When will I leave?

Decision making and trade-offs in relation to timing of spring migration of male Bar-tailed Godwits (Limosa lapponica) at a stopover site

By: Harm Albers (s1705202) University of Groningen
Supervised by: Sjoerd Duijns

Abstract

Male Bar-tailed Godwits of the Afrosiberian population (L. lapponica taymirensis) use the Wadden Sea as a stopover site from migration where they replenish their fuel load and molt further into breeding plumage. In this thesis triggers influencing timing of males are explored in the light of decision making and trade-offs.

An interaction between fuel load and molt exists. Wind has to be studied in the future and plays thus far no role in timing. There are more males in this species and it is suggested that males depart earlier.

Proximate factors that underlie timing of male birds, obtaining a territory and growing a fresh feather pack in order to gain a female, could certainly play a role in Bar-tailed Godwits. Decisions are made by use of an interplay of several ultimate factors (weight and molt) sustained by proximate factors (competition for a mate, a tight migration scheme). Since an interaction between several factors exists, future research is difficult, interesting and necessary to unravel this.

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Introduction

Migration is a widely explored and described natural phenomenon since it implies that the costs it takes to migrate and to leave an area an individual is staying, overcomes the costs to stay at this spot during the year (Landsborough Thomson 1926, Lack 1954). So logically migration exists since of the benefits of the spot an animal migrates to exceed the benefits of staying at the same site all year long plus the costs of migrating. But birds that fly large distances need to obtain stock and carry large amounts of energy to cover large distances (Piersma 1987) and therefore face a large number of trade-offs. So although migration over large distances demands a lot of energy, birds anyhow practice an outward and homeward journey yearly.

The Bar-tailed Godwit (*Limosa lapponica*) for instance, can be termed as a bird that covers large migration distances (Cramp & Simmons 1983). It is assumed that individuals of one subspecies (*L.l. baueri*) fly non-stop intercontinental flights of approximately 10400 km (Gill *et al.* 2005). It is suggested that in general this subspecies uses a stopover site but still travels 8200-8500 km nonstop (Wilson *et al.* 2007). This subspecies is found in South-Eastern Australia and breeds in Alaska, another subspecies (*L.l. menzbieri*) is found in North-Eastern Australia and breeds in North-Eastern Russia (Wilson *et al.* 2007).

In Europe two populations (or subspecies according to Engelmoer & Roselaar 1998) are present during different times of the year (Cramp & Simmons 1983). Both populations take one or two large leaps to get from their wintering grounds to their breeding grounds, which can be perceived as a so called jump migration scheme (Piersma 1987). This results in taking a large amount of fuel load leading to a more costly migration because a heavier bird puts more energy in flying (Piersma 1987). Both the European and the Afro Siberian population reside at the Wadden Sea for a part of the year (Cramp & Simmons 1983). The European population, subspecies *L.l. lapponica* (Engelmoer & Roselaar 1998), winters at the Wadden Sea and breeds in Northern Europe. The Afro Siberian population, subspecies *L.l. taymirensis* (Engelmoer & Roselaar 1998), winters in Western Africa and migrates in two steps to the breeding grounds. During the winter they stay in Western Africa and during early spring they increase their amount of fat and migrate to the Wadden Sea to replenish their fuel stores again in order to fly to the breeding grounds in Western Siberia. This means that the Afro Siberian population migrates over the European population, which is called leap frog migration (Drent & Piersma 1990, Salomonsen 1954).

The Afro Siberian population (*L.l. taymirensis*) is a population with a tight schedule to keep during migration. They migrate to an area stretching from the Pechora River to eastern Taymyr Peninsula in Siberia (Cramp & Simmons 1983). Here the Bar-tailed Godwits often still need to mate (Cramp and Simmons 1983, Yésou *et al.* 1992) and the females have to produce the eggs. This takes a week (Piersma 1987) and then they need to incubate these eggs for three weeks (Piersma 1987, McCaffery & Gill 2001). Finally when the chicks hatch, the four weeks left will be used by the young to develop the ability to fly (Piersma 1987, McCaffery & Gill 2001). The total time to complete the breeding cycle is two months. The appropriate time in which they have to complete it is exactly the same so almost no delay or increase in arrival and departure is possible (Glutz von Blotzheim *et al* in: Piersma 1987). In other words there is very little flexibility in the time it takes and the time they have to complete the breeding cycle. The cause of the tight time scheme Bar-tailed Godwits of the Afro Siberian population face will be further explained as this scheme in the breeding cycle sets the background for the timing of departure from the Wadden Sea during spring. Since these birds can not leave to early because arriving early at their breeding grounds could result in unfavorable conditions, meaning food is scarce (Piersma 1987). And since the breeding cycle requires at least a small two months, leaving too late can result in bad conditions at the end of the breeding cycle probably with food being scarce. For the reason of food scarcity birds have only a fixed period of a few days to leave for their “jump” from their stopover site the Wadden Sea towards their breeding grounds in Siberia (Glutz von Blotzheim *et al.* in: Piersma 1987). Birds have to adapt and know when the time to depart towards the breeding grounds has come so that they can keep track of their schedule. It is proposed that they do this by use of an internal clock or that they respond to the increasing length of the day

(e.g. Piersma *et al*. 1990). Another proposed trigger for departure is wind, but this is variable between heights and yet no correlation has been found of wind speed and direction between ground level and higher (Piersma *et al.* 1990). Though it has been found that wind plays a very positive role in migration in theory (Alerstam 1979) and in practice (Piersma & Jukema 1990). These factors will be further explained during this thesis.

Since the date of departure from the Wadden Sea, the duration of migration towards the breeding grounds and the arrival date in Siberia of these Bar-tailed Godwits are interconnected, knowledge of all these components will be considered in order to get to know about the proximate and ultimate factors determining departure of males. Bar-tailed Godwits are sexual dimorph and have some differences in breeding ecology between males and females, this might cause differences in timing of departure from their stopover site between the sexes. Male Bar-tailed Godwits are about 20% smaller and carry a different molt during the breeding season, whereas their under parts are colored deep rufous-cinnamon these are pink-cinnamon to pale in females (Cramp & Simmons 1983). Besides, males and females play a different role in the breeding ecology (Cramp & Simmons 1983) although little is known about the breeding ecology and the mating system of Bar-tailed Godwits. So this knowledge combined with knowledge about other wader species, intern and extern factors determining departure of male Bar-tailed Godwits (*Limosa lapponica*) from the Wadden Sea to the breeding grounds during spring migration are studied. A difference in the mating system between the sexes can lead to a separated timing of females and males (Gunnarsson *et al.* 2006, Forstmeier 2002). And although no clear evidence has been presented if male Bar-tailed Godwits depart earlier from the Wadden Sea during spring migration (Drent *et al*. 2003, Green *et al*. 2002, Battley 2007), a potential difference is looked upon in this study by determining triggers counting for both sexes and how these triggers could differ between sexes. Since some studies suggest that males depart from their stopover site somewhat earlier than females (Own observations 2010, Prokosch 1988)

Fuel Load

In order to complete the journey from their stopover site to their breeding grounds and afterwards face the sometimes bad weather conditions in the first days at these grounds, the birds from the Afro Siberian population built up a certain amount of reserve energy (Piersma & Jukema 1993). These are large amounts of energy and are called the fuel load, which a bird obtains simply said from taking in more energy than it spends (Piersma 1987). This fuel load is necessary to have for a Bar-tailed Godwit which will migrate and it could therefore be interesting regarding timing. Depositioning of this fuel load is seen as the weight of the average bird increases, but of this weight increase only 52% in females and 48% in males consists of fat, which is the main energy source a bird uses to fly (Piersma & Jukema 1993). A great amount of the total deposited fuel load is depleted during flight, for instance during the flight from the Banc d'Arguin in Mauritania to the Paesenserpolder in the Netherlands the male birds lose all the 178 grams (86 grams of fat) they built up during March and April in Mauritania (Piersma & Jukema 1993). Compared to the journey from Mauritania to the Netherlands, for a journey of somewhat the same distance from the Wadden Sea to the Siberian breeding grounds the male birds increase their weight even more (Piersma & Jukema 1990).

Bar-tailed Godwits, which are on a tight schedule, need to obtain enough fuel to make it from the Wadden Sea to the breeding grounds in a certain time. Several factors have an influence on the speed the fuel load is increasing. Birds can influence this increase themselves by increasing or decreasing the effort put in foraging (Piersma 1987). But sometimes it is physiologically impossible for birds to increase their effort put in foraging although food is available in large amounts (Kirkwood 1983). On the other hand, factors other than the birds themselves influencing the speed fuel load increases are a high ambient temperature which constrains the birds from increasing their effort put in foraging or bad food circumstances (Kersten *et al.* 1983, Drent & Piersma 1990).

So focusing on the Bar-tailed Godwits of the Afro Siberian population (*Limosa lapponica taymirensis*) two periods of weight increase before and during spring migration come forward (Piersma & Jukema 1990). The

first of these periods is at the wintering site in Western Africa, where males and females respectively increase 2.8 and 3.2 g/day on average (Piersma & Jukema 1990). The second increase in weight is at the Wadden Sea, where males and females respectively increase on average 5.9 g/day and 6.7 g/day (own data) and for 1984 to 1988 5.6 g/day and 7.5 g/day. Each year from 1984 to1988 increase showed no difference between years (Piersma & Jukema 1990). At the Wadden Sea the increase in weight starts directly at their arrival and continues linearly (Piersma & Jukema 1990). Their weight has increased largely when they depart during late May and early June with an average median departure date of 31 May in 1984 and 1 June in 1985 and 1986 (Piersma & Jukema 1990).

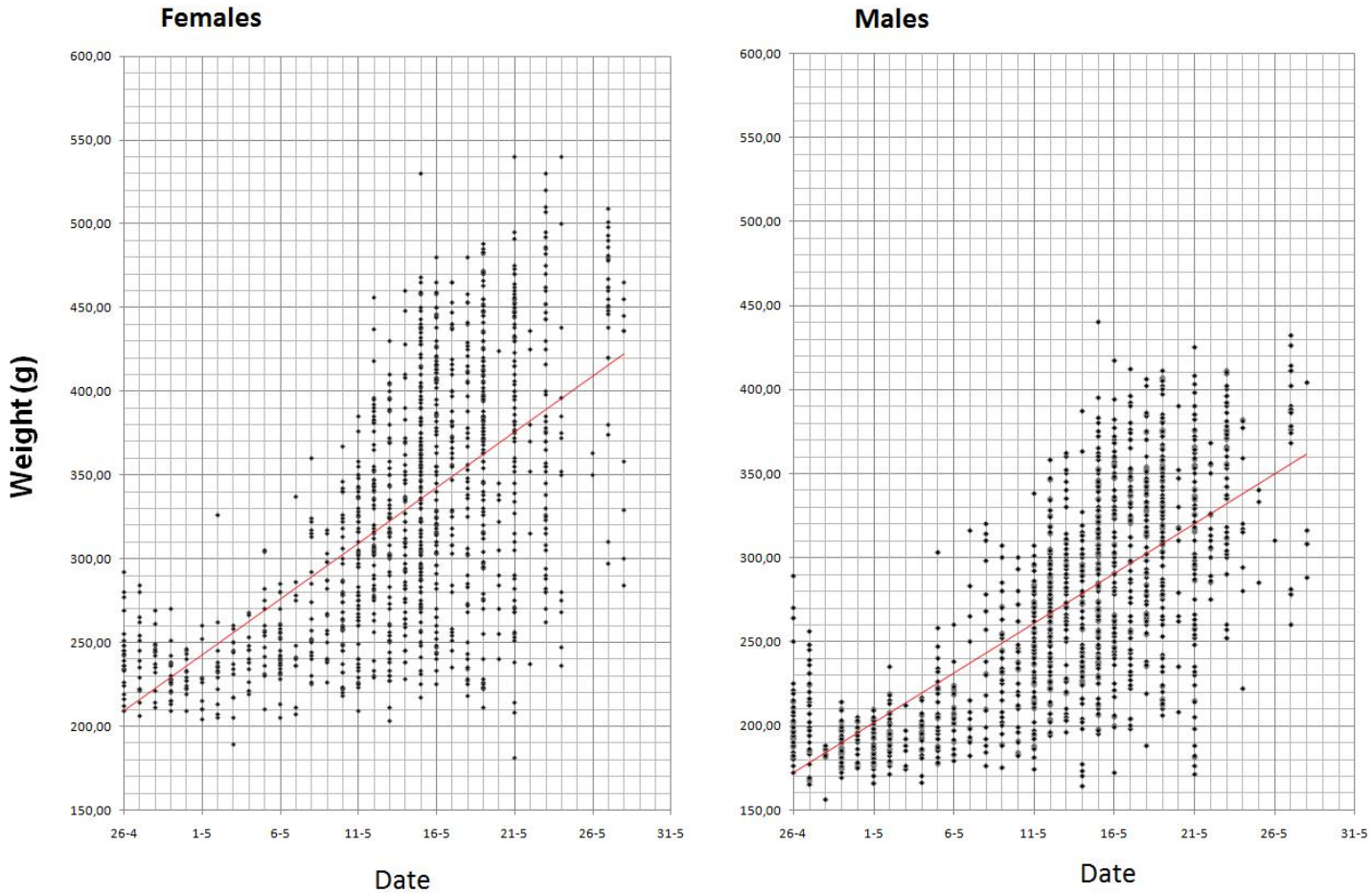

Figure 1 Dots represent weights of Bar-tailed godwits caught between 26-4 and 31-5 in the years 2002-2009 around the Wadden Sea. Red line is the average weight increase of females (left slope=6.7g/d R^2=0.41) and males (right slope=5.9g/d R^2=0.53). Data from the NIOZ Bar-tailed Godwit database.

Molt

Both sexes have a different molt during the breeding season and non-breeding season. Males look much more rufous in breeding plumage since their wing-coverts are grey brown and head and neck are richly chestnut colored (Cramp & Simmons 1983). In the non-breeding plumage males are much paler just like females during that time (Cramp & Simmons 1983). Breeding molt feathers are by half of the birds partly grown at the stopover-site during spring migration (Piersma & Jukema 1993). This growth of feathers is an energetic costly activity and it might be an indicator for the migratory quality of a bird (Piersma & Jukema 1993). So birds that are not able to fulfill their fuel load on time might compensate this with a delay of their molt in order to keep increasing their weight sufficiently.

Before migration to the Wadden Sea males start the partial molt of contour feathers and finish it in several steps (Piersma & Jukema 1993). During migratory flights it is suggested that the Bar-tailed Godwits do not actively

molt since the most of some Bar-tailed Godwits caught just before the average departure date were not in molt (Piersma & Jukema 1993). Of the males that were caught in the Wadden Sea, the ones that were in molt had a higher weight than those that were not, which opposes the general idea that the birds which are in molt are the lighter individuals (Zwarts *et al.* 1990). The combination of being in molt and increasing in weight is an interesting trade-off since these are both energy consuming activities (Piersma & Jukema 1993). In other species it is known that migratory quality is important as indicator of the timing ability of a bird if early individuals have an advantage over the later ones (Daan *et al.* 1990). Male Bar-tailed Godwits can show their migratory quality to the females by growing fresh contour feathers (Piersma & Jukema 1993).

Wind

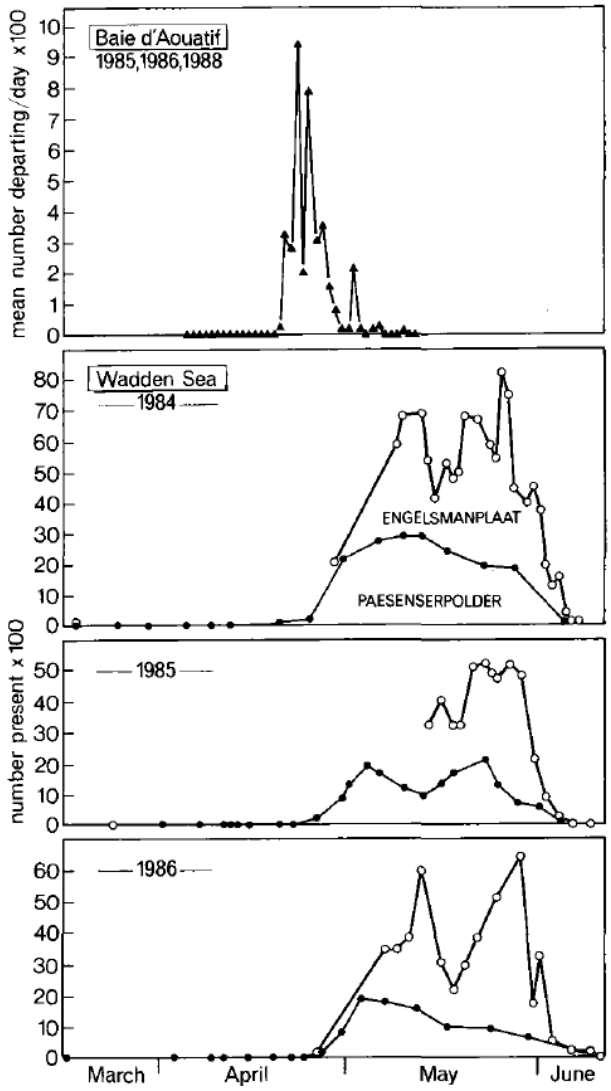

Figure 2 From Piersma & Jukema 1990**. #** of birds departing from the Baie d'Aouatif Banc d'Arguin averaged for the years 1985, 1986 and 1988 (top panel) and # of present birds at the Wadden Sea at the Engelsmanplaat and the Paesenserpolder

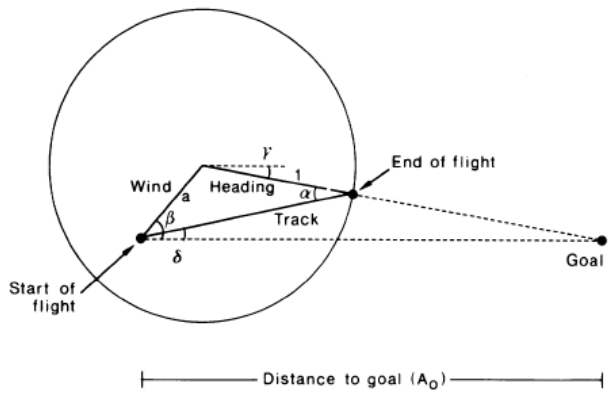

Figure 3 From Alerstam 1979. Theoretical model of wind influencing optimal flight direction for a bird. ß=wind direction, •=start end and goal of the flight, circle=location a bird reaches using a constant amount of effort

When Bar-tailed Godwits fly from the Wadden Sea to their breeding grounds, wind can play a major role in their energy expenditure. Piersma and Jukema (1990) proved that these birds have to make use of favorable high altitude winds or else their energy reserves would be insufficient to reach the Wadden Sea from the Banc d'Arguin. Meaning that wind certainly plays a role in the migration of Bar-tailed Godwits and could play a role in the timing. Not much research has been done on wind determining timing but the theory can give an indication on its role taking timing into account.

The advantage of flying with tailwind is explained in a theoretical model by Alerstam (1979, figure 3). At the start of the flight of a bird the wind blows in a certain constant direction ("Wind" in the figure 3). The dot shows the start spot of the bird and the circle shows all the points a bird can end up if it flies in a constant air speed in that direction. So this figure shows the wind can increase or decrease the distance a bird travels within a certain time and also that in theory when winds are variable across the journey, the bird should drift a bit with the wind although that does not bring it directly to the target spot. In practice this is more difficult because birds have to navigate and going off the known track can disorientate a bird and be of a bigger disadvantage than the advantage of traveling faster (Alerstam 1979).

In short term variation of migration, it is shown that wind is of importance (Richardson 1978), but Bar-tailed Godwits show little variation in departure date from year to year at the Wadden Sea (Piersma & Jukema 1990, table 1). This could either mean that the short term wind conditions are the same from year to year or that these birds use tailwinds only if present. Both explanations make sense in the light of different studies done on different species but also on Bar-tailed Godwits, but that the birds only use tailwinds if present would be most logical. That the short term wind conditions are not the same from year to year at the Wadden Sea is clear from data of the KNMI (table 1). Besides, wind conditions can be in a major different direction on a few kilometers height compared to ground level (Piersma *et al.* 1990). It is known that these birds can fly on great heights and choose the height with the most preferable wind conditions (Piersma *et al.* 1990). Therefore it is possible that an unfavorable ground level wind direction does not keep these birds from departing. Next to that wind data on the ground of the departure period show great variation between years (table 1). Finally Bar-tailed Godwits from the Afro Siberian population are constrained by their tight migration scheme and variation in wind direction between heights allows them to depart even with unfavorable wind directions at ground level. Therefore it is logical that no pattern is observed between the wind direction on ground level and the departure date of Bar-tailed Godwits from the Afro Siberian population at their stopover site. Although no pattern was found, there is also no proof these birds using the wind for their advantage, future research should be done to get behind this.

Table 1 *Wind speed and directions in Leeuwarden during departure of Bar-tailed Godwits from the Paesenserpolder during spring migration in the years 1984 to 1986. Data from the KNMI, red squares are median departure dates from Piersma et al. 1990.*

1984	27 May	28 May	29 May	30 May	31 May	1 June	2 June	3 June	4 June
Wind sp.	3.1	4.6	4.6	4.6	3.6	2.6	4.1	6.2	5.1
Wind dir.	ENE	N	N	NNE	SE	SSW	SSW	ENE	W

1985	27 May	28 May	29 May	30 May	31 May	1 June	2 June	3 June	4 June
Wind sp.	4.1	4.1	5.1	5.1	3.6	4.1	4.1	3.6	2.6
Wind dir.	S	WNW	N	NNE	NNE	NE	NE	NE	O

1986	27 May	28 May	29 May	30 May	31 May	1 June	2 June	3 June	4 June
Wind sp.	7.2	4.6	3.6	3.1	2.6	2.6	2.1	4.6	8.7
Wind dir.	SW	W	NNW	NNW	SSW	SSE	NE	W	WNW

A note on the data collected by Piersma and Jukema (1990) is that for Bar-tailed Godwits it is difficult to predict whether birds which leave earlier from their stopover site the Wadden Sea also arrive earlier at their breeding grounds (Green *et al.* 2002). This is because there is a large variation in breaks during flight per bird. A journey of 650 km from the Dutch Wadden Sea (Texel) to south Sweden that is completed by a Bar-tailed Godwit is fastest tracked in a time of 19.5 hours and slowest in 188.6 hours (Green *et al.* 2002). Mean (± SD) of 13 birds was 80.2 ± 58.1 hour. In this study there were no significant differences found in departure date of males compared to females and fly-over date of males compared to females.

Sex differences

The sex-ratio of Bar-tailed Godwits shows more females than males towards the median departure date at the stopover site (own observations 2010, Prokosch 1988). This does not prove that males are migrating earlier to their breeding grounds (Green *et al.* 2002). But it might indicate an earlier departure of males for the migration to the breeding grounds, which is supported by the theory (Lack 1954). However, using the knowledge shown in this thesis already provides some information of how a different timing of males is constructed.

Fact is that males are smaller and show some difference in behavior on the breeding grounds compared to females (Cramp & Simmons 1983, McCaffery & Gill 2001). While the Bar-tailed Godwit is a gregarious bird on the non-breeding grounds, during breeding season they are territorial. They form small flocks of mixed sex and mixed age before spring migration (Cramp & Simmons 1983). A monogamous mating system exists in the Afro Siberian population of Bar-tailed Godwits. The males display ceremonial flights which are described as a territorial display but it is possibly a mate-seeking display (Cramp & Simmons 1983). On top of that, paired males expose ground chasing against other males. So there seems to be some mate guarding in Bar-tailed Godwits alongside the pair bonding. (McCaffery & Gill 2001). The mating happens when the couples are at the breeding grounds or sometimes during migration (McCaffery & Gill 2001). There seems to be a bias in the population of Bar-tailed Godwits from the Afro Siberian population towards more males (Prokosch 1988, Piersma & Jukema 1993). Males of other species have adjusted to females and often appear at breeding grounds earlier to gain a good territory and a good mate (Lack 1954, Gunnarsson *et al.* 2006, Kokko 1999).

There are many thoughts about males competing for females and the consequence of it for their timing (Lack 1954) but for Bar-tailed Godwits it is suggested that this competition is expressed by the increase of plumage score of males (Piersma & Jukema 1993). Secondly males departing earlier will risk the chance of facing bad weather conditions although they would increase their chance of mating (Drent *et al.* 2003).

Conclusion

Females should lay eggs at a time which results in optimal rearing circumstances (Lack 1954). This is shown in Bar-tailed Godwits where the eggs are laid on a date that not only is an ultimate effect of the offspring being in optimal rearing conditions, but also an effect of the variable weather conditions at the breeding grounds forcing the bird simply to lay her eggs after a certain date (Drent *et al.* 2003). As this date of laying the eggs stays constant of the years, the Bar-tailed Godwits can adapt to the stopover site in an optimal way and depart from there at the moment that will result in optimal rearing circumstances. Males of some bird species adjust to their females and often appear at breeding grounds earlier (Lack 1954), this results in a high yearly reproductive success (Lack 1954, Gunnarsson *et al.* 2006, Kokko 1999). The biased sex-ratio in Bar-tailed Godwits towards more males (Piersma & Jukema 1993) supports this theory since this increases competition for females. So that males are competing not only for good mates but just for a mate. Male Bar-tailed Godwits show little territorial behavior but they do show more of this type of behavior than females, therefore it could be an ultimate factor causing males to leave earlier from the stopover site, since they need to obtain a territory in order to defend one. Nevertheless, the theory says that males not leave, but appear earlier and to conclude this, it has to be assumed that males departing earlier also arrive earlier. But there is not sufficient information about the date of arrival of the different sexes at the breeding grounds to positively correlate departure date from the stopover site with the arrival date on the breeding grounds. Therefore further research still has to be done on arrival and departure date next to research on the territorial quality, territorial behavior, territory choice and partner choice of Bar-tailed Godwits, in order to confirm the hypothesis that males depart earlier to arrive earlier and eventually to gain a good territory for a high yearly reproductive success.

Taking it as simple as possible, males and females differ in size and the females which are larger also have a higher departure mass (Piersma 1990, Prokosch 1988, figure 1). Their increase in mass represents an increase in fuel load and this has to be sufficient in order to complete the journey to the breeding grounds and the conditions they face there (Piersma 1987). What could proximately explain the early departure of males might be the fact that the threshold fuel load is reached earlier by males. Underlying this is that males in proportion have a lower threshold or they have the relatively same threshold but in proportion they increase more in weight (figure 4). So in the figure if the males reach their threshold around 370 grams and the females reach it around 450 grams the males will depart earlier. The average weight of adult females during non-breeding season (without any fuel load for migration) is 273 grams and adult males weigh on average 243 grams (Dick & Pienkowski 1979). This means relatively males increase 2.43 grams per 100 grams of a bird per day against 2.45 grams per 100 grams bird per day regarding females. Meaning increase of weight stays relatively the same and therefore it would be more logical to say that a different relative threshold is the immediate cause of males to depart earlier.

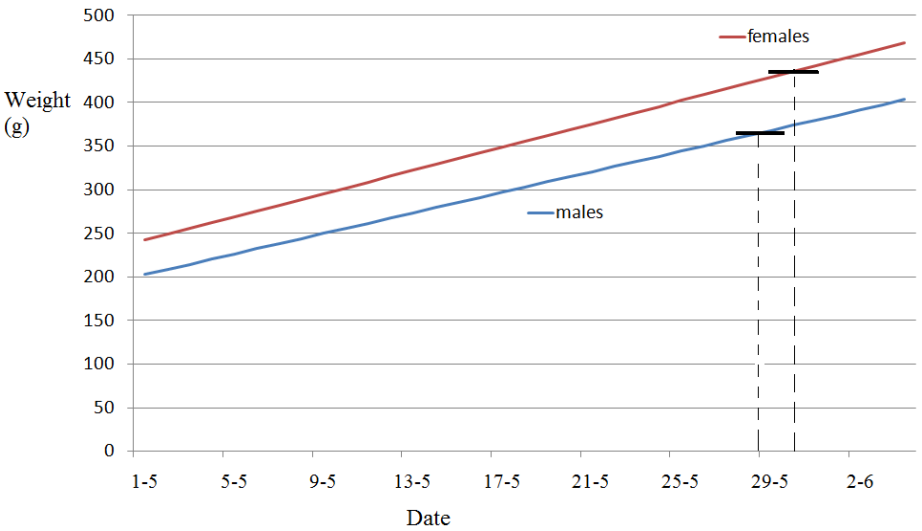

Figure 4 Average weight increase of Bar-tailed godwits caught between 26-4 and 31-5 in the years 2002-2009 around the Wadden Sea. Females (red slope=6.7g/d) and males (blue slope=5.9g/d). Two differing hypothetical threshold weights and the accessory departure dates. Data from the NIOZ Bar-tailed Godwit database. See figure 1.

Wind is proved to be also of importance in the migration of Bar-tailed Godwits, but its speed and direction on ground level has no influence on the moment of departure in this species. This enables unsynchronized migration schemes of males and females since individuals are not dependent on a few days when the wind is in the right direction and at the right speed. But this has to sustained by future research since there might be a pattern over the years that in a certain period at the end of May and the start of June a constant tailwind is originated which is used by the Bar-tailed Godwits to reduce the energy expenditure during this migratory flight (Piersma *et al.* 1990, Alerstam 1979, e.g. Landsborough Thomson 1926).

Among other triggers causing males to depart is, the state of molt might be of importance. Bar-tailed Godwits which have a higher weight invest more often in being in molt, so the other way around males which have the highest quality breeding plumage (freshest and darkest) show a higher migratory quality (Piersma & Jukema 1993). This could be used as indicator for the females (Piersma & Jukema 1993). This fact creates the opportunity for males to show females their quality in two ways, firstly by arriving early at the breeding grounds and obtaining a good territory (e.g. Lack 1954, Gunnarsson *et al.* 2006, Kokko 1999). Secondly by showing a high quality breeding plumage (e.g. Perrins 1965, Daan *et al.* 1990). For this reason the discrepancy in departure date between males and females might be leveled out in comparison with what could be expected from the first system (Kokko 1999) since an increase of the breeding plumage quality takes time and energy which in turn might be translated into time.

Those two opportunities might create a trade-off with an optimal departure date. Because one can expect obtaining a good territory to cause the males to depart earlier, but increasing the quality of the breeding plumage to create a male to delay departure since energy intake is required (Piersma & Jukema 1993). Instantly a very interesting complicated system arises which might not be constant since the food circumstances are not always equal and therefore intake rates differ per year and the effort put in quality of the plumage might differ per year. Especially with the great changes in climate and environment with the extremity of change in the Arctic and subarctic (ACIA 2005). The increase in temperature in the subarctic is an opportunity for the males Bar-tailed Godwits since these can arrive earlier to obtain a territory and not be severed by snow that has not yet melt. For future research it is not only an interesting question if fluctuations per year exist. Also what the underlying causes are for males to choose a certain day to depart. So to look through these fluctuations to the system behind it since a lot is known about the phenomenon of timing but still there is a lot to learn in this complicated but rather exceptional species.

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