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Foraging site selection of two subspecies of Bar-tailed Godwit *Limosa lapponica*: time minimizers accept greater predation danger than energy minimizers

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Different spatial distributions of food abundance and predators may urge birds to make a trade-off between food intake and danger. Such a trade-off might be solved in different ways in migrant birds that either follow a time-minimizing or energy-minimizing strategy; these strategies have been assigned to two subspecies of Bar-tailed Godwits *Limosa lapponica* that use the European Wadden Sea during northward migration. At the study area on Terschelling, we recorded feeding site selection, time budgets and intake rates (prey/min) in the period that both *lapponica* (energy minimizer) and *taymyrensis* (time minimizer) subspecies were present (late April till the end of May 2007). Prey availability (number of prey/m^2) was negatively correlated to the distance from cover. Based on resightings of colour-ringed Bar-tailed Godwits, *taymyrensis* was foraging closer to cover, and for a higher proportion of time than *lapponica* (67% vs. 33%). During the high tide period *taymyrensis* was also foraging on inland coastal meadows. Moreover, *taymyrensis* was more vigilant than *lapponica*, whereas *lapponica* showed more resting and preening behaviour. *Lapponica* had a higher instantaneous intake rate, but *taymyrensis* had a higher overall intake rate and the birds were more successful in taking larger prey items than *lapponica*. Supposedly, due to the increased foraging time and additional foraging on the inland meadows, the time-minimizing *taymyrensis* achieved a higher fuel deposition rate than *lapponica*. *Taymyrensis* shifted towards food-rich areas, apparently accepting higher predation risks, whereas energy-minimizing *lapponica* avoided predation danger by foraging further from cover.

Key words: *Limosa lapponica lapponica*, *Limosa lapponica taymyrensis*, predation, intake rate, migration strategy, feeding site selection, trade-off

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INTRODUCTION

A successful migration strategy results from optimizing at least three selective factors: time, energy and predation (Alerstam & Lindström 1990). Birds may minimize the time for migration, i.e. flight as well as fuelling time (maximize speed of migration), minimize the total energy cost of migration (energy cost of transport), or minimize predation risk during migration. Depending on the migration and energetic status, individuals may

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opt for different solutions to balance these selective factors. Theoretical studies of migration usually incorporated the dichotomy between time and energy minimization (Lindström & Alerstam 1992, Hedenström 1993, Vrught et al. 2007), and only few studies addressed the issue of predation minimization (e.g. Weber *et al.* 1998, Burns & Ydenberg 2002). Most empirical studies that have focused on predation minimization during migration are concerned with passerines (e.g. Lindström 1990, Fransson & Weber 1997, Schmaljohann & Dierschke 2005) and to a lesser extent with shorebirds, such as Western Sandpiper *Calidris mauri* (Ydenberg *et al.* 2002, Lank *et al.* 2003, Pomeroy 2006, Pomeroy *et al.* 2006, 2008), Dunlin *Calidris alpina* (Dierschke 1998) and Ruddy Turnstone *Arenaria interpres* (Metcalfe & Furness 1984). To explore in which way predation danger modulates decisions of birds on migration, we investigated foraging behaviour of two subspecies of Bar-tailed Godwit *Limosa lapponica* that are known to exhibit contrasting migration schedules.

The Bar-tailed Godwit is a long-distance migrant of which two subspecies occur along the East-Atlantic flyway (Engelmoer & Roselaar 1998, Engelmoer 2008). These two subspecies follow a leap-frog migration, with the European Wadden Sea as staging and stopover site (Drent & Piersma 1990). The subspecies *taymyrensis* (600 000 birds; Wetlands International 2006) visits the Wadden Sea twice a year during one month to replenish stores needed for migration between breeding areas in northern Siberia and wintering sites in West Africa (Smit & Piersma 1989, Engelmoer 2008). *Taymyrensis* follows a time-minimizing migration strategy (Scheiffarth *et al.* 2002): it faces a tight time schedule before leaving to the breeding grounds, and devotes as much time as possible for fuel deposition, while minimizing other energy consuming activities. By increasing foraging time, the time at the stopover site is minimized, and consequently time spent on migration is minimized. *Lapponica* (120 000 birds; Blew & Südbeck 2005, Wetlands International 2006), on the other hand, stays in the Wadden Sea for the entire winter before leaving to less distant breeding grounds in northern Scandinavia and the White Sea area (Cramp & Simmons 1983, Prokosch 1988, Engelmoer 2008). *Lapponica* follows an energy-minimizing migration strategy (Scheiffarth *et al.* 2002), as the subspecies builds up the required spring reserves over a long period before leaving to the breeding grounds. These birds do not have to forage the entire available time, which enables them to spend more energy and time on activities as moulting and predation avoidance.

Aerial predators of wader species, such as falcons, often make use of vegetation, hills, dikes and other structures to cover their approach when hunting close to the salt marsh (Bijlsma 1990, Cresswell & Whitfield 1994). Several studies have confirmed that the hunting success of aerial predators is higher on salt marshes than on open mudflats without any cover, suggesting that predation risk declines with distance from cover (Cresswell 1994, Ydenberg *et al.* 2002, Whitfield 2003, Dekker & Ydenberg 2004, van den Hout *et al.* 2008). To study the role of predation minimization on the stopover ecology of the two Bar-tailed Godwit subspecies, we focused on the importance of distance from cover. We recorded feeding site selection, time budgets and intake rates in the period that both subspecies are present in the Wadden Sea during northward migration from late April to the end of May.

METHODS

Study area

Data were collected on the tidal flats and on inland coastal meadows of the Dutch Wadden Sea island Terschelling (53°24'N, 05°21'E; Fig. 1). Bar-tailed Godwits are known to primarily forage on tidal flats (Cramp & Simmons 1983), although in spring they also use inland coastal meadows for feeding (Piersma *et al.* 1993, van de Kam *et al.* 2004).

Population identification

In 2001 the Royal Netherlands Institute for Sea Research (NIOZ) on Texel, in association with various ringing

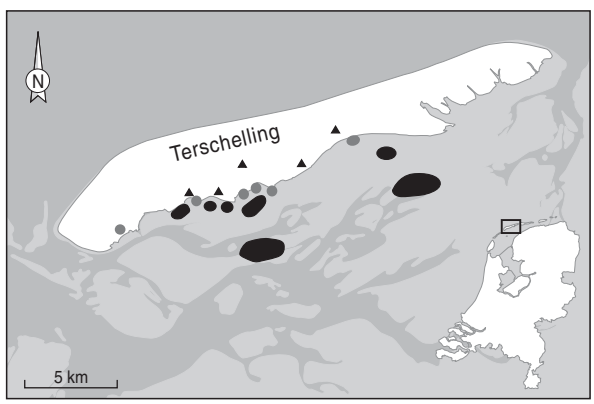


Figure 1. The island Terschelling located in the Dutch Wadden Sea. Sites of benthic sampling and main foraging areas of Bar-tailed Godwits are indicated in black. The small grey circles indicate the most important high water tide roosts. The small inland triangles represent the main feeding sites on the meadows.

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groups, started a colour-ringing program on the Bar-tailed Godwit. Based on the catching and/or previous resighting dates of colour-ringed individuals, they can be assigned to either the subspecies *lapponica* or *taymyrensis*. Birds caught and/or resighted between October and March in the Wadden Sea were assigned to the subspecies *lapponica*, and individuals caught and/or resighted in West Africa to the subspecies *taymyrensis*. In the Dutch Wadden Sea area, many birds were caught with 'wilsternets' (Jukema *et al.* 2001) on inland coastal meadows in May, or were resighted only in May. It is estimated that only a small fraction (6.7%) of the birds caught in May are *lapponica* (B.S., unpubl. data). We therefore assume that all birds caught and/or resighted only in May are *taymyrensis*. Up to March 2007, a total of 2173 Bar-tailed Godwits were colour-ringed, of which 15% were *lapponica* and 85% *taymyrensis*.

Since only a small fraction of the birds observed were colour-ringed, we tested the degree to which the two subspecies mixed while foraging. If they would not mix, the presence of colour-ringed individuals in a flock could indicate to which subspecies the flock belonged. In all flocks observed on inland coastal meadows and on tidal flats during low tide (3 hours before and after low water) that contained multiple colour-ringed individuals ($n = 32$), it never occurred that an assigned colour-ringed *lapponica* was foraging together with an assigned *taymyrensis* (Fisher's exact test, $P < 0.001$). Therefore, we assumed that flocks could be assigned to a subspecies on the basis of the identity of single individuals in the flock. In total we resighted 371 different colour-ringed Bar-tailed Godwits, of which 69 were *lapponica* and 302 *taymyrensis*.

Observations and benthos sampling

Behaviour of Bar-tailed Godwits was recorded during daylight on tidal flats, high water roosts and inland coastal meadows. Within each flock, 2-min focal animal observations were conducted (Martin & Bateson 1993) of randomly chosen birds with 20–60x zoom spotting scopes. Five different categories were distinguished: foraging, resting, preening, vigilance and flight. Vigilant behaviour was scored when the bird had raised the head from the head-down foraging position to at least a horizontal position ('head-up vigilance', Metcalfe 1984). Flight behaviour was scored when a focal bird flew in the air. Bar-tailed Godwits are highly dimorphic in bill and body size, which can affect their foraging behaviour (Smith & Evans 1973, Cramp & Simmons 1983, Glutz von Blotzheim *et al.* 1985), therefore the sex of each focal bird was recorded. Sex was determined by body size, coloration and bill length (Both *et al.* 2003). Abdominal profiles (ranging from 1 – lean – to 5 – abdomen bulging) were scored to estimate the body condition of the birds (Wiersma & Piersma 1995). Every 30 min the number of individuals was estimated, and the contours of the flock were plotted on Google Earth maps.

Prey items were scored to determine the intake rate. Bar-tailed Godwits in the Wadden Sea mudflats mainly feed on lugworm *Arenicola marina*, ragworm *Nereis diversicolor*, catworm *Nephtys hombergii* and bristleworm *Scoloplos armiger* (Scheiffarth 2001). When foraging on inland coastal meadows, Bar-tailed Godwits mainly feed on cranefly larvae *Tipula paludosa* (Piersma *et al.* 1993, van de Kam *et al.* 2004). The prey items were scored in four classes: (1) small polychaetes (all items up to half the bill length; i.e. smaller than 5 cm), (2) large polychaetes (all items exceeding half the bill length; i.e. larger than 5 cm), (3) lugworms, and (4) cranefly larvae.

To assess food availability of the tidal areas, soil samples were taken on spots where foraging flocks had been observed. Per foraging area, 10 random samples with a depth of 15 cm (equal to ±1.5 times the bill length) were taken with a standard PVC tube (1/56 m^2) in a randomly placed square of 100 x 100 m. The samples were sieved over a 1-mm mesh sieve and the four main polychaetes species were identified and measured by a ruler to the nearest 5 mm. Per sample, we calculated the abundance of prey/m^2. As our sampling sessions on inland coastal meadows failed, we took cranefly densities from a similar grassland polder on another Dutch Wadden Sea island, Schiermonnikoog (Tinbergen 1981).

Cover

To assess the distance from cover per subspecies, the location of each colour-ringed individual on the tidal flat and the inland coastal meadows was mapped. The distance from each foraging location to cover (e.g. dike, tree, scrub) was measured (m) from the centre of the flock. In this way the distance of each foraging colour-ringed individual from cover could be determined.

Data analysis

For the analysis we merged observations into so-called 'sessions', with a mean for both sexes. Each session ended when the observed flock flew up, the flock size changed or the session exceeded one hour. Over all tidal hours, we performed 1569 observations (692 low tide hours; i.e. 3 hours before and after low water) which we pooled per sex into 445 sessions (195 low tide hours), resulting in a mean number of 3.5 observations (3.5 low tide hours) per session. In the meadows

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we conducted 192 observations which were also pooled per sex into 49 sessions, resulting in 3.9 observations per session. Analyses are based on the sessions, with mean values for males and females to correct for sex in the model, hence sample sizes refer to sessions and not to individual birds. In all models sex is included as fixed factor to allow for morphological and behavioural differences between the sexes. Tidal and weather (i.e. temperature, wind speed, wind direction) data were obtained from Rijkswaterstaat Rijksinstituut voor Kust en Zee and the Royal Netherlands Meteorological Institute (KNMI), and were used as covariates whenever they were significant in the model.

Taymyrensis shows fast increases in body mass when staging in the Wadden Sea in May, whereas *lapponica* increases with a rather slow rate (Prokosch 1988, Drent & Piersma 1990). To determine the fattening rate of the two subspecies, mean abdominal profiles (±SE) per session of all tidal hours during the fattening period of both subspecies were used. A GLM was performed, with date as covariate, to assess differences between the two subspecies.

To assess differences in intake rate between the two subspecies, we calculated the instantaneous intake rate (prey/min) as the number of prey items taken when foraging. Only sessions of low tide hours were used in the calculation. The overall intake rate (prey/min) is defined as the number of prey items taken during entire focal observation periods (2 min) and further includes all tidal hours, including the inland coastal meadows. Besides the overall intake rate, we calculated the intake rate for each of the four prey items (i.e. small polychaetes, large polychaetes, lugworm, cranefly larvae), which were all natural-log transformed. For the instantaneous and overall intake rate calculations, a GLM was performed with sex as an additional fixed factor. Data were natural-log-transformed to satisfy the assumption of normality (Zar 1996). Time budgets of both subspecies were determined by the percentage of time spent per activity within the 2-min observations.

Effects of cover (as proxy for predation danger) on foraging behaviour were tested by correlation analysis. The mean time (s) per session spent on each behavioural category was converted into percentages and arcsin-transformed. Only data of the low tidal hours have been used, as during high tide birds are much limited in where to forage. Moreover, we examined whether intake rate and prey availability were correlated with distance to cover. Analyses were performed with Pearson correlation (r) or Spearman's Rho (r_s). Graphical data of these correlations were pooled into 250-m points. Meadows are shown in graphs, but are excluded from correlation analyses. We performed GLM's to test for differences in behavioural activity between the two subspecies, with sex as additional fixed factor, by pooling data from all tidal hours. The behavioural category flight did not satisfy the assumption of normality, and therefore the non parametric Mann–Whitney U test was used. Differences in foraging mean distance (±SE) from cover between the two subspecies were analysed with a Student's t-test, in which data of low tide hours and meadows were used.

Basic assumptions of parametric tests were examined by testing for normality, residual analysis, and the application of the Levene's test for equality variances. The reported mean values and SE were back-transformed without corrections. All analyses were performed using SPSS version 15.0.

RESULTS

Seasonal occurrence

From March until mid-April 2007, only colour-ringed *lapponica* individuals were seen. An influx of colour-ringed *taymyrensis* began on 22 April (Fig. 2). From the beginning of May, *lapponica* started to leave the study area and gradually decreased in numbers in May. *Taymyrensis* did not leave the study area until the end of May.

Fuelling patterns

Taymyrensis were on average slimmer than *lapponica* individuals (GLM, $F_{70,650} = 5.30$, $P < 0.001$). However, in *taymyrensis* the daily increase of abdominal profile was almost 10 times faster than in *lapponica* (Fig. 3).

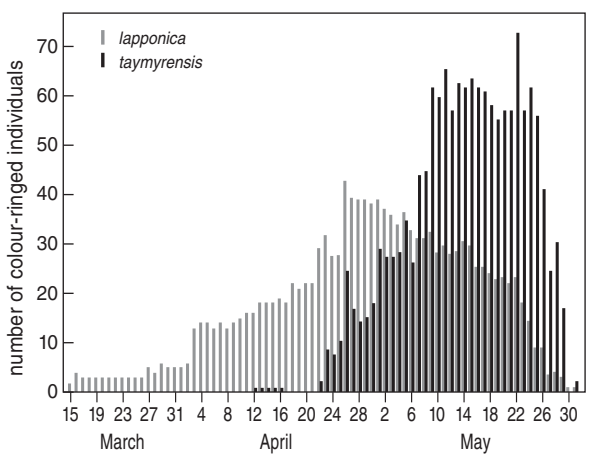


Figure 2. Daily number of resighted colour-ringed *lapponica* and *taymyrensis* Bar-tailed Godwits on Terschelling, spring 2007.

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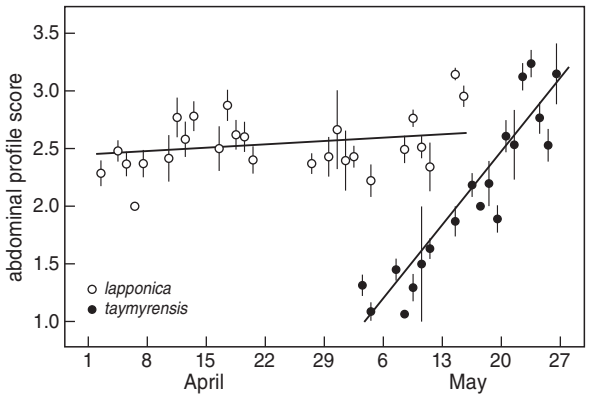


Figure 3. Abdominal profile score (mean ± SE) of two Bar-tailed Godwit subspecies throughout spring 2007. Regression coefficients are 0.004 AP-units/d for *lapponica* ($F_{1,434}$ = 7.14, R^2 = 0.016, P = 0.008) and 0.043 AP-units/d for *taymyrensis* ($F_{1,283}$ = 136.13, R^2 = 0.325, P < 0.001).

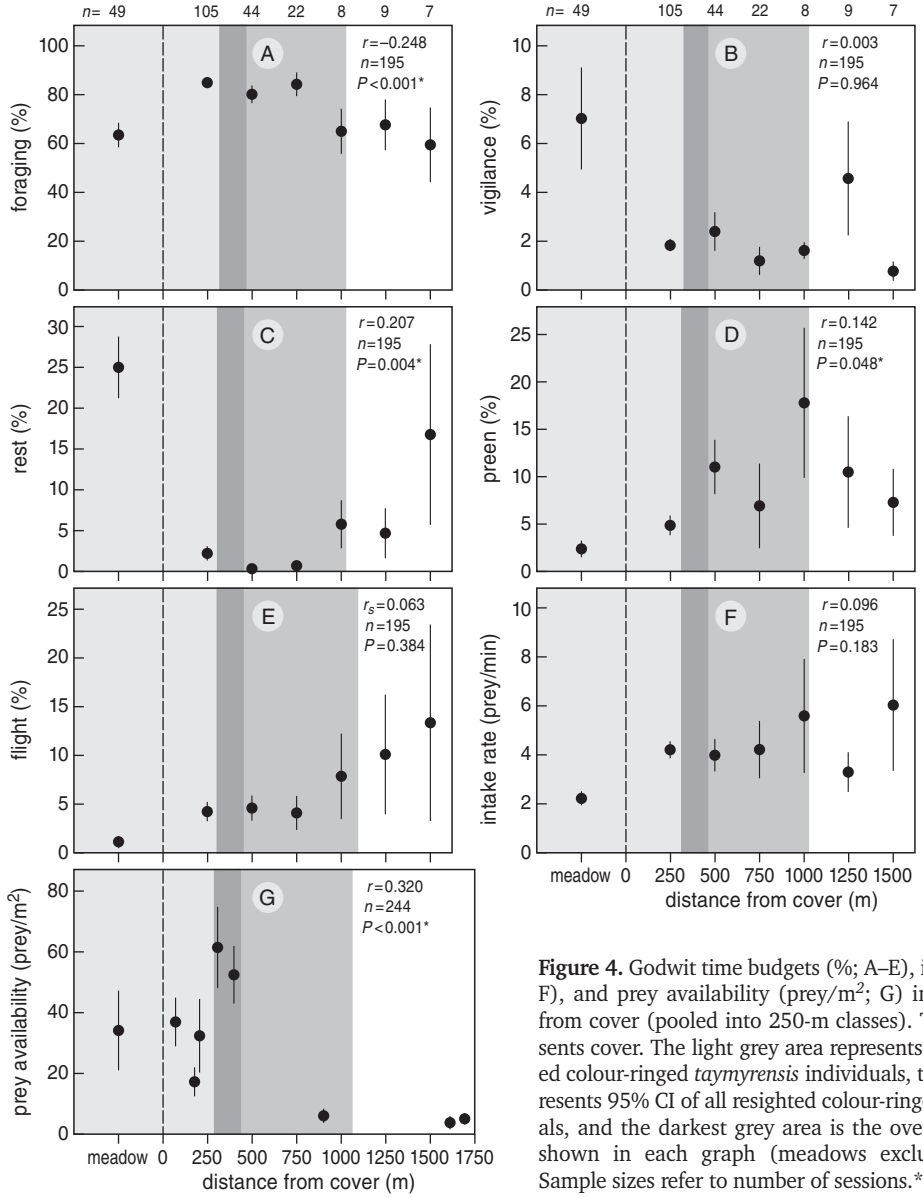


Figure 4. Godwit time budgets (%; A–E), intake rate (prey/min; F), and prey availability (prey/m^2; G) in relation to distance from cover (pooled into 250-m classes). The dotted line represents cover. The light grey area represents 95% CI of all resighted colour-ringed *taymyrensis* individuals, the dark grey area represents 95% CI of all resighted colour-ringed *lapponica* individuals, and the darkest grey area is the overlap. Correlations are shown in each graph (meadows excluded from analysis). Sample sizes refer to number of sessions.* indicates P < 0.05.

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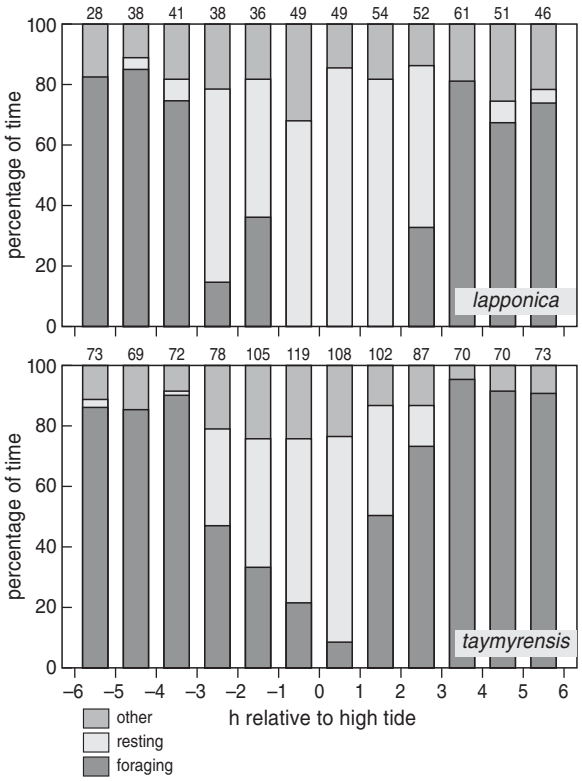


Figure 5. Activity pattern of two Bar-tailed Godwit subspecies in relation to tidal stage. The category 'other' includes preening, vigilance and flight. Sample sizes (total number of birds recorded) are given for each hour.

Correlations with distance to cover

Resting and preening increased with distance from cover, whereas time spent foraging and prey availability decreased with distance (Fig. 4). Vigilance, intake rate and time spent flying were not correlated with distance from cover.

Lapponica foraged at a mean distance of 397 ± 67 m from cover, and *taymyrensis* at a mean distance of 85 ± 21 m from the nearest cover (*t*-test, $t_{21} = 4.26$, $P < 0.001$). In particular *taymyrensis* on inland coastal meadows were foraging close to cover.

Foraging behaviour

Taymyrensis spent more time foraging than *lapponica* (Table 1) as the subspecies was still foraging during high tide when *lapponica* was roosting (Fig. 5). *Lapponica* spent more time resting and preening, whereas *taymyrensis* was more vigilant. There was no difference in time spent flying between the subspecies.

During low tide, *lapponica* had a higher instantaneous intake rate (3.5 prey/min) than *taymyrensis* (2.8 prey/min; $F_{1,188} = 4.27$, $P = 0.040$). However, the overall intake rate showed an opposite trend (1.1 and 1.3 prey/min, respectively; $F_{1,431} = 6.56$, $P = 0.011$). *Taymyrensis* ingested large polychaetes at a higher rate than *lapponica*, whereas intake rates of small polychaetes and lugworms did not differ between the subspecies (Table 2). No comparison was made for cranefly

Table 1. Time budgets (% of time) of two subspecies of Bar-tailed Godwit, based on 2-min observation periods. Means and SE are based on arcsin-transformed data, given are back-transformed values.

	Lapponica (*n* = 166)		*Taymyrensis* (*n* = 285)			
Behavioural category	Mean	Upper / lower SE	Mean	Upper / lower SE	Test	*P*
Foraging	33.12	5.22/4.92	66.82	4.46/4.52	$F_{1,439} = 20.47$	<0.001
Rest	34.69	5.12/4.89	14.77	2.40/2.22	$F_{1,437} = 8.68$	0.003
Preen	5.27	1.18/1.06	1.84	0.37/0.34	$F_{1,442} = 15.80$	<0.001
Vigilant	2.21	0.33/0.31	3.42	0.50/0.47	$F_{1,440} = 16.93$	<0.001
Flight	5.00	0.93/0.93	3.70	0.58/0.58	$U = 22072.50$	0.151

Table 2. Overall intake rate (prey/min) by prey class taken by two subspecies of Bar-tailed Godwit. Means and SE are based on log-transformed data, given are back-transformed values.

	Lapponica (*n* = 160)		*Taymyrensis* (*n* = 236)			
Prey item	Mean	Upper / lower SE	Mean	Upper / lower SE	Test	*P*
Small polychaetes	1.05	0.14/0.13	1.22	0.11/0.10	$F_{1,393} = 1.04$	0.310
Large polychaetes	0.07	0.01/0.01	0.13	0.01/0.01	$F_{1,393} = 9.49$	0.002
Lugworms	0.02	0.00/0.00	0.01	0.00/0.00	$F_{1,393} = 0.86$	0.354

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larvae, as only *taymyrensis* was foraging on inland coastal meadows. For *taymyrensis*, intake rates on tidal flats and meadows were similar (1.2 prey/min; $F_{1,277} = 0.97$, $P = 0.326$).

DISCUSSION

By using resightings of colour-ringed individuals, we confirmed the established patterns of *lapponica* and *taymyrensis* presence in the Wadden Sea (Prokosch 1988, Piersma & Jukema 1990, Scheiffarth *et al.* 2002, Engelmoer 2008). *Lapponica* was present during winter till mid May and *taymyrensis* from late April to late May. The idea that 20% of the wintering Bar-tailed Godwit population in the Wadden Sea consists of *taymyrensis*, as suggested by Engelmoer (2008) on the basis of biometry, was not supported by our resightings.

Body stores of *taymyrensis* arriving in the Wadden Sea at the end of April were close to depletion. Throughout their stay of only one month they were able to prepare for the next leg of the migration route of more than 3000 km. The apparently high daily food intake was achieved by (1) foraging a large proportion of time per day, which they achieved by feeding during high and low tide close to cover on mudflats, (2) feeding on inland coastal meadows, and (3) selecting sites where they found large prey species. Thus, our results confirm that *taymyrensis* follows a strategy of a time minimizer (Scheiffarth *et al.* 2002).

Taymyrensis foraged close to cover in areas with a higher prey density. By foraging close to cover, birds are more vulnerable to surprise attacks by raptors (e.g. Cresswell & Whitfield 1994, van den Hout *et al.* 2008), and apparently *taymyrensis* accepted a higher predation danger in favour of better feeding opportunities. The trade-off between food and danger has inspired many investigators (e.g. Milinski & Heller 1978, Sih 1980, Brown & Kotler 2004). Dark-eyed Juncos *Junco hyemalis* which had been deprived of food opted for a riskier habitat to enhance their feeding rates (Lima 1988). In a study of Western Sandpipers, heavy birds predominated at safe stopover sites, while leaner birds used sites where predation danger was greater (Pomeroy 2006). Our observations of Bar-tailed Godwits add well to these findings: initially heavier Bar-tailed Godwits foraged further from cover, and leaner birds closer to cover. Thus, the benefit of better feeding opportunities outweighed the risk of selecting more dangerous areas. This was clearest during high tide, when *taymyrensis* using inland coastal meadows, necessarily foraged close to cover (i.e. ditches, trees and buildings). A study on Ruffs *Philomachus pugnax* showed that birds foraging on meadows avoided fields that were located near trees and buildings (Verkuil & de Goeij 2003). We suspect that especially individuals that face difficulties in reaching their departure fuel load in time, would supplementary forage in the meadows. Caldow *et al.* (1999) showed that Oystercatchers *Haematopus ostralegus* tend to feed in meadows to supplement their low-tide intake on the tidal flats. Piersma & Jukema (1993) found that Bar-tailed Godwits at a coastal site were 40 g heavier than those feeding on inland meadows. In line of this finding, we found the mean abdominal profile score (corrected for date) of 1.8 in meadows compared to 2.2 on tidal flats (GLM, $F_{1,279} = 10.424$, $P = 0.001$).

We suggest that Bar-tailed Godwits traded distance to cover against food abundance. By increasing foraging time and by facing a higher predation risk, the time-minimizing *taymyrensis* ensured the accumulation of a sufficient fuel load, within a short stopover period, whereas the energy-minimizing *lapponica* minimized predation by foraging in the safer areas. It is expected that these strategies influence survival rates, and we predict higher mortality rates due to a higher predation risk for the *taymyrensis* subspecies during the migration seasons.

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SAMENVATTING

In deze studie is onderzocht in hoeverre bij de Rosse Grutto *Limosa lapponica* predatierisico een rol speelt bij de plaatskeuze tijdens het foerageren. In de Waddenzee komen twee ondersoorten voor: *lapponica* en *taymyrensis*. Zij houden er in het voorjaar een verschillende trekstrategie op na (*lapponica*, die in het waddengebied overwintert, een energie minimaliserende strategie; *taymyrensis*, die het waddengebied tijdens de noordwaartse trek alleen in mei gebruikt om op te vetten, een tijd minimaliserende strategie). We hebben van beide ondersoorten in 2007 op Terschelling de voedselplaatskeuze, tijdsbesteding en opnamesnelheid bepaald tijdens de periode dat beide ondersoorten hier aanwezig zijn (midden april tot eind mei). Bij de keuze van de foerageerplek is als maat voor gevaar de afstand tot de dekking (bijv. dijk, bomen of struiken) genomen. Het bleek dat er meer wordt gepoetst en gerust en minder wordt gefoerageerd naarmate de afstand tot de dekking groter is (voedselbeschikbaarheid is hoger dichter bij de dekking dan verder weg). Individueel gekleurringde vogels lieten zien dat de twee ondersoorten tijdens de laagwaterperiode niet mengen, zodat de groepen van beide ondersoorten goed zijn te onderscheiden. Het bleek dat *lapponica* gemiddeld verder van de dekking foerageerde dan *taymyrensis*. De laatste foerageerde langer en was waakzamer dan *lapponica*, maar rustte en poetste minder. De dagelijkse voedselopname lag bij *taymyrensis* hoger dan bij *lapponica*, voornamelijk doordat *taymyrensis* langer foerageerde (67% tegen 33% van de tijd) en tijdens hoogwater ook in de weilanden foerageerde. Het lijkt erop dat bij de afweging tussen voedselopname en predatierisico *taymyrensis* meer voor een maximale voedselopname kiest. Ze foerageren in rijkere voedselgebieden, maar moeten hiervoor wel een hoger predatierisico accepteren. Vanuit de noodzaak om in korte tijd het noodzakelijke vertrekgewicht te bereiken, ligt deze keus in de lijn met hun trekstrategie. *Lapponica* daarentegen heeft veel langer de tijd om lichaamsreserves op te bouwen. Omdat hun broedgebied minder ver weg is, hebben ze waarschijnlijk ook minder reserves nodig. Deze vogels kunnen het zich blijkbaar permitteren te foerageren in de minder rijke gebieden waar het predatierisico veel kleiner is.

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