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Afro-Siberian Bar-tailed Godwits on inland coastal meadows during spring migration



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Abstract

The Bar-tailed Godwit is a wader species of which two subspecies occur along the East-Atlantic flyway. The European population *Limosa lapponica lapponica* winters in Western Europe and breeds in Northern Scandinavia. The Afro-Siberian population *Limosa lapponica taymyrensis* breeds in Siberia and winters in West Africa and use the Wadden Sea twice a year as a stopover site. During spring migration a part of the subpopulation *taymyrensis* use inland coastal meadows to build up their reserves for the next part of their journey. We studied foraging Bar-tailed Godwits on inland coastal meadows during spring migration.

At the study area on Texel, we recorded foraging time, intake rate (prey/min), disturbance, kleptoparasitism and prey availability. During the short stopover at the Wadden Sea small flocks with a mean of 110 individuals forage on inland coastal meadows. Flock sizes decreased over time and the sex ratio changed by a decrease in percentage of males. On inland coastal meadows Bar-tailed Godwits forage primarily on crane fly larvae which were locally available in high densities. However prey densities did not affected the instantaneous intake rate of 1.78 prey/min for females and 1.5 prey/min for males. Kleptoparasitic attacks hardly affected the intake rate of Bar-tailed Godwits. Bar-tailed Godwits lost 0.2% of their foraging time and 0.56% of the total prey items at kleptoparasitic attacks. Kleptoparasitic attacks were exclusively done by Black-headed Gulls. In 78.3% of the focal bird observation Black-headed Gulls were present in the flock and 60% of the attacks on Bar-tailed Godwits were observed in flock sizes, varying between 50 and 150 individuals. On inland coastal meadows Bar-tailed Godwits experience an disturbance rate 1.25 times per hour and they spent 8.5% of their time to vigilant behaviour. The daily energy intake of Bar-tailed Godwits on inland coastal meadows is higher compared to the tidal mudflats.

Eventually we conclude that inland coastal meadows enables Bar-tailed Godwits the opportunity of a high energy intake, however they face a higher predation and disturbance risk.

Contents

Abstract

Introduction 8
 1.1 Problem description..... 10

2 Methods 13
 2.1 Study area..... 13
 2.2 Observations..... 13
 2.3 Sampling Crane fly larvae..... 14
 2.4 Data analysis 14

3 Results 17
 3.1 Flock size..... 17
 3.2 Migratory qualities 18
 3.3 Food availability and intake rate 19
 3.4 Disturbance..... 21
 3.5 Comparison between tidal mudflats and inland coastal meadows 21

4 Discussion 25

5 Conclusion and recommendation 29
 5.1 Conclusion..... 29
 5.2 Recommendation..... 30

Acknowledgements..... 31

References

Appendix 1

1 Introduction

The Dutch Wadden Sea is an important stopover and wintering site for many wader species that use the East-Atlantic flyway. One of this wader species is the Bar-tailed Godwit *Limosa lapponica* which occurs along this flyway. Within the Bar-tailed Godwits population two sub-populations are distinguished (i.e. the European population and Afro-Siberian population). The European population *Limosa lapponica lapponica* winters in Western Europe, mainly in Great Britain and the Western Part of the Wadden Sea (Smit & Piersma 1989). Their breeding grounds are in Northern Scandinavia and around the White Sea (Engelmoer 2008). This population follows an energy-minimizing migration strategy (Scheiffarth et al. 2002), as they slowly build up reserves all winter for spring migration. They do not forage the entire available time, which enables them to spend more energy and time for other activities such as moulting and predation avoidance. In contrast, the Afro-Siberian population *Limosa lapponica taymyrensis* breed from Yamal peninsula to the delta of the Anabar River, Siberia, and winters in West Africa (Drent & Piersma 1990; Engelmoer 2008). In spring, they conduct two 4.000 km non-stop flights with the Wadden Sea as stopover site to reach their breeding ground in Siberia. During this stop of one month, they have to build up reserves for the next part of their journey. The *taymyrensis* population follows a time-minimizing migration strategy (Scheiffarth et al. 2002; Duijns et al. 2009), i.e. they have a tight time schedule and therefore they spend as much time as possible foraging and reduce time to other energy consuming activities. By increasing their foraging time, reserves are build up sooner and stopover time is shortened (Scheiffarth et al. 2002; Duijns et al. 2009).

Every year around 600.000 individuals of the *taymyrensis* population use the East-Atlantic flyway to migrate from their breeding ground to their winter ground and vice versa. Based on high tide counts, the population of *taymyrensis* seems to be decreasing over the last years (Wetlands International 2006). The population of *lapponica* is stable with a total of 120.000 birds (Wetlands International 2006). In May, both populations are present in the Wadden Sea and more than 300.000 birds can be counted (Reneerkens et al. 2005; Duijns et al. 2009).

The Bar-tailed Godwit is usually found in silty or sandy parts of the intertidal area. They are able to find prey even when the sediment is covered with 10 cm of water (van de Kam et al. 2004). In spring, individuals of *taymyrensis* can be found on inland coastal meadows where they feed on crane fly larvae *Tipula paludosa* (van de Kam et al. 2004; Duijns et al. 2009). Crane fly larvae live between the grass and stay in small j-shaped burrows. They eat the roots of grass and reach their final weight at the end of May (Tinbergen 1980), exactly when Bar-tailed Godwits need them the most.

Previous studies have shown that Bar-tailed Godwits at a coastal site were 40 g heavier than those feeding on inland coastal meadows (Piersma & Jukema 1993) and Duijns et al. (2009) showed that the mean abdominal profile score (i.e. abdominal profile score is used as an index for the fat content of individual shorebirds) of meadow foraging birds was lower compared to the birds foraging on the tidal flats. This indicates that individuals that face difficulties in reaching their departure fuel load use inland coastal meadows. Nevertheless, the intake rate (prey/min) on tidal flats and inland coastal meadows were similar (Duijns et al. 2009). However, they also face higher predation risk, since birds that feed closer to cover are more vulnerable to surprise attacks by raptors (Bijlsma 1990; van den Hout et al. 2008).

Not only a higher predation risk is a disadvantage, also different quality of food and kleptoparasitism might affect their foraging efficiency. Kleptoparasitism is defined as stealing by one animal of food that has been caught by another and is common in some groups of birds, especially seabirds. Many kleptoparasitic species are opportunists, they take advantage

of any small supply of food they can find (Rand 1954). Gulls, *Laridae*, and Carrion Crows, *Corvus corone*, regularly steal food found by waders (Goss-Custard 1980). However the effects of kleptoparasitism on the foraging behaviour and consequently the intake rate of Bar-tailed Godwits along the East Atlantic flyway is unknown. A study in Australia shows that Bar-tailed Godwits on mudflats facing with a reduction of 36% in the prey capture rates when food-stealing Silver Gulls *Larus novaehollandiae* were present compared with times when they were not (Dann 1979). Another study in Australia (Parramatta estuary) Taylor et al. (1996) showed that the amount of foraging time and percentage of prey items lost by Bar-tailed Godwits was very low, 1.9% of foraging time loss and 0.56% of prey items lost.

This raises the question what the consequences are for Bar-tailed Godwits feeding on inland coastal meadows. Kleptoparasitism, higher predation risk, affected intake rate, different quality of food, possibilities to feed during high tide, effect of tidal stage on flock size and changes flock size over time are some of the characteristics that will be studied for the Afro-Siberian population feeding on inland coastal meadows.

1.1 Problem description

The Wadden Sea is a large coastal wetland environment with a variety of different habitats like, sandy shoals, sea-grass meadows, mussel beds, sandbars, mudflats, salt marshes, estuaries, beaches and dunes. It is a very important stopover and wintering site for many different wader species. Besides Bar-tailed Godwits, many other species use the Wadden Sea as wintering or stopover site; Ringed Plover *Charadrius hiaticula*, Grey Plover *Pluvialis squatarola*, Red Knot *Calidris canutus* and Dunlin *Calidris alpina* to name a few. It is considered one of the most important areas for migratory birds along the East Atlantic flyway (Fig. 1).

The Wadden Sea area is protected by the Convention on Wetlands; i.e. the Ramsar Convention and Natura 2000 policy from the European Union. In June 2009, the Wadden Sea was added to the UNESCO World Heritage List, stressing the natural importance of this area.

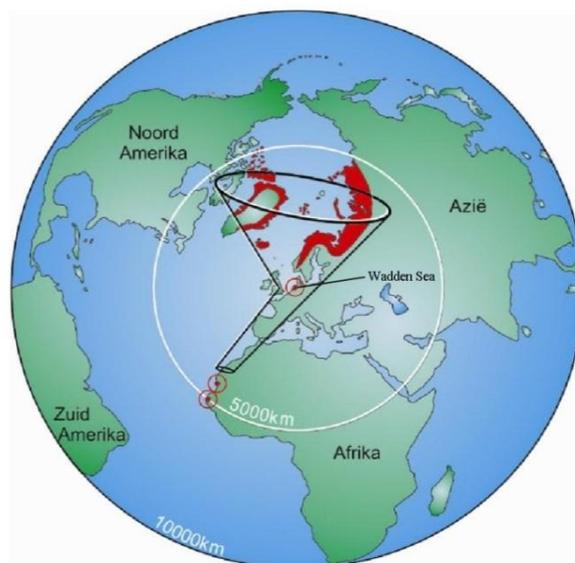


Figure 1 The East Atlantic flyway is shaped like a funnel, with central the Wadden Sea. The Wadden Sea act as a stepping stone between West Africa and Siberia/Greenland (Reneerkens et al. 2005).

The Wadden Sea is one of the last remaining natural, large-scale, intertidal ecosystems in Europe where natural processes continue to function largely almost undisturbed. Thus, for the

protection of this international important stopover site for waders, it is useful to gather information about how waders use this ecosystem. In this case, little is known how important inland coastal meadows are for Bar-tailed Godwits and what the consequences are of foraging at those locations. Through the following research question we will try to find out how important inland coastal meadows are for migratory Bar-tailed Godwits.

Research question:

Why do some Bar-tailed Godwits foraging on inland coastal meadows during spring migration

Sub questions:

- Does flock size of *taymyrensis* on inland coastal meadows relate to the tidal stage?
- What is the mean flock size of foraging *taymyrensis* on inland coastal meadows and does flock sizes change over time?
- What is the fuelling rate of *taymyrensis* on inland coastal meadows?
- What is the instantaneous intake rate (prey/min) of *taymyrensis* on inland coastal meadows?
- Is kleptoparasitism common and if so, how does this effects their intake rate?
- How often are foraging *taymyrensis* disturbed by human activities or disturbed/predated by predators?
- What is the difference of daily energy intake (KJ/day) between inland coastal meadows compared to the adjacent mudflats?

2 Methods

2.1 Study area

All observations and crane fly larvae sampling were carried out on the inland coastal meadows of the Dutch Wadden Sea island Texel. The fieldwork, was performed on the locations depicted in Figure 2.

2.2 Observations

All the observations were performed in May, when the influx of *taymyrensis* started and the first Bar-tailed Godwits were seen foraging on meadows. Observations were carried out during daylight hours. Within a flock a randomly chosen foraging bird, was observed for 5 minutes. In those 5 minutes the following activities were recorded: foraging, preening/resting, and vigilant behaviour which were measured in seconds. Vigilant behaviour was recorded when the focal bird raised his head from the head-down foraging position to at least a horizontal position (Metcalf 1984), also intake rates were measured by counting the number of preys ingested. The captured preys were easily identified, since the important prey species the crane fly larvae are relatively large.

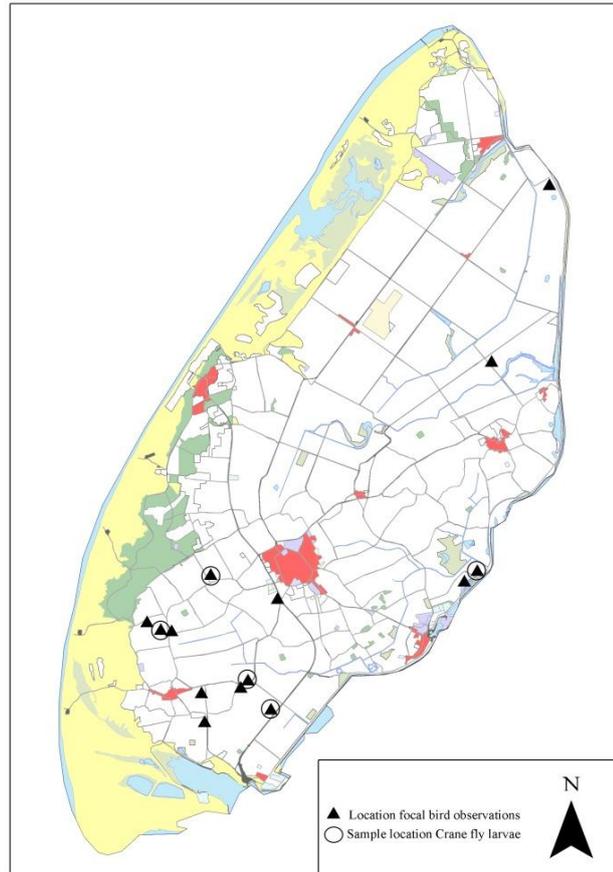


Figure 2. A map of the Dutch Wadden Sea Island Texel where fieldwork was performed. The triangles represent the locations of focal bird observations and the circles represent the sample locations of crane fly larvae.

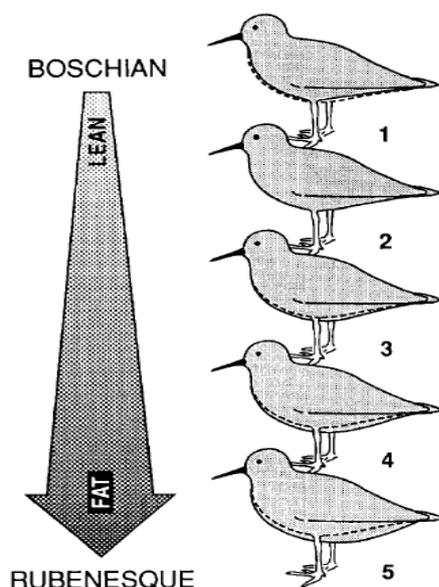


Figure 3. Example of the typology of abdominal profile by Red Knots as scored in the field, ranging from 1 (very lean) to 5 (very fat) (Wiersma & Piersma 1995).

Besides these behavioural activities the following events were recorded: (1) kleptoparasitic attacks by Gulls and (2) disturbance by humans or predators. Every time a Gull attacked the focal bird the time loss and the prey items loss were recorded (William & Hockey 1995). When the focal bird was disturbed and flew up the observation was ended.

Individual traits such as sex, moulting stage (male only) and abdominal profile were scored. To determine the sex of Bar-tailed Godwits, the moulting stage was used, since males moult into their red breeding plumage when they are present in the Wadden Sea. Additionally the field estimate of general body size and bill length was used to differentiate between the sexes (Cramp & Simmons 1983; Both et al. 2003). Abdominal profile scores were recorded by using a scale from 1 to 5 (Fig. 3). A score of 1 implying the bird is very lean and a

score of 5 when the abdomen is bulging (Wiersma & Piersma 1995) and is used as a proxy for their fuelling rate. The moulting stage of males was determined as this yields information on their migratory quality (Piersma & Jukema 1993). The extension of breeding plumage was evaluated on the basis of the colour of the back, breast and belly and was scored on a seven-point scale; (1) winter plumage, (2) trace of breeding plumage, (3) $\frac{1}{4}$ breeding plumage, (4) $\frac{1}{2}$ breeding plumage, (5) $\frac{3}{4}$ breeding plumage, (6) trace of winter plumage, (7) full breeding plumage (Piersma & Jukema 1993).

Every 30 minutes the numbers of individuals were counted, males and females were counted separately to determine the sex ratio of the flock. Other birds (primarily Gulls) were also counted.

2.3 Sampling Crane fly larvae

To assess food availability of inland coastal meadows, samples were taken on locations where foraging flocks has been observed regularly. The sampling was performed in the second part of May at five different locations (Fig. 2). At each location 2 transects of 3 samples of 20x20x20 cm (0.04m²) were taken with a distance of 50 m between each sample. The crane fly larvae were manually removed from the soil sample and collected and conserved in saline formalin (6%) and taken to the NIOZ for determine the ash free dry mass (AFDM). The larvae were measured and consequently dried for 72 hours in a ventilated drying oven at 55-60°C. The resulting dry mass contains both organic and inorganic contents of the sample. The dry mass was weighted (expressed in g) and incinerated at 550°C for two hours. After cooling all of the organic contents were burned. The ash that's left over is the inorganic contents of the sample. The ash was reweighed. To determine the AFDM, the weight of the dry mass minus the ash (inorganic contents) gives the weight of the organic contents (AFDM).

2.4 Data analysis

Number of Bar-tailed Godwits in relation to tidal stage

To examine whether the tidal stage affected flock size on inland coastal meadows the flock sizes during focal observations were used. The observations were grouped in observation sessions (i.e. series of observations performed on the same day and location) and for every observation session the mean number of present birds in a flock was calculated. The mean flock size for an observation session was determined as 100%. Of each individual observation within a session the percentage relative to the mean flock size was calculated. For the final analysis the observations were separated into two groups, see appendix 1. To examine if there was an optimum of Bar-tailed Godwits on inland coastal meadows during high tide, a quadratic regression analysis was used.

The changes of flock sizes during the month May were analysed. Analyses were performed with a Pearson correlation, flock size were natural log transformed to satisfy the assumption of normal distribution. The sex ratio of the flocks was given in percentages and the data for both sexes followed the assumption of normal distribution. To test for increasing or decreasing in numbers of Bar-tailed Godwits present on a daily base a Pearson correlation for both sexes was used.

Migratory qualities

The development of the fuelling rate for Bar-tailed Godwits was estimated by using the mean abdominal profile score on a daily base. This development of fattening rate was analysed by using a linear regression. For males the development of their moulting stage was also

analysed on a daily basis. For every day the mean moulting score was calculated and the analyses were performed by using a linear regression.

Food availability and intake rate

To assess differences in intake rate between both sexes, the instantaneous intake rate (prey/min) was calculated. The instantaneous intake rate followed the assumption of normal distribution and differences between the sexes was tested by using a GLM (General Linear Model), and flock size, food availability, flock density, abdominal profile score and number of present Gulls were included as covariates whenever they were significant in the model.

The effects of kleptoparasitism was analysed by using the percentage of loss foraging time, loss captive prey items and success rate. A comparison was made between the intake rate of observations when the focal bird was attacked by Gulls and without attacks. The data followed the assumptions of normality and were analysed with a GLM.

Disturbance

An overview of the different factors causing disturbance is given. In total, five different factors were distinguished which were identified during fieldwork, (1) Humans, (2) Raptors, (3) Carrion Crows, (4) Sheep and (5) Unknown. For each disturbed factor the percentage relative to the disturbance moments were calculated. Raptors, were described in more details. Therefore data was used of disturbances by raptors between the focal observations.

Comparison between tidal mudflats and inland coastal meadows

The total energy intake KJ for one day was calculated for four different scenarios, i.e. (1) Bar-tailed Godwits foraging only on inland coastal meadows, (2) Bar-tailed Godwits foraging on inland coastal meadows and were affected by kleptoparasitism, (3) Bar-tailed Godwits foraging only on tidal mudflats, (4) Bar-tailed Godwits foraging on the tidal mudflats and during high water at the inland coastal meadows. A basic assumption is that birds forage for the same time and with the same intensity day and night (Scheiffarth et al. 2002).

For both sexes the minimum daily energy requirement was calculated. The minimum energy requirements consisting the existence metabolism (EM) and thermostatic cost. The EM was calculated by using the equation; $EM (kj/day) = 912 BW(kg)^{0.704}$ (Kendeigh 1970; Kersten and Piersma 1987). The EM is calculated based on the mean body weight (BW) of Bar-tailed Godwits in the month May, respectively 400 g for females and 300 g for males (unpublished data NIOZ). The calculated EM is equal to $1 * BMR$ (Basal Metabolic Rate). Thermostatic cost for Bar-tailed Godwits were calculated by Scheiffarth (2003) and were $1.9 * BMR$ for females and $2.25 * BMR$ for males, respectively.

Scenario 1 and 2.

During crane fly larvae sampling all individuals were collected and the AFDM was determined. Zwarts & Blomert 1996, calculated that 1 gram of AFDM of crane fly larvae contained a mean of 23.45 KJ. This enables us to calculate the mean energy content of 1 crane fly larvae. By multiplying the mean energy content of one crane fly larvae with the mean intake rate, the mean energy intake rate (KJ/min) for each sex was calculated. The percentage of time spent at foraging was calculated by using the data from the focal observations. The results of the 5 minutes observations were combined with the mean foraging time from 30 minutes observations since the 5 minutes observations prefer foraging birds. With these two parameters (i.e. energy intake rate and percentage foraging time) and assuming an assimilation efficiency of 85% (Zwarts et al. 1996) the energy intake per day was calculated. For the situation where Bar-tailed Godwits dealing with kleptoparasitism, the energy intake rate for both sexes are corrected with prey loss.

Scenario 3 and 4

By calculating the energy intake for the tidal mudflats literature values were used (Scheiffarth et al. 2002). The mean energy intake was converted into energy intake (KJ/min) for both sexes. The percentage of time spent foraging was obtained from Duijns et al. 2009. These parameters (i.e. energy intake rate and percentage foraging time) and assuming an assimilation efficiency of 80% (Castro et al. 1989; Kersten and Piersma 1987; Scheiffarth et al. 2002; Zwarts and Blomert 1990) the energy intake for a day was calculated. The energy intake for Bar-tailed Godwits foraging on tidal mudflats and during high water on inland coastal meadows was calculated. We assumed these birds were able to forage 16 hours on tidal mudflats and 8 hours on inland coastal meadows.

3 Results

3.1 Flock size

Flocks size fluctuated from hour to hour and day to day, but the mean flock size was 110 birds. Overall no trend was found, suggesting the tidal stage affects flock size (Quadratic regression, $R^2 = 0.005$, $P = 0.381$; Fig. 4A). Also when the locations nearby the Wadden Sea dike (appendix 1, group 2) were analyzed separately from the rest, no significant trend was found (Quadratic regression, $R^2 = 0.056$, $P = 0.210$; Fig. 4B).

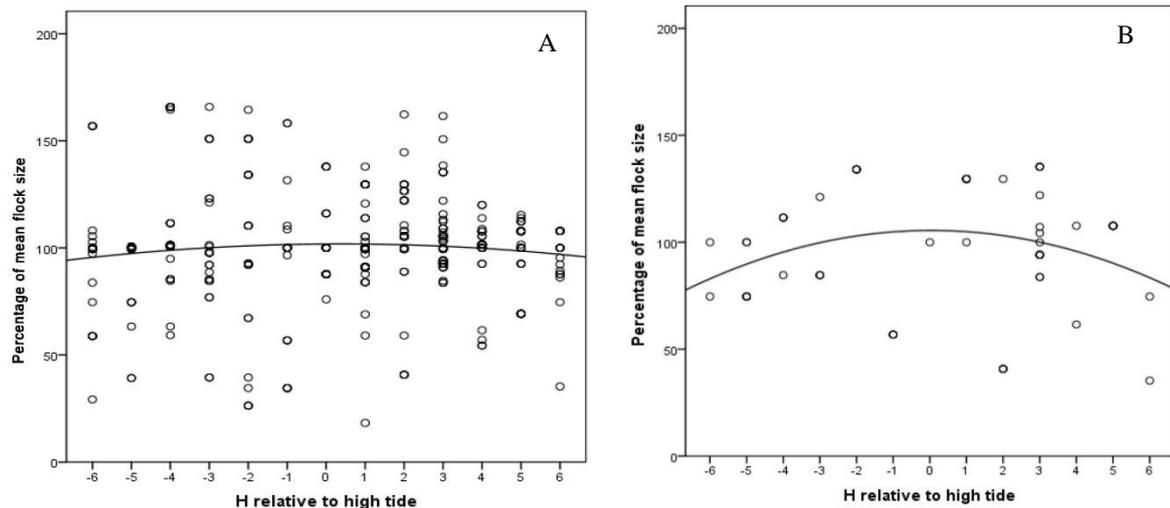


Figure 4. (A) Trend of flock sizes (represented in percentage of mean flock sizes) in relation to the tidal stage. Date includes all the performed observations. (B) To examine whether flocks nearby the Wadden Sea dike were affected by the tidal stage, these locations (appendix 1, group 2) were also analysed.

Flock size decreased over time ($r = -0.325$, $P < 0.001$). At the end of May significant fewer birds used inland coastal meadows (Fig. 5). Besides the decreasing flock sizes, the sex ratio within the flocks also changed. In the beginning of May the sex ratio was equal, but gradually over time the percentage of males in a flock show a significant decreasing trend ($r = -0.354$, $P < 0.001$; Fig. 6A) and consequently the females an significant increasing trend ($r = 0.347$, $P < 0.001$, Fig. 6B). Based on the mean numbers of females and males in a flock, females are in higher numbers present on inland coastal meadows (GLM, $F_{1,789} = 65.106$ $P < 0.001$).

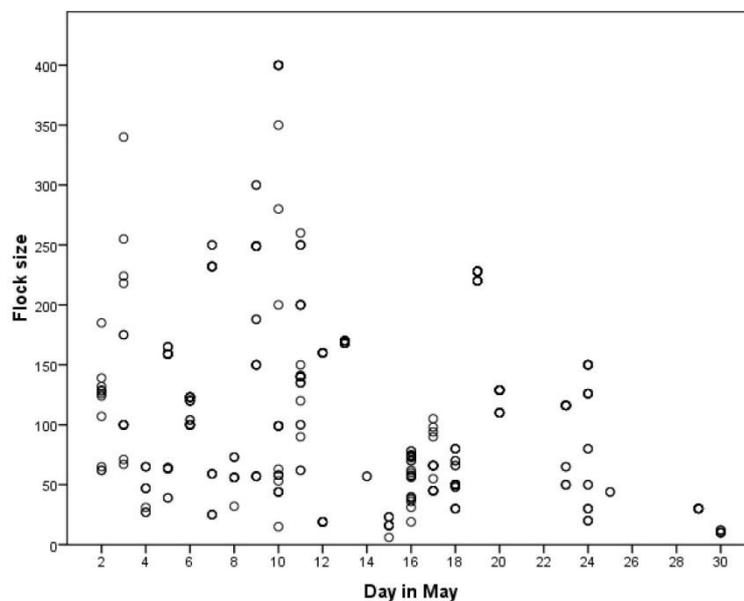


Figure 5. Trend of the daily changes in flock sizes on inland coastal meadows.

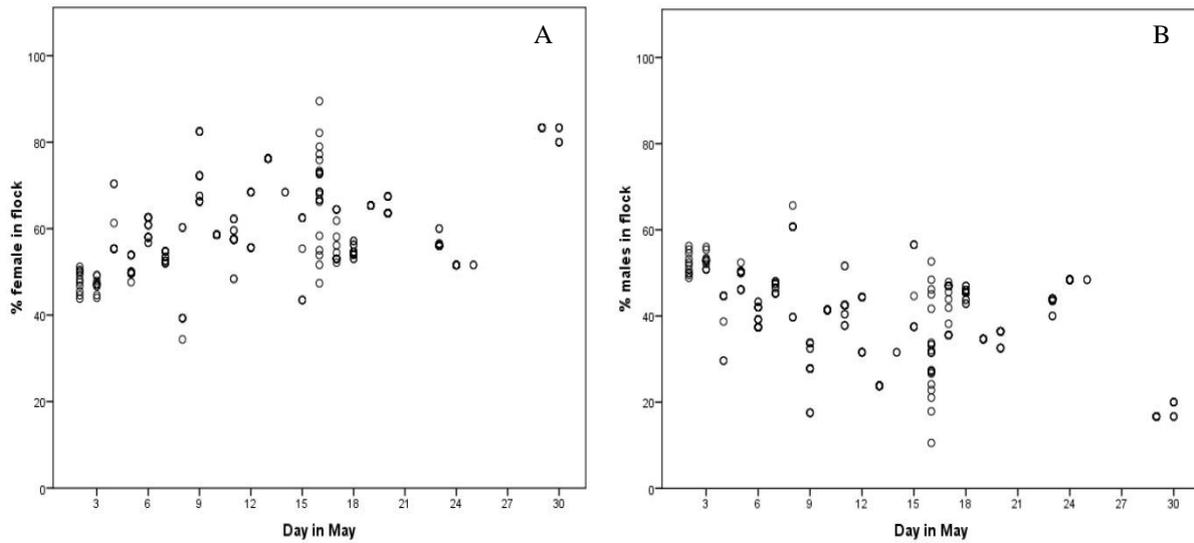


Figure 6. Trend of the presence (%) of females (A) and males (B) in flocks on inland coastal meadows in the course of May.

3.2 Migratory qualities

Bar-tailed Godwits arrived around 28 April and started quickly with foraging on inland coastal meadows. These birds just flew 4000 km before arriving in the Wadden Sea and were close to depletion, with a mean abdominal profile for the first day (2 May) of 1.1 (Fig. 7A). The mean abdominal profile (fattening rate) increased significantly ($F_{1,393} = 560.720$, $P < 0.001$) with 0.119 per day.

Overall the mean moulting score was 5.76 in contrast of the maximal score of 7. The moulting score shows a significant linear increase over time ($F_{1,191} = 6.824$, $P = 0.01$, Fig. 7B).

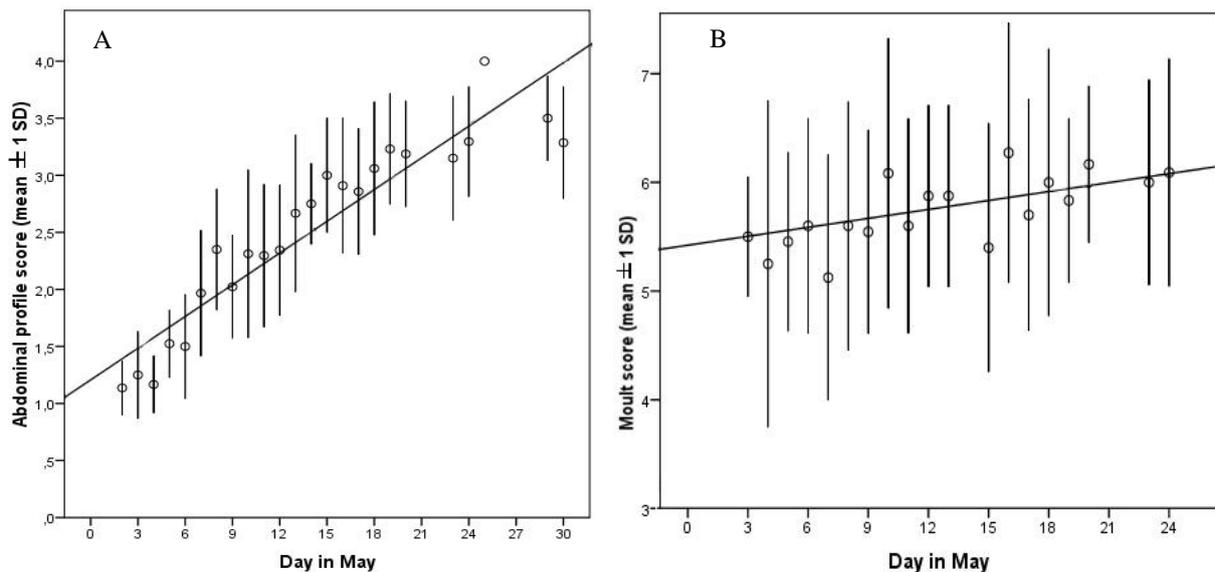


Figure 7. (A) The development of the abdominal profile score (mean \pm 1 SD) for Bar-tailed Godwits on inland coastal meadows. (B) For the male Bar-tailed Godwits the moulting score (mean \pm 1 SD) were determined and shown in relation to time (day in May).

3.3 Food availability and intake rate

In our study area (Fig. 8) densities measured end of May varied between 33 to 204 per m² (Table 1), with a mean of 100 crane fly larvae per m². During the sampling session 120 individuals of crane fly larvae were collected with a length between 21.61 and 28.18 mm (Table 1). The mean AFDM on inland coastal meadows was 6.4 gram/m². However the data gives no indication that prey densities affected the overall intake rate (GLM, $F_{3,249} = 0.246$, $P = 0.863$).

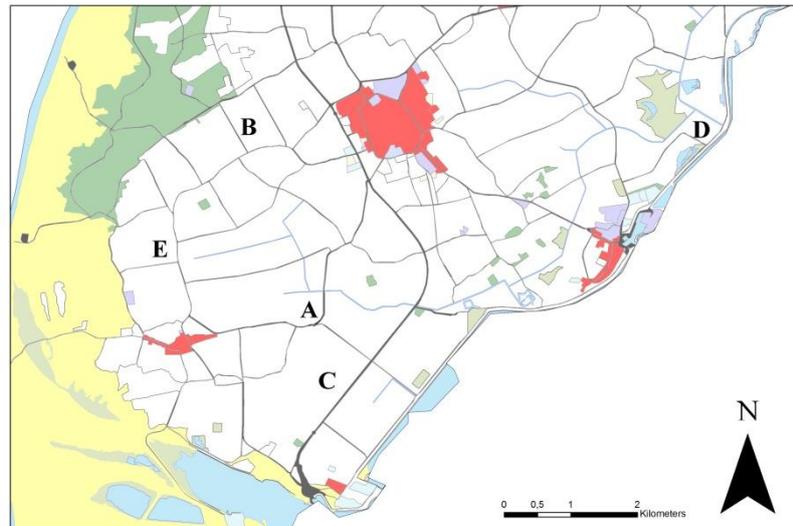


Figure 8. Detailed map of the crane fly larvae sampling location, the characters (A-E) represent the sampling location and correspond with table 1.

Table 1. Details of food availability sampled at five sample locations. For each location the mean crane fly larvae densities per m² were calculated, also the mean AFDM per m² and the mean length of crane fly larvae. Per location the mean intake rate for both sexes are given.

Location	Mean density of crane fly larvae per m ²	Density g AFDM/ m ²	Mean length crane fly larvae (mm)	Mean intake rate (items per min)	
				Males	Females
A	204	10.6	23.88	1.30	1.58
B	88	4.46	23.31	1.16	1.58
C	33	2.28	28.18	1.23	1.53
D	100	4	21.61	1.63	1.83
E	75	3.37	23.59	1.26	1.54

Female Bar-tailed Godwits had a higher instantaneous intake rate (1.78 prey/min) than males (1.5 prey/min; GLM, $F_{1,393} = 16.270$, $P < 0.001$).

The effects of kleptoparasitism by Black-headed Gulls on the intake rate of Bar-tailed Godwits were minor. In 78.3% of the observations (N= 396) one or more Black-headed Gulls were present within the flock. The highest numbers of Black-headed Gulls were present within flocks between 150 and 250 Bar-tailed Godwits (quadratic regression, $R^2 = 0.140$, $P < 0.001$; Fig. 9). Of all the attacks 60% of the attacks on Bar-tailed Godwits were observed in smaller flock sizes, between 50 and 150 individuals. From the total recorded foraging time Bar-tailed Godwits lost only 0.2% of their foraging time to kleptoparasitic attacks (Table 2).

An average kleptoparasitic attack lasted 2.7 second. From the total number of attacks observed during the observation sessions 46.88% were successful (Table 4). Foraging Bar-tailed Godwits lost only 0.56% of their captured preys at Black-headed Gulls (Table 2). Almost 60% of the attacked Bar-tailed Godwits were males (Table 3).

By comparing the overall intake rate of the observation without attacks and observation where the focal bird was attacked, no significant difference was found between the total intake rate (GLM, $F_{1,391} = 0.056$, $P = 0.812$).

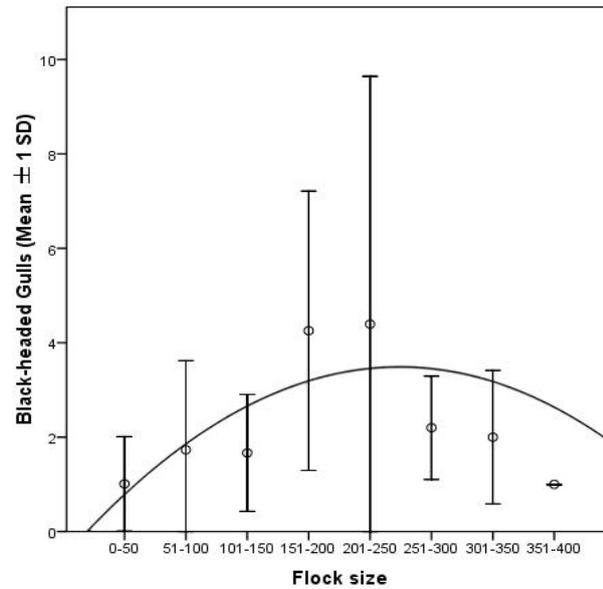


Figure 9. The numbers of present Black-headed Gulls (mean \pm 1 SD) are shown in relation to the flock sizes. The observations were separated in eight different categories of flock size.

Table 2. Details of the effects of food stealing behaviour by Black-headed Gulls from Bar-tailed Godwits observed on inland coastal meadows, separated for both sexes.

	Observation time (s)	Time loss (s)	Time loss (%)	Mean time (s) loss per attack	Total prey items	Prey loss (%)
Males	45132	130	0.29	6.8	1161	0.69
Females	49772	85	0.17	6.5	1486	0.47
Overall	94904	215	0.2	7.2	2647	0.56

Table 3. Details of the success rate of food stealing Black-headed Gulls based on the number of attacks during observations.

Number of observations	Number of attacks	Successful attacks (%)	Attacks males (%)	Attacks females (%)	Attacks per min
396	32	46.88	59.37	40.63	0.02

3.4 Disturbance

Disturbance of foraging Bar-tailed Godwits on inland coastal meadows were caused by 5 different factors, (1) Humans, (2) Raptors, (3) Carrion Crows (4) Sheep and (5) Unknown. Of 34% when a foraging flock was disturbed, the reason of disturbance was not detected (Fig. 10A) and 29% was caused by human activity. Most of the flocks were present nearby roads and bicycle paths. Often when a tractor or truck passed they flew up, they were also regularly disturbed by stopping cars and cyclists. In 18%, raptors were the cause of disturbance. Four different raptor species were identified, (1) Peregrine Falcon (*Falco peregrinus*), (2) Buzzard (*Buteo buteo*), (3) Marsh Harrier (*Circus aeruginosus*) and (4) Goshawk (*Accipiter gentilis*). Of those four raptor species buzzard were responsible for 50% of the disturbances (Fig. 10B). In all cases Buzzards flew over and were no threat to Bar-tailed Godwits. The other three raptor species can be a threat to Bar-tailed Godwits, but during the observations only one unsuccessful attack of a Peregrine falcon at a flock was observed. The consequence of the presence of raptors is that the flock flew up and many times they did not return or remained in the air for a long time.

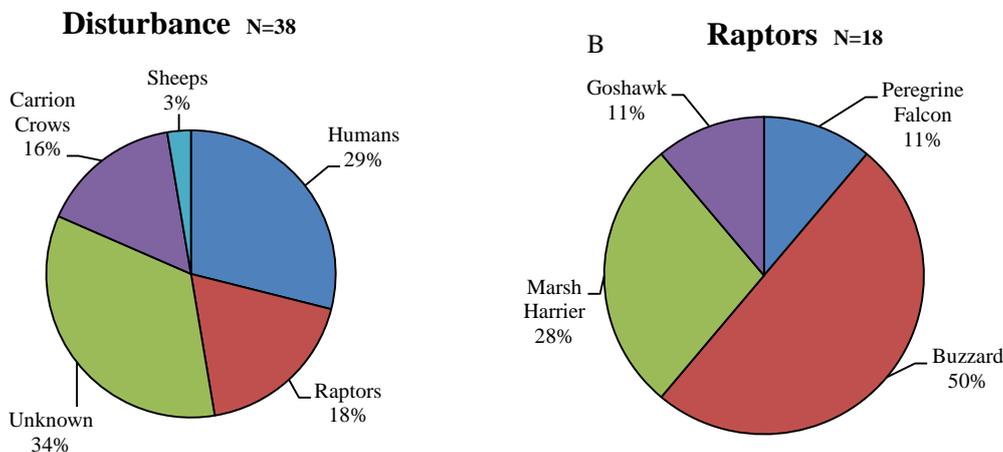


Figure 10. Disturbances were caused by different factors when Bar-tailed Godwits forage on inland coastal meadows, (A) represent the disturbed factors which were encountered during observations. From the raptors, the species were identified and shown in (B). N reference to the number of observation when foraging Bar-tailed Godwits were disturbed.

The other two factors (i.e. Carrion Crows and sheep) had no major impact on the flock. When Carrion Crows were present or flew over, the flock flew up and landed further to continue with their normal activities. Sheep had the same effect on Bar-tailed Godwits. Overall, a flock of Bar-tailed Godwits present on inland coastal meadows were disturbed 1.25 times per hour based on 30.3 hours of observation. Of the total observation time Bar-tailed Godwits were 8.5% vigilant.

3.5 Comparison between tidal mudflats and inland coastal meadows

When Bar-tailed Godwits forage on inland coastal meadows, they had a mean energy intake rate of 1.66 KJ/min, 1.45 KJ/min for males and 1.88 KJ/min for females respectively (Table 4). Foraging time fluctuated between 66% for males and 78% for females in May, with a total energy intake of 1171.2 KJ/day for males and 1790.8 KJ/day for females respectively. The difference between Bar-tailed Godwits affected by kleptoparasitism and without kleptoparasitism was 6.7 KJ/day by males and 10.2 KJ/day by females.

Table 4. For four different scenarios the total energy intake is calculated. The energy intake of Bar-tailed Godwits foraging on meadows was corrected with the assimilation efficiency of 85%. And the energy intake of Bar-tailed Godwits foraging on tidal mudflats was corrected with the assimilation efficiency of 80%.

	Sex	% for	Min. day	intake kj/min	Corrected intake kj with efficiency	Source
Meadow	♂	66	950.4	1.45	1171.2	own data
	♀	78	1123.2	1.88	1790.8	
Meadow with kleptoparasitism	♂	66	950.4	1.44	1164.5	own data
	♀	78	1123.2	1.87	1780.6	
Meadows and Tidal mudflats	♂	66	950.4	1.39	1089.6	own data; Scheiffarth et al. 2002;
	♀	72	1036.8	1.82	1509.6	Duijns et al. 2009
Tidal mudflats	♂	66	950.4	1.29	980.6	Scheiffarth et al. 2002;
	♀	66	950.4	1.72	1304.5	Duijns et al. 2009

When Bar-tailed Godwits forage only on tidal mudflats, they forage for 66% of the available time, with a total energy intake of 980.7 KJ/day for males and 1304.5 KJ/day for females respectively. If they also would forage during high tide on inland coastal meadows their energy intake could have increased to 1089.6 KJ/day for males and 1509.6 KJ/day for females.

From the perspective that Bar-tailed Godwits need every day a minimum energy requirements to survival, 879.2 KJ for males and 909.1 KJ for females both sexes reach their necessary requirements in all the four given scenarios. As shown in figure 11A and B, Bar-tailed Godwits on inland coastal meadows reach their daily requirement earlier than Bar-tailed Godwits on the tidal mudflats. Males which forage on the tidal mudflats reach their daily requirements after 21.5 hours compared to the inland coastal meadows were males reach their daily requirements after 18 hours.

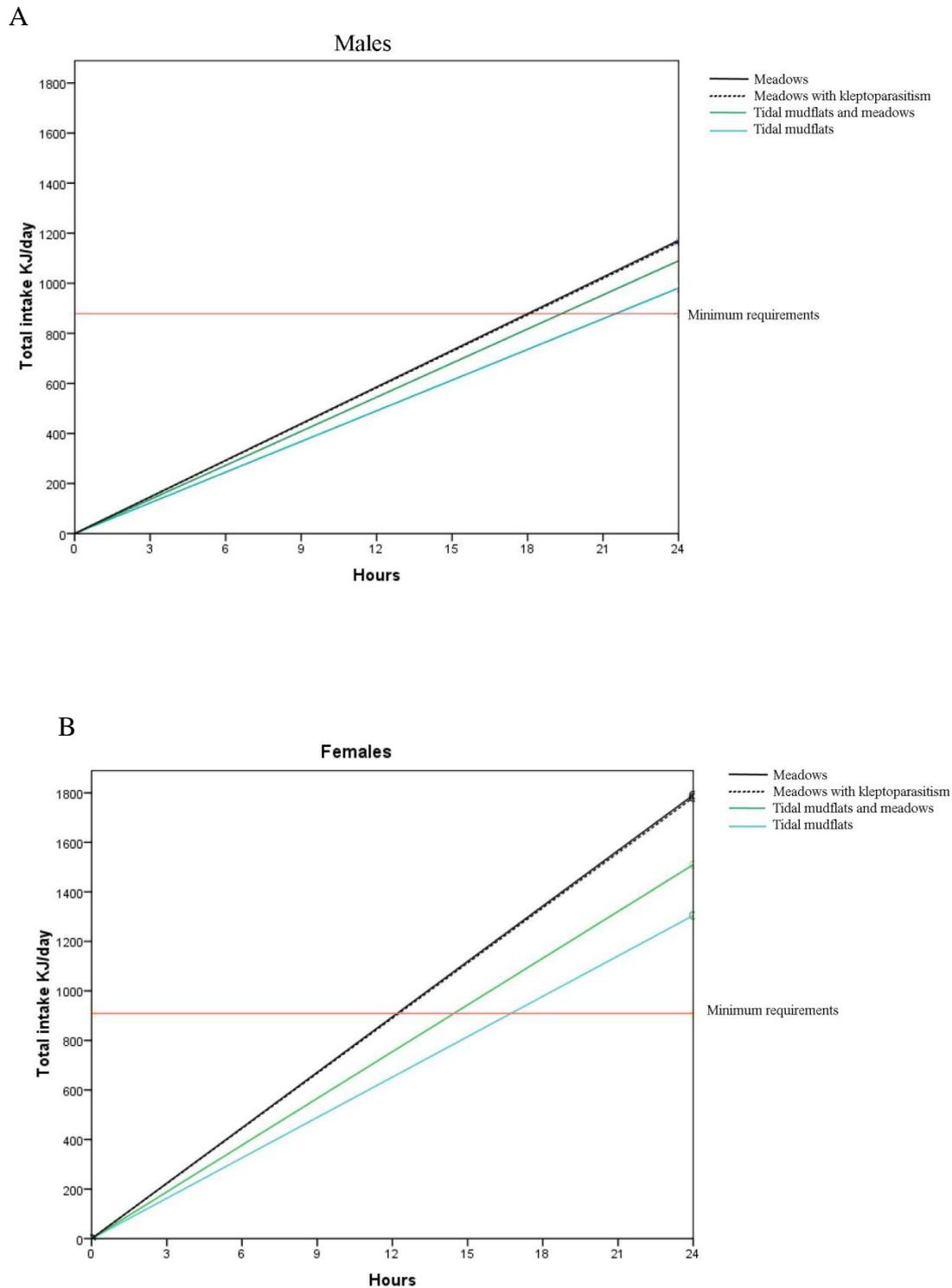


Figure 11. For four situation the total energy intake was calculated and for both sexes. These results are shown in relation to a day of 24 hours. Besides the energy intake for both sexes the minimum requirement for one day was calculated. The energy intake for males (A) does not differ from each other. However males on inland coastal meadows achieve a higher daily energy intake compared to the tidal mudflats. All extra achieved energy above the minimum requirement can be used for other activities as moulting and refill there departure fuel load. The same trend is found by females (B) only larger differences were found between daily energy intake of the tidal mud flats and the meadows.

4 Discussion

On inland coastal meadows Bar-tailed Godwits forage primarily on crane fly larvae and achieve a higher daily energy intake compared to the tidal mudflats. However, Prey densities on inland coastal meadows were lower compared with tidal mudflats. Prey density (g AFDM per m²) on inland coastal meadows varied between 2.3 and 10.6 while prey densities on the tidal mudflats varied between 20 and 27 (Beukema 1976; Beukema et al. 1978; Zwarts & Wanink 1993). Besides on the tidal mudflats food is not always available (e.g. tidal stage) for Bar-tailed Godwits, compared to the inland coastal meadows where food is available for 24 hours per day. Nevertheless Bar-tailed Godwits spent at both habitats almost the same amount of time on feeding activities and on inland coastal meadows they reach a higher daily energy intake at lower prey densities.

Crane fly larvae are an easy prey for Bar-tailed Godwits since crane fly larvae live in V-shaped burrows, usually close to the surface at 2 to 4 cm deep. Even in spring it is not always necessary to extract the crane fly larvae from their burrow, since they are then often found at, or just beneath, the surface (pers. obs.; Zwarts & Blomert 1996). Other possible prey species like earthworms also live in burrows but are usually buried 5 to 10 cm and are thus less easy to find (Zwarts & Blomert 1996). Crane fly larvae also have a higher energy content compared to the earthworm, 23.3 KJ and 21.5 KJ, respectively (Ralph 1957; Zwarts & Blomert 1996).

Crane fly larvae populations fluctuate from year to year with a peak year at approximately 5 year intervals (Blackshaw & Coll 1999; White 1963). During the study period (May 2011), densities between 33 and 204 individuals per m² were found. In contrast, Tinbergen (1980) measured crane fly larvae densities over 4 years on the Wadden Sea Island Schiermonnikoog and found densities between 9.5 per m² and 69.4 per m². In Great Britain Blackshaw & Petrovskii (2007) measured for 31 years crane fly larvae densities divided over three different locations, they found densities between < 20 per m² and 140 per m². This suggests crane fly densities measured in 2011 were locally above average. However the different crane fly larvae densities did not affect the intake rate of Bar-tailed Godwits.

The intake rate on inland coastal meadows was hardly affected by kleptoparasitic attacks. Kleptoparasitic attacks on inland coastal meadows were exclusively done by Black-headed Gulls *Chroicocephalus ridibundus*. Bar-tailed Godwits lost only 0.2% of their total foraging time to kleptoparasitic attacks and 0.56% of their prey items. The amount of lost prey items is similar to what Taylor et al. (1996) found by Bar-tailed Godwits on three intertidal sites on the estuary of the Parramatta River Australia. When actually attacked, Bar-tailed Godwits move quickly away from the Black-headed Gull in an attempt to avoid the attack and at the same time swallow their prey item. Of all kleptoparasitic attacks 46% were successful, which is much higher than 13% found by Taylor et al. (1996) and 7% by Dann (1979). These two studies were performed on tidal mudflats in Australia. Barnard & Thompson (1985) found a success rate of attacks by Black-headed Gulls of 74% on Lapwings *Vanellus vanellus* and 36% on Golden Plovers *Pluvialis apricaria* performed on meadows in Nottinghamshire. These species forage mainly on earthworms and larger worms could not be swallowed rapidly and this increased the handling time. A longer handling time provides an opportunity for a kleptoparasitic attack (Barnard & Thompson 1985). The handling time of crane fly larvae was not measured, however crane fly larvae are small prey items and likely this decreases the handling time. When the handling time decreases it is likely that kleptoparasitic attacks will occur less frequently.

In this study the effects of predation and disturbance on Bar-tailed Godwits on inland coastal meadows has not been studied in detail. However it seems that Bar-tailed Godwits adapt to the circumstances and tolerate more human activity and fly up earlier by natural causes. We found that human activity caused 29% of the disturbance and 37% had a natural cause. Nevertheless Smits & Visser (1993) shown that Bar-tailed Godwits on a high tide roost, in a cultivated grassland area at Terschelling, were disturbed in 64% of the time by human activity and 18% had a natural cause. These finding correspond with Scheiffarth et al. (2002) and Duijns et al. (2009), as they confirmed that *Taymyrensis* uses a time minimizing migration strategy whereas *Taymyrensis* shifted towards food-rich areas, while accepting more disturbance and an increased predation risk. The increase of the disturbance and predation risk was also supported by the percentage of time Bar-tailed Godwits spent to vigilant behaviour. When foraging on inland coastal meadows Bar-tailed Godwits were vigilant for 8.5% of their time, similar as the 7% found by Duijns et al. (2009). This compared to the tidal mudflats were Duijns et al. (2009) found that Bar-tailed Godwits were 2% of their time vigilant. Thus, Bar-tailed Godwits on inland coastal meadows spent 4 times more time at vigilant behaviour compared to Bar-tailed Godwits on the tidal mudflats.

During spring migration only a small part of the Bar-tailed Godwit population use inland coastal meadows which was also supported by colour-ringed birds which were frequently resighted on inland coastal meadows (unpublished data NIOZ). Within these flocks, sex ratio changed over time, resulting in a decrease in percentage of males. It appears that males depart earlier to their breeding grounds than females. Green et al. (2002) found no clear difference between females and males in timing of migration from the Dutch Wadden Sea Island Texel. However, when Bar-tailed Godwits migrated over South-Sweden males pass in higher numbers in the first three-days (Green et al. 2002).

It seems that Bar-tailed Godwits on inland coastal meadows face difficulties to reach their departure fuel load. Duijns et al. (2009) showed that the mean abdominal profile score of meadow foraging birds was lower compared to the birds foraging on the tidal flats and Piersma & Jukema (1993) showed that Bar-tailed Godwits at a coastal site were 40 g heavier than those feeding on inland coastal meadows. The moulting stage can also be used as an indicator for the migratory qualities of Bar-tailed Godwits, Piersma & Jukema (1993) suggest that only individuals which have sufficient energy/nutrient reserves can moult to their full breeding plumage. In the line of this findings, we found that the mean moulting score (for males only) on inland coastal was 5.8 compared with 6.5 (unpublished data S.Duijns) on the tidal mudflats.

We suggest that the most important advantage of inland coastal meadows is a higher energy intake, whereas the prey availability is lower compared with the tidal mudflats. Still it seems that only Bar-tailed Godwits which face difficulties during their stopover period in the Wadden Sea area use inland coastal meadows, but given the advantages of inland coastal meadows it raises the question; why don't more Bar-tailed Godwits use inland coastal meadows during spring migration?

Bar-tailed Godwits (*taymyrensis*) follow an time minimizing migration strategy (Scheiffarth et al. 2002; Duijns et al. 2009) and must accumulate a sufficient amount of fuel load, within a short stopover period. During this stopover period they face a trade-off between food and danger. Bar-tailed Godwits which face difficulties to reach their departure fuel load will choose for the benefits of better feeding opportunities outweigh the risk of selecting more dangerous areas (i.e. inland coastal meadows). This in contrast to the Bar-tailed Godwits which encounter no difficulties, they opt for safety at the tidal mudflats above food

availibility. Thus, it seems that the group Bar-tailed Godwits which encounter difficulties during spring migration is small.

5 Conclusion and recommendation

5.1 Conclusion

- *Does flock size of *taymyrensis* on inland coastal meadows relate to the tidal stage?*
Flock sizes on inland coastal meadows are not related to the tidal stage, figure 4A and B shows that there is no significant increase of Bar-tailed Godwits on inland coastal meadows during high tide.
- *What is the mean flock size of foraging *taymyrensis* on inland coastal meadows and does flock sizes change over time?*
The mean flock size was 110 birds and decreased over time (Fig. 5). In the beginning of the month May the sex ratio was equal. However gradually over time the percentage of males shows a significant decreasing trend (Fig. 6B).
- *What is the fuelling rate of *taymyrensis* on inland coastal meadows?*
Bar-tailed Godwits on inland coastal meadows shows an fuelling rate of 0.119 per day (§ 3.2)
- *What is the instantaneous intake rate (prey/min) of *taymyrensis* on inland coastal meadows?*
Female Bar-tailed Godwits had an instantaneous intake rate of 1.78 prey/min what is significant higher than male Bar-tailed Godwits with an instantaneous intake rate of 1.5 prey/min (§3.3).
- *Is kleptoparasitism common and if so, how does this effects their intake rate?*
Kleptoparasitic attacks occurs with a frequency of 0.02 attacks per minute (Table 3) and were exclusively done by Black-headed Gulls. Through kleptoparasitic attacks Bar-tailed Godwits lost 0.2% of their foraging time and 0.56% of their prey items (Table 2). This translated to their daily energy intake, males lost 6.68 KJ/day and females 10.21 KJ/day compared with Bar-tailed Godwits without kleptoparasitic attacks (Table 4, §3.5). Thus, kleptoparasitic attacks hardly affected the intake rate of Bar-tailed Godwits.
- *How often are foraging *taymyrensis* disturbed by human activities or disturbed/predated by predators?*
Foraging Bar-tailed Godwits were disturbed 1.25 times per hour (§3.4). Mostly the reason of disturbance was unknown, however 29% of the disturbed was caused by human activity (Fig. 10A).
- *What is the difference of daily energy intake (KJ/day) between inland coastal meadows compared to the adjacent mudflats?*
On inland coastal meadows both sexes of Bar-tailed Godwits obtained more energy per day compared to Bar-tailed Godwits on the adjacent mudflats, males obtained 190.6 KJ more energy per day and females 486.3 KJ (§3.5). The effect is that Bar-tailed Godwits on inland coastal meadows reach their daily minimum energy requirement earlier than Bar-tailed Godwits on the mudflats, males will reach their daily minimum energy requirements 3.5 hours earlier and females 4.5 hours (§3.5).

Eventually we conclude that inland coastal meadows enables Bar-tailed Godwits the opportunity of a high energy intake, however they face a higher predation and disturbance risk.

5.2 Recommendation

The advice is to continue this research since measurements from one season could give a distorted picture as variations per year occurs. And for future research, we advise to examine subject as behavioural activity patterns, night foraging and effect of predation/disturbance on the foraging efficiency of Bar-tailed Godwits on inland coastal meadows in more details.

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Appendix 1

