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FORAGING IN A TIDALLY STRUCTURED ENVIRONMENT BY RED KNOTS (*CALIDRIS CANUTUS*): IDEAL, BUT NOT FREE

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Abstract. Besides the “normal” challenge of obtaining adequate intake rates in a patchy and dangerous world, shorebirds foraging in intertidal habitats face additional environmental hurdles. The tide forces them to commute between a roosting site and feeding grounds, twice a day. Moreover, because intertidal food patches are not all available at the same time, shorebirds should follow itineraries along the best patches available at a given time. Finally, shorebirds need additional energy stores in order to survive unpredictable periods of bad weather, during which food patches are covered by extreme tides. In order to model such tide-specific decisions, we applied stochastic dynamic programming in a spatially explicit context. Two assumptions were varied, leading to four models. First, birds had either perfect (ideal) or no (non-ideal) information about the intake rate at each site. Second, traveling between sites was either for free or incurred time and energy costs (non-free). Predictions were generated for three aspects of foraging: area use, foraging routines, and energy stores. In general, non-ideal foragers should feed most intensely and should maintain low energy stores. If traveling for such birds is free, they should feed at a random site; otherwise, they should feed close to their roost. Ideal foragers should concentrate their feeding around low tide (especially when free) and should maintain larger energy stores (especially when non-free). If traveling for such birds is free, they should feed at the site offering the highest intake rate; otherwise, they should trade off travel costs and intake rate. Models were parameterized for Red Knots (*Calidris canutus*) living in the Dutch Wadden Sea in late summer, an area for which detailed, spatially explicit data on prey densities and tidal heights are available. Observations of radio-marked knots (area use) and unmarked knots (foraging routines, energy stores) showed the closest match with the ideal/non-free model. We conclude that knots make state-dependent decisions by trading off starvation against foraging-associated risks, including predation. Presumably, knots share public information about resource quality that enables them to behave in a more or less ideal manner. We suggest that our modeling approach may be applicable in other systems where resources fluctuate in space and time.

Key words: *Calidris canutus*; daily routine; foraging; patch use; Red Knot; state-dependent decisions; stochastic dynamic programming; tidal regime; Wadden Sea.

INTRODUCTION

Resources are usually patchily distributed in space (Levin 1992, Wiens 2000). This poses a real challenge for foragers to exploit them effectively. For example, a forager that is uncertain about the quality of the patch that it is currently exploiting either risks the penalty of spending too *much* time in it, or the penalty of spending too *little* time in it (Oaten 1977, McNamara 1982, Olsson and Holmgren 1998, van Gils et al. 2003b). Alternatively, a forager may be fully informed about the quality of the current patch (prescience; Valone and Brown 1989), but may lack information about the

quality of alternative patches in its environment. For reasons of simplicity, many models of forager distributions have assumed so-called “ideal” foragers, i.e., foragers that are omniscient with respect to the quality of *each* patch in their environment, which enables them “to choose the patch that maximizes their fitness” (sensu Fretwell and Lucas 1970). As a further simplification, these models assume “free” traveling between patches (in terms of time and energy); hence, the name “ideal, free models” (Fretwell and Lucas 1970). In a world that is inherently dynamic and unpredictable, these models may be oversimplified; nevertheless, they have generated a wealth of empirical and theoretical studies that have brought the science of distributional ecology leaps forward (Tregenza 1995).

Apart from informational and travel constraints, foragers in a patchy world still bear other problems. Since the best food patches usually attract the most foragers, such patches will in turn attract the most

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predators, leading to trade-offs between energy gain and the avoidance of, respectively, interference competition and predation (Lima and Dill 1990). Moreover, the best solution today might not be the best solution tomorrow, as optimal solutions are usually state dependent and, therefore, vary with, for example, energy stores (Olsson et al. 2002, Lendvai et al. 2004).

On top of these environmental hurdles, shorebirds living in intertidal habitats face additional restrictions. Their feeding grounds are only available during low tide (occurring twice per day, for ~12 hours per day, in most parts of the world; Piersma et al. 2005). Therefore, time and energy costs need to be paid to travel, twice per day, to and from the high-tide roost. Moreover, due to spatial heterogeneity in elevation of sites and timing of low water, not all food patches will be available at the same time (van Gils et al. 2005b). In order to obtain adequate amounts of food, intertidal foragers should, therefore, follow itineraries along the best patches available at a given time (Connors et al. 1981, van Gils et al. 2004, 2005b). Finally, shorebirds need additional energy stores in order to survive unpredictable periods of bad weather, for example, series of stormy days during which food patches are covered by extreme tides (Zwarts et al. 1996).

Among shorebirds, the Red Knot (*Calidris canutus*; henceforth called knot) typically faces all these problems and is also a suitable species to study at the individual level. Knots mainly feed on mollusks (Prater 1972, Zwarts and Blomert 1992, Piersma et al. 1993a, van Gils et al. 2003a), whose abundance and availability are quantified relatively easily because of their immobility (Piersma et al. 1993a, Zwarts and Wanink 1993, Goss-Custard et al. 2001, Wanink and Zwarts 2001). The relative ease with which knots can be kept in captivity has enabled us to quantify their functional responses (Piersma et al. 1995), information use (van Gils et al. 2003b), digestive processing capacity (van Gils et al. 2003a) and energetic costs of foraging (Piersma et al. 2003a), locomotion (Bruinzeel et al. 1999, Kvist et al. 2001), and thermoregulation (Wiersma and Piersma 1994, Bruinzeel and Piersma 1998). In addition, free-living individual knots roaming through vast intertidal areas can be successfully tracked using radiotelemetry, especially through the use of arrays of automated receiving stations (van Gils and Piersma 1999, Nebel et al. 2000, van Gils et al. 2000, Battley et al. 2004, Leyrer et al. 2006, Rogers et al. 2006).

Using this extensive database, we predicted and analyzed how knots cope with spatial and tidally caused temporal variability in food abundance in the western Dutch Wadden Sea in terms of area use, foraging routines (i.e., intensity of foraging), and energy storage. In order to capture the dynamic nature of these factors, we constructed spatially explicit, stochastic dynamic programming models (SDP; Houston and McNamara 1999, Clark and Mangel 2000). The main input values were energy intake rates per site, calculated by using

empirically derived functional responses and fine-scale measurements on prey densities and prey qualities. We varied two assumptions, leading to four models. First, birds had either perfect (ideal) or no (non-ideal) information about the intake rate at each site. Second, traveling between sites was either for free or incurred time and energy costs (non-free). Predictions were tested using data on radio-marked birds (area use) and unmarked birds (foraging routines, energy stores). By focusing on the *islandica* subspecies (Piersma and Davidson 1992) at the onset of its overwintering period in Northwest Europe (late July and August), we ensured that preparations for reproduction or long-distance migrations could be ignored, which makes survival rate a realistic currency to model.

MATERIAL AND METHODS

Spatial distribution of the prey

Each year from 1996 to 2000, during late July and August, prey densities in the western Dutch Wadden Sea (53°14' N, 05°11' E; Fig. 1A) were sampled at fixed stations in a grid, with grid intersections at 250-m intervals (Fig. 2). In selected sites (bordered by thick straight lines in Figs. 1 and 2, which excludes stations sampled in the most recent years only), an average of 1880 stations were sampled yearly. Stations were located using handheld GPS devices (Garmin 45; Garmin Corporation, Lenexa, Kansas, USA). At each station, one sediment core (1/56 m²) was taken to a depth of 20 cm. In order to distinguish accessible from inaccessible prey (knots have bills of 3–4 cm), a top layer (0–4 cm) was separated from a bottom layer (4–20 cm), and both layers were subsequently sieved over a 1-mm mesh. Mudsails (*Hydrobia ulvae*) were sampled by sieving smaller cores (1/267 m²) over a finer mesh (0.5 mm). All potential prey items (mollusks, crustaceans) that remained on the sieve were frozen for later analysis.

Prey were considered available when they were both accessible and ingestible (Zwarts and Wanink 1993). We therefore distinguished ingestible prey from prey too large to be swallowed by identifying each prey item with respect to species and size (to nearest mm or, in the case of *H. ulvae*, to nearest 0.5 mm). Maximally ingestible lengths were taken from Piersma et al. (1993a) and Zwarts and Blomert (1992). Metabolizable energy content and amount of indigestible ballast mass were determined by removing soft, fleshy parts from indigestible shell material, drying both flesh and shell to constant mass for 3 d in a ventilated oven at 55°–60°C, and weighing shell mass using an electronic balance (to nearest 0.1 mg). Subsequently, dried flesh was incinerated at 550°C for 2 h, after which flesh ash-free dry mass (AFDM_{flesh}) was determined (to nearest 0.1 mg). Metabolizable energy content was calculated as AFDM_{flesh} × energetic density × assimilation efficiency; the latter two were assumed to be constant with values of, respectively, 22 kJ/g AFDM_{flesh} (Zwarts and Wanink 1993) and 0.725 (Piersma 1994). As soft parts could not be separated from hard parts in the

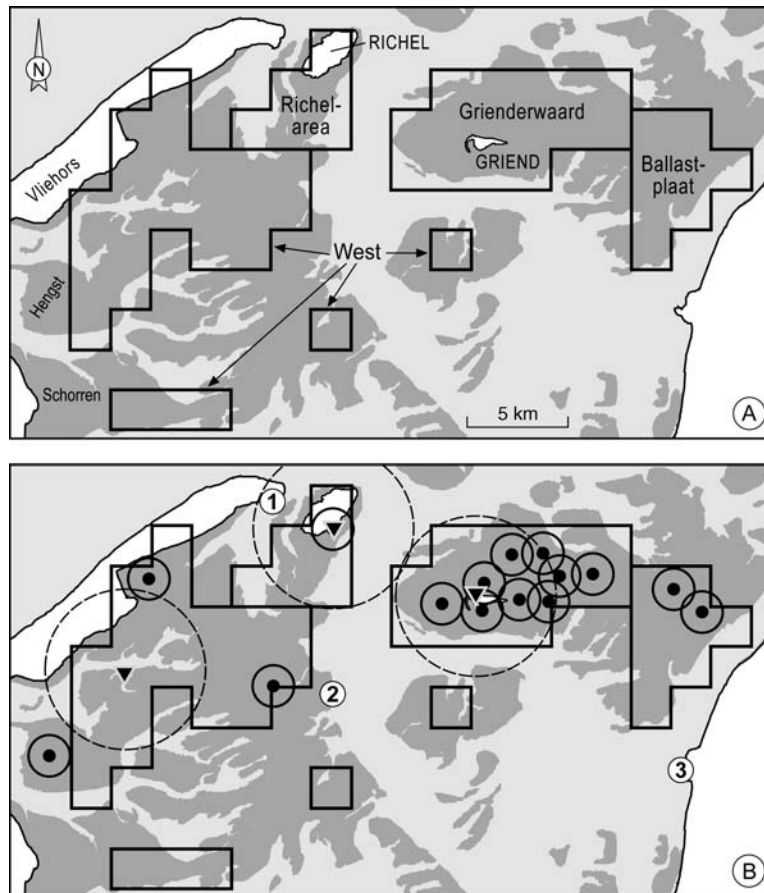


FIG. 1. Maps of the study area, the western Dutch Wadden Sea, The Netherlands. (A) Thick-lined areas border the four areas in which prey were sampled yearly (Richel-area, "West," Grienderwaard, and Ballastplaat). Main roosts are shown (Schorren, Hengst, Vliehors, Richel, and Griend) with the most frequently used roosts considered in the models (Richel and Griend) written in capitals. (B) Position and detection range of radio receivers, shown by solid dots encircled by solid-lined circles (automated systems) or by triangles encircled by dashed-lined circles (handheld systems; the most westerly positioned triangle represents the mobile handheld station at RV *Navicula*). Numbered circles give positions of tidal-height recording stations: 1, Vlieland Harbor; 2, Inschot; 3, Harlingen; the fourth station, West-Terschelling, is north of Griend, just beyond the scale of the map. White areas indicate land, light gray areas indicate water, and dark gray areas indicate mudflat exposed at low tide.

case of non-bivalve species, we determined dry mass and ash-free dry mass of entire specimens and assumed that 12.5% of organic matter resides in the hard parts of *H. ulvae* (Dekker 1979) and 30% in those of crustaceans (Zwarts and Blomert 1990). See Piersma et al. (1993a, 2001) for more details on our benthic-sampling program.

From prey densities to energy-intake rate predictions

Using a multiple prey species functional response, the energy intake rate was predicted from measured available prey density for each year and each fixed station in the 250-m grid. The applied functional response was based on the rate-maximizing prey selection model by Hirakawa (1995), who generalized the classical "prey model" (Pulliam 1974, Charnov 1976) for situations in which rates of ballast intake are subject to a digestive constraint. Whether a prey type is included in the diet not only depends on its energy content and required handling time (profitability; classical model),

but also on its amount of ballast mass. Due to their habit of ingesting and processing their bulky bivalve prey whole (Piersma et al. 1993b), this model explained diet choice in knots significantly better than the classical prey selection model (van Gils et al. 2005c).

Functional response parameters were based on observed values. Search efficiency was set at $5 \text{ cm}^2/\text{s}$ (Piersma et al. 1995). Size-specific handling times for *Carcinus maenas*, *Crangon crangon*, and *Hydrobia ulvae* were taken from van Gils et al. (2005c), and those for *Macoma balthica* and *Cerastoderma edule* were taken from Piersma et al. (1995). Handling Gammaridae was assumed to be similar to handling *C. crangon*, while handling relatively rare bivalve species (*Abra tenuis*, *Ensis directus*, *Mya arenaria*, *Mytilus edulis*, and *Tellina tenuis*) was assumed to take as long as handling *M. balthica*. Since knots handle their prey quickly relative to rates of finding and internal processing, the predicted intake rate is rather insensitive to natural variations in

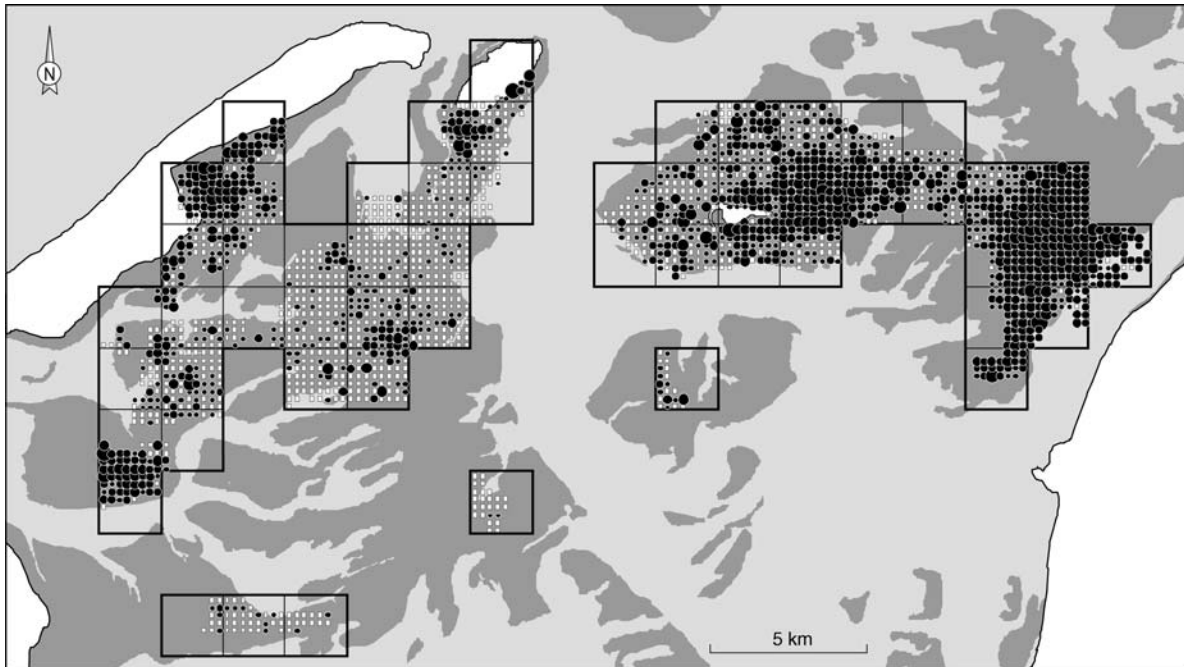


FIG. 2. All prey sampling stations (250-m grid), shown by small symbols, are scaled to predicted intake rate averaged across all years (intake rate is zero for open symbols; note that in the models, we used year-specific values rather than these averages). In the models, sample stations were grouped into 55 blocks of 2×2 km, shown by the larger squares. See Fig. 1 for an explanation of white and shaded areas.

handling time (van Gils et al. 2005c). Upper rate of processing ballast material (mostly shell mass) was set at 1.83 mg/s, a value specific for knots with the average and most frequent fresh gizzard mass of 6 g (van Gils et al. 2003a). Besides this gizzard size-related constraint on the rates of shell crushing, rates of energy intake were subject to an additional constraint on rates of digestion in the gut as measured by Kvist and Lindström (2003), which we modeled according to Piersma et al. 2003a, van Gils et al. 2003a, 2005a. Birds that hit this constraint are forced to take digestive breaks such that the intake rate over total time equals the upper rate of flesh digestion (McNamara and Houston 1997, van Gils et al. 2003b).

The stochastic dynamic programming models

Four stochastic dynamic programming (SDP) models were constructed. (1) In the so-called non-ideal/non-free model, we assumed that the birds expected the same intake rate at each site, which represented the year-specific average across the entire study area. Even though they would *obtain* the actual intake rate that we predicted for each site, these model birds were assumed to be unable to collect and store this information (non-ideal). Furthermore, traveling (i.e., flying) between sites incurred time and energy costs (non-free; see Appendix A for detailed calculations of these costs). (2) The so-called non-ideal/free model differs from the first model in the sense that traveling between sites was for free, both energetically and in time.

(3) In the ideal/non-free model, the birds had perfect knowledge about the intake rate for each site (ideal) but paid for traveling (non-free). (4) Finally, the ideal/free model differs from the latter model in the sense that traveling was for free.

To economize on computing time, fixed stations in the 250-m grid were grouped into 55 blocks of 2×2 km (Fig. 2). Such 4-km² blocks contained 7–64 stations per year. The minimum of seven samples per block yielded standard errors in prey density estimates of $\leq 30\%$ of the mean (Piersma et al. 1993a). The 55 blocks formed the spatial units in our stochastic dynamic programming models. Predicted energy intake rate in each block was (1) year specific, (2) constant within a season (i.e., we assumed no seasonal depletion, which seems not unrealistic given that available prey densities at the applied scale tend to decline slowly [M. van der Geest, *unpublished manuscript*] and given the relatively short two-month period that we modeled), and (3) constant throughout the tidal cycle (J. A. van Gils and A. Brans, *unpublished data*).

A block could be available (exposed during low tide) or unavailable (inundated during high tide) for foraging. For each time step in the models (50-min intervals), availability was calculated for each block using measured elevation (-45 ± 78 cm [mean \pm SD]; fine-scaled data collected and interpolated in a 20-m grid by the National Institute for Coastal and Marine Management [RIKZ], The Netherlands, in 1992–1999; relative to

Normaal Amsterdams Peil [NAP]) in comparison with empirical measurements of water height (3 ± 62 cm relative to NAP). Water heights were measured automatically at regular 10-min intervals at four different stations (Inschot, Harlingen, Vlieland Harbor, and West-Terschelling; Fig. 1B; Data Opslag Natte Rijkswaterstaat [DONAR, *available online*]),⁴ of which we used the nearest station per block.

In each model, five different types of tidal cycles, w , occurred, each with a different probability P_w (Appendix B, Fig. B1). The values of P_w were based on the frequency distribution of tidal cycle types observed during late summer 2000 (DONAR). They were 10% for very good tides (many blocks available for feeding; $w = 1$, represented by neap tide observed at 26 August 2000, wind force 4 Bft [Beaufort scale] from east-southeast direction), 35% for good tides ($w = 2$; neap tide at 12 August 2000, 2 Bft north-northeast), 30% for intermediate tides ($w = 3$; 10 August 2000, 4 Bft west), 20% for poor tides ($w = 4$; spring tide at 8 September 2000, 3 Bft west-southwest), and 5% for very poor tides ($w = 5$; spring tide at 6 September 2000, 5 Bft west-southwest). We assumed that all foragers (also those in the two non-ideal models) knew (1) the values of P_w , (2) the current cycle's type (w), and (3) the availability of each block throughout the cycle for each type (w). However, due to unpredictable wind effects overriding the astronomical tide effects, the value of w in future cycles behaved stochastically and, therefore, birds did not know it for future cycles (see Zwarts et al. 1996).

For all tidal cycles, availability was set to 0 for all 55 blocks during a cycle's final time step (Appendix B, Fig. B1). Availability of the roost was set to 1 in all time steps. This forced foragers to roost at least during a cycle's final time step, while they *could* go to roost as early as they "liked." The roost was located either at Richel or at Griend (Fig. 1A), which are the most used roosts in the western Wadden Sea (Piersma et al. 1993a). For reasons of simplicity, model birds did not switch roosts.

We modeled fitness-maximizing foragers, where fitness was defined as the probability of surviving until some defined final time. Mortality occurred either through starvation or predation. In this sense, our models are similar to so-called "small-bird-in-winter" models (Houston and McNamara 1999, Pravosudov and Lucas 2001), and seem appropriate for *islandica* knots at the beginning of their nonbreeding period in late summer (August-September). Starvation occurs when energy stores, x , reach critical level X_{crit} . This parameter therefore played a prominent role in the model: At all times, the animal should try to avoid reaching X_{crit} . Energy stores varied from 0 g ($=X_{\text{crit}}$) to 100 g (Piersma et al. 2005), in discrete steps of 5 g. We assumed that foraging incurs a higher risk of predation than non-foraging activities, which is based on obser-

vations showing that feeding knots are more frequently disturbed by raptors than roosting knots (when expressed per individual bird; B. Spaans, *personal observation*; see also work by Hilton et al. [1999] showing that Redshanks (*Tringa totanus*) on attack by an avian predator had slower escape-flight response when their head was down compared to when their head was up). As we have no actual data on risks of predation, we performed sensitivity analyses (presented in Tables 1-3) in which we varied the risk of predation (in steps of one order of magnitude) during foraging (10^{-2} - 10^{-6} per single time step) and during non-foraging activities (i.e., resting or flying; 10^{-3} - 10^{-6} per single time step). This range in risk of predation covers the range observed in knots (P. J. van den Hout and T. Piersma, *unpublished data*) and in other shorebirds (notably Redshanks; Cresswell 1994, Whitfield 2003).

Time proceeded in discrete steps of 50 minutes. As tidal cycles last 12.5 hours, they were made up of 15 such time steps ($t = 1 \dots T$, where $T = 15 =$ high tide; t will be referred to as "tidal time"). We considered a sequence of 120 tidal cycles (i.e., approximately two months), and used d to indicate cycle number ($d = 1 \dots D$, where $D = 120$). At each time step, the forager makes two "sequential decisions" (Clark and Mangel 2000). At the onset of a time step, it decides whether it will feed or rest, at the end of a time step it decides which 4-km² block to go to next. Which action is optimal, i.e., which action maximizes the chance of surviving until the final time, depends on the actions taken in the future; this problem should therefore be solved using dynamic programming by working backwards in time (Houston and McNamara 1999, Clark and Mangel 2000). We therefore started with the final time step in the whole sequence, where $t = T$ and $d = D$. Obviously, the chance of surviving until the final time, at the final time, equals 1 for all individuals that have energy stores $x > X_{\text{crit}}$. Thus, the so-called "terminal reward function" is given by

$$F(x, s, D_w, T) = 1 \quad \text{for } x > X_{\text{crit}} \quad (1a)$$

$$F(x, s, D_w, T) = 0 \quad \text{for } x = X_{\text{crit}} \quad (1b)$$

where s indicates the bird's location (which is at the roost for $t = T$) and subscript w indicates the type of tidal cycle $d = D$ ($w = 1 \dots 5$; see Appendix B: Fig. B1). The chance of surviving until the final time for all other time steps t at d_w is the maximum of the survival chance until final time of all possible actions taken at t at d_w , assuming that the animal behaves optimally from $t + 1$ at d_w onward (i.e., assuming that from that moment onward, it always selects the option yielding the maximum survival chance; note that this is an assumption made in all dynamic programming models; Houston and McNamara 1999, Clark and Mangel 2000):

$$F(x, s, d_w, t) = \max_{i,k} V_{ik}(x, s, d_w, t) \quad (2)$$

⁴(<http://www.waterbase.nl>)

where

$$V_{ik}(x, s, d_w, t) = (1 - \mu_{is})F(x + \Delta x, s', d_w, t + 1). \quad (3)$$

In these equations, V_{ik} indicates the survival chance (until final time) of actions i (feed or rest) and k (block to go to for the next time step). These two actions lead to a change in energy stores by Δx (Appendix A) and a new location s' at the next time step ($d_w, t + 1$), contingent on the probability of not being taken by a predator ($1 - \mu_{is}$) during the current time step (d_w, t). In order to make $x + \Delta x$ discrete, we used linear interpolation (Clark and Mangel 2000). As predation risk differs between foraging and non-foraging, risk of predation μ_{is} over a full time step obviously depends on the time spent actively feeding. Therefore, μ_{is} depends on whether the bird chooses to feed or rest (indicated by i). Through foraging time loss to digestive breaks (during which non-foraging predation risks apply), μ_{is} also depends on where the bird currently is (indicated by s ; see Appendix C for a graphical explanation).

Note that V_{ik} at the last time step $t = T$ in tidal cycle d is "sequentially coupled" (Clark and Mangel 2000) to the first time step $t = 1$ in the next tidal cycle $d + 1$. As the value of w (cycle type from 1 ... 5) of cycle $d + 1$ is a stochastic variable, V_{ik} at $t = T$ is calculated for each value of w , and subsequently averaged across all values of w (weighted for the probability P_w of occurrence of w):

$$V_{ik}(x, s, d_w, T) = \sum_{w=1}^5 p_w (1 - \mu_{is})F(x + \Delta x, s', d_w + 1, 1). \quad (4)$$

Because of this stochasticity in feeding opportunities generated by uncertainty about the types of cycles to expect in the future, our models show strong backward convergence (Houston and McNamara 1999). This means that survival probability as a function of both states (energy stores and current location) becomes independent of the terminal reward initially assumed (Eq. 1) at times well before the final time ($d \ll D$). In other words, no matter what terminal reward is assumed, the predictions of the models will always be the same at times well before the final time. We checked this by varying the terminal reward and found that 50–60 tidal cycles are enough to generate convergence (tested over 1000 cycles). For this reason, we selected the first 60 cycles (i.e., $d = 1 \dots 60$) when analyzing the results from the forward simulations, which corresponds with our period of field observations (i.e., late July–August). Per model, per roost, per year, we performed 1000 Monte Carlo forward simulations (Clark and Mangel 2000). Note that years differed in the distribution and quality of the food (in both back and forward simulations) and in the initial distribution of energy stores x (in forward simulations only; based on the distribution of body masses among the radio-tagged birds and assuming a lean mass of 92 g [Piersma et al.

1996]). When pooling the output of forward simulations across years (such as in Figs. 3–5), years were weighted according to the number of radio-tagged birds. To compare the relatively fine-scaled modeling results on area use with the relatively large-scaled empirical data on area use (especially those collected by handheld radio receivers), we categorized the 4-km² blocks into four larger areas (Fig. 1A).

Area use

Each year from 1996 to 2000, during late July or in August, we mist-netted knots near Richel (53°17' N, 05°07' E), an important high-tide roost used by knots in the western Dutch Wadden Sea. For each bird, we measured body mass (to nearest gram) as a measure of energy stores (van der Meer and Piersma 1994). Using ultrasonography to make an image of gizzard diameter (Dietz et al. 1999), we predicted gizzard size of birds that we radio-tagged from 1997 onward as a measure of digestive processing capacity (van Gils et al. 2003a). Indeed, mean gizzard size did not differ from the 6 g that we applied in the models (6.3 ± 0.2 g [mean \pm SE], $P > 0.05$, $N = 103$; GLM, SYSTAT 10; Systat Software 2000). Before release, each bird was fitted with a small (1.4 g) radio transmitter glued to its back (172–173 MHz [Holohil Systems, Carp, Ontario, Canada] following Warnock and Warnock 1993, but using superglue, see Nebel et al. 2000). Subspecific identity was based on presence or absence of active primary molt (*islandica*, the subspecies that we focus on here, changes primaries in northwest Europe, while the subspecies that uses the Wadden Sea as its stopover, *canutus*, changes primaries in West Africa; Nebel et al. 2000, Boyd and Piersma 2001), presence of bare brood patches on the belly (regrown at first stopover in Iceland in *islandica*, while usually still completely bare in *canutus* that arrive directly from the Siberian tundra; T. Piersma, unpublished data), and body mass (in the Wadden Sea, *islandica* usually weighs <160 g in early autumn; Piersma 1994). In all, 121 *islandica* were radio-tagged (11 in 1996, 13 in 1997, 7 in 1998, 45 in 1999, and 45 in 2000).

Daily movements of radio-tagged birds were followed using a combination of handheld radio receivers (TRX-2000S, Wildlife Materials, Carbondale, Illinois, USA; see also van Gils and Piersma 1999, Nebel et al. 2000) and automated radio-tracking systems (Telemetry, Arnhem, The Netherlands; see also van Gils et al. 2000, Green et al. 2002, Battley et al. 2004). Handheld systems were used in 1996–1998 at two fixed stations (Griend and Richel) and at a mobile station (research vessel RV *Navicula*). At each station, a directional three-element Yagi-antenna was mounted on a mast (3–4 m), which enabled radio signals to be detected up to distances of 4–8 km. Each bird was scanned at half-hour or hourly intervals (day and night; knots also feed during nighttime low waters; van Gils and Piersma 1999, van Gils et al. 2000). If a valid radio signal was detected,

direction and time was recorded. Automated systems were used in 1997 (1 station), 1998 (6 stations), 1999 (14 stations; see Fig. 1B), and 2000 (13 stations). At each station, a receiver (ICOM IC-R10, Amcom v.o.f., Nieuw-Vennep, The Netherlands) was connected to a non-directional antenna (1.2 m) and, through an interface, to a palmtop computer. Each bird was scanned every 10–15 min. The system recorded background noise and signal strength and detected valid signals up to 1 km. An additional system used in 1997 was of a different type (Aktiv500 [GFT, Gesellschaft für Telemetriesysteme, Horst, Germany]; described in Exo et al. 1992), connected to a three-element Yagi and having a detection range of ~3 km. Because available prey densities change seasonally through depletion, shell growth, and changes in burying depth (Piersma et al. 1993a, Zwarts and Wanink 1993, de Goeij et al. 2001), we restricted the analyses of movement data to the time period when prey sampling was ongoing, i.e., late July and August.

For each *islandica* individual, we calculated frequency of use per tidal area (i.e., Ballastplaat, Grienderwaard, Richel-area, and “West”; Fig. 1A), specified per 50-min tidal time step per roost used (Griend or Richel). Frequencies were arcsine square-root transformed before comparison with model outputs. Differences between observed and predicted values were analyzed using GLM in SYSTAT 10 (Systat Software 2000).

Foraging routines

During low tide (1988–2000; mostly in August), groups of 2–4 observers covered tidal flats during low tide in search of flocks of knots. Upon encounter of a flock, time of day was noted and individual birds were observed through a 20–60× telescope at a distance of 60–100 m. By means of scan sampling (Martin and Bateson 1993), behavior (foraging or non-foraging) was scored instantaneously for a number of individuals (mostly 100). In the analyses we used the (arcsine square-root transformed) proportion of knots feeding per scan sample. Note that, due to the inability to distinguish *islandica* from *canutus* in the field, data on foraging routines are, in contrast to radio-tracking data, partly collected on fueling *canutus*. However, overall proportion *canutus* in our observations will be minor, as only 16% of the observations stem from periods that *canutus* is the prevailing subspecies (late July and early August; Nebel et al. 2000).

For each model, we analyzed foraging routines across the first 60 tidal cycles. In the comparison with empirical data, we pooled model outputs across both roosts, as we did not know where the knots in our scan samples had roosted during the latest high tide (most likely they either came from Griend or Richel; Piersma et al. 1993a). Differences between observed and predicted values were analyzed using GLM in SYSTAT 10 (Systat Software 2000).

Energy stores

For each model, we analyzed the stabilized distribution of energy stores x after 60 tidal cycles. At such a time point far into the future, the distribution of x becomes independent of the distribution initially assumed (due to strong forward convergence because of stochasticity in feeding conditions; Houston and McNamara 1999). In order to compare these data with the real world, we analyzed body masses of adult knots caught in the Dutch Wadden Sea in September ($N = 69$; 1990 and 2001–2002), which is more or less 60 tidal cycles after their arrival in our study area. By that time, almost all *canutus* knots have left the Wadden Sea for West Africa (Nebel et al. 2000), which ensures that our sample mainly comprised knots of the *islandica* subspecies. As before, we assumed a lean mass of 92 g in order to estimate x from body mass (Piersma et al. 1996). Model output and empirical data were compared using two-sample t tests (variances pooled; SYSTAT 10; Systat Software 2000).

RESULTS

Area use

The four models made distinct predictions with respect to area use throughout the tidal cycle (Fig. 3), in which the location of the roost also mattered, especially in the models that assumed travel costs (i.e., non-free). In contrast, varying the risk of predation hardly had any effect on area use (Table 1 and 95% CI in Fig. 3).

Basically, non-ideal/non-free knots best feed close to the roost (always when roosting at Richel; Fig. 3A) or make only a single move to another area nearby (often when roosting at Griend; Fig. 3B). Reasons for this move by Griend roosters to the Richel-area are: (1) some sites near Richel are fairly elevated, which makes them available for feeding longer than the sites around Griend; (2) non-ideal/non-free knots need long foraging periods, as they experience low incomes (non-ideal) at relatively large costs (non-free); and (3) Richel-area is relatively close to Griend (8–9 km).

In contrast, non-ideal knots traveling for free best feed at a random site once off the roost (Fig. 3). Therefore, predicted use of *feeding* sites does not vary with roost use, but rather reflects availability of feeding sites (note that in all graphs in Fig. 3, area use includes roost use, which is why the use of Grienderwaard [which includes Griend] and the use of Richel-area [which includes Richel] vary with roost use).

Ideal/non-free knots face a trade-off between intake rate and travel costs. In that case, the best feeding area, Ballastplaat, should not be used as intensely by knots roosting far away (at Richel, 16–18 km away; Fig. 3G) as by knots roosting relatively close by (at Griend, 8–9 km away; Fig. 3H). By contrast, a poor feeding area, such as “West,” should almost never be used (Fig. 3E, F), even if it is located near the roost (Richel, 5–6 km

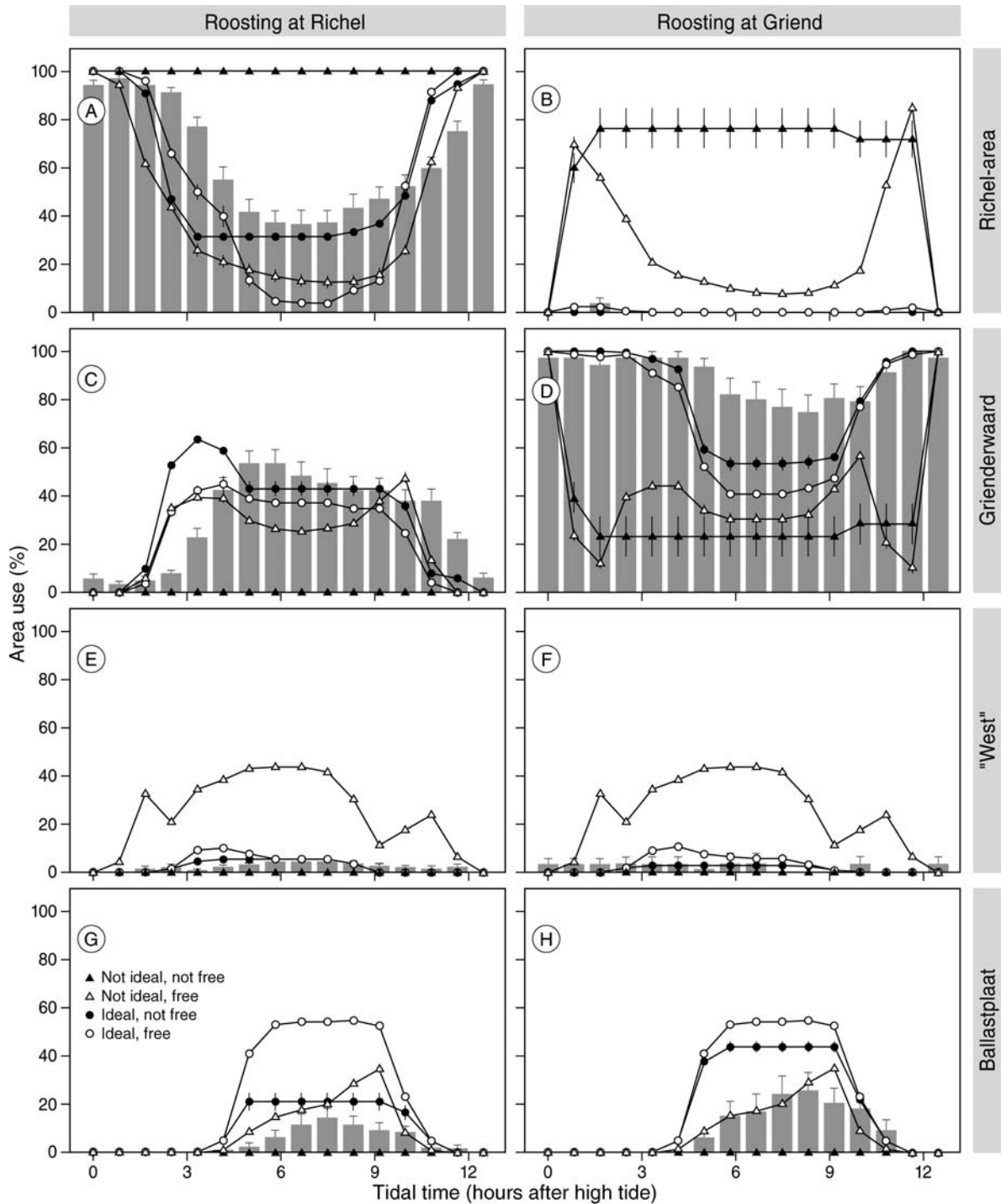


FIG. 3. Area use at four sampling areas throughout the average tidal cycle, predicted (symbols; key in panel G) or observed (gray bars) for birds roosting at Richel (left panels) and Griend (right panels). Error bars give 95% CI for the model predictions (i.e., variation between sensitivity runs) and SE for the observations (i.e., variation between individual birds). Note that area use includes roost use during high tide.

away; Fig. 3E). Finally, most Richel-roosting knots should leave the vicinity of their roost to feed at Grienderwaard (Fig. 3C), being the second-best feeding area, while most Griend-roosting knots should feed

closer to their roost (i.e., at Grienderwaard; Fig. 3D) and virtually never visit the Richel-area (Fig. 3B).

Ideal/free knots should always feed at the site yielding the highest intake rate, which, if available for feeding, is

TABLE 1. Area use: residual sum of squares (RSS) of the four models (rows) and their sensitivity runs (columns; italic numbers indicate \log_{10} -transformed predation risks per 50-min interval during feeding and non-feeding, respectively).

Model		$\log_{10}(\text{predation risk foraging}), \log_{10}(\text{predation risk non-feeding})$									
Ideal	Free	-2, -3	-2, -4	-2, -5	-2, -6	-3, -4	-3, -5	-3, -6	-4, -5	-4, -6	-5, -6
No	No	2054.9	2002.7	1998.2	2001.3	2481.9	2463.6	2468.4	2491.7	2500.3	2502.2
No	Yes	1620.9	1613.5	1613.5	1613.1	1743.6	1743.0	1742.5	1774.5	1774.6	1778.1
Yes	No	1205.7	1196.6	1195.3	1194.4	1147.8	1155.6	1152.9	1137.8	1140.4	1147.7
Yes	Yes	1416.0	1414.3	1415.9	1418.5	1443.6	1448.8	1447.4	1479.5	1457.8	1503.4

Notes: Residuals are the differences between observed frequency of area use (averaged per individual, per area, per roost, per 50-min time step) and predicted frequency of area use (specified per x , per area, per roost, per 50-min time step). Analyzed per area per roost (i.e., $N = 15$ per analysis), these residuals differed from 0, except in three parameter sets in the ideal, non-free model (indicated in boldface type). Note that we combined significance probabilities of each separate test by a method proposed by Sokal and Rohlf (1995), which compares test statistic $-2\sum \ln P$ with $\chi^2_{2 \times 8}$. Furthermore, we set the critical P value to 0.0125 by taking the Bonferroni correction ($\alpha/n = 0.05/4$) into account, since the sum of frequencies across the four areas is constrained to 1 (Krebs 1999).

located at Ballastplaat (Fig. 3G, H). Only early in the tidal cycle and during the entire worst cycle type ($w = 5$; Appendix B, Fig. B1), when sites at the relatively low-lying Ballastplaat are unavailable for feeding, should knots mainly feed at the second-best area, Grienderwaard. As traveling is for free, these predictions, with respect to feeding sites, do not vary with the location of the roost.

Observations of area use by the radio-tagged birds match best with the ideal/non-free model (Fig. 3; see Table 1 for residual sums of squares [RSS] per model per sensitivity run). More explicit, observations did not differ from ideal/non-free predictions when risk of predation while feeding was set to 10^{-3} , while they differed from all other models and parameter settings (Table 1). Confirming ideal/non-free predictions, a majority of the birds roosting at Richel were observed

to leave the Richel-area for Grienderwaard (4985 observations of 67 individuals in 512 cycles; Fig. 3A, C), and almost all Griend roosters stayed at Grienderwaard in the vicinity of their roost (1565 observations of 37 individuals in 164 cycles; Fig. 3D). Moreover, Ballastplaat was used relatively little, and the proportional usage of this area was found to be twice as high for Griend roosters as for Richel roosters (Fig. 3G, H).

Foraging routines

In each model, intensity of foraging was lowest during high tide and peaked during low tide (symbols in Fig. 4). However, the models again made distinct quantitative predictions. For each 50-min time step, both non-ideal models predicted higher intensities than both ideal models (compare triangles with dots in Fig. 4). Non-ideal foragers generally obtained low intake rates and, therefore, required long feeding times to compensate. Lowest intensities, especially early in the tidal cycle, were found in the ideal/free model, simply because those model birds obtained high intake rates (they know where to go) at a low price (no travel costs). Again, as in the area use predictions, varying risk of predation within each model hardly had any effect on foraging routines (Table 2 and 95% CI around symbols in Fig. 4).

Observed routines (1,124 observations collected during 300 tidal cycles on a total of 367950 birds; bars in Fig. 4) also match best with the ideal/non-free model (Fig. 4; see Table 2 for RSS per model per sensitivity run). More explicitly, observations did not differ from ideal/non-free predictions when risk of predation while feeding was set to 10^{-3} , while they differed from all other models and parameter settings (Table 2).

Energy stores

Energy stores (after 60 simulated tidal cycles) were predicted to be relatively low in the models assuming non-ideal knots (Fig. 5; two most left boxes). This is because those birds generally obtained low intake rates. In order to maintain energy balance, they should try to minimize metabolic costs, which is feasible by carrying as little mass as possible (we modeled mass-dependent

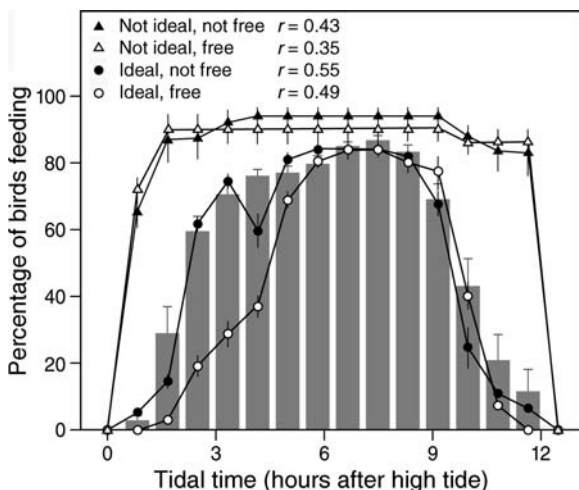


FIG. 4. Foraging routine throughout the average tidal cycle (expressed as hours after high tide), predicted by the four models (symbols) and observed (gray bars). Error bars give 95% CI for the model predictions (i.e., variation between sensitivity runs after pooling both roosts) and SE for the observations (i.e., variation between scan samples). The numbers in the key show Pearson's correlation coefficient between predictions and observations.

TABLE 2. Foraging routines: residual sum of squares of the different models (rows) and their sensitivity runs (columns; italic numbers indicate \log_{10} -transformed predation risks per 50-min interval during feeding and non-feeding, respectively).

Model		$\log_{10}(\text{predation risk foraging}), \log_{10}(\text{predation risk non-feeding})$									
Ideal	Free	-2, -3	-2, -4	-2, -5	-2, -6	-3, -4	-3, -5	-3, -6	-4, -5	-4, -6	-5, -6
No	No	188.5	186.1	185.6	185.9	275.9	274.5	274.8	324.2	324.3	343.7
No	Yes	182.1	181.3	181.4	181.4	246.1	246.2	246.0	309.1	309.2	334.7
Yes	No	132.4	132.8	133.0	132.8	124.6	125.0	125.0	124.8	124.9	124.1
Yes	Yes	188.4	188.4	188.3	188.5	242.5	213.0	201.4	182.1	176.0	168.1

Notes: Residuals are differences between observed and predicted proportion of knots foraging (arcsine square-root transformed). Residuals differ from 0 (GLM; $P < 0.05$; $N = 1124$), except in three parameter sets in the ideal, non-free model (indicated in boldface type).

energy costs through locomotion; Appendix A). In doing so, they take account of the trade-off between minimizing starvation risk and minimizing metabolic costs, i.e., they need some energy storage in order to buffer against stochastic periods of poor feeding conditions when the tides are bad (cycle types $w \geq 4$; Appendix B, Fig. B1). Because of this trade-off, ideal (model) birds should and do store more energy (Fig. 5): They obtain higher intake rates and can therefore afford higher metabolic rates. As ideal/free birds experience lowest risks of starvation (they always obtain the highest intake rates possible and travel for free), they can do with a somewhat lower storage level than ideal/non-free birds.

Observations of September body masses as a proxy for energy stores 60 tidal cycles after arrival ($N = 69$) also match best with the ideal/non-free model ($P > 0.35$, pooled variance $t = 0.88$; while $P < 0.00001$ for each of the other models, pooled variance t from 5.04 to 13.54; x predicted per roost, per year, per risk-parameter setting;

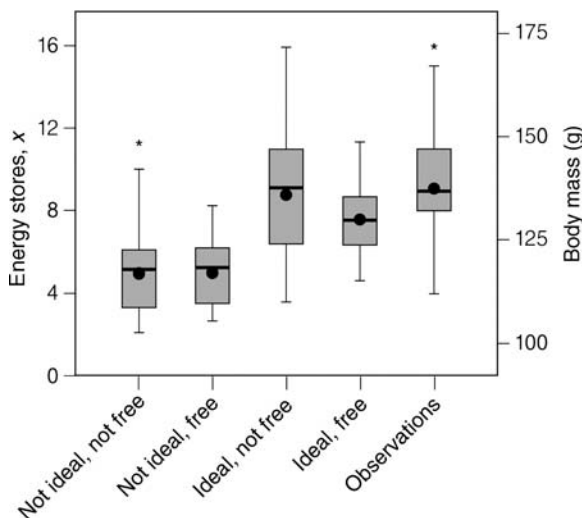


FIG. 5. Distribution in energy stores, x , predicted by the four models after 60 tidal cycles and observed indirectly through measurements on body mass (scaled on the right vertical axis). These box-and-whisker plots give mean (solid dot), median (horizontal line within box), interquartile range (box), range (bars), and outliers (stars).

Fig. 5). When analyzed per sensitivity run, observations did not differ from ideal/non-free predictions when the risk of predation while feeding was set to 10^{-3} ($P > 0.9$, pooled variance t from -0.12 to 0.07) and from one parameter setting in the ideal/free model (albeit at a much lower P values of 0.42 , pooled variance $t = -0.81$), while they differed from all other models and parameter settings ($P < 0.05$, negative pooled variance t from -10.47 to -6.03 , positive pooled variance t from 2.00 to 24.78 ; Table 3). Note that Table 3 shows that optimal storage levels tend to go down with an increase in risk of predation while feeding; this reflects the trade-off between risk of starvation and risk of predation (even though we did not assume mass-dependent predation risks). When feeding is dangerous it is better to feed less (which, in turn, makes you lighter, alleviating the need to feed) at the expense of an increase in risk of starvation.

DISCUSSION

Observations of area use, foraging routines, and energy stores are all in best agreement with the model assuming ideal/non-free knots. With respect to area use, we conclude that knots trade off energy intake rates against travel costs: Sites near a roost are skipped in case they offer low intake rates (e.g., “West” in case of Richel roosters). Sites offering high intake rates are only used frequently if roosting occurs close by (e.g., Ballastplaat is used more often by Griend roosters [8–9 km one-way] than by Richel roosters [16–18 km]; Fig. 3G, H). Observed foraging routines seem to reflect the trade-off between the risk of starvation and the risk of predation, both directly and indirectly. Directly, if foraging would indeed incur higher risks of predation than resting, knots would aim to feed for as short a time as possible under the constraint of maintaining energy balance. They would best do so by feeding most intensely in the middle of the low-tide period, which is when the best feeding sites are available. More indirectly, feeding should be as short and efficient as possible, as feeding leads to a heavier body, leading to higher metabolic costs when carrying the extra mass, leading to more feeding to compensate, leading to higher risks of predation on a daily basis. Note that mass-dependent predation risk, which we did not include in

TABLE 3. Energy stores: differences between mean observed value ($N = 69$) and mean predicted value ($N = 100$; x predicted per roost per simulation) per model (rows) per sensitivity run (columns; italic numbers indicate \log_{10} -transformed predation risks per 50-min interval during feeding and non-feeding, respectively).

Model		$\log_{10}(\text{predation risk foraging}), \log_{10}(\text{predation risk non-foraging})$									
Ideal	Free	-2, -3	-2, -4	-2, -5	-2, -6	-3, -4	-3, -5	-3, -6	-4, -5	-4, -6	-5, -6
No	No	5.91 (24.12)	6.07 (24.77)	6.07 (24.78)	6.07 (24.77)	3.59 (14.64)	3.62 (14.76)	3.62 (14.77)	2.56 (10.48)	2.58 (10.55)	2.02 (8.24)
No	Yes	5.76 (23.57)	5.93 (24.27)	5.93 (24.28)	5.93 (24.27)	3.78 (15.45)	3.80 (15.53)	3.79 (15.51)	2.58 (10.56)	2.59 (10.61)	1.90 (7.75)
Yes	Yo	2.49 (10.09)	2.59 (10.53)	2.59 (10.53)	2.60 (10.57)	-0.03 (-0.12)	0.01 (0.06)	0.02 (0.07)	-1.68 (-6.07)	-1.66 (-6.03)	-3.09 (-10.47)
Yes	Yes	2.69 (11.00)	2.78 (11.37)	2.79 (11.42)	2.79 (11.41)	1.25 (5.12)	1.30 (5.33)	1.31 (5.37)	0.49 (2.00)	0.52 (2.11)	-0.20 (-0.81)

Note: Differences deviate from 0 ($P < 0.05$, with pooled variance t given in parentheses), except in three parameter sets in the ideal, non-free model ($P > 0.9$) and in one set in the ideal-free model ($P > 0.4$; indicated in boldface type).

the model, could also underlie such an indirect effect (Lind 2004). More general, we note that mortality risks other than predation should lead to similar routines (Yearsley et al. 2002). For example, if the activity of feeding itself would reduce a bird's condition, e.g., through bill damage (Johnstone and Norris 2000) or the build-up of free radicals (Finkel and Holbrook 2000), then foraging should also be as short and efficient as possible. We therefore conclude that the observed behavior does not necessarily reflect the starvation–predation trade-off, but a more general starvation–mortality trade-off instead. The same precautionary conclusion should be drawn from the analyses on energy stores. Not necessarily just the risk of predation, but also other causes of mortality associated with foraging should lead to the observed submaximal energy stores: Larger stores lead to higher metabolic costs, which lead to longer feeding periods, which in turn lead to higher risks on a daily basis (e.g., predation risk), which should be traded off against starvation risk.

Although the predation–starvation trade-off thus played a crucial role in the models, the sensitivity analyses revealed that the *actual* risk of predation hardly affected the predictions (95% CI in Figs. 3 and 4, Tables 1–3). This was especially so for area use and foraging routines, and to a lesser degree for energy stores. Energy stores decreased with an increase in risk of predation (Table 3), a pattern now verified in the field for several species (Gosler et al. 1995, and see references in Piersma et al. 2003b). Of course, the effects on area use would increase once spatial variability in risk of predation was brought in. This would also affect foraging routines, as birds would need to compensate by feeding longer in safer but lower quality sites (van Gils et al. 2004).

The fact that the models assuming free travel were rejected may not come as a surprise. Traveling obviously takes energy (Kvist et al. 2001) and time (knots do not fly with infinite speeds; Gudmundsson 1994). The fact that the models assuming ideal knowledge were upheld may be more surprising. Overall home ranges of individual knots in the Dutch Wadden Sea are large (up to 800 km²; Piersma et al. 1993a, van Gils et al.

2005b), and prey densities and, hence, intake rates, vary tremendously between sites, seasons, and years (Zwarts et al. 1992). Their prey live buried in the sediment, which makes it likely that knots actually need to feed at a site before they know what it yields (e.g., prescient assessment from the air seems improbable). Even though knots can be perfect Bayesian foragers when feeding in small-scale experimental environments (50 m²; van Gils et al. 2003b), it seems unlikely that, on their own, free-living individuals would be able to collect sufficient information across their entire home range. Presumably, knots not only collect personal patch sample information (Valone 1991), but share public information while feeding (Danchin et al. 2004, J. A. van Gils and J. Bruin, unpublished data), and possibly while roosting (Wright et al. 2003, J. A. van Gils and T. Piersma, unpublished data), in addition to rapid discoveries of food patches by local enhancement (Pöysä 1992). Due to the openness of the intertidal landscape, finding food patches through local enhancement is likely to be very efficient in knots. Adding the sedentary lifestyle of their prey (which only move vertically through the mud), makes knots virtually “ideal” in relatively short periods of time (presumably upon return from their breeding grounds, they need 5–10 days to “get the picture”). This contrasts with other social foragers that exchange public information but live in spatially more complex environments and/or feed upon more mobile prey (e.g., mammalian carnivores).

The dynamic programming technique enabled us to study survival-rate maximization in a stochastic environment and link three relevant aspects of foraging in the same model (area use, foraging routines, and energy stores). With alternative modeling techniques based on intake-rate maximization, one is usually bound to study only one of those aspects in isolation (e.g., West et al. 2005). The main limitation of our approach would be the exclusion of density-dependent costs (around which Fretwell and Lucas' (1970) theory of ideal-free distribution centers). For example, as recently shown by Vahl et al. (2005), short-term prey-encounter rates in knots are decreased by interference competition (although such negative effects are overruled by digestive constraints when considering long-term intake rates; van Gils and

Piersma 2004). Here, stochastic dynamic games, a blend between game theory and SDP, should be employed (Houston and McNamara 1999). Furthermore, it would be challenging to allow a free choice of where to roost (Rogers 2003), a feature that we kept fixed in our models. In this way, one would obtain a prediction on the relative uses of the two different roosts (76% of the observations of area use were of knots roosting at Richel, 24% at Griend) and on the occurrence of switches between roosts. Between different days, individual knots regularly switch roosts (mean \pm SE, 13.1% \pm 2.3%, $N = 668$ observations of 73 birds switching between Griend–Richel–Hengst), which appears to be driven by inter-roost differences in predation risk (Piersma et al. 1993a). As Griend is closer to good feeding grounds than Richel, it seems likely that roosting knots accept a greater risk of predation at Griend than at Richel (especially so when energy stores x are low; for which we have empirical support; J. A. van Gils, A. Dekinga, T. Piersma, and B. Spaans, unpublished data). It would be insightful to explore the (state-dependent) differences in predation risk at which model knots make such roost switches.

In spite of such inherent shortcomings of our models, we feel that the approach applied here is likely to be fruitful in other studies on foragers dealing with large-scale temporal and spatial variability in food resources. For example, herds of herbivores tracking seasonal fluctuations in grass quality face similar problems as knots in intertidal areas, albeit at larger spatiotemporal scales: where to go for feeding, how intensely to feed when on the move, and how much energy stores to carry around (Owen-Smith 2002). Modeling such problems sheds new light on the ecological requirements of a species (home range sizes, food availability), which could help us making science-based decisions for conservation (Sutherland et al. 2004).

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APPENDIX A

On the calculation of Δx (*Ecological Archives* E087-069-A1).

APPENDIX B

A figure showing availability of feeding sites as a function of tidal time and cycle type (*Ecological Archives* E087-069-A2).

APPENDIX C

On the calculation of risk of predation μ_b (*Ecological Archives* E087-069-A3).