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Authors: Piersma, Theunis, and Jukema, Joop

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BUDGETING THE FLIGHT OF A LONG-DISTANCE MIGRANT: CHANGES IN NUTRIENT RESERVE LEVELS OF BAR-TAILED GODWITS AT SUCCESSIVE SPRING STAGING SITES

THEUNIS PIERSMA[1,2,3] & JOOP JUKEMA[4]

ABSTRACT A single population of Bar-tailed Godwits *limosa lapponica* was studied before departure from their wintering grounds on the Banc d'Arguin in Mauritania, and at a spring staging site in the Dutch Wadden Sea. On the Banc d'Arguin the godwits started gaining body mass in the course of March at rates of about 2.8 g d^{-1} in ♂♂ and 3.2 g d^{-1} in ♀♀, before leaving north between 25 and 27 April. In the Wadden Sea, body mass increased linearly over the entire staging period (29 April-31 May) at 5.6 g d^{-1} in ♂♂ and 7.5 g d^{-1} in ♀♀. Half of the mass increase was due to the deposition of fat, the other half to increases in fat-free tissue (mainly muscle protein). If the godwits flew at the heights with most tail wind assistance by varying their flight altitude up to 5.5 km, they gained an average wind assistance of 18 km h^{-1}, which would add considerably to their estimated air speed of 57 km h^{-1}. At an average ground speed of 57 + 18 = 75 km h^{-1} the godwits would cover the required 4300 km in 57.3 h. During this flight, ♂♂ and ♀♀ were estimated to lose 136 g and 178 g respectively. Since half of these mass losses consisted of fat, they represent energetic equivalents of 3163 kJ and 3857 kJ respectively, leading to estimated flight costs of 55 kJ h^{-1} for ♂♂ and 67 kJ h^{-1} for ♀♀. The energy reserves stored on the Banc d'Arguin would not enable the Bar-tailed Godwits to cover the distance between W. Africa and the Wadden Sea in one flight without making good use of favourable high-altitude winds.

[1]Zoological Laboratory, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands; [2]Netherlands Institute for Sea Research (NIOZ); [3]Foundation Working Group for International Wader and Waterfowl Research (WIWO); [4]Haerdawei 44, 8854 AC Oosterbierum, The Netherlands

INTRODUCTION

Energy, time, safety against predators and the spatial distribution of suitable habitats have all been put forward as factors that constrain the migratory options available to birds (e.g. Moreau 1972, Alerstam 1981, Gauthreaux 1982, Alerstam *et al.* 1986, Piersma 1987, Bairlein 1988, Alerstam & Lindström 1990). To find out which are the crucial factors that mould the variety of bird migration systems, detailed descriptive studies of the migration of specific populations are a first requirement. In spite of an abundance of general knowledge about patterns of bird migration (e.g. Baker 1978, Mead 1983) and much data on the energy cost of flight (recent reviews by Masman & Klaassen 1987, Castro & Myers 1988, Rayner 1990), such comprehensive analyses of itinerary, timing and energy gains and losses during migrations of specified populations are not readily available (but see Alerstam 1985, Dick *et al.* 1987 and Biebach 1990 for a variety of recent approaches).

This study sets out to provide a detailed description of the northward migration of Bar-tailed Godwits *Limosa lapponica* that have wintered in W. Africa. Since these Bar-tailed Godwits show a very synchronized spring migration, we can use the changes in the average nutrient reserves levels at the two studied staging sites to realistically estimate the energy loss of individual godwits during a

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single long-distance flight. We will examine the possibility that the godwits use favourable high altitude winds to balance their rather constrained time and energy budgets.

The Bar-tailed Godwit is a sexually dimorphic (♀♀ larger and paler than ♂♂), middle-sized wader species, breeding on low to high Arctic tundra (Cramp & Simmons 1983). The breeding populations from N. Europe and W. Siberia winter in respectively W. Europe (115 000 birds) and W. Africa (707 000 birds), the species thus representing a clear example of a leap-frog migrant (Smit & Piersma 1989, Drent & Piersma 1990; see Salomonsen 1955 for identifying this interesting category of migrants). About 156 000 birds winter in Guinea-Bissau (Zwarts 1988), but the majority of the W. African birds winters on the Banc d'Arguin in Mauritania (540 000 birds, Trotignon *et al.* 1980, Altenburg *et al.* 1983), where we studied their departure from the wintering grounds. The spring staging before the flight to the breeding grounds was studied at a site in the Dutch Wadden Sea during the same seasons.

METHODS

Fieldwork

On the Banc d'Arguin in Mauritania, Bar-tailed Godwits were captured in the neighbourhood of Iouik (19°53'N, 16°17'W) in the periods 22 March-29 April 1985 and 8 February-12 April 1986. The majority of individuals (101 of the total of 115) were captured in mistnets in the Baie d'Aouatif, the remaining 14 were caught with a cannon-net in Ebelk Aiznay, a bay NW of Iouik, in early April 1985 (see Wolff & Smit 1990 for site descriptions and Ens *et al.* 1990 for further details). Mistnets were set over the exposed mudflats during nocturnal low tides and checked 3-4 times per night. Birds were carried to base camp for ringing, measuring and, in 1985, colour-marking. Wing length (maximum chord, Evans 1986), bill length (exposed culmen) and tarsus plus toe length (Piersma 1984b) were measured. Since a lot of the godwits captured early in the season still had to moult into summer plumage (Piersma 1989), birds could not always be sexed in the hand. For this reason sex was estimated from bill length (see below). Birds were weighed with Pesola spring-balances and the time elapsed between catching and weighing was estimated. Thirty godwits were kept in boxes and weighed twice after capture. Over a period of 10 h after first weighing they lost body mass at a constant rate of 1.9 g h^{-1} ($r = 0.54$, Piersma 1989). Using this value, body masses were standardized to the estimated mass at one hour after capture. In spring 1985 the under-tails of captured godwits were dyed yellow with picric acid, and a piece of coloured tape was applied around the ring to allow resightings within that season at the site of capture and further along the migration route.

In the Dutch Wadden Sea, Bar-tailed Godwits were captured with wilsternets (large wind-swept 'clap-nets', see Eenshuistra 1973, Koopman & Hulscher 1979) in the Paesenserpolder (53°21'N, 6°06'E) during the periods 30 April-3 June 1984-1988. Birds in flight were attracted to the netting site with 1) whistles (made on a 'wilster-flute') specifically developed for the purpose, 2) a 'flock' of ca. 25 Golden Plover *Pluvialis apricaria*-decoys on and around the netting site, and 3) in many cases a live Bar-tailed Godwit acting as a, particularly attractive, additional decoy. Birds were taken out of the net immediately after capture. They were weighed and measured within about one h after capture, so body mass values were not transformed. Since all the birds were in summer plumage, they could reliably be sexed on the basis of plumage colour (dark brown-red in ♂♂, beige with sometimes a brown-reddish glow in ♀♀) and sometimes overall size (♀♀ largest, Cramp & Simmons 1983).

Observations in the Baie d'Aouatif on departing flocks (Piersma *et al.* 1990a) and series of counts on the high tide roost in the Paesenserpolder (P.M. Zegers & A.A. Goede pers. comm.) and on the nearby island of Engelsmanplaat (H. Smit pers. comm.) in the springs of 1984, 1985 and 1986, yielded information on the timing of the migrations of Bar-tailed Godwits at and between the two sites.

Body composition analysis

During the catching operations some birds died accidentally. Such individuals were weighed as soon as possible, measured in the standard way, and dissected to determine their sex by gonadal inspection. The carcasses were cut in parts and dried to constant mass in an oven at 60-80°C. Birds from the Banc d'Arguin were vacuum-packed in plastic bags and stored in plastic containers with silica-gel. The latter was to ensure that the carcasses kept dry during transport to The Netherlands. Fat extraction of the dry carcasses took place in a large Soxhlet apparatus using petroleum-ether (boiling traject 40-60°C) as the solvent. Fat masses were obtained by subtracting fat-free dry from dry masses. Birds from the Banc d'Arguin suffered from some dehydration before analysis (see Piersma & van Brederode 1990): their water content (percentage of fat-free mass) amounted to 66.5%. This compares with an average of 70% (*SD* is only 2%) in the sample of birds from the Wadden Sea. In order to make the two samples fully comparable, body mass values of birds from the Banc d'Arguin were corrected to water percentages of 70% of fat-free mass.

Analysis of wind speeds and directions

Synoptic wind data for the northern hemisphere are given in the European Meteorological Bulletin, issued daily by the Deutscher Wetterdienst in Offenbach, W. Germany. This bulletin summarizes air pressure (isobars), wind speed and wind direction at ground level, and height, wind speed and wind direction at pressure levels of 850 mb (ca. 1.5 km), 700 mb (ca. 3 km) and 500 mb (ca. 5.5 km) at 00 h GMT. Wind speed is given in the following categories (indicated by different symbols, see e.g. Elkins 1983: Table 2): 0, 3, 9, 16, 24, 35, 44, 56, 68, 81, 95, 110 and 121 km h^{-1}, corresponding to Beaufort-forces of 1-12.

If we assume that the godwits fly along the shortest possible route between the Banc d'Arguin and the Dutch Wadden Sea (i.e. the great circle route, see Fig. 8), they have to adjust track direction from 20° at departure to 32° at arrival. In the absence of the required information (or the tested predictive equations) on differences in flight speed relative to changing flight altitudes and body masses (Pennycuick 1975, 1978, 1989 and see Fig. 10), we furthermore assume that Bar-tailed Godwits fly at a constant air speed of 57 km h^{-1}, as was measured during their spring departure from the Banc d'Arguin (own obs.) and during autumn migration along the Baltic coast of Sweden (T. Alerstam pers. comm.).

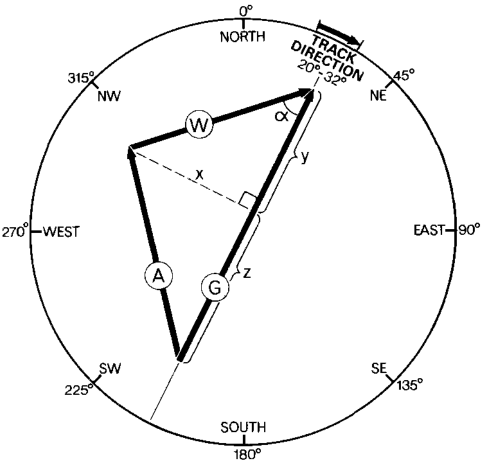

Fig. 1. Scheme to outline the way to calculate the wind effect ΔW (= G-A) for birds flying in a fixed track direction, and with a constant air speed, in a case where the wind blows from WSW. The three vectors A (bird's air speed and direction), W (wind speed and direction) and G (ground speed and [track] direction) are indicated by the encircled letters.

The synoptic weather maps of the European Metereological Bulletin allowed us to 'read out' wind speed and wind direction at seven different locations evenly spread along the great circle route (see Fig. 8): each represents a partial-traject of 4300/7 = 614 km. To read out the wind data for the appropriate date and time, we first constructed a travel scheme assuming that the birds started at 18 h on the Banc d'Arguin (Piersma *et al.* 1990b) and travelled with a constant ground speed of 65 km h^{-1} (which is somewhat higher than air speed in view of the expected tail wind assistance) along the great circle route. The first wind measurement read is from the date after the birds had started, at midnight (00 h).

The head or tail wind vectors at different locations and altitudes are calculated as follows (see the scheme in Fig. 1). If α is the angular difference between the track (migratory) direction (t, changing from 20° to 32°) and the wind direction (w, the direction from where the wind is blowing) then $\alpha = w \pm 180° - t$. If W is wind speed, A is the bird's air speed (i.e. 57 km h^{-1}) and G is the bird's ground speed, then the 'wind effect' (ΔW) is G-A. Since birds try to remain on course, the heading of G is always in the fixed track direction. According to Fig. 1 and simple geometrics, $\sin\alpha = x/W$ and therefore $x = W \bullet \sin\alpha$. Also $z = \sqrt{(A^2 - x^2)}$ and $z = \sqrt{\{A^2 - (W \bullet \sin\alpha)^2\}}$. Furthermore $\cos\alpha = y/W$ and therefore $y = W \bullet \cos\alpha$, and since $G = y + z$, it follows that:

$$G = W \bullet \cos\alpha + \sqrt{\{A^2 - (W \bullet \sin\alpha)^2\}}.$$

The wind effect ΔW is G-A, and therefore:

$$\Delta W = W \bullet \cos\alpha + \sqrt{\{A^2 - (W \bullet \sin\alpha)^2\}} - A.$$

In the text we may also call the wind effect the tail wind vector (when $\Delta W > 0$) or head wind vector (when $\Delta W < 0$).

The calculated wind vectors were averaged over the appropriate migration periods, and for flights at constant or varying altitudes. Sometimes, hard winds from unfavourable sideways directions made it impossible for the birds to stay on the 'great circle track' (that is, when $W \bullet \sin\alpha > A$). Such instances were handled as missing cases, and were not used when calculating average wind vectors en route. Although it never occurred, the birds would also be unable to move if the head wind vectors were stronger than their own flight speed (i.e. when $-W \bullet \cos\alpha > A$).

Aerodynamic properties of the godwits

Both wing span and wing area were measured on birds in the only reproducible position: with the wings maximally (but not over-) stretched, and with the arm perpendicular to the bird's body (see Pennycuick 1989: Fig. 2.3). Wing area is the surface covered by the two wings as they extend from the body plus the body area between the wing-attachments (Norberg 1981a: Fig. 2). The data are presented in Table 1. Our measurements suggest an aspect ratio of more than 9, which would mean that Bar-tailed Godwits have wings that are as long and pointed as swallows and swifts according to Fig. 6 of Masman & Klaassen (1987). The expected wing spans (S in m) on the basis of body mass (BM in kg) as based on the interspecific allometric relationship: $S = 1.165 \bullet BM^{0.394}$, derived by Rayner (1988: Fig. 1). These wing spans are 70.4 cm for ♂♂ (278 g, see Table 6) and 76.2 cm for ♀♀ (340.5 g). The expected wing areas ($A = 0.1576 \bullet BM^{0.722}$) are 625.4 cm^2 and 724.0 cm^2 respectively (A in m^2, BM in kg, from Rayner 1988: Fig. 13). The expected aspect ratio's are thus 7.9 and 8.0 for ♂♂ and ♀♀ (Rayner 1988) or ca. 7.5 (Norberg 1981b: Fig. 5). This leads us to infer that the wing spans reported on in the literature were measured in the very ambiguous 'natural flight position'. Note that Rayner (1988: Fig. 7) shows that in Pigeons *Columba livia* almost any position is natural. Wing span measured in the 'natural flight position' in five of our godwits was 12% smaller than in the maximally stretched position and the

Table 1. Wing span (in cm) and wing area (in cm^2) of Bar-tailed Godwits from the Paesenserpolder, Dutch Wadden Sea. Aspect ratio is defined as $span^2$/area.

Variable	Males (n = 8)			Females (n = 6)		
	Mean	*SD*	Range	Mean	*SD*	Range
Wing span	66.0	4.2	60- 72	71.1	3.5	67- 75
Wing area	464.6	38.7	373-484	554.9	32.8	465-556
Aspect ratio	9.4	0.8	8.4-10.5	9.1	0.5	8.5- 9.9

aspect ratio averaged 7.4. The correct measurement of wing span and area is a major problem in the theoretical estimation of the energy cost of flight. For this reason it is very unfortunate that the papers extensively using or reporting on wing span (e.g. Pennycuick 1969, 1975, Norberg 1981a, Rayner 1982, 1988, 1990) do not give the details of their measurement. Recently, however, ways to make standardized wing measurements were published by Pennycuick (1989).

Statistics

Bird data were entered in a mainframe computer and analysed with a standard statistical package (SPSS, Nie *et al.* 1975). In the linear regression analyses to estimate the relative contributions of fat and fat-free (muscle) mass to changes in total mass, the assumptions underlying the standard regression model about the relative variances of the x- and y-variables were not met. In such cases, we calculated the *reduced major axis* to quantify the relationship (i.e. the geometric mean of the x-y and y-x slopes; see Rayner 1985). This procedure deviates from the statistic exercises carried out by Piersma & van Brederode (1990) on a similar data set. The difference in approach is defensible, however, since here we are interested in correctly estimating the value of a slope (the ratio between fat and fat-free mass gain), whereas Piersma & van Brederode (1990) examined the more straightforward problem of how best to estimate fat mass from body mass and structural size variables.

Unless stated otherwise we use two-tailed Student's t-tests.

RESULTS

Are we dealing with one population?

Morphometrics The frequency distributions of bill lengths of Bar-tailed Godwits captured on the Banc d'Arguin and in the Dutch Wadden Sea show no obvious differences (Fig. 2). The presence of two peaks separated at a bill length of approximately 86 mm, indicates two slightly overlapping normal distributions. A discriminant analysis with bill length, on the sample of birds from the Dutch Wadden Sea (sexed in the field according to plumage), gave the following discriminant function (where DS is discriminant score, if $DS < 0$ the bird should be a ♀, if $DS > 0$ a ♂): $DS = 17.78 - 0.214 \bullet BILL$ (96.9% correctly identified). This function gives a discriminating bill length value of $17.78/0.214 = 83.1$ mm. Although bill length and wing length are correlated (over all birds caught in the Paesenserpolder, $r = 0.75, p < 0.05$, for the 576 ♂♂ in the sample $r = 0.25, p < 0.05$ and for 290 ♀♀ $r = 0.30$, $p < 0.05$), they might still contribute independently to a morphometric separation of the two sexes. A discriminant analysis with bill length and wing length on the same sample of live birds

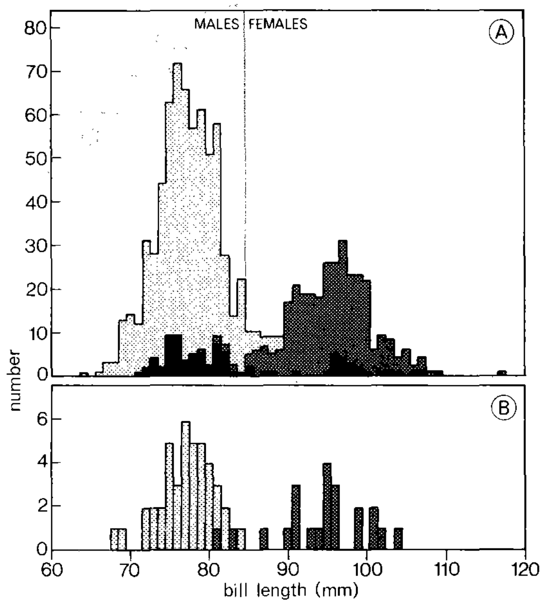

Fig. 2. Frequency distributions of bill lengths of adult Bar-tailed Godwits captured in spring on the Banc d'Arguin, Mauritania and in the Paesenserpolder, Dutch Wadden Sea. A: data for all birds captured on the Banc d'Arguin (heavily shaded) and in the Paesenserpolder (rest). The open block represents individuals that were called ♂♂ on the basis of plumage colour and overall size, the hatched block ♀♀. The boundary line separates presumed ♂♂ and presumed ♀♀ in the sample from the Banc d'Arguin. B: data for individual ♂♂ (open bars) and ♀♀ (hatched bars) that were dissected after their death (birds from both Banc d'Arguin and Wadden Sea).

(sexed on plumage characteristics) gave the following discriminant function: $DS = 31.87 - 0.176 \cdot BILL(\mathrm{mm}) - 0.078 \cdot WING(\mathrm{mm})$ (in 97.6% of 868 cases, sex was correctly identified). For the sample of dissected birds the respective discriminant functions are: 1) $DS = 18.30 - 0.219 \cdot BILL$ (96.3% correctly identified, discriminating bill length-value is 83.6 mm), and 2) $DS = 30.26 - 0.190 \cdot BILL - 0.065 \cdot WING$ (96.3% of 61 cases correct). Since the percentages correctly sexed birds hardly differ between the functions incorporating bill only and incorporating both bill and wing dimensions, we here used a discriminating bill length of 84 mm to assign sex to the adult godwits from the Banc d'Arguin. The discriminating value of 84 mm compares to a value of 92 mm in a British wintering population of Bar-tailed Godwits (Green 1973). These two values differ, but fit nicely with the finding of Prokosch (1988: Fig. 81) in the W German Wadden Sea, that the dip between the two peaks in bill length distributions decreases from 91 mm in April, when the presumed European wintering birds are involved, to 85 mm in May, when the birds that have wintered in W. Africa are present in his samples.

The averages for linear measurements of Bar-tailed Godwits captured on the Banc d'Arguin and in the Dutch Wadden Sea differ significantly in two of the six cases (Table 2). The absolute differences between the averages for the two study sites amount to only 0.8% (for wing length of ♂♂) and 2.1% (for tarsus plus toe length of ♂♂). In view of the large sample sizes, small systematic differences in the methods of measuring, easily allow statistically significant differences to occur. We therefore do not attach much weight to the differences and feel that the morphometric information does not disprove our notion that the godwits studied at the two sites belong to the same population.

Although at either study site, in spite of the difference in catching method, the number of captured ♂♂ is larger than the number of ♀♀ (69% ♂♂ on the Banc d'Arguin and 67% in the Dutch Wadden Sea), the value for the sex-ratio of birds captured at Paesens is certainly biased. The value for the Banc d'Arguin fits nicely with earlier reports on the sex ratio of Bar-tailed Godwits on the Banc d'Arguin: Dick (1975) found that 67% of the 70 adults captured in autumn were ♂♂ (and 56% of the 61 juveniles), whereas visual observations of foraging birds in winter suggested a ♂ percentage of 76% (Piersma 1982).

Evidence from ringing and resightings There are now two spring recoveries in the Wadden Sea of Bar-tailed Godwits captured on 20 December 1986

Table 2. Linear body measurements (in mm) of adult Bar-tailed Godwits captured in spring on the Banc d'Arguin and in the Dutch Wadden Sea. Birds from the Banc d'Arguin were sexed according to their bill length: individuals with a bill larger than 84 mm were called females (see Fig.2 and text). Birds from the Dutch Wadden Sea were sexed according to plumage and overall size.

Dimension	Sex	Banc d'Arguin			Wadden Sea				
		n	Mean	*SD*	*n*	Mean	*SD*	*t*	*p*
Bill	♂♂	58	77.6	3.1	574	77.2	4.1	0.82	N.S.
	♀♀	26	97.2	6.4	289	95.1	5.6	1.58	N.S.
Wing	♂♂	58	213.8	5.9	576	215.6	4.6	2.29	<0.05
	♀♀	26	229.1	6.4	289	228.1	5.5	0.80	N.S.
Tarsus +toe	♂♂	57	87.0	2.9	441	88.8	2.6	4.48	<0.05
	♀♀	26	94.0	3.1	229	95.3	2.9	2.03	N.S.

at Ilha de Formosa in Guinea-Bissau (one originally ringed on 23 May 1985 at Norderheverkoog, W. German Wadden Sea, the other recaptured on 16 May 1987 at Noorderleech, Dutch Wadden Sea, E. Wymenga pers. comm.), but no direct ringing evidence for a spring connection between the Banc d'Arguin and the Dutch Wadden Sea is yet available. (Note that a godwit ringed on the Banc d'Arguin on 16 November 1973 was recaptured along the Frisian Wadden Sea coast on 14 August 1980.) However, two times a ♂ Bar-tailed Godwit colour-marked on the Banc d'Arguin between 22 March and 23 April 1985 was resighted at our Dutch study site a few weeks after their release in Mauritania. The first sighting was of a bird in flight as it (only just) escaped the wilsternet in the Paesenserpolder on 9 May 1985. The second sighting (of the same or another individual) was on 18 May 1985. Mauritanian colour-marked birds were not resighted at other locations along the coasts of NW. Africa and W. Europe, despite intensive observer effort (see Piersma 1985).

Timing of migration Most Bar-tailed Godwits left the Banc d'Arguin in the period 22-27 April (Fig. 3, and see Piersma *et al.* 1990a). They arrived in the Paesenserpolder between 27 April and 3 May, and apparently slightly later on the roosts on Engelsmanplaat (Fig. 3). There were no obvious differences in departure or arrival timing between years. The average departure date from the Banc d'Arguin was 25 April, the median arrival date in the Paesenserpolder was 29 April in each of the three years. Assuming that all birds staging in the Paesenserpolder departed from the Banc d'Arguin, the delay suggests an average travel time of four days. This is slightly longer than it would take a godwit to cover the distance in one non-stop flight (see below) and might imply that some individuals stage for a couple of days at unknown intermediate staging sites.

There is evidence that ♂♂ leave and arrive before the ♀♀. From 20-24 April 1985 only two of the 18 (11%) departing Bar-tailed Godwits that were sexed in flight were ♀♀. Unquantified observations over the same period in 1988 confirm this predomi-

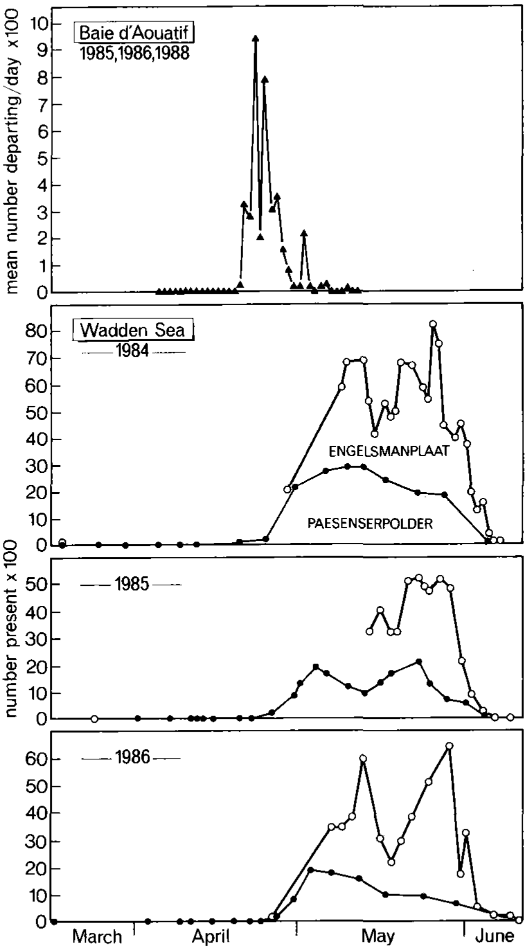

Fig. 3. Schedule of departure from the Baie d'Aouatif, Banc d'Arguin (top panel) and the occurrence in the Paesenserpolder and on the Engelsmanplaat (lower three panels) of Bar-tailed Godwits. The departure schedule from the Banc d'Arguin is given by the mean number of birds leaving the area each day during the late afternoon (averaged for data from 1984, 1985 and 1988, see Piersma *et al.* 1990 for comparison between years). The occurrence in the Paesenserpolder is given by the numbers counted at the high tide roost in the springs of 1984, 1985 and 1986 (data collected by P.M. Zegers & A.A. Goede pers. comm.). The numbers counted on Engelmanplaat (H. Smit pers. comm.) are added to the (interpolated) numbers at Paesens, and the open dots therefore refer to the overall totals.

nance of ♂♂. In the periods 25-27 April 1985 and 1988, 57% of 470 departing godwits, and from 28 April-6 May 1988, 89% of 182 departing birds were ♀♀. Of the 31 birds captured in the Paesenserpolder on 30 April, 8 (26%) were ♀♀ and of 60 birds captured on 3-4 May, 35% were ♀♀, the increase in the percentage of ♀♀ giving some support to the sexual difference in the timing of spring migration. Male Bar-tailed Godwits might thus schedule their travels earlier in spring than ♀♀. This suggestion is in agreement with the remark of Prokosch (1988: p.400) that in the German Wadden Sea ♂♂ seem to leave the area, for the flight to the arctic breeding grounds, a few days before the ♀♀ do so.

Bar-tailed Godwits use the high tide roost in the Paesenserpolder during the entire month of May, leaving the area in late May and in early June (Fig. 3). The godwits feed along the north Frisian shores between Paesens and Wierum, and can also fly to the offshore island Engelsmanplaat to roost (L. Zwarts pers. comm.), a bee-line distance of 7 km from the Paesenserpolder. In 1984 and 1986, numbers in the Paesenserpolder were lowest in the second half of May, but these decreases were compensated by simultaneous increases on the Engelsmanplaat-roost. Local distributional changes during May are recorded for godwits elsewhere in the Wadden Sea, e.g. on the nearby island of Schiermonnikoog (de Goede *et al.* 1985). In fact, some birds may actually have shifted to Schiermonnikoog (a distance of 10 km). A ♂ ringed on 6 May 1988 was recaptured on Schiermonnikoog on 21 May 1988, the timing of which movement coincides with the annually recurring dip in combined numbers on the Paesens- and Engelsmanplaat-roosts halfway through May (Fig. 3). The changes in total numbers (Fig. 3), indicate a median departure date of 1 June in 1984, and of 31 May in 1985 and 1986.

To summarize, the overlapping biometrics, the resightings at our Dutch study site of one or two individual godwits a few weeks after they were colour-marked on the Banc d'Arguin, and the close fit between the timing of departures and arrivals, lead us to believe that we are dealing with the same Bar-tailed Godwit population at the two study sites.

Changes in total body mass

On the Banc d'Arguin, Bar-tailed Godwits started to gain mass in the course of March at rates of about 2.8 g d^{-1} for ♂♂ and 3.2 g d^{-1} for ♀♀ (Fig. 4). Males captured between 8 and 20 April

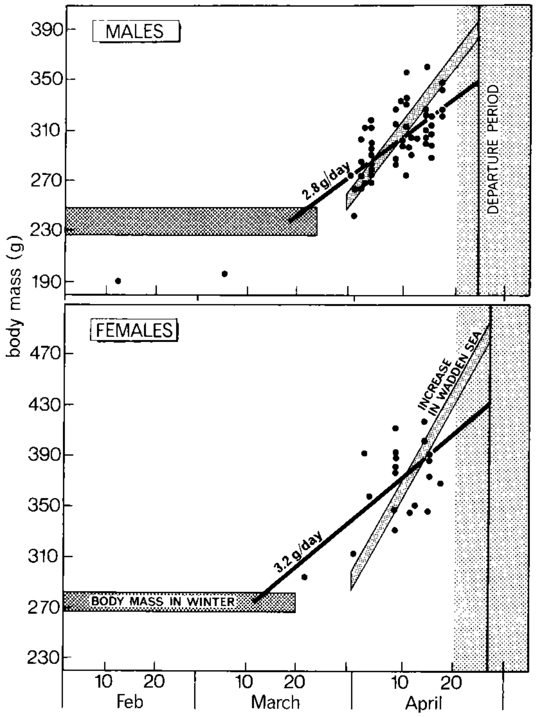

Fig. 4. Body mass gains of ♂ and ♀ Bar-tailed Godwits on the Banc d'Arguin (individual data points from 1985 and 1986) relative to the dates of departure (vertical bars) and the body mass levels in winter (indicated by horizontal bars, which give the 95% confidence intervals around the mean masses in January-February in Guinea-Bissau, corrected for mass loss after capture; from Zwarts *et al.* 1990b). For comparison, the mass increases in the Dutch Wadden Sea are also indicated (relative to departure date again; from Fig. 5). The regression line for ♂♂ is based on the 50 data points from late March and April ($r^2 = 0.40$, $p < 0.0001$). Incorporation of the two low values from February and early March in the regression equation leads to an increase in explained variance ($r^2 = 0.62$) and a decrease in slope (2.42 g d^{-1}). The slope for ♀♀ is significantly different from zero ($r^2 = 0.37$), and not dependent on the earliest and lowest data point (if it is left out of the regression, $r^2 = 0.15$, $p = 0.05$ and slope = 2.4). See also Table 3.

Table 3. Comparison between the body mass increase rates (Slope: *b*) on the Banc d'Arguin (see Fig.4) and in the Dutch Wadden Sea (see Fig.5), and the relative arrival masses in the Dutch Wadden Sea (Intercept: *a* = mass on 29 April) of adult Bar-tailed Godwits in the springs of 1984-1988.

Sex	Site	Years	*n*	*b*	*SE*	*a*	*SE*	r^2
♂♂	Wadden Sea	1984	134	6.55	0.56	198.9	12.8	0.51
		1985	231	4.88	0.37	229.7	6.1	0.43
		1986	92	5.99	0.41	209.5	7.6	0.70
		1987	62	5.59	0.68	225.5	9.9	0.53
		1988	51	7.29	0.55	208.9	6.4	0.78
		1984-1988	570	5.65	0.19	219.1	3.5	0.60
	Banc d'Arguin	1985-1986	50	2.83	0.50	(-)	(-)	0.40
♀♀	Wadden Sea	1984	51	8.04	1.05	236.3	24.3	0.54
		1985	115	8.36	0.50	242.6	7.6	0.71
		1986	62	7.90	0.60	233.0	10.4	0.74
		1987	30	7.76	1.09	260.0	13.9	0.64
		1988	14	8.35	1.52	267.9	14.7	0.71
		1984-1988	272	7.52	0.30	252.1	5.1	0.70
	Banc d'Arguin	1985-1986	20	3.22	0.99	(-)	(-)	0.37

with a full summer plumage and no body moult (probably ready to depart; see Zwarts *et al.* 1990b), weighed on average 320 g (*SD* = 20, *n* = 12). This is almost 30 g more than the body mass of ♂♂ which were fully in moult at the time, and which had less than half the summer plumage completed (293 g, *SD* = 12, *n* = 6; the difference is significant, Student's *t*-test, $p < 0.05$). After 15 April 1985 a few very light non-moulting birds (of either sex) with rather incomplete summer plumages were captured: they possibly represented immigrants from more southerly wintering areas and were excluded from our analysis (see Piersma 1989 for the details). The regressions of body mass on date were significant for both sexes (Table 3).

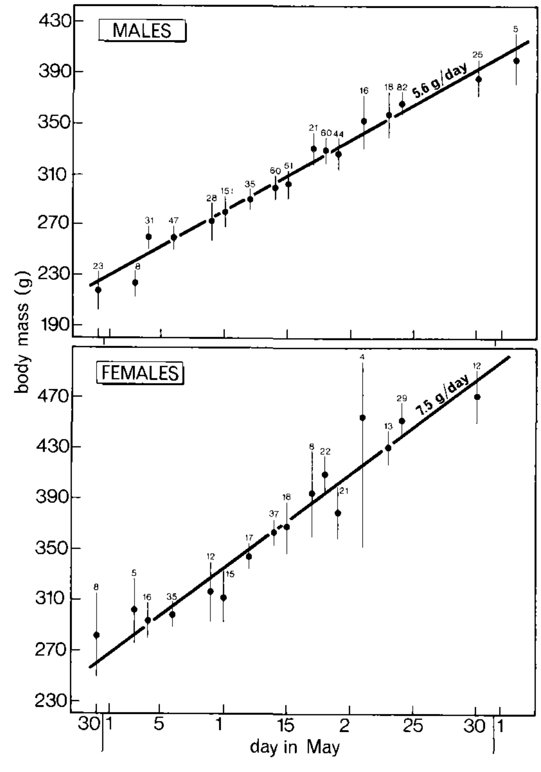

Fig. 5. Body mass gains of Bar-tailed Godwits in the Paesenserpolder, Dutch Wadden Sea. The average values for different dates (with 95% confidence intervals) are given for data from the springs of 1984-1988. The slopes of the regression equations are significantly different from zero (♂♂: $r^2 = 0.60$, ♀♀: $r^2 = 0.70$). See Table 3 for the equations for different years.

In the Dutch Wadden Sea body mass increased linearly over the entire staging period, both when the data for different years were examined (not shown), as when all data were pooled (Fig. 5). An analysis of covariance showed no significant ($p > 0.05$) inter-year effects on the body mass increase rates nor on the arrival masses (intercepts) in either ♂♂ or ♀♀, but note that the body mass increase rates as calculated for the pooled data were nevertheless slightly lower than the averages for the slopes in different years (Table 3).

In the Wadden Sea, ♂♂ (at 5.6 g d^{-1}) gained mass at a 25% lower rate than ♀♀ (at 7.5 g d^{-1}; Student's *t*-test, $p < 0.05$). Male and female Bar-tailed Godwits on the Banc d'Arguin gained body mass at a 57% lower rate (Student's *t*-test, $p < 0.05$) than in the Dutch Wadden Sea (see Fig. 4 for a direct comparison).

Individual ♂ Bar-tailed Godwits which were recaptured at or near the Dutch study site on different dates in spring, showed body mass changes which closely followed the average for the population (Fig. 6). On average, the mass increase was 4.6 g d^{-1} ($SD = 6.9$, $n = 8$). If we take only the 7 birds which we captured 9 days or more apart showing a body mass increase, the average is 6.9 g d^{-1} ($SD = 1.8$). Since neither value is statistically different from the population average of 5.6 g d^{-1} (Student's *t*-tests, $p > 0.05$), there is no reason to believe that the body mass increase patterns for the population of Bar-tailed Godwits in the Dutch Wadden Sea are much different from (i.e. lower than) those of individuals (cf. Davidson 1984).

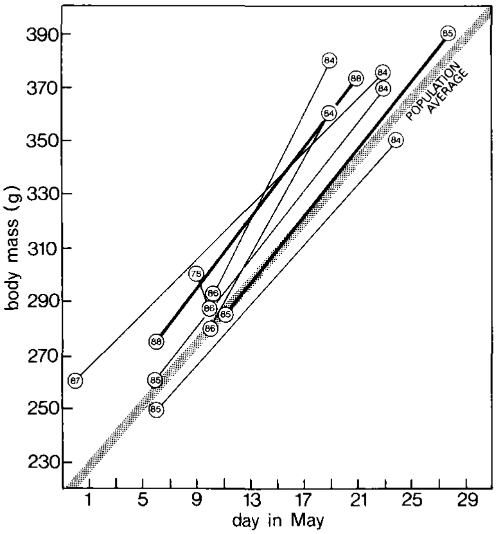

Fig. 6. Body mass changes with respect to date of individual ♂ Bar-tailed Godwits captured twice in or near the Paesenserpolder. Data points connected with a double line indicate birds captured twice in the same season. The figure in the circle stands for the year of capture.

The fact that we find no delay in the onset of body mass gain after Bar-tailed Godwits have arrived in the Dutch Wadden Sea from W. Africa, is perhaps surprising in itself. Most studies on body mass changes in migrant birds have shown that recaptured migrants at stopover sites tend to lose mass during the first few days after first capture, before starting to put on extra mass (see e.g. Mascher 1966, Page & Middleton 1972, van Brederode *et al.* 1982, Mehlum 1983), but it is possible that this is an effect of capture stress (see Lank 1983 for the latter interpretation, and Carpenter *et al.* 1983 and Biebach *et al.* 1986 for cases where the initial mass loss is not paramount).

Estimating fat and non-fat components

In order to estimate the energetic equivalent of the body mass changes in migrating Bar-tailed Godwits (Figs. 4 and 5), it is critical to know whether the changing mass consists entirely of dry fat (energetic density is 39.4 kJ g^{-1}, Schmidt-Nielsen 1975: p.211), or whether some of it consists of fat-free tissue (probably mainly 'wet muscle tissue', with a water content of 70% (measured), a protein content of 95% of dry matter (estimated, the remainder mainly being minerals) and an energetic yield of $0.3 \cdot 0.95 \cdot 17.8 = 5.1$ kJ g^{-1}, Schmidt-Nielsen 1975). If fat-free body mass is plotted as a function of total body mass (Fig. 7), the slope of the reduced major axis should give a good approximation of the relative contributions of the fat and non-fat components to the deposited mass. The regression equations for ♂♂ from the Banc d'Arguin and from the Dutch Wadden Sea (no ♀♀ from Banc d'Arguin available) were similar (analysis of covariance, and slopes and intercepts com-

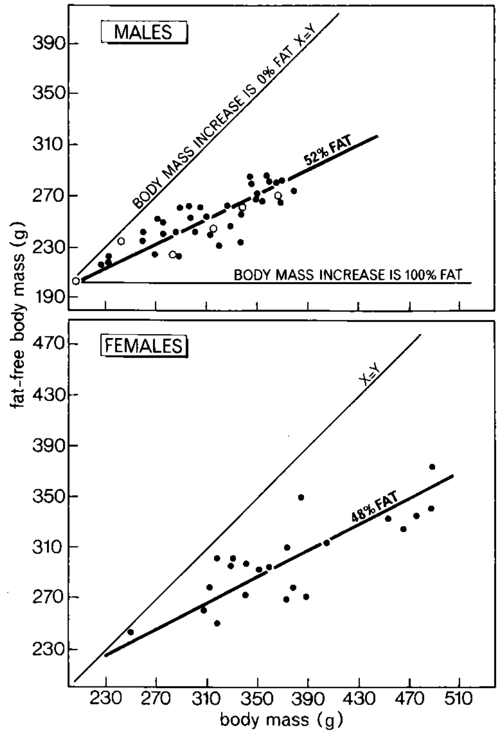

Fig. 7. Fat-free body mass as a function of body mass in Bar-tailed Godwits captured during spring migration on the Banc d'Arguin (open circles) and in the Dutch Wadden Sea (closed dots). The thin lines present two theoretical possibilities: all or none of the mass gain consists of fat. The thick lines are the reduced major axes, with r^2-values of 0.70 for all ♂ ♂, and 0.64 for the ♀ ♀. In ♀ ♀, body mass values were transformed to correct for variations in structural size, as expressed by wing length (corrected to an average wing of 227.6 mm; see text).

pared, Student's *t*-tests, $p > 0.05$). The body composition data for the two sites can therefore be taken together.

To control for systematic variation in structural size (sensu Wishart 1979, Piersma 1984a) that might influence the regressions of fat-free mass on total body mass, we have correlated total body and fat-free mass with bill and with wing length. In ♂ ♂, total and fat-free body mass did not correlate with either bill or wing length. In ♀ ♀, however, total and fat-free body mass were correlated with both bill length ($r = 0.51$ and $r = 0.50$, $p < 0.05$, respectively) and wing length ($r = 0.50$ and $r = 0.54$, $p < 0.05$, respectively). For this reason the mass values for ♀ ♀ were corrected to their average wing length of 227.6 mm (wing chosen as a good estimator of structural size).

In ♂ ♂, 52% of the deposited mass appears to consists of fat (equation: *fat-free mass* (g) = 0.48•*body mass* (g) + 103, $r^2 = 0.70$, $n = 40$). In ♀ ♀ the percentage fat is somewhat lower, 48% (equation: *fat-free mass* = 0.52•*body mass* + 107, $r^2 = 0.65$, $n = 21$), but note that the slopes for the linear regressions do not differ between ♂ ♂ and ♀ ♀ (Student's *t*-tests, $p > 0.05$). Although the intercepts of the axes at zero body mass are the same for ♂ ♂ and ♀ ♀, at realized body masses fat-free mass of ♀ ♀ is 10-20 g greater than in ♂ ♂.

The apparent linearity of the relationship between fat-free body mass and total body mass (Fig. 7) may come as a surprise since we might expect that fat-free muscle tissue is deposited before fat is (Kersten & Piersma 1983: Fig. 7.44, Piersma & van Brederode 1990, Zwarts *et al.* 1990b, but see Piersma 1984: Fig. 2A). Although in ♂ ♂ the fat-free masses of the lightest birds are above the linear axis (Fig. 7 top), the present sample gives no further evidence for a curve with a decreasing slope: a regression of y on $\ln(x)$ does not increase the explained variance relative to a linear regression, either in ♂ ♂ or in ♀ ♀. In addition, if fat-free mass is plotted as a direct function of date, linearity also appears to characterize this relationship.

Winds aloft during the flight

The following analysis assumes that Bar-tailed Godwits are able to estimate their ground speed with reference to landmarks, that they are able to migrate at altitudes of at least 5 km (see Richardson 1979) and that, by comparing their own performance over a range of altitudes, they are able to select the best altitude for forward flight. Studies on the Banc d'Arguin in spring 1988 have shown that departing waders gain much height (up to 1.5 km and beyond) as they leave the Baie d'Aouatif (Piersma *et al.* 1990b). There is empirical evidence that long-

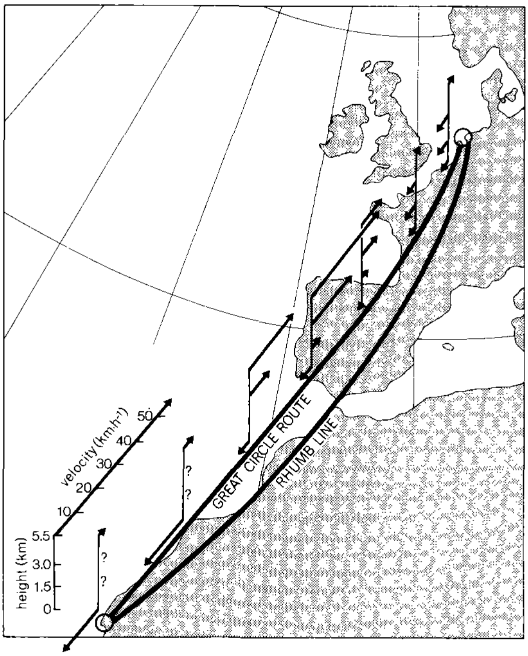

Fig. 8. Relative strengths of the head and tail wind vectors encountered by Bar-tailed Godwits at different heights along the great circle route between the Banc d'Arguin and the Dutch Wadden Sea. Averages for eight starting dates (22-29 April) in 1984-1987; based on data for 23 April- 3 May from the European Metereological Bulletin, Offenbach. Apart from the great circle route, the route via the rhumbline (a flight of 4600 km with constant heading) is shown.

distance migrants may 'sample' the winds at various altitudes before choosing which one is best (Alerstam 1985), and that migrants generally seek the altitudes with most favourable winds (Bruderer 1971, 1975, Steidinger 1972, Richardson 1976, Williams 1985).

The wind data for the godwits' migration periods in 1984-1988 are summarized in Table 4. It stands out that the spring of 1987 could have provided much more wind assistance than the other three. At ground level head winds predominate all along the route (Table 4, Fig. 8), but the winds ameliorate with height. In the 1984-migration period the average wind vectors were negative at all altitudes, but if birds had regularly changed flight height to where the best winds were, they would have gained an average tail wind vector of 10 km h^{-1}. Over the four seasons, birds following the optimal height track would have incurred an average wind assistance of 18 km h^{-1}.

Table 4 suggests that flying at heights of 3 km or more is generally a reasonable strategy. Indeed, the average tail/head wind vectors depicted in Fig. 8 suggest that birds should generally carry on at an altitude of 5.5 km during the trip from the Banc d'Arguin to the Wadden Sea. At great heights temperatures are low (an average decrease of 6.5°C per 1000 m increase in latitude), and this may give the additional advantage of reducing water loss due to evaporative cooling (Yapp 1956, 1962, Torre-Bueno 1978, Biesel & Nachtigall 1987). Instead,

Table 4. Tail or head wind vectors (km h^{-1}) experienced by Bar-tailed Godwits when flying from the Banc d'Arguin to the Dutch Wadden Sea along the great circle route, under different assumptions about the followed height track. See Methods-section for details of calculations and assumptions.

Flight condition	Mean tail/head wind vector, km h^{-1}								
	1984		1985		1986		1987		Overall
	Mean	(*SD*)	Mean	(*SD*)	Mean	(*SD*)	Mean	(*SD*)	mean
ground level	-8.5	(2)	-5.6	(3)	-9.4	(3)	-7.8	(3)	-7.8
ca. 1.5 km	-6.9	(11)	-7.9	(6)	-5.6	(12)	+12.0	(14)	-2.1
ca. 3 km	-3.4	(10)	-0.3	(13)	-0.7	(12)	+28.8	(5)	+6.1
ca. 5.5 km	-4.6	(11)	+4.5	(20)	+11.1	(13)	+30.4	(17)	+10.4
optimal track	+9.7	(10)	+9.7	(7)	+16.5	(10)	+35.3	(13)	+17.8

most of the heat produced during flight can be carried off by convection. However, the higher the godwits fly, the more unpredictable the winds get (see the increasing *SD* values in Table 4). At ground level, winds are never strong enough to prevent godwits flying at 57 km h^{-1} to keep track, but at higher altitudes the percentage of times that birds are blown off course (scored as a missing case, see methods) increases (1.5 km: 1%, 3 km: 4% and 5.5 km: 16% of the cases). Thus it might generally be best to fly high along the NW. coast of Africa (above the trade-wind inversion at 500-800 m the winds are reasonably predictable and favourable, and the view only rarely obscured by clouds), and to start flying at low and least 'risky' altitudes when approaching the Strait of Gibraltar.

Budgeting the flight

The data on timing of the Bar-tailed Godwit migration from the Banc d'Arguin to the Dutch Wadden Sea suggest an average departure date of 25 April. We have taken this as the average departure date for ♂♂, and assume that ♀♀ left two days later, on average on 27 April. To construct a model of body mass changes of the studied population of Bar-tailed Godwits in spring, we additionally assumed that they covered the distance along the great circle route (4300 km, see Fig. 8), following the best wind conditions at heights up to 5.5 km (i.e. an average tail wind vector of 18 km h^{-1}, Table 4), which leads to an average ground speed of 57 + 18 = 75 km h^{-1}. This gives a total flight time of 4300/75 = 57.3 h or 2.4 days, and arrivals in the Wadden Sea in the early mornings of 28 and 30 April for ♂♂ and ♀♀ respectively. The birds leave the Wadden Sea on 31 May. The data on body mass increase rates at the two sites can then be combined to construct a model of the average changes in total body mass of Bar-tailed Godwits in spring (cf. Dick *et al.* 1987 for Siberian Knots *Calidris c.canutus*). The information on the composition of body mass changes furthermore allows a quantitative interpretation in terms of fat and fat-free body tissue. The resulting models for ♂♂ and ♀♀ are presented in Fig. 9.

The quantified mass loss of the two nutrient

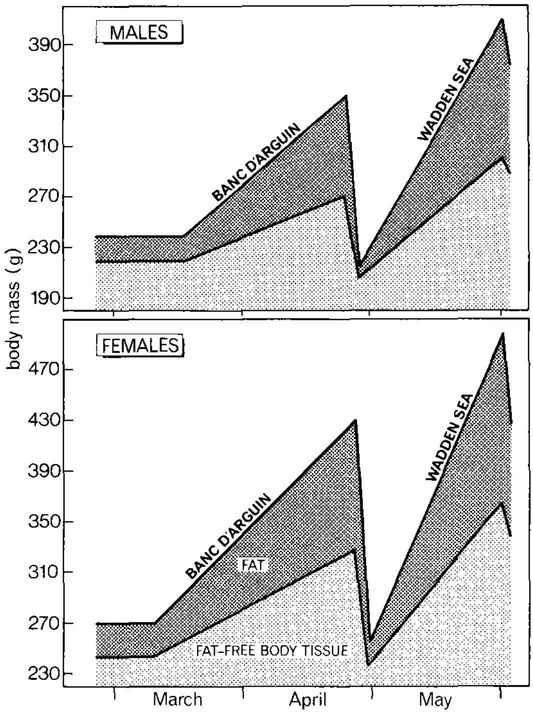

Fig. 9. Body mass and composition changes of an average ♂ (top) and an average ♀ (bottom) Bar-tailed Godwit during their spring migration from the Banc d'Arguin to the Siberian breeding grounds.

Table 5. Nutrient reserve losses of Bar-tailed Godwits between their departure from the Banc d'Arguin and their arrival in the Dutch Wadden Sea (values from Fig. 9). Energetic value of fat is 39.4 kJ g^{-1}, and of fat-free body tissue (FFBT) 5.1 kJ g^{-1}.

Sex	Reserve	Mass loss		Energy loss	
		(g)	(%)	(kJ)	(%)
♂♂	Fat	72	53	2837	90
	FFBT	64	47	326	10
	Total	136	100	3163	100
♀♀	Fat	86	48	3388	88
	FFBT	92	52	469	12
	Total	178	100	3857	100

reserves, as based on Fig. 9, and their energetic equivalents, are given in Table 5. Male Bar-tailed Godwits lost on average 3163 kJ during the flight and ♀♀ 3857 kJ (the ratio is 0.82). Like the mass gain, the mass loss consists only half of fat, the rest being fat-free body tissue, although fat provides almost 90% of the combusted energy.

Mass losses over a flight period of 57.3 h with energetic equivalents of 3163 kJ and 3857 kJ for ♂♂ and ♀♀ respectively, leads to empirical estimates of flight costs of 55 kJ h^{-1} for ♂♂, and 67 kJ h^{-1} for ♀♀. Note that the estimated mass loss for a 4300 km flight is not sensitive to a relaxation of the assumption of a single flight and two to three

Table 6. Comparison between the flight costs of male and female Bar-tailed Godwits as estimated by various predictive equations based on empirical data provided by the three most recent reviews: (1) Masman & Klaassen (1987), (2) Castro & Myers (1988) and (3) Rayner (1990), and as estimated by one theoretical model: (4) Pennycuick (1989, for details see Fig. 10). We used the estimated mean body mass during the flight from the Banc d'Arguin to the Dutch Wadden Sea, i.e. the mean of the respective departure and arrival masses. This is 282 g for males and 340.5 g for females (Fig. 9). Body mass (*BM*) in g, wing length (*L*) in cm, wing span (*S*) in cm and wing area (*A*) in cm^2; e_f= flight cost. For (3) *BM* in kg, *S* in m and *A* in m^2. *n* gives the number of species-average data points, R^2 is the explained variance of the regressions yielding the predictive equations.

Review	Model	Equation	e_f (kJ h^{-1})	
			♂♂	♀♀
(1)	Non-windtunnel studies	$e_f = 0.305 \bullet BM^{0.756}$ (W) ($n = 23, R^2 = 0.84$)	78.2	90.1
(1)	Aerodynamic properties incorporated	$e_f = 17.36 \bullet BM^{1.013} \bullet S^{-4.236} \bullet A^{1.926}$ (W) ($n = 14, R^2 = 0.84$)	41.1	51.0
(1)	Idem with wing span in "natural flight position" ($S_{males} = 58.1$, $S_{females} = 62.6$)	idem	70.4	87.5
(2)	All available data	$e_f = 0.679 \bullet BM^{0.818}$ (kJ h^{-1}) ($n = 39, R^2 = 0.80$)	68.6	80.0
(2)	Idem, incorporating wing span	$e_f = 67.29 \bullet BM^{1.763} \bullet S^{-2.275}$ (kJ h^{-1}) ($n = 20, R^2 = 0.83$)	101.9	120.0
(2)	Idem, incorporating wing length	$e_f = 3.167 \bullet BM^{1.464} \bullet L^{-1.614}$ (kJ h^{-1}) ($n=38, R^2 = 0.89$)	86.3	103.5
(3)	All available data for cruising flights	$e_f = 114.61 \bullet BM^{1.145} \bullet S^{-1.225} \bullet A^{0.253}$ (W) ($n = 64, R^2 = 0.86$)	72.1	85.3
(3)	Idem, with wing span in "natural flight position"	idem	84.3	99.8
(4)	Power curve (minimum power)	see legend Fig. 10	73.5	88.5
(4)	Power curve (maximum range)	see legend Fig. 10	92.5	111.5

travel days. If some birds would stop for a few days we just need assume that their body mass gains at the stopover site averaged the gains on the Banc d'Arguin and the Wadden Sea. However, the empirical estimate of flight cost is sensitive to variations in flight duration, and hence in variations in flight speed. How do these estimates compare with the predicted flight costs for birds like Bar-tailed Godwits?

The three recent reviews of flight costs of birds show that the incorporation of aerodyamic properties of birds other than body mass (notably wing span and wing area, i.e. aspect ratio) greatly increases the explained variance of the predictive regression models (Masman & Klaassen 1987, Castro & Myers 1988, Rayner 1990). We measured wing span and wing area in a sample of our birds (see methods and Table 1) and Table 6 summarizes the estimates of flight costs for ♂ and ♀ Bar-tailed Godwits. The estimates based on regression equations not incorporating wing size variables, range from 68 to 77 kJ h^{-1} for ♂♂ and from 80 to 90 kJ h^{-1} for ♀♀. Incorporating aerodynamic properties leads to a reduced estimated flight costs according to Masman & Klaassen (1987), but, surprisingly and unexpectedly, to higher costs according to Castro & Myers (1988). The flight costs as estimated by the 'aerodynamic equation' of Masman & Klaassen and our measured wing span and area (Table 1), results in exceptionally low estimated flight costs (40.5 and 51.0 kJ h^{-1} for ♂♂ and ♀♀ respectively). In case we calculate flight costs using the estimated wing span according to measurement in the 'natural flight position', the estimated costs increase to 70.4 and 87.5 kJ h^{-1} for ♂♂ and ♀♀ respectively. A 12% reduction in wing span leads to a 71% increase in estimated flight costs. Qualitatively the same effect is shown by Rayner's predictive equation, but here the estimated flight costs increase with only 17%. Although the published predictive equations may point the way to accurate flight cost estimates on

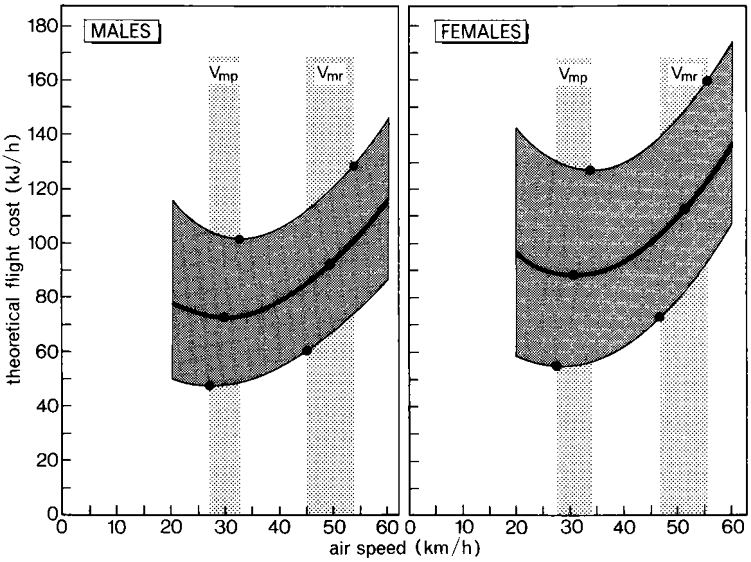

Fig. 10. Theoretical power consumption during flight of ♂ and ♀ Bar-tailed Godwits in relation to flight speed according to Pennycuick's (1989: PROG_1.BAS) model for non-passerine birds. We used wing span values of 66.0 cm for ♂♂ and 71.1 cm for ♀♀ (Table 1), and overall body mass values (from Fig. 9) at the start of flight (upper curve, BM_{males} = 350 g, BM_{females} = 430 g), halfway through the journey (thick middle curve, BM_{males} = 282 g, BM_{females} = 341 g) and upon arrival in the Wadden Sea (lower curve, BM_{males} = 214 g, BM_{females} = 252 g). The dots indicate estimated V_{mp} (minimum power speed) and V_{mr} (maximum range speed) at different body masses.

the basis of bird morphology, more efforts on standardizing morphological measurements are certainly required.

Theoretical estimates of flight costs based on the power curve of Pennycuick (1989, see Fig. 10) give figures in the same order of magnitude as the earlier predictions (Table 6). Yet, theoretical flight costs at minimum power speed are still about 33% higher than our estimates based on energy loss during the flight, and the costs at maximum range speed (a more likely assumption for a long-ditance migrant) even more so. The steep increase in flight costs at air speeds above 50 km h^{-1} (Fig. 10), indicates that it is unlikely that the air speed for Bar-tailed Godwits of 57 km h^{-1} used here, is much too low (see also Zwarts *et al.* 1990b).

A confounding factor that has gone undiscussed is the saving on flight costs that the godwits may have gained from flying in flock formation with narrow wing tip spacing (cf. Piersma *et al.* 1990b). Studies by Lissaman & Shollenberger (1970) and Hummel (1973) suggest flight power reductions by 20% or more by flying in closed flocks. Obviously, the empirical flight cost estimates used to derive the predictive equations which are based on mass change over long flights (Table 6), implicitly take this factor into account.

A last insight in the approximate costs of flight may be gained from a comparison with *BMR*. In early June, *BMR* was measured in two ♂♂ captured two weeks earlier in the Paesenserpolder (L. Groenewold pers. comm.). Their *BMR*-values were 2.126 W and 1.658 W. Because 1 W equals 3.6 kJ h^{-1}, they average 6.8 kJ h^{-1}. These values are close to a *BMR* level of 2.01 W predicted on the basis of the equation for waders: $BMR = 5.06 \bullet BM^{0.729}$ (Kersten & Piersma 1987), where $BM = 0.282$ kg and *BMR* in W. An estimated flight cost of 41 kJ h^{-1} is therefore 41/6.8 = 6 times *BMR*, and for an estimated flight cost of 70 kJ h^{-1}, 70/6.8 = 10 times *BMR*. The first value seems a bit low, the latter a bit high for a bird like the Bar-tailed Godwit (Masman & Klaassen 1987).

Our empirical estimates for the flight costs of ♂ and ♀ Bar-tailed Godwits are between the lowest and the higher theoretic estimates presented in Table 6. This gives a comfortable feeling, but the correspondence also implies that, to balance their energy budget, Bar-tailed Godwits are apparently forced to keep flight-time low by optimally using the available tail winds en route. To fly from the Banc d'Arguin to the Dutch Wadden Sea in one go (i.e. to perform a direct flight with a balanced budget), the godwits apparently require the help of favourable winds.

DISCUSSION

Flying along the great circle route?

An aerial voyage along the great circle route implies that during the flight Bar-tailed Godwits 1) are able to constantly adjust track direction relative to the north and 2) are able to use the available landmarks to orient themselves 'precisely' over the route, compensating completely for wind drift (see Evans 1966, 1968, Alerstam 1976, 1979). In turn this implies that flying birds are able to accurately relate their actual (projected) flight path to the known patterns of visual (Tinbergen 1956) and possibly auditory (e.g. sound of surf along the Atlantic shores, infrasound from winds around mountain ranges, Griffin 1969, Kreithen & Quine 1979, Kreithen 1983) reference systems of landmarks. It would perhaps be easier to follow the rhumbline (300 km longer than the great circle, Fig. 8): the shortest route with a constant heading. We have no information on the orientational abilities of godwits, or indeed any other wader. However, a glance on a map (Fig. 8) suggests that taking either route from the Banc d'Arguin to the Strait of Gibraltar should offer no difficulties since the birds should be able to follow the coast, even at a distance. Since the visible distance (*d*, in km) for objects at heights above ground level h_1 (in m) as a function of flight height (h_2) follows the relationship: $d = 3.5 \bullet \sqrt{(h_1 + h_2)}$ (T. Alerstam pers. comm.), godwits flying at 5000 m would in clear weather be able to see the ca. 100 m high Moroccan coastline from a distance of $3.5 \bullet \sqrt{5100} = 250$ km, i.e. when cruising over the central Canarian Islands. In reaching Iberia, the birds can stay west of the Sierra Nevada and head for central Spain. Those that follow the great circle route pass west of the Pyrénées, fly along the SW coast of France, pass over Paris and arrive in The Netherlands. Birds following the rhumbline may have a harder time since they have to cross the Pyrénées and fly an inland route. An inland route means perhaps that orientation is more difficult, but also that the birds are not overflying possible additional (emergency) stop-over stations, such as those along the French Atlantic coast (see Bredin & Doumeret 1986 for the occurrence of godwits in spring).

In the comprehensive analysis of Alerstam (1979), it is pointed out that under relatively constant winds (such as one finds along the NW. African coast) complete compensation for wind drift is the optimal behaviour. As birds approach their goal (such as in NW. Europe, with rather unpredictable wind directions and speeds) birds are also predicted to compensate for wind drift. For all these reasons we feel that it is likely that the Bar-tailed Godwits flying from Mauritania to The Netherlands try to follow a 'fixed' track that is reasonably close to the great circle route. Observations of southward migrating Bar-tailed Godwits at heights of more than 2400 m over the Picos de Europa in northern Spain (exactly on the great circle route) in September 1988 (N.F. van der Ham pers. comm.), are the first of the radar and visual registrations along the envisaged route, which are now required to substantiate this flight scenario.

Reserve dynamics during long-distance migrations

Although it is well established that premigratory 'fattening' in migrant birds involves, in addition to fat storage, increases in some non-fat components such as the breast muscles (Fry *et al.* 1972, McLandress & Raveling 1981, Marsh 1984, Davidson & Evans 1988, Johnson *et al.* 1989: Fig. 3), some authors nevertheless maintain that premigratory body mass increases do not involve significant increases in the total fat-free mass of birds (Odum *et el.* 1964, Marsh 1983). It may therefore come as somewhat a surprise (as conveyed by Cherel *et al.* 1987: pp. 260-261), that no less than 50% of the body mass gained by Bar-tailed Godwits during two successive premigratory periods in one spring season, consisted of fat-free body tissue (Fig. 7), most of which is likely to be muscle protein. About 40% of the increase in fat-free mass of birds on the Banc d'Arguin, but only 15% of the increase in the Dutch Wadden Sea, can be accounted for by the mass increase of the breast muscles: hypertrophy is clearly going on in most parts of the body (own obs.). Part of the apparent discrepancy between this and earlier studies may be due to our use of an 'alternative' regression model. The application of reduced major axes to quantify the relationships between total and fat-free mass leads to higher estimated contributions of fat-free tissue than simple regression models. If the latter model is used, the estimated 'slopes' are 40% and 41% for ♂♂ and ♀♀ respectively (cf. Piersma & van Brederode 1990, Zwarts *et al.* 1990b). The issue clearly awaits more data and similar types of analyses for other species.

The 136 g (in ♂♂) or 178 g (in ♀♀) of body mass lost by Bar-tailed Godwits during their flight from Mauritania to The Netherlands, also consisted for about 50% of fat (Table 5), the remainder being fat-free body tissue (muscle protein). The loss of fat-free mass in ♂♂ can only for 20% be accounted for by a decrease in the mass of the breast muscles (own obs.). Davidson & Evans (1988) have shown that Knots also lose breast muscle mass during their long-distance flight from northern Norway to the breeding grounds in high arctic Canada. Davidson & Evans (1988) argue that this mass loss is less than predicted by aerodynamic theory (Pennycuick 1978) and infer that a protein reserve is being saved during the flight.

Apart from Pennycuick's (1978) argument from aerodynamic design to explain the loss of breast muscle mass, physiological mechanisms must account for the large losses of fat-free mass during long-distance flights too. Since migrants in flight do not normally ingest any food for one or more days, their mass loss may best be compared to the well studied mass loss in starving animals (e.g. Le Maho *et al.* 1981, Cherel & Le Maho 1985, Cherel *et al.* 1987). Indeed, long-distance migration may be viewed as a very rapid starvation process. In domestic geese *Anser domesticus* it was shown that 58% of the total mass loss during a prolonged fast of more than 40 days, was due to fat loss and 34% to the loss of muscle tissue (Le Maho *et al.* 1981). Fat and muscle protein contributed respectively 94% and 6% of the total energy expenditure during the fast, values which are close to the values of ca. 89% and ca. 11% in migrating Bar-tailed Godwits (Table 5). Taken at face value, the comparison suggests that the starving geese were employing better protein saving mechanisms than the flying godwits.

We conclude that the loss of fat-free tissue during a long-distance flight can be explained by the minimum requirement for protein for repair (and after replacement as fuel) in a fasting but hard working organism. We must expect similar patterns in other long-distance migrants.

The small margins of a balanced budget

Figure 11 explores to which extent variations in the estimation of flight costs, the energetic equivalent of the mass losses and a given air speed (57 km h^{-1}), influence our conclusion that tail winds are required to balance the travel budget of Bar-tailed Godwits. Since it is likely that the contribution of fat to mass loss is between 40% and 60% (or alternatively, that mass loss was estimated with an accuracy of ± 15%), and that flight costs are between 50 and 70 kJ h^{-1} for ♂♂ and between 60 and 80 kJ h^{-1} for ♀♀ (cf. Table 6), an examination of Fig. 11 (shaded area) leads to the conclusion that some wind assistance is likely to be required if godwits fly with an average air speed of 57 km h^{-1}. Without considerable errors made in the description of the reserve dynamics of migrating Bar-tailed Godwits, in the estimates of air speed and potential wind assistance, and henceforth in the estimation of the cost of flight, the conclusion that the energy budget (and, almost by implication, the time budget) of Bar-tailed Godwits during their spring migration from W. Africa to W. Europe makes a close fit, cannot be avoided (Fig. 11).

This is not to say that all individuals are equally

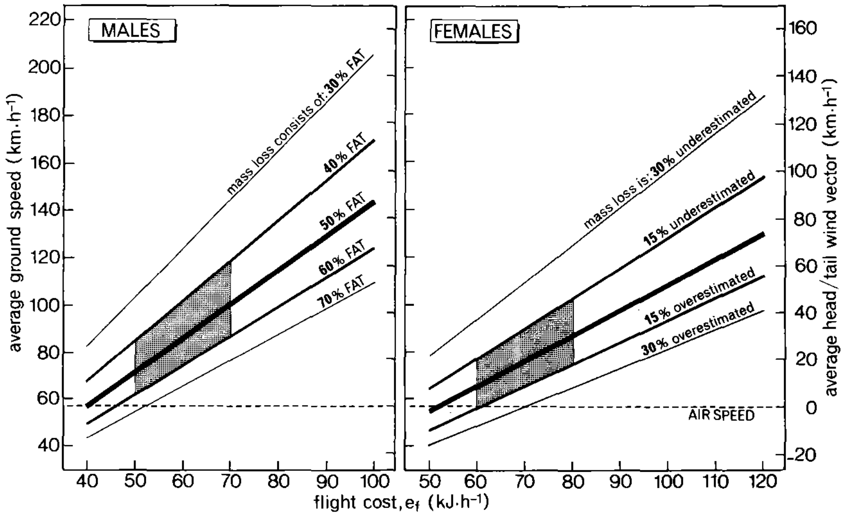

Fig. 11. Ground speeds (and tail wind assistance) required by Bar-tailed Godwits (♂♂ at left, ♀♀ at right) to cover the 4300 km between the Banc d'Arguin and the Dutch Wadden Sea, as a function of flight cost and the energetic density of the estimated mass loss. Since a 10% difference in the proportional contribution of fat to mass loss (at left) equals a 15% difference in total mass assuming a 50/50 fat/fat-free tissue ratio, variations in energetic density can also be expressed as under- or overestimates of mass loss (at right). The shaded areas give the ranges in reasonable values for flight cost and energy loss during the migration.

close to the edge, that all individuals require wind assistance to cover the distance between the Banc d'Arguin and the Dutch Wadden Sea and that a constrained travel budget to fly from W. Africa to Europe necessarily implies that the entire seasonal time and energy budgets of all individuals are constrained. The fact that five of the six individual ♂♂ that were captured near Paesens in two different years, showed a larger than average body mass for the time of the year, when first captured (Fig. 6), may suggest that some birds do better than others: the heaviest birds returned to the same spring staging site, while others moved or died.

Why then, do the Bar-tailed Godwits not leave from the Banc d'Arguin with larger reserves? Do the relatively small food stocks and small individual prey items available (Piersma 1982, Piersma & Engelmoer 1982, Wolff & Smit 1990) prevent an earlier start of premigratory fattening, or do the high temperatures in spring in with a high required intake for each g of mass increase (Klaassen *et al.* 1990) give rise to a constrained time budget (Zwarts *et al.* 1990a), preventing the godwits from attaining higher daily mass gains (Zwarts *et al.* 1990b)? Or might it be evolutionary best to make this flight as energetically cheaply as possible, in spite of the risks of timing incurred?

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SAMENVATTING

De voorjaarstrek van Rosse Grutto's van hun overwinteringsgebied op de Banc d'Arguin in Mauretanië naar de Nederlandse Waddenzee wordt beschreven aan de hand van wegtrekwaarnemingen en vangstgegevens verzameld op de Banc d'Arguin, en vangst- en telresultaten uit de Paesenserpolder aan de Friese Waddenzee kust. Het laatste gebied wordt door de Rosse Grutto's als pleisterplaats gebruikt voordat ze vertrekken naar hun Siberische broedgebieden.

We gaan er van uit dat we in beide gebieden met dezelfde populatie te maken hebben. Hiervoor zijn drie redenen: 1) de biometrie van de vogels op beide plekken komt sterk overeen; 2) twee op de Banc d'Arguin gekleurmerkte Rosse Grutto's werden enkele weken later in de Paesenserpolder teruggezien; 3) de timing van vertrek van de Banc d'Arguin en aankomst in de Paesenserpolder sluit zo mooi op elkaar aan. Op de Banc d'Arguin beginnen de vogels in de eerste helft van maart met opvetten. De mannetjes nemen dan tot hun vertrek naar het noorden (rond 26 april) met ongeveer 2,8 g/dag in gewicht toe, de -wat grotere- vrouwtjes met 3,2 g/dag. Bij Paesens neemt hun gewicht tussen aankomst (29 april) en vertrek (31 mei) toe met 5,6 g/dag voor mannetjes en 7,5 g/dag voor vrouwtjes. Deze gewichtstoenames bestaan voor de helft uit vet (droog en energie-rijk) en voor de andere helft voornamelijk uit (spier-)eiwit.

Aangezien we zowel het wegtrekgewicht van de Banc d'Arguin als het aankomstgewicht in de Wadden-

zee aardig kunnen schatten, hebben we geprobeerd een energiebudget op te stellen voor de nonstop vlucht van 4300 km (langs de kortste afstand: de zgn. grootcirkelroute) van de Banc d'Arguin naar de Waddenzee. We nemen daarbij aan dat de Rosse Grutto's in staat zijn steeds die hoogtes te vinden waar zich de meest gunstige (rug) winden bevinden, tot op 5,5 km hoogte. Tijdens de trekperiode profiteren ze dan gemiddeld van een wind van 18 km/uur in de rug. Dat scheelt nogal op een eigen vliegsnelheid van 57 km/uur. Met een gemidelde snelheid ten opzichte van de grond van 57 + 18 = 75 km/uur hebben de dieren 57,3 uur nodig om 4300 km af te leggen. Tijdens deze vlucht verliezen ze naar schatting zo'n 136 g (mannetjes) of 178 g (vrouwen) lichaamsgewicht, dat (weer) voor de helft uit vet bestaat. Dit gegeven wijst erop dat de trekvogels tijdens zulke meerdaagse vluchten in feite in een toestand van hevige verhongering komen.

Er bestaat altijd een minimum eiwitbehoefte voor het onderhoud van organen en weefsels. Bij verhongerende dieren wordt daar aan voldaan door spieren en organen af te breken. We schatten de energie-verliezen tijdens de trek op 3163 kJ (mannetjes) en 3857 kJ (vrouwtjes). Gedeeld door 57,3 uur komen we uit op een schatting van de vliegkosten voor mannetjes van 55 kJ/uur, en voor vrouwtjes van 67 kJ/uur. Dat is laag vergeleken met de vliegkosten-schattingen aan de hand van literatuurgegevens. Dat betekent dat als de Rosse grutto's niet van de gunstige winden in de hogere luchtlagen gebruik zouden maken, ze meer uren in de lucht zijn. Dan wordt de schatting voor de vliegkosten onwaarschijnlijk laag. Dit houdt in dat de Rosse Grutto's er alleen in slagen om non-stop van de Banc d'Arguin naar de Waddenzee te vliegen door van deze rugwinden gebruik te maken.

RÉSUMÉ

Cet article traite de la migration printanière des Barges rousses à partir de leur zone d'hivernage, sur le Banc d'Arguin en Mauritanie, vers la Mer des Wadden aux Pays-Bas. Elle est basée sur des observations de départs et sur des données fournies par des captures éffectuées sur le Banc d'Arguin, ainsi que sur les résultats de captures et de recensements effectués dans le Paesenserpolder sur la côte frisonne de la Mer des Wadden. Cette dernière zone leur sert d' escale avant qu'elles ne partent vers leurs zones de reproduction en Sibérie. Vu la grande analogie de la biométrie des oiseaux dans les deux zones, vu le fait que deux Barges rousses marquées sur le Banc d'Arguin furent ré-observées deux semaines plus tard dans le Paesenserpolder et vu le fait que le moment du départ du Banc d'Arguin et celui de l'arrivée au Paesenserpolder correspondent, il est pratiquement certain que nous avons affaire à la même population dans les deux zones. Sur le Banc d'Arguin les Barges commencent à constituer leurs réserves de graisse dans la première quinzaine du mois de mars. Jusqu'à leur départ vers le nord (aux environs du 26 avril) la croissance pondérale des mâles est de 2,8 g/jour, celle des femelles, un peu plus lourdes, de 3,2 g/jour. Dans la Mer des Wadden le poids des males s'accroît de 5,6 g/jour et celui des femelles de 7,5 g/jour depuis leur arrivée (le 29 avril) jusqu'à leur départ (le 31 mai). Ces croissances pondérales se composent pour moitié de graisse (sèche et riche en énergie), pour moitié de poids corporel libre de graisse (pauvre en énergie) surtout compose d'eau et de protéines (musculaires). Etant donné que nous pouvons estimer tant le poids de départ que le poids d'arrivée des Barges rousses, nous avons essayé d'établir le budget énergétique d'un vol sans escale sur 4300 km (la distance la plus courte) depuis le Banc d'Arguin jusqu'á la Mer des Wadden. Pour ce faire nous supposons les Barges rousses capables de parvenir aux altitudes où règnent les vents (arrières) les plus favorables, c'est à dire vers 5500 m. Pendant la période de migration ils profitent en moyenne d'un vent arrière soufflant à 18 km/heure, ce qui présente un grand avantage quand on vole à 57 km/heure. Avec une vitesse-sol moyenne de 57+18=75 km/heure les Barges rousses mettent 57,3 heures à parcourir 4300 km. On estime que lors de ce vol la perte de poids corporel est de 136 g (mâles) ou de 178 g (femelles), dont -de nouveau- la moitié seulement se compose de graisse. D'après nous, cela est dû au fait que les oiseaux migrateurs souffrent énormément de faim pendant ces vols de plusieurs jours. Il y a toujours un besoin minimal de protéines pour le maintien des organes et des tissus, besoin auquel est satisfait dans ces animaux souffrant de faim au dépit des muscles et des organes. Nous estimons à 3163 kJ (mâles) et à 3857 kJ (femelles) les pertes énergétiques subies pendant la migration. Divisées par 57,3 heures, cela revient à une estimation des frais de vol des Barges rousses mâles à 55 kJ/heure, et des Barges rousses femelles à 67 kJ/heure. C'est peu, comparé aux estimations de la littérature. Cela signifie que si les Barges rousses ne profitent pas des vents favorables soufflant dans les couches atmosphériques supérieures, elles volent plus longtemps et nous finissons par obtenir une estimation trop basse (inacceptable) des frais de vol. Ce n'est qu'en profitant des vents arrières que les Barges rousses réussissent à accompli sans arrêt le voyage à partir du Banc d'Arguin vers la Mer des Wadden aux Pays-Bas au printemps.