prey capture rate (Fig. 3c) of SBs was higher than when LBs had a higher chance of winning confrontations between SBs and LBs. Similar to the results for LBs, the probability of SBs chasing away LBs from grid locations did not affect the other foraging performance metrics used here (Fig. 3).

DISCUSSION

In waders, certain morphological traits and foraging behaviours tend to be strongly linked. Waders with a larger body and longer legs are typically tactile foragers that use their longer bills to probe for prey in the sediment. Smaller birds generally have shorter bills and hunt visually by pecking prey from the sediment surface (Jing *et al.* 2007, Kuwae *et al.* 2012). These suitable combinations of characteristics likely represent different adaptive peaks in a trait landscape (Barbosa & Moreno 1999, Nebel *et al.* 2005). However, we do not know to what extent these traits are linked to the foraging performance of waders when they are foraging in the same landscape, nor which trade-offs are most important for explaining these differences. In this study, we therefore simulated the foraging performance of short (SB)- and long-billed (LB) waders in landscapes with varying resource distribution patterns. We found that the small-scale spatial structure of resources in a foraging area had strong effects on the waders' energy gains and prey capture rates. Interestingly, the horizontal prey distribution appeared to be more important for LBs than the vertical prey profile. SBs maintained higher prey capture rates, but in most landscapes their energy gain was distinctly lower than that of LBs.

Catching fewer but larger prey items pays off for LBs, while SBs rely on high prey capture rates

Contrary to our expectations, we found no indication of SBs performing better than LBs when prey was distributed randomly, nor of an advantage of LBs when prey was clustered (***first hypothesis***). Instead, SBs gained less energy than LBs, irrespective of the horizontal prey distribution. SB waders foraged better in uniform landscapes where prey was found at each location, but their performance was similar when prey was distributed randomly or clustered. LBs, in contrast, foraged better in landscapes with a random than with a clustered prey distribution. In the latter, LB waders had a higher chance to encounter larger contiguous groups of cells either with or without prey. This can lead to higher mean but lower maximum net energy gains in landscapes with random versus clustered prey distributions.

The differences in energy requirements and prey handling efficiency of the two types of waders were less important than we anticipated. The lower prey handling efficiency, higher absolute energy requirements, and higher absolute movement costs of LBs (Taylor *et al.* 1982, Kersten & Piersma 1987, Zwarts & Wanink 1993) were adequately compensated by LBs catching larger, higher-energy prey items than SBs. As a result LBs accumulated energy more easily, which in turn allowed them to continue foraging in the landscape even when they failed to feed for several (consecutive) time steps. The higher energetic requirements specified in the model for SBs ensured that they required very high prey capture rates (> 75 %) to remain in the landscape. Relative to their body mass SBs require more than twice as much energy as LBs to sustain their metabolism (*cf.* minimal energy intake) and to forage (*cf.* searching cost, Supporting Information Table S2, Taylor *et al.* 1982, Zwarts & Wanink 1993). Combined with a more restricted size (range) of profitable prey (Supporting Information Table S3; Kersten & Piersma 1987, Vahl *et al.* 2005, Duijns *et al.* 2015) and, relative to their body mass, only a slightly larger capacity for metabolising energy from food (Kersten & Piersma 1987), SBs have smaller energy reserves. Therefore, SBs struggled more to meet their energetic demands than LBs in our simulations, and left more quickly to look for food elsewhere.

In reality, longer-billed birds are tactile foragers that must probe to detect prey, so they have less information about the prey availability in their immediate surroundings than visual foragers (Santos *et al.* 2009). Longer-billed waders must bridge longer periods between successful foraging attempts, but can catch large prey with a higher energetic content from deeper sediment layers compared to visually foraging, smaller-bodied waders. Being able to catch high-quality prey, even if only occasionally, appeared to offer an important competitive advantage for LBs in the simulations. It is thought that this has been a main driving force for the evolutionary lengthening of bills in waders (Nebel *et al.* 2005).

Our sensitivity analysis indicated that, if they cannot find high-quality prey, the foraging performance of both wader species plummets, regardless of the spatial distribution and density of prey (Supporting Information Figs. S3a-g). The model suggests that SBs would then benefit more from leaving such suboptimal foraging grounds more quickly than LBs to explore other (nearby) locations in search of prey. This implies that smaller, shorter-billed birds with higher energetic demands and lower metabolic ceilings (Kvist & Lindström 2000) may rely more on the availability of alternative suitable foraging grounds in close proximity. This aligns with observations of Common Redshanks (*Tringa totanus*), which forage visually. Disturbances to the sediment that result from their foraging activity cause preys to retreat to deeper sediment layers or stop moving, making them less detectable. Therefore, Common Redshanks need to regularly move to different locations to maintain sufficiently high intake rates (Dias *et al.* 2009).

Horizontal rather than vertical prey distribution matters for LBs

The ***second hypothesis***, which proposed that LB waders would benefit more from landscapes where a higher proportion of prey is present in the upper part of the sediment, was not confirmed by the main results of this study. LBs maintained similar energy gains and prey capture rates irrespective of the vertical prey distribution or prey density – even when prey was locally depleted in this layer at the lowest prey density (Supporting Information Table S7) or during longer simulations (Supporting Information Table S8, Fig. S3g). The foraging performance of LBs remained high because there was sufficient energy to cater for their needs in both sediment layers combined in the simulations. In most cases, LBs continued to peck prey from the upper layer until depletion in this layer stimulated them to switch to probing in the lower sediment layer. This aligns with the behaviour displayed by Western Sandpipers (*Calidris mauri*). They alternately peck for small prey or probe for larger macrobenthos depending on the local availability to maximise their intake rates (Sutherland *et al.* 2000). Similarly, Eurasian Curlews adjust their foraging technique in response to the seasonal and tidal activity patterns of polychaete Ragworms *Nereis diversicolor*. Ragworms that filter-feed near the sediment surface or graze near their burrow are easily pecked by Curlews. When ragworms retreat into their burrows, Curlews more often forage by probing into the burrow or by waiting until the worm resurfaces (Zwarts & Esselink 1989).

Energetic costs lead to stronger decreases in SB performance when competing with LBs

Interspecific competition between SB and LB populations resulted in a decrease in the foraging performance of both species in our simulations, especially in landscapes with lower prey densities. LB waders, however, were less affected by the presence of foraging SBs than *vice versa* – even when LBs were easily chased away by SBs from a location, as specified in the model. The SBs' maximum energy gain and prey capture rate decreased more strongly than the LBs' when the two species competed in the same foraging landscape, as LBs were able to catch larger prey and required less energy relative to their body size (Supporting Information Table S2, Kersten & Piersma 1987, Vahl *et al.* 2005). The ease with which LBs chased SBs from their foraging spot strongly reduced the maximum energy gain and prey capture rate of SBs, although there was a lot of variation between different replicates. Each time a bird was chased away, it could not feed and only lost energy. Being chased away and re-entering the landscape, however, means the individual can by chance move from a cell without prey to a cell with prey. This may be especially advantageous in landscapes with few and small prey clusters.

When competing for resources, the energy reserves of SBs dropped faster than those of LBs because flying off and relocating costs at least 50% more energy for SBs. For SBs, the decrease in the prey capture rate and maximum energy gain due to competition was more pronounced in landscapes with a clustered than with a random prey distribution, as in the former there was a higher probability of encountering larger contiguous groups of grid cells without prey.

Limitations

The current simulations explored foraging and both intra- and interspecific interactions at small spatial scales, which in reality correspond to a relatively small section of a mudflat in a wetland area during a brief period. The evolution of wader phenotypes is driven by diverse selection pressures and different trade-offs in addition to those that are operating at small spatiotemporal scales (Franks *et al.* 2013, Henry & Cumming 2017). Thermoregulatory costs are an important driver for wader body size and shape, affecting their required daily energy intake (González-Medina *et al.* 2020, McQueen *et al.* 2022). For instance, migratory Charadriidae have shorter legs, as longer body appendages entail a larger metabolic cost because of wind-induced stress at their Arctic breeding grounds (Cartar & Morrison 2005). In contrast, in warmer environments, longer bills and legs are more advantageous to dissipate heat (McQueen *et al.* 2022). Also, larger birds are more conspicuous and lose more energy when taking flight (Collop *et al.* 2016), which makes them more vulnerable to predation. So, while LBs appear to outperform SBs under the conditions defined for this study's foraging simulations, other trade-offs exist for other activities – including predator avoidance (Glover *et al.* 2011, Collop *et al.* 2016) and migratory flights (Nebel *et al.* 2013, Zhao *et al.* 2018).

A central assumption of the model is that individuals always feed when they land on a cell that contains prey, but whether prey is ingested by waders is in reality also influenced by the bird's abilities or experience (*e.g.* skill of cropping siphons; Santos *et al.* 2010), vegetation (Jing *et al.* 2007), sediment properties such as sediment penetrability (Piersma *et al.* 1998), tidal exposure (Granadeiro *et al.* 2006), interactions with other birds (*e.g*. kleptoparasitism); and the prey's (hiding) behaviour (Yates *et al.* 2000, Duijns & Piersma 2014), size (Zwarts & Blomert 1992), or palatability (van Gils *et al.* 2013). The location also matters, as suboptimal foraging grounds may be preferred over higher-quality sites if they are closer to the nesting or roosting areas (Piersma *et al.* 1993b, Folmer *et al.* 2010).

In this study we considered all prey as a certain amount of energy distributed in the landscape, as uncertainties remain on which prey species are selected by different waders. Still, although SBs and LBs partly caught prey of similar sizes, we found no major effect of interspecific competition on the waders' foraging performance. We did include variation in prey size and energetic content, but further diversifying preferred prey species in future work would allow to compare the performance of waders with lower levels of dietary overlap, for example. Similarly, by favouring prey of certain species or sizes, birds can influence the composition of the prey community (Fonseca & Navedo 2020) and even locally deplete prey (Schneider & Harrington 1981). Although depletion did not occur during the relatively short simulations from this study, it would be interesting to keep track of the prey items remaining in the landscape more explicitly. This way, we could investigate longer-term changes in the prey community due to the waders' selective feeding on prey community composition.

An interesting added complexity would be to simultaneously adjust the birds' horizontal and vertical searching behaviour and handling times based on whether prey is found or not, and which type of prey is available. Modelling foraging behaviour with greater biological realism by increasing the 'intelligence' of the virtual birds may allow to address which fraction of the available prey is actually ingested by waders. In this, the waders' field of vision plays an important role. Generally, visual foragers possess a sensitive 'binocular' visual zone to *e.g.* guide fine bill tip movements, whereas tactile foragers benefit from a broader 'panoramic' vision to detect predators while probing (Martin & Piersma 2009, Martin 2012). Here, all individuals continued to perform random walks regardless of prey encounters or other types of environmental feedback. Waders in reality follow 'informed trajectories' based on sensory cues, such as feeling prey movements, spotting burrow openings, and tasting whether a burrow is occupied or not (Davidson *et al.* 1986, Jing *et al.* 2007). Especially longer-billed tactile foragers use an area-restricted search to maximise their intake rates (Dias *et al.* 2009). Black-tailed Godwits, for instance, explore foraging grounds by probing at widely spaced locations, and increase their effort in close vicinity of their location if a prey item is discovered (van Gils *et al.* 2003). Our model might therefore underestimate the performance of particularly LBs in clustered landscapes. However, even if we would account for the higher energy gains of LBs using an area-restricted search strategy, it would only strengthen our conclusion that LBs are more efficient foragers in clustered landscapes. Still, the increase in the energy gain in clustered landscapes would depend on the size and number of prey-rich clusters in the landscape. Hence, landscapes with a random prey distribution could still prove to be better foraging grounds than landscapes where prey is only present in few small and widely scattered clusters (Santos 2009). Finally, waders respond to social information from con- and heterospecifics. Bar-tailed Godwits (*Limosa lapponica*), for example, typically forage in flocks, as opposed to Common Redshanks that avoid patches where conspecifics had fed before to maintain higher intake rates (Yates *et al.* 2000). Accounting for social interactions is especially important for modelling the habitat use based on resource distribution patterns for wader species that are sensitive to interference (Folmer *et al.* 2010, Oudman *et al.* 2018).

Conclusion

By integrating existing knowledge about energetic trade-offs in waders, we simulated the foraging performance of two different wader phenotypes to explore in which types of resource landscapes they could obtain the highest energy gains and persist the longest. Similar tests in the field with real wader populations would be logistically unfeasible. Despite the simplified behaviour of virtual birds and resource landscapes, the model provides support for the idea that the suitability of mudflats as foraging areas for different waders depends on the spatial clustering of prey. Thanks to their ability to catch larger prey and their more modest energetic requirements, larger longer-billed waders could remain foraging for longer periods than smaller, short-billed birds. The latter, however, were less sensitive to the spatial distribution of prey.

As an extension of our approach, it would be interesting to incorporate changes in the energy budget of individual waders over longer temporal scales (*e.g.* daily or weekly time allocation to foraging) and over larger spatial scales (*e.g.* relocation between distinct foraging areas). This may help explain why certain resource landscapes are more suitable than others for breeding, migrating, and wintering waders. Such insights can help to identify which sets of morphological features and behaviours are advantageous during certain circumstances and resulted in the emergence of different adaptive peaks in waders.

Technological advances for close observation of the wader's foraging behaviour by video recording (Touhami *et al.* 2020) as well as their movement and activity patterns by fine-scale GPS and accelerometer logging (Schwemmer *et al.* 2016, van der Kolk *et al.* 2020) provide a promising avenue for calibrating and refining foraging models. Because benthic surveys are time-consuming and birds do not necessarily select those areas where prey is most abundant or of the highest quality (Zwarts & Wanink 1993), modelling approaches such as ours could help assess which wetland areas could be most profitable for different types of foraging waders.

Acknowledgements

E.D. was funded by the Research Foundation – Flanders (FWO), grant number 11ZH518N. B.V.S. acknowledges support from ResPond: a Biodiversa+, Joint Programming Initiative ERA-NET-Cofund (European Research Network- Cofund) BiodivRestore project, www.respond.eu. All authors kindly thank the editors and two anonymous reviewers for their constructive feedback which helped us improve the manuscript.

Conflict of interest statement

The authors declare that there is no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Figures

Figure 1

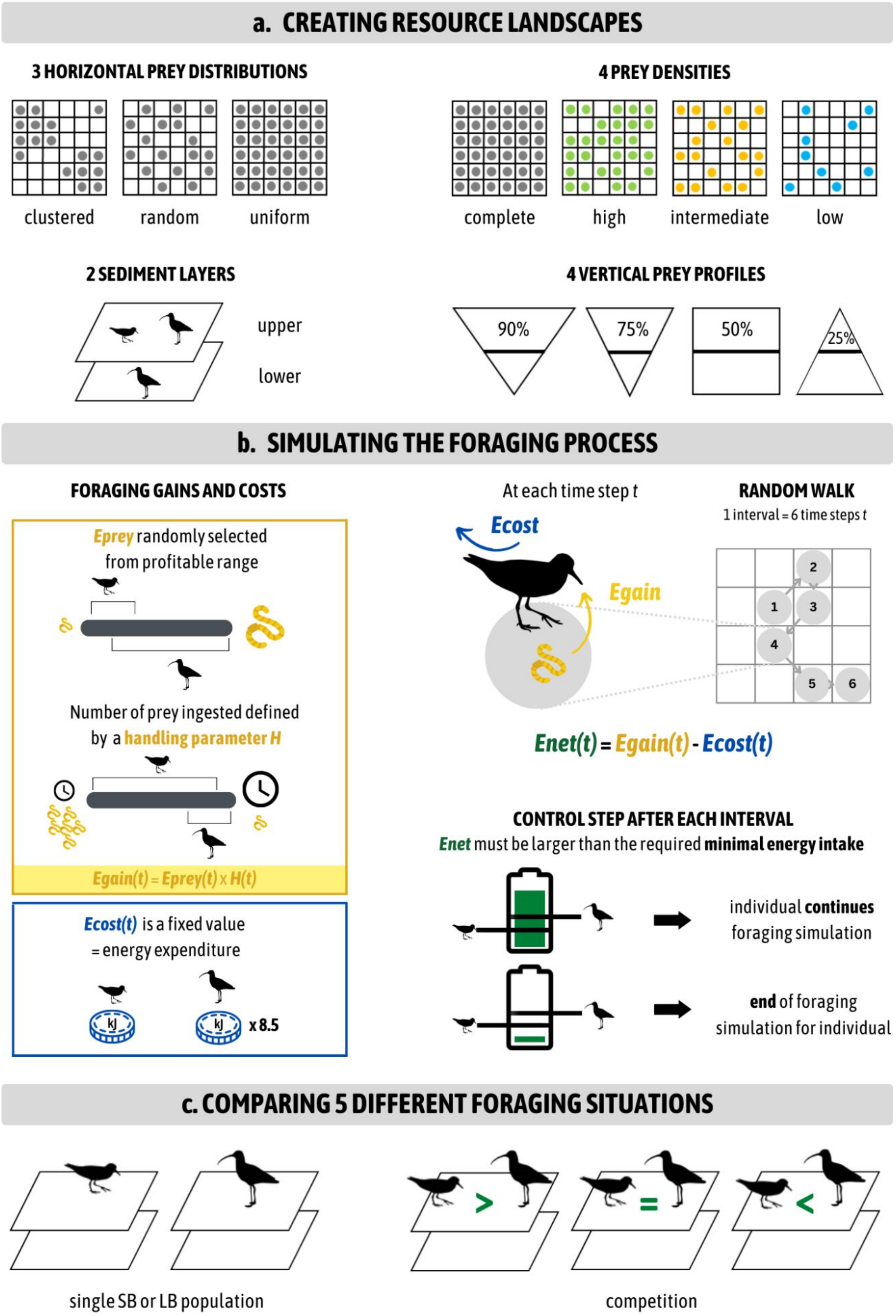

Figure 1 The effect of different spatial resource distributions on the foraging performance of short- (SB) and long-billed (LB) waders is simulated by first **(a) creating different types of resource landscapes**. Filled circles indicate grid cells occupied by prey. Prey, under the form of energy units (kJ), is ***horizontally distributed*** across the landscape in a clustered, random, or uniform pattern, at *4*

different densities where prey is present in 25 % (low, blue), 50 % (intermediate, yellow), 75 % (high, green), or 100 % (complete cover, grey) of all grid cells (Supporting Information Table S1). The sediment consists of ***two layers***, of which the upper layer is accessible to both SBs and LBs. Prey from the lower layer can only be taken by LBs. At the start of each simulation, prey distribution is identical in both layers. Prey density, however, may vary between the upper and lower layer to assess the effect of ***vertical variation in resource availability*** on the waders' foraging performance. The percentage of the total energy at a grid cell present in the upper layer is here set to 90, 75, 50 or 25 %. Different resource landscapes are then used in **(b) foraging simulations**, which are sequences of 60 time steps. At each time step ***t***, an individual obtains energy if it is located on a grid cell that contains prey. The **energy from prey** (***Eprey***) is multiplied by **handling parameter *H***, which corresponds to how many prey items birds can consume within one time step. The net energy gain ***Enet*** is obtained by subtracting the fixed searching cost ***Ecost*** from the energy gain ***Egain***, with ***Ecost*** 8.5 times larger for LBs than for SBs . After every interval of six time steps, the sum of the net energy gains is compared to a minimal energy intake threshold (Supporting Information Table S2), to decide whether the wader can continue foraging or not. Finally, simulations are repeated for **(c) five different foraging situations**: only SBs or LBs forage in the landscape in situations without competition ('single-species model'), or both species forage alongside each other ('competition model'), mimicking exploitative and interference competition. Three variants of competitive simulations exist: either SBs or LBs have a higher chance of chasing away the other wader species (' > ' or ' < '), or the probability of chasing away a heterospecific individual is equal for both species (' = ').

Figure 2

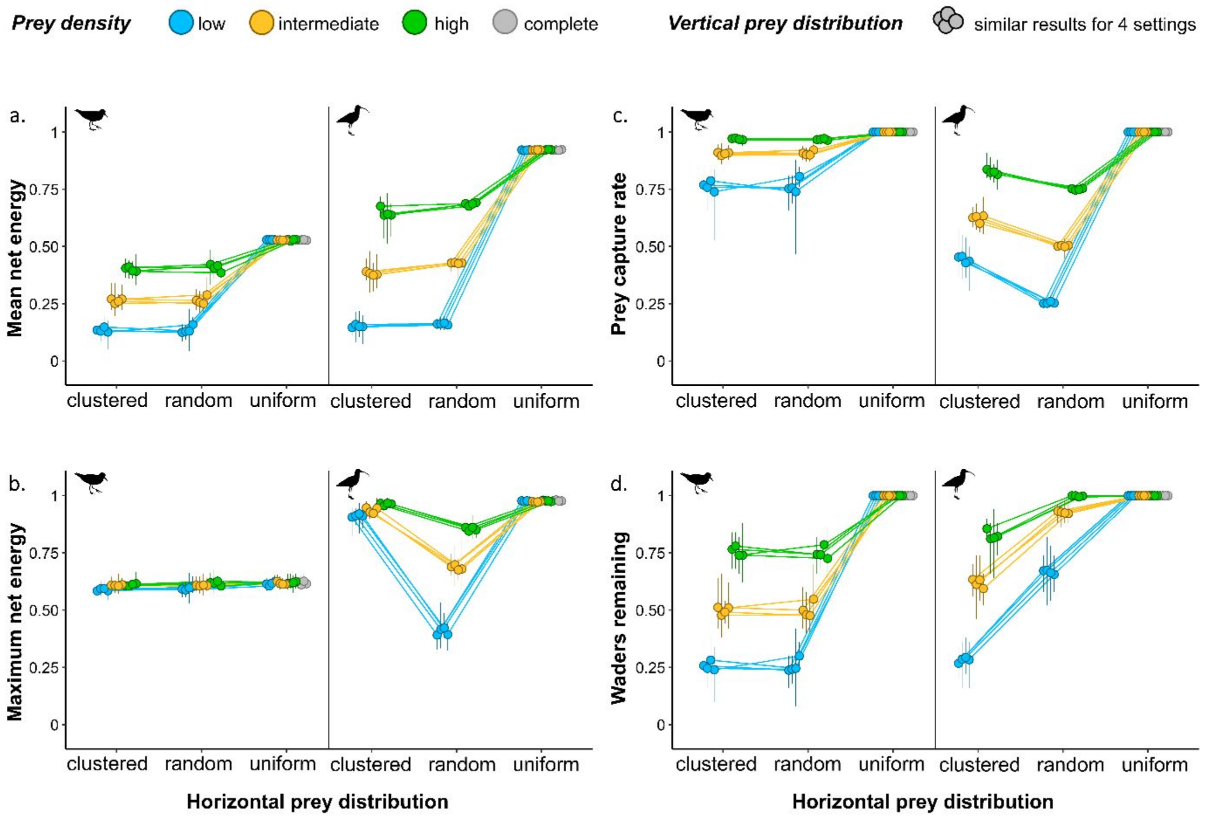

Figure 2 Impact of **horizontal prey distribution** and **prey density** on the foraging performance of short-billed (SB) and long-billed (LB) waders in single-species simulations, calculated by four different metrics: (a) **mean** and (b) **maximum net energy** gained by individuals ($E_{net,i}$), both expressed as the percentage of the maximum gross net energy intake of a SB or LB individual, (c) the **prey capture rate**, indicating during how many time steps waders caught prey in comparison to the total number of cells they visited in the foraging landscape, and (d) the **waders remaining** in the foraging landscape, which is calculated as the proportion of the initial population (50 individuals) that continue foraging until the end of the simulation. Mean energy gains (a), prey capture rates (c), and population size (d) are averaged across 10 replicates performed in each type of foraging landscape. For these foraging metrics (a,c,d), error bars indicate the minimum and maximum value obtained by individuals of the SB or LB populations. Results for different prey densities are visualised in different colours: low (blue), intermediate (yellow), and high prey density (green), and complete prey cover (grey). For each combination of prey density (low, intermediate, high, complete) and horizontal distribution pattern (clustered, random, uniform), the four circles that are placed closely together represent different **vertical prey distribution** settings.

Figure 3

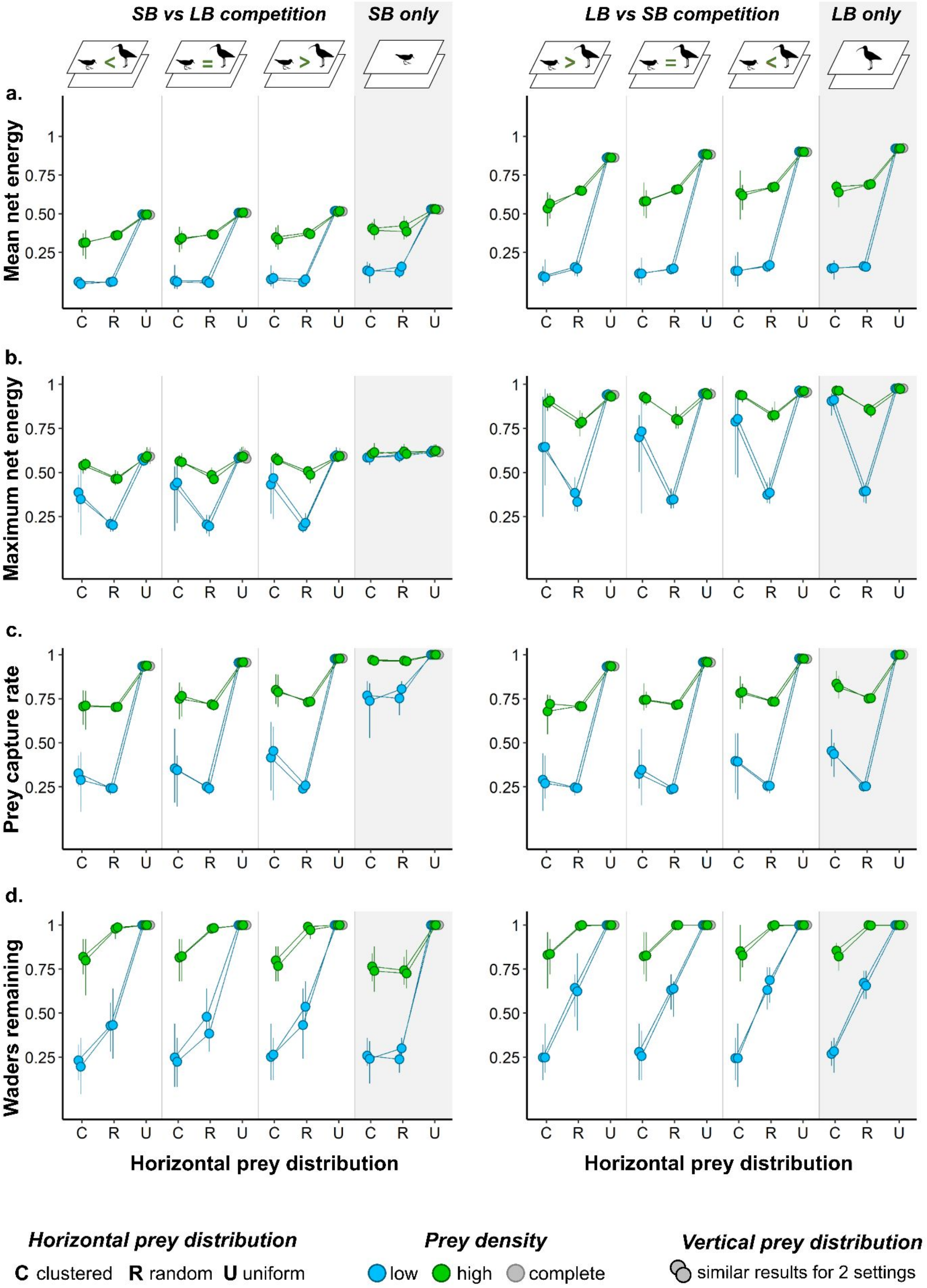
SB vs LB competition
SB only
LB vs SB competition
LB only
<
=
>
a.
Mean net energy
b.
Maximum net energy
c.
Prey capture rate
d.
Waders remaining
1
0.75
0.50
0.25
C R U
Horizontal prey distribution
Horizontal prey distribution
C clustered R random U uniform
Prey density
low high complete
Vertical prey distribution
similar results for 2 settings

Figure 3 Impact of interspecific competition on the foraging performance of short-billed (SB) and long-billed (LB) waders, calculated by four different measures: (a) **mean** and (b) **maximum net energy** gain ($E_{net,i}$), both expressed as the percentage of the maximum gross net energy intake of a SB or LB individual, (c) **prey capture rate**, indicating during how many time steps waders caught prey in comparison to the total number of cells they visited in the foraging landscape, and (d) SB (left) and LB (right) **waders remaining**, calculated as the proportion of the initial population that continues foraging until the end of the simulation. Results are visualised as a function of horizontal prey distribution patterns, with C = clustered, R = random and U = uniform. For competition simulations, individuals had a 25% ('loses'), 50% ('neutral') or 75% ('wins') chance of chasing away a heterotypic individual when competing for the same grid cell location. As a reference, results for simulations without competition are added as the rightmost side for panels of both wader populations, shaded in grey. Simulations were performed for the lowest (blue) and highest (high: green; complete: grey) prey densities, and for landscapes in which the upper layer contained 25% or 90% % of the total available prey. For each combination of prey density and horizontal distribution pattern, the two symbols that are placed closely together represent these two **vertical prey distributions**. Based on simulations where waders were foraging in absence of individuals of the other species (**Figure 2**), results are expected to be similar for landscapes with intermediate prey density and 50% or 75% of available prey residing in the upper layer. Error bars indicate the minimum and maximum values of each foraging metric for 10 replicate simulations in each landscape type.

Tables

Table 1 Overview of model parameters, their definition, and selected values for this study. Parameters that are related to the one that is discussed are indicated in bold. Details and calculations can be consulted in Tables S2 & S3.

Parameter	Definition	Values
Area (m²)	Surface area of the foraging landscape	20 cells × 20 cells = 400 m²
Time step	Smallest time unit considered for all simulations. Within one time step, all individuals perform a set of activities based on the model's rules defined for foraging and moving through the landscape.	5 seconds
Total simulation time	Duration of the simulation after which foraging performance is evaluated. Here, each simulation consists of 60 time steps.	300 seconds = 5 minutes
Control step	After each set of six time steps, those individuals are removed from the landscape that failed to gain a **minimum amount of energy** from prey.	30 seconds
Minimal energy intake (kJ)	Energy birds must ingest within one time step to remain foraging in the landscape, required for maintaining metabolism and performing activities (foraging).	SB: 0.015 kJ LB: 0.283 kJ
Lean body mass *LBM* (g)	Average body mass of an individual wader excluding fat reserves. LBM is used to determine the **minimum intake rate** and the **searching cost** of both wader species (Davidson 1983).	LBM_{SB} = 40.07 g LBM_{LB} = 870.98 g
Energy gain from prey E_{gain} (kJ)	The energy acquired by an individual bird when taking prey from the sediment within one time step. The **maximum gross energy intake** is set as the upper limit of consumption by waders (Kersten & Piersma 1987, Zwarts & Wanink 1993, Kvist & Lindstrom 2003).	$E_{gain,SB}$ = 0 to 0.2 kJ $E_{gain,LB}$ = 0 to 3.3 kJ
Prey handling parameter *H* (number of prey per time step)	Parameter correcting for the time required for a wader to recognise, capture, lift, handle, and swallow a prey, and move its bill downward again to continue foraging. It is equal to the amount of prey that can be caught and ingested by waders within one **time step** (Zwarts & Esselink 1989, Zwarts & Wanink 1993).	$H_{SB,\ small}$ = 7.5 (prey ≤ 50 mm) $H_{SB,\ large}$ = 2.5 (prey > 50 mm) $H_{LB,\ peck}$ = 2.2 $H_{LB,\ probe}$ = 0.625

Searching cost E_{cost} (kJ)	Energy expenditure of waders when moving from the midpoint of a grid cell to the midpoint of a vacant adjacent grid cell, for one **time step**. Based on the metabolic rate for the general locomotion of birds (Taylor *et al.* 1982), for waders moving through the landscape at a speed of 0.2 m•s^{-1} (Dias *et al.* 2009).	$E_{cost,SB} = 0.00439$ kJ $E_{cost,LB} = 0.03712$ kJ
Peck-to-probe rate	Preference of LBs for pecking, *i.e.* how likely an LB will peck instead of probe (Navedo & Masero 2008)	0.70
Interference	Probability that an LB can chase away an SB from its location when individuals are placed in the landscape, or when they move while foraging. After being chased, an individual can return to the landscape in the next **time step**. Only applies to the competition mode.	0.25, 0.50, 0.75
Population size	Number of individuals of an SB or LB population present in the landscape for a certain time step.	Single-species: 50 SBs or 50 LBs Competition: 25 SBs and 25 LBs

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Relationship between mean body mass (in g, sqrt-transformed) and mean bill length (mm) of 35 wader species.

Figure S2. Number of SB (top) and LB (bottom) waders remaining in the landscape during single species simulations (without interspecific competition).

Figure S3. Mean and maximum individual energy gain, prey capture rate and the number of waders remaining until the end of the simulation.

Table S1. Calculation of prey density for generating different types of foraging landscapes.

Table S2. Overview of energetic and foraging parameters characterising the two species of waders.

Table S3. Biomass, length (size) and energetic content of macroinvertebrate prey that both waders feed on.

Table S4. Summary of foraging scenarios that have been simulated.

Table S5. Calculation of maximum net individual energy gain for both species of foraging waders.

Table S6. Overview of simulations performed for assessing the foraging model's sensitivity to parameter variation.

Table S7. Minimum and maximum proportion of energy from prey that is taken from the upper sediment layer compared to the total net energy gain of individual longer-billed waders.

Table S8. Minimum and maximum proportion of energy from prey that is taken from the upper sediment layer compared to the total net energy gain of individual longer-billed waders.