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MOULT, MASS AND FLIGHT RANGE OF WADERS READY TO TAKE OFF FOR LONG-DISTANCE MIGRATIONS

LEO ZWARTS[1,2], BRUNO J. ENS[2,3], MARCEL KERSTEN[2,3] & THEUNIS PIERSMA[2,3,4]

ABSTRACT Wader species wintering on the Banc d'Arguin increased their body mass by about 40% during the 4-6 weeks before their departure in spring. This estimate is based on 1) the empirical fact that most waders which had finished or suspended their body moult into summer plumage were heavy and thus ready to take off, and 2) the assumption that only the heaviest birds in the population left, which allowed the mass of disappearing waders to be estimated from counts and the frequency distribution of body masses in samples of captured birds. The mass gain on the Banc d'Arguin is just over 1% per day, when expressed as a proportion of winter mass. A review of studies on waders preparing for migration shows that 1) the total migratory reserve adds 20-80% to winter mass, 2) the rate of mass gain is 0.1-4% per day and 3. the period of mass increase lasts four weeks on average, but longer if waders prepare for spring migration on the wintering areas. We suggest that all wader species leaving the Banc d'Arguin at the end of April and the beginning of May are able to reach SE. and NW. Europe without refuelling. This seems only possible if current equations to predict flight range systematically underestimate this range, even when the energetic benefits of favourable winds at high altitude are taken into account.

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INTRODUCTION

A preliminary analysis of the spring migration of waders from the Banc d'Arguin in Mauritania suggested that different species employed different migration strategies: 'hoppers' would make many short flights and use many staging areas, whereas 'jumpers' would fly large distances in one go, using few staging areas in- between (Piersma 1987). The birth of this special issue of ARDEA, in which we attempt to synthesize what is known on the spring migration from W. Africa, seems a timely occasion to reexamine this thesis.

The departure mass is an essential parameter in such a study of long-distance migration of birds, since it allows the estimation of flight ranges using equations for flight metabolism and loss of mass during flight, ignoring effects of wind (Summers & Waltner 1978, Davidson 1984a, Castro & Myers 1989). Departure mass can be estimated directly if birds are captured just before departure. In many cases this is impossible and an estimate must be obtained by extrapolating the increase in body mass during the premigration period, to the day of departure. Both methods are reliable only if departure time and the body mass increase are synchronized between the individuals in the population. This appears to be the case, for example, in waders arriving in the Wadden Sea around 1 May and leaving 3.5-5 weeks later (Goede *et al.* 1990, Piersma & Jukema 1990).

However, if the departure time spans a long period (Evans & Pienkowski 1984, Metcalfe & Furness 1985) so that the body mass increases are not synchronized amongst individuals, such methods are less reliable. Unfortunately, this is the situation for many waders departing from the Banc d'Arguin in spring. The period during which wad-

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ers leave varies from more than two months (Redshank *Tringa totanus*, Piersma *et al.* 1990) to about a week (Bar-tailed Godwit *Limosa lapponica*, Piersma & Jukema 1990). Moreover, as discussed by Zwarts & Piersma (1990), there is probably an influx in some species of lean immigrants during the premigration period, thus distorting the frequency distribution of body masses.

If the mass increase is not synchronized exactly during the premigration period, the mean increase in body mass is always less than the rate at which individual birds gain body mass. Figure 1 illustrates the errors which can arise if a mean rate of increase is derived from a regression of the mass of captured birds against the date. The discrepancy between the mass increase of individuals and the average increase in the population is not only affected by the varying strategies of mass gain used by the waders (Fig. 1A-D), but also by the duration of the departure time relative to the duration of the period during which birds increase their body mass (Fig. 1E-F). Furthermore, the error in the population estimate of mass gain becomes even larger if birds remain behind and do not deposit extra body mass, such as occurs in many wader species in Europe during late summer and autumn (Steventon 1977, Clapham 1978, Branson *et al.* 1979, Clapham 1979, Pienkowski *et al.* 1979, Insley & Young 1981, Johnson 1985).

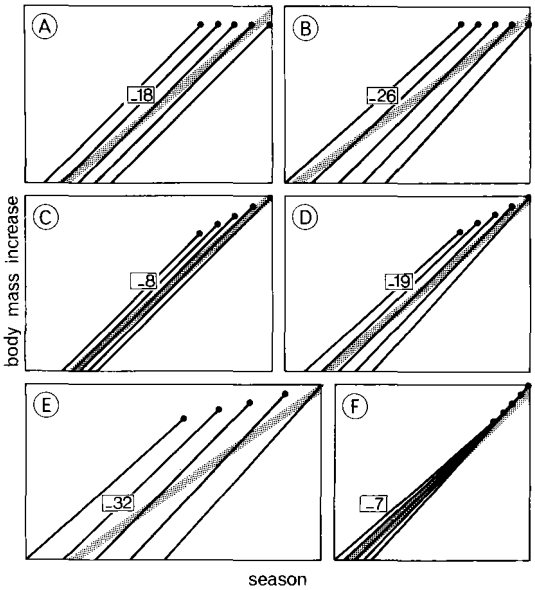

Fig. 1. The body mass increase during the premigration period in a theoretical population of five birds. The birds leave as soon as the departure mass is reached (●). The unsynchronized increase in mass is given according to 6 models: rate of body mass gain either increases during the season (B, D) or does not (A, C) and the departure mass increases during the season (C, D) or does not (A, B). Model E and F are similar to D, but the departure period is twice as long (E) or twice as short (F). The average increase according to a linear regression of body mass against season is given in grey. The decrease (%) in the calculated slope of mass gain of the population from the mean slope of the 5 individuals is indicated in the boxes.

While a direct estimate of the rate of increase in body mass can be made if individuals are captured more than once during the premigration period, capture itself may lead to a long-term depression in mass (Ens *et al.* 1990), so this technique cannot be easily used either. This brings us back to the problem how to identify individuals that are about to migrate in a population where migration is not synchronized. We will use two methods to pinpoint waders on the Banc d'Arguin that are ready to go. First, the increase of body mass and the transition from winter to summer plumage appeared to occur simultaneously and since waders that suspended prenuptial moult prior to departure were also relatively heavy, such birds could be used to estimate the body mass of waders ready to leave. Second, it is also possible to compare, over different periods, the numbers that have disappeared with the frequency distribution of body masses. Assuming that only the heaviest birds leave, the mass of the departing birds can then be estimated.

In this paper the first method is employed to arrive at an estimate of departure mass for as many species of waders as possible. The second method could only be applied to a few species with sufficient data and was used to calibrate the estimates from the first method. Subsequent application of flight range formulae to find out where the waders departing from the Banc d'Arguin go next, then leads us to question the validity of these formulae

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and into a review of their empirical basis. While doing so we could not resist the temptation to reflect on optimal trajectories of mass gain.

METHODS

Waders were captured on the Banc d'Arguin during March-April 1985 and February-April 1986 (see Ens *et al.* 1989 for an analysis of the biometric data obtained for each species). Further data were obtained from waders captured on the Banc d'Arguin in April-May 1988 (P. Duiven & M. Engelmoer pers. comm.) and waders caught in Guinea-Bissau in December 1986-February 1987 (Wymenga *et al.* 1990).

The transition from winter to summer plumage was divided into seven classes: winter plumage (= 1), trace of summer plumage, 1/4, 1/2 and 3/4 summer plumage, trace of winter plumage, and full summer plumage (= 7). The last two categories will be combined here. The less conspicuous change in ♀♀ Bar-tailed Godwits from winter to summer plumage was described using four categories (1 = winter, 4 = summer and two classes in-between).

The prenuptial moult was recorded in four categories; body moult being (0) absent, (1) light, (2) moderate, or (3) heavy. Wing length and bill length were measured to the nearest 1 and 0.1 mm, respectively, according to the standard procedures of maximum chord and exposed culmen, respectively. Body mass was determined to the nearest g with Pesola spring balances and/or electronic digital balances.

Captive waders which were reweighed lost on average 0.78% of their body mass per h (Fig. 2A). Birds lost most mass just after capture (Fig. 2B), but since waders were generally captured on the incoming tide, the trend in Fig. 2B might be due to waders defecating more frequently during the first hours of the roosting period. Indeed, they lost less mass per h the greater the time elapsing since feeding (Fig. 2C). These estimates of mass loss in captivity agree with those of waders caught in Europe: Dunlin *Calidris alpina* (Goede & Nieboer 1983, Davidson 1984b), Knot *C. canutus* (Davidson 1984b) and Oystercatcher *Haematopus ostralegus* (Zwarts pers. obs.; see Fig. 2C). According to G.

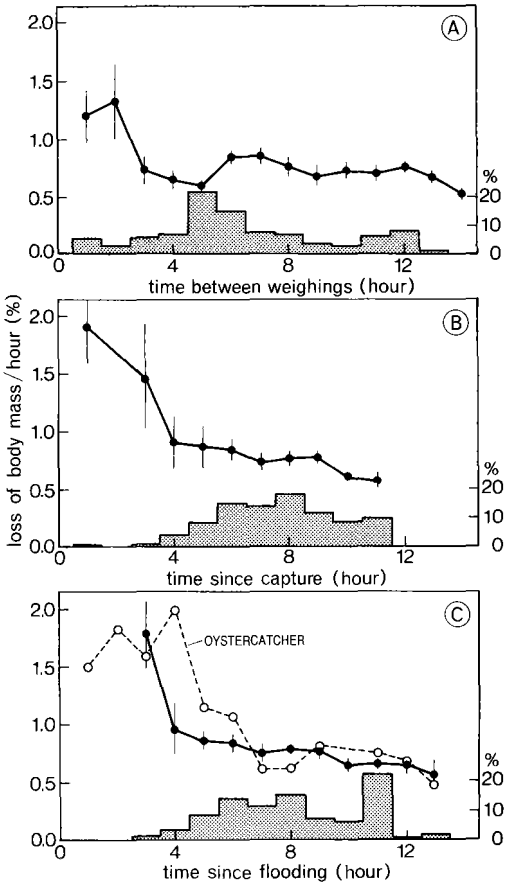

Fig. 2. Loss of body mass per h in relation to A) time between first and second weighing (% ± *SE* relative to total body mass at first weight) B) time since capture time (time is the midpoint of the period between successive weighings) and C) time since the flooding of the tidal flats (time is the midpoint of the period between successive weighings); for comparison the mass loss in Oystercatchers captured in the Wadden Sea is also given (Zegers & Zwarts own obs.). In all three panels, the histograms show the frequency distribution of times (n=449). All birds except the Dutch Oystercatchers were captured on the Banc d'Arguin, the sample consisting of 23 Ringed Plovers, 1 Kentish Plover, 1 Oystercatcher, 93 Knots, 7 Sanderlings, 26 Little Stints, 19 Curlew Sandpipers, 225 Dunlins, 31 Bar-tailed Godwits, 1 Whimbrel, 2 Redshanks and 20 Turnstones.

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Castro (pers. comm.) rate of mass loss increased with temperature above a threshold level of 30°C but it is unlikely that such temperatures were ever reached in any of the previously mentioned studies.

Clearly, body mass might be best obtained 4-6 h after the end of the feeding period, so most of the food would have been digested and defecated. However, this was not possible as the time when the feeding area was flooded was not always known. It was possible though to add another refinement. We had expected that smaller waders would lose relatively more mass as they might dehydrate faster than the larger species (Piersma & van Brederode 1990; see also Nagy & Peterson 1989). Indeed, according to a one-way analysis of variance ($R^2 = 0.036$, $p = 0.04$, $n = 443$; analysis on seven species with more than seven individuals reweighed; see Fig. 2), the relative loss of mass (L in % of mass per h) differed between the species. The average relative loss decreased with mass (M in g), being 1% per h for Little Stint (*C. minuta*) and 0.6% per h for Bar-tailed Godwit (253 g):

$$L = 1.55 - 0.17 \cdot \ln(M) \; (r = 0.21, p < 0.001).$$

Therefore, body mass was converted to mass at capture by adding the species-dependent loss (varying between 0.6% and 1% per h) to body mass for each h after capture. In fact, the correction is small because most of the waders were weighed 2-7 h after capture.

There were no differences between the masses of adult waders caught in February on the Banc d'Arguin and those captured in Guinea-Bissau, 950 km to the south. The relations between winter mass and wing length, used as a measure of structural size (Piersma & van Brederode 1990), were also similar in the two sites. The covariance analyses performed for the different species showed that 'site' explained only a small and, in all cases, non-significant part of the variance (p ranging from 0.11 to 1.00 and R^2 from 0.06 to 0.0). Therefore the data for the two sites were combined.

The large variation in winter body mass within species can partly be attributed to size differences

Table 1. Regression of body mass on wing length for adult waders caught in Guinea-Bissau and on the Banc d'Arguin in January/February. Regression has been used to calculate relative winter mass (see Fig. 5, where also numbers of cases are given). Intercept = a; slope = b and correlation coefficient = r. Mean body mass of adults ($\bar{x}$, SE, in g; number = n_m) concern waders captured during both months; birds in wing moult are included. Wing length ($\bar{x}$, SE in mm; number = n_w) is given for all adults captured at both sites (December/May). The two-letter code is used elsewhere in the paper to indicate the species.

		regression			body mass (g)			wing length (mm)		
species	code	a	b	r	$\bar{x}$	SE	n_m	$\bar{x}$	SE	n_w
Kentish Plover	KP				38.3		1	111.8	1.0	11
Grey Plover	GP	-39.42	1.124	0.39	187.4	1.5	100	198.7	0.6	59
Ringed Plover	RP	-136.80	1.400	0.92	48.7	1.9	4	131.5	0.4	78
Knot	Kn	-80.74	1.189	0.51	119.4	0.8	164	169.0	0.2	550
Sanderling	Sa	-9.60	0.447	0.68	46.9	1.2	4	126.2	0.6	40
Little Stint	LS	-22.56	0.456	0.61	22.1	0.5	12	97.9	0.2	232
Curlew Sandpiper	CS	0.97	0.386	0.37	51.6	0.3	151	131.5	0.2	202
Dunlin	Du	-19.50	0.540	0.53	42.0	0.5	38	114.5	0.1	504
Bar-tailed Godwit	BG	-395.06	2.987	0.79	253.2	8.7	78	217.0	0.6	211
Whimbrel	Wh	-328.65	2.960	0.61	413.6	4.2	94	255.8	1.0	89
Curlew	Cu	-1531.87	7.360	0.84	718.2	33.3	13	305.7	3.9	13
Redshank	Re	-75.16	1.150	0.41	107.6	1.7	43	159.8	0.4	75
Turnstone	Tu	38.04	0.390	0.19	99.4	0.8	110	157.4	0.2	409

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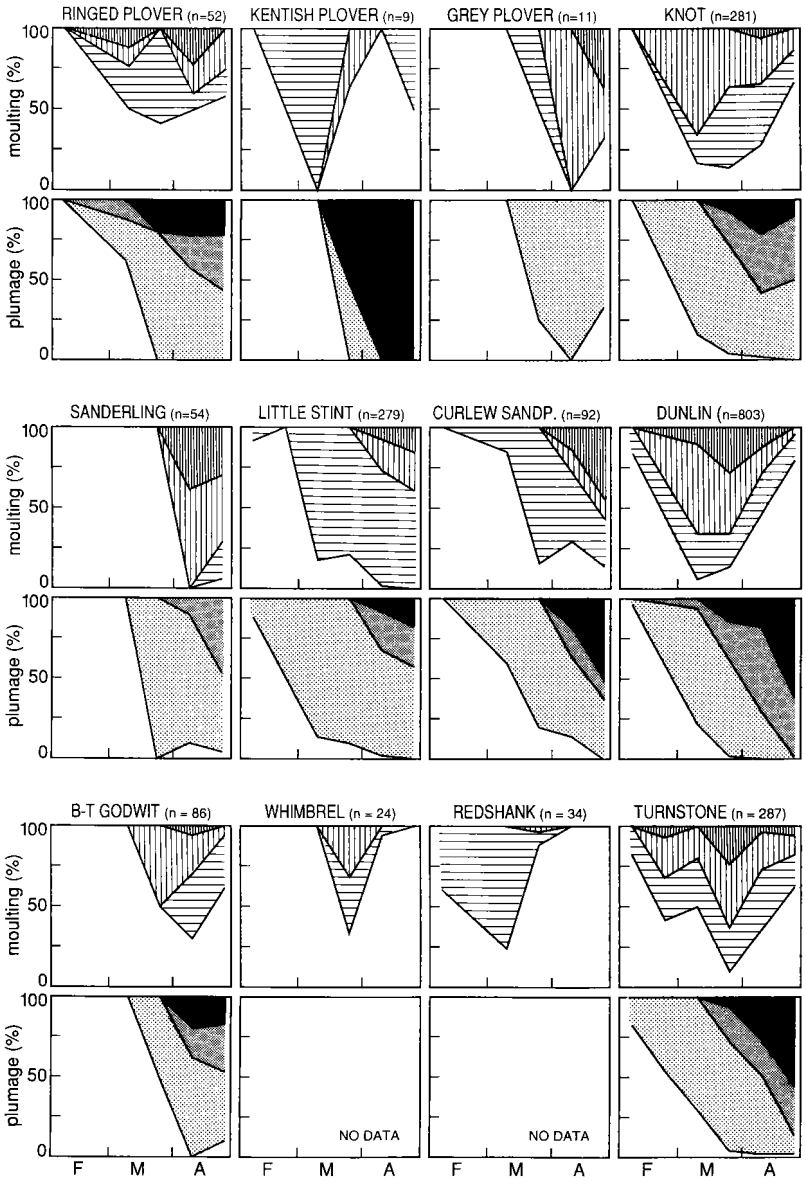

Fig. 3. Body moult scores (upper panel) and the development of the summer plumage (lower panel) per fortnight over a period of three months in the adult population of 12 wader species on the Banc d'Arguin. The sample size is indicated. Moult is scored in four categories: no (white), light (vertical light hatching), middle (horizontal light hatching) and heavy (dark hatching). Plumage is also given in 4 classes in increasing intensity of grey: 1) winter (white), 2) trace of summer to 1/2 summer, 3) 3/4 summer and 4) trace of winter to completely summer plumage (black).

between individuals. The regressions of body mass on wing length (Table 1) were used to predict winter body mass against which the measured body mass was calculated as a percentage deviation. The reader wishing to transform the percentages into absolute body mass is referred to the average winter mass (Table 1), and papers giving the original data (Ens *et al.* 1989, 1990, Piersma & Jukema 1990).

The seasonal timing of wader departure from the Banc d'Arguin has been quantified (see Piersma *et al.* 1990), while the numbers leaving during spring were derived from a series of counts (Zwarts & Piersma 1990).

The statistical analyses were performed using SPSS (Norusis 1989).

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RESULTS

Moult and plumage

With the exception of a few Ringed Plovers *Charadrius hiaticula* and Little Stints, all adult waders caught on the Banc d'Arguin in March-April had finished their wing moult. In fact, the majority of individuals of all species had done so in February. They start their wing moult in September or even earlier (Pienkowski & Dick 1975, Pienkowski *et al.* 1976, Johnson & Minton 1980, Wilson *et al.* 1980). Waders wintering in Africa and Australia extend the wing moult to continue through the whole autumn and winter (e.g. Middlemiss 1961, Thomas & Dartnall 1971a, 1971b, Elliott *et al.* 1976, Schmitt & Whitehouse 1976, Dean 1977, Paton & Wykes 1978, Tree 1979, Pearson 1987, Barter 1989, Summers *et al.* 1989), in contrast to waders wintering in the temperate zone which finish their wing moult in autumn (e.g. Boere 1977, Summers *et al.* 1989; see Smit & Piersma 1989: Fig. 29 for a review).

The adults of most wader species on the Banc d'Arguin were in winter plumage until late February and commenced moulting their body feathers only in March (Fig. 3). The adults in nearly half of the species were completely in summer plumage at the end of April, but there were large differences between the species in the timing. Redshanks completed body moult at the end of March, when Sanderlings *C. alba* and Bar-tailed Godwits had just started. The latter two species left the Banc d'Arguin three weeks later than the Redshank (Piersma *et al.* 1990, Zwarts & Piersma 1990), suggesting that the timing of prenuptial moult coincides with that of departure. Figure 4A shows that prenuptial moult was most intense about four weeks before the average date of departure.

Species which departed early from the Banc d'Arguin bred in the temperate zone, while the species leaving later returned to the high arctic, where the breeding season is later (Piersma *et al.* 1990). If moult is completed before departure, the timing of moult may ultimately depend on the timing of the start of breeding. Indeed, in an interspecies comparison there is a positive association between the time of prenuptial moult and the latitude of the midpoint of the breeding area, a measure of the time when breeding starts (Fig. 4B).

Increase of body mass

Since winter mass did not systematically change during January and February and since no differences were observed between the Banc d'Arguin and Guinea-Bissau, the data were pooled (Table 1). For all species, the body masses in Table 1 approximated those of waders captured on the Banc d'Arguin in autumn and early winter (Dick & Pienkowski 1979, R. Lensink & P.L. Meininger pers. comm.). Comparison with the masses of waders in S. Africa (Summers & Waltner 1978, Summers *et al.* 1987, 1989), reveals that winter masses were about 10% lower in Guinea-Bissau and Mauritania.

From March until their departure, body mass increased in all species, but there were differences in timing (Fig. 5). Redshanks and Dunlins began earlier than both Sanderlings and Curlew Sand-

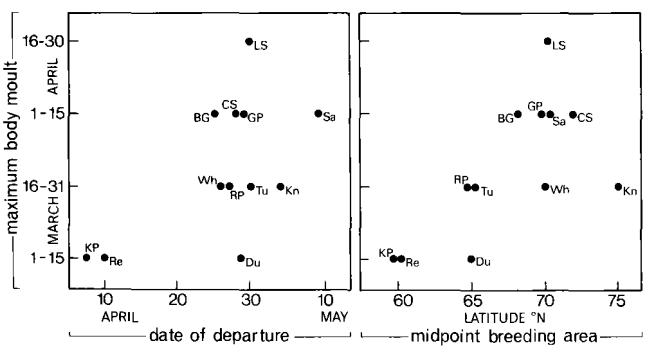

Fig. 4. The fortnight at which body moult was most intense in 12 wader species on the Banc d'Arguin (from Fig. 3) as a function of (A) their average date of departure (from Piersma *et al.* 1990) or (B) the average latitude of their breeding areas (from Piersma *et al.* 1990 and Cramp & Simmons 1983). Species are indicated with two-letter codes (see Table 1).

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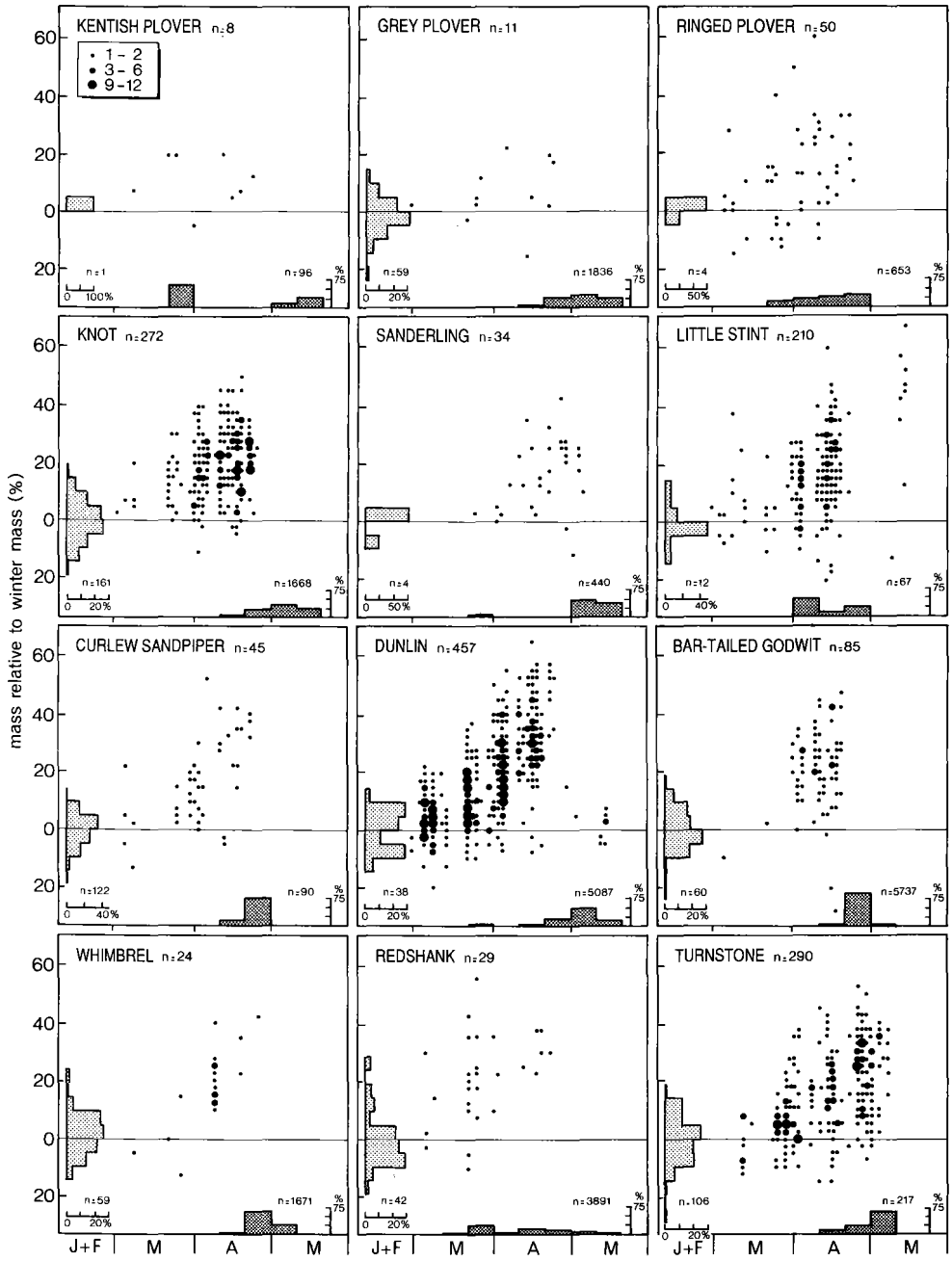

Fig. 5. Frequency distribution of body mass in mid-winter (histogram along y-axis), and the change in body mass during spring (scatterplots). The timing of departure is indicated by the histograms along the x-axis (from Piersma *et al.* 1990). The body masses are adjusted for variation in wing length (Table 1). Sample sizes are indicated and refer to the total number of adult waders captured in Guinea-Bissau and on the Banc d'Arguin in January and February (histogram), the total numbers of adult waders captured on the Banc d'Arguin later in the season (scatterplots), and the numbers of waders observed to leave the Banc d'Arguin (histogram).

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pipers *C. ferruginea*. The scatterplots (Fig. 5) suggest that the mass gain started about a month before the departure. The maximum increase in mass was 50-60% relative to winter mass. Kentish Plovers *Charadrius alexandrinus* and Grey Plovers *Pluvialis squatarola* were exceptions to this rule since they seemed to gain only half as much mass, but very few birds were caught.

Identification of waders 'ready to take off'

Only Knot, Little Stint, Dunlin, Bar-tailed Godwit and Turnstone were caught in sufficient numbers to allow a detailed investigation between the increase in body mass (expressed as a % deviation relative to winter mass), summer plumage, body moult and season.

From January onwards, the body mass of adults in winter plumage remained low, even in the rare individuals which still had winter plumage in April (Fig. 6). This suggests that no birds prepared to migrate from the Banc d'Arguin without first having commenced the prenuptial body moult. In the majority of species, body mass reached a maximum in those birds which had nearly completed their moult towards summer plumage. For some species there was a clear trend for individuals with the same plumage score to be heavier as the season progressed (Fig.6, Table 2). Interestingly, in May, when most of the adult Dunlins in summer plumage had already left the Banc d'Arguin, those remaining had a low body mass (Fig. 6). This suggests that adult Dunlins

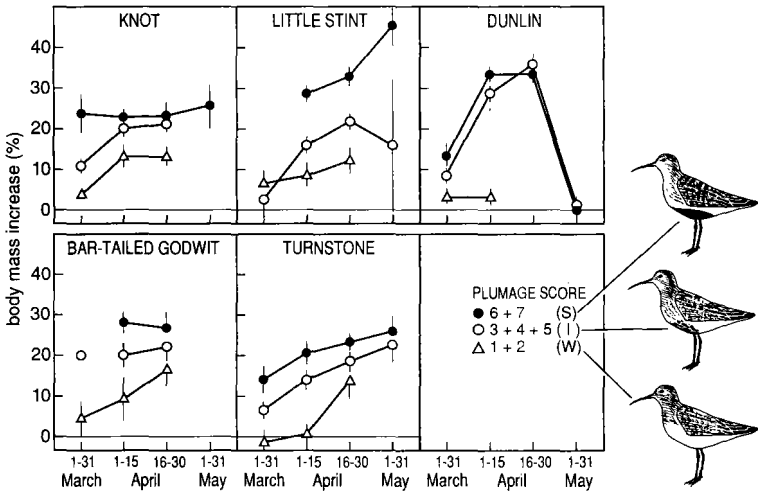

Fig. 6. The relation between body mass (% increase relative to winter mass) and season (March, first and second half of April and May) for adult waders with a different plumage. The isolated symbol concerns a case with sample size one. Statistical analyses are given in Table 2.

Table 2. Results of five 3-way analyses of variance to investigate the variation in body mass (relative to winter mass) of adult waders captured in March, April and May, as dependent on plumage (3 categories: score 1+2, 3+4+5 and 6+7, but for ♀♀ Bar-tailed Godwit 1, 2+3 and 4), body moult (2 classes: yes or no) and season (4 classes: March, first and second half of April, first half of May). The factors are accessed successively; the interaction could not be calculated in three species. Same data are given in Figs. 6 and 7.

species	plumage		moult		season		interaction		
	R^2	p	R^2	p	R^2	p	R^2	p	n
Knot	0.058	0.000	0.095	0.000	0.039	0.000	0.044	0.089	274
Little Stint	0.239	0.000	0.009	0.115	0.043	0.002			210
Dunlin	0.194	0.000	0.179	0.000	0.124	0.000			445
Bar-tailed Godwit	0.125	0.005	0.004	0.571	0.021	0.395			84
Turnstone	0.181	0.000	0.095	0.000	0.051	0.000	0.053	0.000	286

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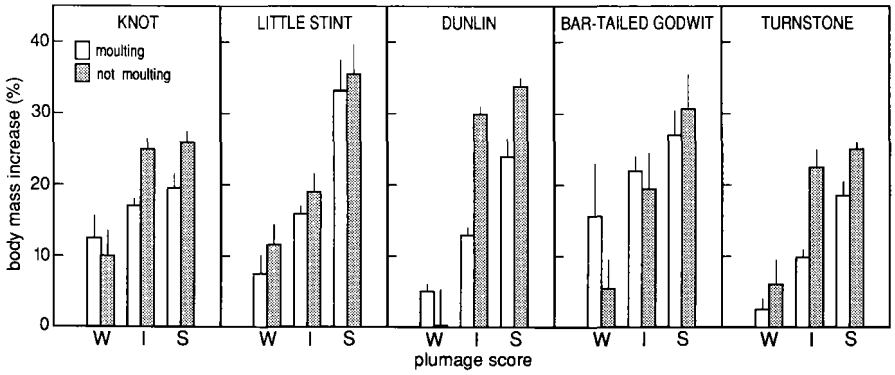

Fig. 7. Average body mass (% increase relative to winter mass) in moulting (black) and non-moulting adult waders (white) in March, April and May, given separately for winter plumage (W: scores 1 + 2), summer plumage (S: scores 6 + 7) and intermediate plumage (I: in-between). Statistical analyses are given in Table 2.

which spend the summer on the Banc d'Arguin slowly complete their body moult to summer plumage.

The increase of body mass in the course of the season for individuals with a comparable plumage score might be due to individuals gaining mass after having finished or suspended moult. Indeed, the occurrence of prenuptial moult appears to be related to body mass (Fig. 7). With the exception of Little Stint and Bar-tailed Godwit, non-moulting waders which were in transitional or summer plumage were heavier than birds that were moulting (Fig. 7). The effect of season on body mass (Fig. 5) becomes less pronounced when stage of summer plumage and body moult score are also taken into account (Table 2). Therefore, we identified waders as ready to take off when they had suspended or finished their prenuptial body moult.

For waders captured before and after 15 April, Fig. 8 shows the frequency distribution of the increase in body mass in all birds as well as those which were considered as ready to go. Very few individuals deposited more than 50% of the winter mass before migration, and most individuals ready to go laid down only 20-40%. The body masses of some waders, considered as ready to take off according to moult and plumage scores, were still on winter level, and so not able to depart. This might be explained by the fact that for instance adult Dunlins reach full summer plumage when they spend the summer on the Banc d'Arguin (and thus are scored as ready to go), while the body mass of these birds remains on winter level (Fig. 6). This is one of the reasons why we believe that distinguishing waders according to plumage or moult during the premigration period can only give a minimal estimate of departure mass. The degree of underestimation will be evaluated in the discussion.

DISCUSSION

Timing of mass gain and moult to summer plumage

That waders start their prenuptial moult before the departure from the wintering grounds has been shown for Knots and Bar-tailed Godwits in Australia (Barter, Jessop & Minton 1988b, Barter 1989), Little Stints in S. Africa (Middlemiss 1961) and Kenya (Pearson 1987), Curlew Sandpipers in Australia (Thomas & Dartnall 1971b, Barter 1986) and S. Africa (Elliott *et al.* 1976), Turnstones in S. Africa (Summers *et al.* 1989), Least Sandpipers *Calidris minutilla* in California (Page 1974), Red-necked Stints *C. ruficollis* in Australia (Thomas & Dartnall 1971a), Pacific Golden Plovers *Pluvialis fulva* on Hawaii (Johnson & Johnson 1983, Johnson *et al.* 1989), Golden Plovers *P. apricaria* in The Netherlands (Jukema 1986) and 12 different wader species in Venezuela (McNeil 1970).

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In waders on the Banc d'Arguin, the increase in body mass and the moult from winter to summer plumage occur simultaneously. Comparing species, there is a tendency that species that depart early in the season also moult early in the season (Fig. 4A). Variations in timing in different geographical areas have even been described within a species. Curlew Sandpipers leaving S. Africa or Australia in early April start their prenuptial moult a month before their conspecifics departing from the Banc d'Arguin a month later (Elliott *et al.* 1976, Barter 1986). A similar difference occurs with Bar-tailed Godwits wintering in Australia (Barter 1989) and on the Banc d'Arguin. The Australian birds depart at the end of March and the African birds at the end of April.

Not all waders complete prenuptial moult before leaving the wintering area. Many waders that are ready to go apparently suspend body moult (Fig. 7), as originally suggested by Thomas & Dartnall (1971a, 1971b). That waders do not migrate long-distances in active body moult is supported by Piersma & Jukema (pers. obs.). They found that Bar-tailed Godwits were not moulting when they arrived in the Dutch Wadden Sea but restarted body moult some days later. Prokosch (1988) also found that Bar-tailed Godwits staging in the Wadden Sea continued body moult. Since Stresemann & Stresemann (1966) it is widely accepted that migration and wing moult are mutually exclusive processes. Though Boere (1976) and Pienkowski *et al.* (1976) suggest that Redshank migrate while in active wing moult, neither paper compares the number of individuals caught in arrested moult with an expectation of this number based on the amount of time it takes to arrest moult and depart. Flying while in wing moult would reduce flight performance, but it is less clear why body moult should be suspended before migration. Perhaps, the active growth of feathers is not compatible with the fast drain of energy during long-distance flights, or birds in heavy body moult would suffer an extra energy drain when flying in cold air at high altitudes.

Estimation of departure mass

That waders which have reached full summer plumage have a greater mass than other birds was earlier reported by Jukema (1986) for Golden Plovers and by Pearson (1987) for Little Stints. Here we want to go a bit further and explore to what extent plumage can actually be used to identify those waders which are approaching departure mass. If successful, it would allow us to reliably estimate departure mass for the majority of wader

Table 3. The total mass increase (%) relative to the winter mass of departing waders, assuming that only the heaviest waders leave (see Fig. 5 for a frequency distribution of the adults; note that for these analyses juveniles are included). Mean departure mass (with range between brackets) was calculated for the proportion of the population leaving the Banc d'Arguin during ten-day periods in March (M) and April (A), as derived from either the numbers observed to leave in departing flocks or from the series of high water counts.

species	10 day	departures		counts	
	period	leaving (%)	mass gain (%)	decrease (%)	mass gain (%)
Knot	A II	5	45 (41-50)	19	37 (31-50)
	A III	24	30 (28-36)	45	27 (20-36)
Dunlin	M III	1	36 (34-38)	14	26 (20-38)
	A I	0		14	38 (30-55)
	A II	3	54 (53-64)	14	44 (36-64)
	A III	25	53 (48-57)	32	47 (26-57)
Turnstone	A III	30	34 (28-53)	43	31 (22-53)

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species departing from the Banc d'Arguin.

Premigratory fattening was not observed in birds which had not started their prenuptial body moult. The average body mass of individuals which had finished or suspended prenuptial moult would underestimate their actual departure mass if birds continued to deposit still more mass after finishing or suspending moult. Figure 7 shows that this occurred with near certainty in some species. Moreover, as shown earlier, summering waders with low body masses were erroneously marked as ready to go. It is therefore necessary to quantify by what amount departure mass is underestimated.

To this end the departure mass of the three species caught in highest numbers was calculated from 1) the frequency distribution of the body masses per 10 day period (as shown in Fig. 5, but in this case including the juveniles), and 2) the proportion of the population actually leaving during that period. For each period it was assumed that only the heaviest birds (moulting or not moulting) left. The juveniles are included in the frequency distribution since the proportion leaving refers to all birds present. Two measures for the proportion leaving were available: 1) the series of counts at high tide (Piersma *et al.* 1989) or at low tide (Zwarts *et al.* 1990a) and 2) the systematic direct observation of departing flocks (Piersma *et al.* 1990; see also Fig. 5 in this paper). In Knots and Dunlins, high water counts suggested many waders departed in April, while direct observations suggested the main exodus occurred around early May (Fig. 2 in Zwarts & Piersma 1990). Therefore, when counts were used to estimate the proportion of birds leaving, the estimate of departure mass turned out lower than when direct observations were used, but the differences were surprisingly small (Table 3). Dunlin departing early in the season did so at a lower mass than Dunlin departing late (see also Kersten 1989), but there is no indication that the Knots departing in the middle of April did so at a lower mass than the Knots departing by the end of

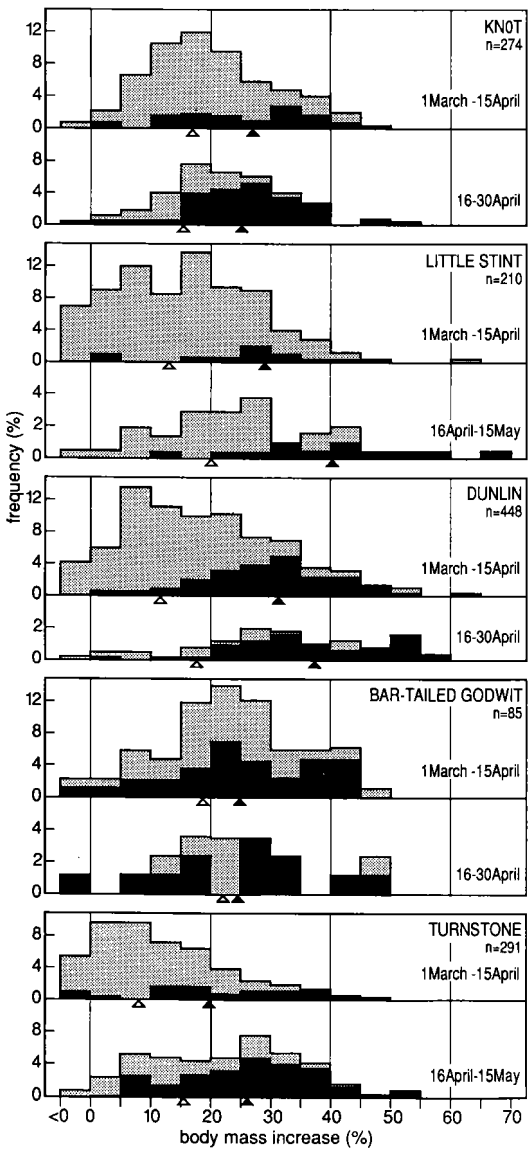

Fig. 8. Frequency distribution of body mass (% increase relative to winter mass) in waders on the Banc d'Arguin in March and first half of April (upper panel) and in second half of April and in May (lower panel). Indicated with grey are waders which either had suspended or finished their moult and had reached a stage of > 1/4 summer plumage (score > 2) (Knot, Dunlin or Turnstone), or waders which had reached the stage of summer plumage (score > 6, moulting or non-moulting taken together) (Little Stint and Bar-tailed Godwit). See Fig. 7 why different criteria were used to indicate for the five species waders ready to go. Triangles along the x-axis indicate the means of all waders involved (white) or waders which were assumed to be ready to go (black).

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April. Most important is that on all accounts the departure masses in Table 3 were higher than the average body masses of birds which had suspended or finished prenuptial moult (Fig. 8). Therefore departure mass should not be estimated as the mean mass of all of the waders which, on the basis of plumage, are 'ready to go'. Comparison of both data sets (see Fig. 8 and Table 3) suggest that the best estimate of the body mass is the mean of the upper half in the frequency distribution of such birds.

Further support comes from an independent estimate of the departure mass of Turnstones by Ens *et al.* (1990). They showed that in Turnstones the discrepancy between body mass predicted from the rate of body mass gain in recaptured birds and the mean body mass of the population increased during the season. It was concluded that heavy birds left first and that lighter ones stayed behind to deposit more mass. Departure mass of Turnstones was estimated at ca. 135 g, equivalent to an increase of 35%, which is close to the results in Table 3.

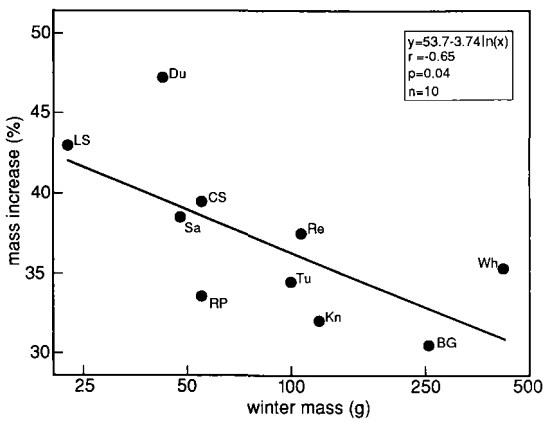

Fig. 9. Relative body mass increase (mean of the upper half of the frequency distribution of body mass of waders, caught from 15 April onwards which, according to the stage of plumage and/or moult, were considered as ready to go) as a function of the winter mass (Table 1). Species are indicated with a two-letter code (Table 1). The selection criteria are given for five species in Fig. 8 and are for the five other species: non-moulting birds in Redshank and Whimbrel (in both species plumage was not scored); summer plumage in Curlew Sandpiper (in this species all birds captured were still moulting) and waders at least in intermediate plumage and non-moulting in Sanderling and Ringed Plover.

Hence, the mean of the upper half of the frequency distributions of waders ready to go in Fig. 8 is used as the estimate of departure mass. This averaged 1.3 times both the median and the mean mass of these waders. Figure 9 shows that the larger the species, the lower is the migratory reserve as a percentage of body mass.

Rate of body mass gain and duration of the premigration period

One additional reason for believing that many waders in summer plumage were ready to go is that, in April, Knots, Dunlins and Bar-tailed Godwits in summer plumage fed much less actively than birds in transitional plumage (Zwarts *et al.* 1990b). So perhaps some individuals with completed body moult no longer needed to feed intensively having already (almost) attained departure mass and were waiting for a good opportunity to depart. This makes us aware that a wader must solve four problems during the premigration period: 1) when to start preparations for migration, 2) at what rate to gain mass, 3) at what mass to depart and 4) when to depart. For convenience we assume in the following that there exist a fixed optimal departure date and a fixed optimal departure mass and discuss rate of mass gain and duration of the premigration period. Waders cannot depart without sufficient levels of reserve tissue, but it is very likely that carrying the reserve before the grand moment of departure is costly. The excess body mass probably increases the daily cost of living and will decrease agility in flight making the waders more vulnerable to aerial predators. All else being equal we would expect the waders to gain mass at a maximal rate so as to minimize the period during which they are gaining mass.

Our first task is to put a value to the maximal rate of mass increase and investigate whether these rates are observed in nature. Assuming that net energy intake has to increase by 25-30% to achieve a daily mass increase of 1% (calculated from Klaassen *et al.* 1990), the maximum potential rate

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Table 4. Estimations of the increase of body mass in coastal waders during spring and autumn migration; month and, if relevant, subspecies are indicated. The total mass gain and the gain per day are both given as percentages relative to body mass before the premigration period. Both variables are, for the purpose of comparison, expressed in relation to the 'tropical winter mass', even if they prepare for migration in the temperate zone. The mass gains per day are estimated from mass gain in the population (pop.) or from average mass gain in retrapped individuals (ind.).

area	species	month	mass (g)	gain (g)	gain/day pop.	gain/day ind.	sources
Wadden Sea	Dunlin (*alpina*)	4	48	15	0.2	0.4	Goede, Nieboer & Zegers 1990[1]
Wadden Sea	Bar-tailed Godwit	4	264	35	0.4		Prokosch 1988[2,3]
Mauritania	Curlew Sandpiper (juv)	10	42	35	0.7		Wilson, Czajkowski & Pienkowski 1980[1]
Australia	Red-necked Stint	3	30	45	0.9		Barter 1984
Australia	Curlew Sandpiper	3	52	65	0.9		Barter 1986
Kenya	Little Stint	4	21	55	0.9	1.1	Pearson 1987[1]
S. Africa	Turnstone	4	100	65	1.0		Summers *et al.* 1989
S. Africa	Curlew Sandpiper	3	52	55	1.0		Elliott *et al.* 1976
S. Africa	Sanderling	4	47	80	1.1		Summers *et al.* 1987
Mauritania	different wader species	4	40	1.1			this paper: Fig. 9[4]
E. England	Dunlin (*alpina*)	5	48	55	1.1		Pienkowski, Lloyd & Minton 1979[1]
W. England	Ringed Plover (*tundrae*)	5	49	55	1.1	1.2	Eades & Okill 1976[1]
Mauritania	Turnstone	4	100	40	0.7	1.3	Ens *et al.* 1990[5]
S. Africa	Knot	4	120	60	1.2		Summers & Waltner 1979
S. Africa	Grey Plover	4	187	70	1.2		Summers & Waltner 1979
W. England	Knot	4	129	65	1.2		Prater & Wilson 1972
Canada	Semipalmated Sandpiper	7/8	25	35	1.4	1.5	Morrison 1984[6]
S. Africa	Little Stint	4	21	50	1.5		Middleniss 1961
W. England	Turnstone	5	100	60	1.5		Clapham 1979[1]
W. England	Ringed Plover (*tundrae*)	5	49	65	1.5	3.0	Clapham 1978[1]
E. USA	Semipalmated Sandpiper	8	25	55	1.6	1.5	Dunn *et al.* 1988[7]
Hawaii	Golden Plover	4	117	50	1.7		Johnson *et al.* 1989
Scotland	Turnstone	5	100	55	1.7		Summers *et al.* 1989
Scotland	Sanderling	5	47	45	1.8	1.9	Clark, Turner & Young 1982[1,8]
E. England	Grey Plover	5	187	70	1.8		Branson & Minton 1976, Johnson 1985
Wadden Sea	Dunlin (*alpina*)	5	48	65	1.9	2.1	Goede, Nieboer & Zegers 1990[1]
Wadden Sea	Grey Plover	5	187	78	1.9	4.6	Prokosch 1988[5]
E. England	Sanderling	5	47	80	2.1		Davidson 1984a
Iceland	Turnstone	5	100	60	2.1		Morrison 1975
Iceland	Knot	5	120	50	2.1		Morrison 1975
Norway	Knot	5	120	55	2.2		Davidson & Evans 1986
Wadden Sea	Knot	4	120	60	2.2		Prokosch 1988
W. England	Dunlin (juv. *alpina*)	5	48	60	2.2	2.3	Eades & Okill 1977[9]
Sweden	Dunlin (juv. *alpina*)	9	42	?25	2.4		Mascher 1966[10]
Wadden Sea	Bar-tailed Godwit	5	254	80	2.6	2.8	Piersma & Jukema 1990[1]
Wadden Sea	Knot	5	120	75	2.5	3.6	Prokosch 1988[5]
Alaska	Turnstone	9	100	55	3.7		Thompson 1974[11]
England	Dunlin (*schinzii*)	8	42?	60	(0.2)	3.9	Steventon 1977[12]
E. USA	Semipalmated Sandpiper	8	25			4.0	Page & Middleton 1972[1]
Wadden Sea	Bar-tailed Godwit	5	254	75	4.5		Prokosch 1988
W. Scotland	Knot (juv.)	8	96			4.9	Buxton 1989[1]
England	Curlew Sandpiper	9	52	55	3.6	5.4	Stanley & Minton 1972[1]

[1]ind. mass gain over same year; no correction made for possible long-term mass loss after first capture; [2]departure mass probably too low because of influx of newcomers; [3]mass estimated to be 10 g above mass of birds wintering in the tropics, given the longer wing (Table 1); [4]departure mass according to Fig. 9; the average mass in the population before and during the departure amounts to 25-30% (Fig. 5); [5]ind. mass gain over different years since waders lost too much mass after first capture; [6]ind. mass gain from 7 days after first capture onwards; [7]ind. mass gain from 1 day after first capture onwards; [8]departure mass given too low since departure week after last capture; [9]average mass gain within same year, excluding 3 individuals which had lost mass; [10]ind. mass gain from 3 days after first capture onwards; [11]ind. mass gain from 4 days after first capture onwards; [12]greater part of birds did not leave within the study period.

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of mass gain can be calculated since the maximum amount of energy that can be metabolized (calculated from body mass using the equation of Kirkwood 1983) is 3.9 times the basal metabolic rate of waders (Kersten & Piersma 1987) or 2.2 times the metabolic rate in the field in Mauritania (Zwarts & Dirksen 1990, Zwarts *et al.* 1990a). The maximum rate of increase in mass must be ca. 4-5% d^{-1}.

This theoretical value has to be compared to empirical data, compiled in Table 4 (see legend for details). This table must be interpreted with caution as rate of mass gain was often calculated from departure mass and duration of premigration period. Departure mass itself was calculated from data on the mean mass of the population at the average date of departure, which, as argued above, will usually provide underestimates. Though we are fully aware of the difficulties with estimating rate of mass gain from either changes in mean mass of the population or from changes in mass of retrapped individuals (see introduction) we present both; if the same trend emerges from both data sets, it reinforces the conclusion.

Bearing these caveats in mind, it appears that high rates of increase in mass are predominantly found in the spring 'refuelling sites' when birds stop on migration, but gains of up to 4.5% d^{-1} have also been measured in some stopover sites during autumn migration (Table 4). The highest observed rates in Table 4 are thus close to the maximum level. However, Hicklin (1983a) noted the extremely high rate of gain of 0.9-2.5 g per day in Semipalmated Sandpipers *Calidris pusilla* refuelling in the Bay of Fundy, Canada, equivalent to 3.6-10.0% d^{-1} relative to winter mass. Though more data are needed to confirm this exceptionally high rate of mass gain in this rich intertidal area (e.g. Hicklin 1983b, Wilson 1990), Lank (1985) too found indications that this species is able to gain mass very quickly.

Low rates of mass gain were reported for waders departing from the wintering areas. The rate of body mass gain on the Banc d'Arguin (Fig. 5) could not be estimated directly because waders departed over a prolonged period (cf. Fig. 1). The period over which Redshank left was so long that, in retrospect, it is not surprising that there was no seasonal trend in body mass (Fig. 5). However, a rough estimate of the rate of mass gain could be obtained indirectly. Waders deposited 30-50% mass before leaving (Figs. 5-9) and did not start to increase body mass before the first or second week of March (Fig. 5). In the 4-6 weeks before departure, the average mass increase must therefore have been 1.0-1.2% per day. This rate of increase is similar to rates measured in waders wintering elsewhere (Table 4). Waders wintering in S. Africa deposited more reserve mass than did waders on the Banc d'Arguin. The mass increase in most of 11 wader species wintering in SE. Australia species is 50-70% (Lane 1987), rather similar to waders wintering in S. Africa (Table 4). In both the S. African and Australian wintering areas, the mass gain per day is about 1%.

Why do not all waders gain mass at the maximum rate? Probably, the 'advantage' of carrying excess mass during as short a period as possible must be weighed against the risk of falling short of the optimal departure mass at the optimal departure date. This suggestion resembles the proposal of Lima (1986) that the body mass of a wintering bird should be viewed as a trade-off between the risk of starvation and the risk of predation. If feeding conditions in a certain area are often so poor that gaining mass at the maximum rate is impossible, the waders may be selected to start gaining mass early and slowly. If feeding conditions early in the season do not predict feeding conditions later on very well, the birds would do best by attempting to follow the same trajectory of mass gain each year, compensating through behavioural adjustments for the vagaries of the outside world. From this point of view we predict high rates of mass gain when circumstances are predictably good (e.g. longer feeding periods because of the increase of the length of the daylight period; higher intakes rate because more prey are available; no heat stress). Indeed, highest rates of mass gain are observed in late summer and early autumn when benthic food stocks are maximal in the European estuaries (Fig. 10). Also, rates of mass gain tend to be higher in May, compared to April, when food availability tends to be lower (Fig. 10).

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However, we also predict that, within limits, different feeding conditions between years need not translate into different patterns of mass gain as the birds may compensate by feeding for longer or by increasing the intake rate while foraging (Swennen *et al.* 1989). Indeed, the pattern of mass gain in Dunlins and Bar-tailed Godwits in the eastern Dutch Wadden Sea in May (Goede *et al.* 1990, Piersma & Jukema 1990) hardly differs between years, in spite of considerable variations in their food supply (Zwarts pers. obs.).

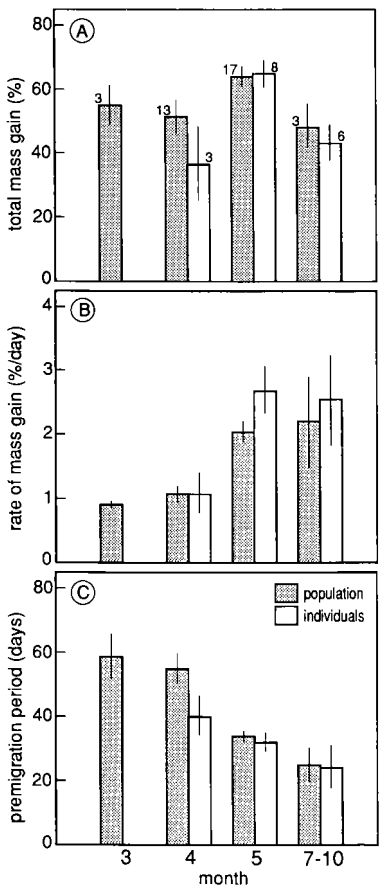

Fig. 10. Seasonal variation in A) total mass gain, B) mass gain per day and C) premigration period, for estimates of rate of mass change derived from either changes in the population mean or changes in the mass of retrapped individuals. All values represent mean ± *SE*; *n* is given in panel A. All data are given in or can be derived from Table 4.

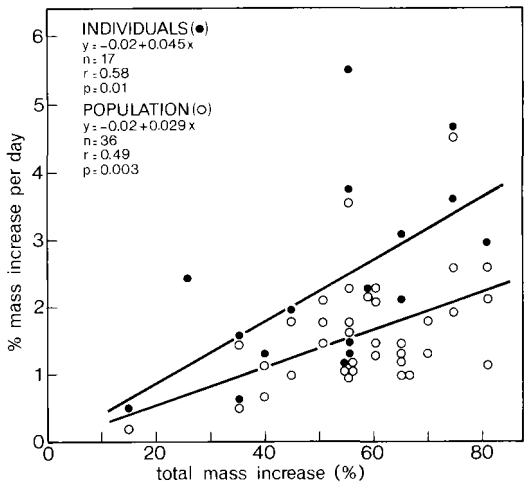

Fig. 11. Mass gain per day (given as % of winter mass) as a function of total mass increase (also as % of winter mass). All data are summarized in Table 4. Statistical analysis is given in Table 5.

Along the same lines it is to be expected that different populations of a same species migrating through the same area at different times of the year, will show consistent differences in the patterns of mass gain. Dunlins refuelling in the eastern part of the Dutch Wadden Sea in May, gain mass at least five times faster than birds in April (Goede *et al.* 1990). The same trend is found in Bar-tailed Godwit populations staging in the Wadden Sea in April and May (Prokosch 1988, Drent & Piersma 1990). While the feeding conditions in the Wadden Sea

Table 5. Two analyses of covariance to investigate the significance the effect of total mass increase and season on the mass increase per day, calculated separately for mass gains in the population ($n = 36$ studies) and in individuals ($n = 17$); same data are given in Table 4 and Fig. 10.

	population		individuals	
	R^2	p	R^2	p
total mass gain	0.242	0.001	0.321	0.02
season (month)	0.265	0.001	0.154	0.21

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almost certainly improve during the course of the spring, it is unlikely to account for this sudden increase in the rate at which mass is laid down. Prey mass (Beukema 1974, see also Chambers & Milne 1979) and availability (Zwarts 1984, Esselink & Zwarts 1989) gradually increases during April and May, but there is no evidence that these changes are abrupt and occur at the same moment each year.

Superficially it may seem that our scheme is so flexible that it is untestable, but this is not true. We predict that differences in rates of mass gain between different populations or between different times of the year should persist when the birds are provided with food ad libitum. As we see it, departure mass is adapted to the travel distance and rate of mass gain to the average feeding conditions. Travel distance and feeding conditions bear no obvious relation to each other and we were therefore surprised to find that the higher the departure mass, the faster the rate at which mass is deposited (Fig. 11). The covariance analyses (Table 5) show that the total increase in mass itself explained a significant part of the variance. As the length of the period during which waders deposit mass, is determined by the quotient of total departure mass and the rate of mass gain (Table 4), it follows from the near-zero intercepts in Fig. 11 that this period is independent of the total mass increase (Fig. 12). The data from retraps suggest that the premigration period lasts 25-35 days while the population estimate suggests it lasts ca. 40-45 days. Since the latter is itself based on underestimates of the rate of mass gain (Fig. 1), it seems that waders usually spend about a month to reach their departure mass regardless whether they gain 20% or 80% of their lean mass. Perhaps, waders only prepare for long-distance flights from places and at times when feeding conditions are predictably good, so that the premigration period does not become unbearably long.

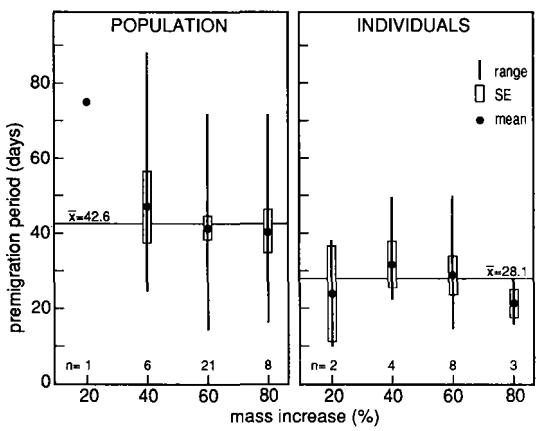

Fig. 12. Duration of the period before departure during which waders gained mass as a function of total mass increase (% relative to winter mass), given separately for estimates based upon mass increase in the population and for individuals (retraps). All data are given in or can be derived from Table 4 (see text).

Departure mass and flight range

Once departure mass has been established it can be used to estimate flight range, which would inform us about the whereabouts of the next spring staging area. Flight range can be estimated if the following are known: body composition and mass of the departing wader (1), the minimum body composition and mass that allow the wader to survive after a flight (2), flight costs (3), flight speed (4) wind conditions 'en route' (5). The amount of 'fuel' burned is estimated from (1) minus (2), while the fuel needed per km is the product of (3) and (4). The flight distance can only be estimated from these parameters by taking into account (5). These parameters are measured as follows:

Energy reserve at departure (1) The relative increase of mass for waders identified as being ready to go (shown in Fig. 9) is calculated as a deviation from winter mass (Table 1) to give the body reserve in grams. The fat-free winter mass is, on average, 94% of the winter mass (Fig. 13; compiled from the data set of Piersma & van Brederode 1990), which agrees closely with Davidson's (1983) estimate. The composition of the migratory body reserve is similar for all the species on the Banc d'Arguin (Fig. 13); on average 60% of the reserve is fat. Waders departing from Venezuela also deposit ca. 60% fat (McNeil 1969, 1970), but waders preparing for

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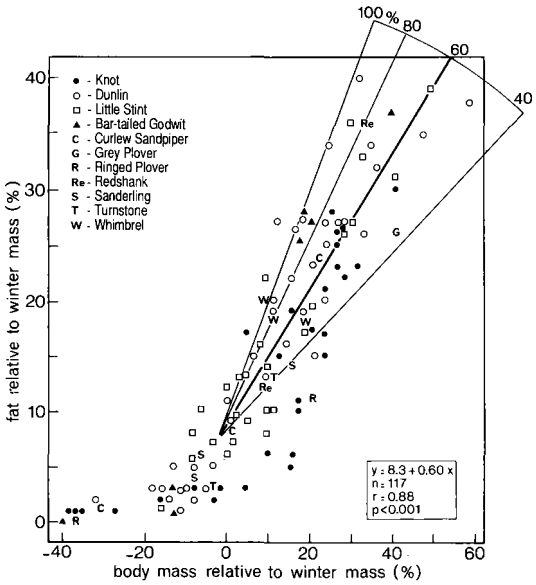

Fig. 13. Relative fat mass (fat expressed as % of winter mass; winter mass derived from wing length, see Table 1) as a function of the relative body mass (% deviation from winter mass) in 11 species captured on the Banc d'Arguin ($n = 117$). The original data are given by Piersma & van Brederode (1990). The regression line is calculated for all waders with a mass > average winter mass. The three other lines refer to a predicted fat content if the reserve consists for 100, 80 and 40% of fat. The intercept of the line (8.3%) can be interpreted as the average relative fat mass in wintering waders. When this is subtracted from the total relative fat mass, the remaining fat as proportion of the migration reserve appears to be 68% ($y = -2.6 + 0.68x$, $r = 0.84$), implying that fat in wintering waders is 5.7% (8.3-2.6%). The estimate of the relative amount of fat was reduced to 58% if the slope is forced through the origin ($SE = 2$; $r = 0.91$), i.e. winter fat is set to 8.3% of winter mass.

Table 6. Relative fat mass as function of the relative body mass: *a* (= intercept) gives the fat content as % of winter mass in waders wintering in Africa or relative to mass before the premigration period in waders staging in the temperate zone; see text); *b* (= slope) gives the fat percentage of the migratory reserve.

area	species	*a*	*b*	source
NW. Africa	Dunlin	8.0	50	Piersma & van Brederode 1990
NW. Africa	Knot	6.8	54	Piersma & van Brederode 1990
NW. Africa	Redshank	5.9	56	Piersma & van Brederode 1990
Wadden Sea	Bar-tailed Godwit	8.3	57	Piersma & Jukema 1990[1]
NW. Africa	Little Stint	8.0	59	Piersma & van Brederode 1990
Mauritania	all waders	8.2	60	this paper: Fig. 13[2]
Sweden	Dunlin	11.2	61	Mascher & Marcström 1976
Wadden Sea	Dunlin	2.6	72	Goede *et al.* 1990
Kenya	Little Stint	6.7	80	Pearson 1987
Hawaii	Golden Plover	11.9	84	Johnson *et al.* 1989
S. Africa	Turnstone	5.5	90	Summers *et al.* 1989
S. Africa	Sanderling	5.9	94	Summers *et al.* 1987
S. Africa	Curlew Sandpiper	4.6	100?	Elliott *et al.* 1976[3]
E. USA	Semipalmated Sandpiper	±5.0	100?	Page & Middleton 1972[4]
Pacific	Golden Plover	12.0	112?	Johnston & McFarlane 1967[5]

[1]Piersma & Jukema (1990) give the ratio fat/reserve using the combinated regression *y* on *x* and *x* on *y*; for the purpose of comparison, the regression *y* (fat) on *x* (body mass) is given here; [2]Fig. 13 uses data given by Piersma & van Brederode (1990), but excludes waders with a very low mass; [3]Elliott *et al.* (1976) found a much lower slope but assumed that b = 100 (because of errors made); [4]Page & Middleston (1972) gave no details, but showed that the error is small if all mass deposited would be fat; see also Dunn *et al.* 1988; [5]Johnston & McFarlane (1967) presumably calculated the slope of X on Y.

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spring migration from S. Africa or Kenya store ca. 90% fat (Pearson 1987, Summers *et al.* 1987, 1989) (Table 6).

The energy yield from fat is high (38.9 kJ; Whittow 1986) but is low for fat-free reserves. The lean mass consists of 65-70% water (Mascher & Marcström 1976, Pienkowski, Lloyd & Minton 1979, Davidson 1984b, McEwan & Whitehead 1984, Summers *et al.* 1987, Johnson *et al.* 1989, Piersma & van Brederode 1990). Assuming that the lean dry mass consists of protein with an energy content of 22.6 kJ g^{-1}, of which 80% is metabolizable (Whittow 1986), the energy yield of the non-fat reserves can be estimated as 5.8 kJ g^{-1}. From this it can be calculated that the energy yield of the nutrient reserve therefore varies between 25.7 kJ g^{-1} for waders leaving the Banc d'Arguin to 35.6 kJ g^{-1} for waders leaving S. Africa.

Energy reserve at arrival (2) After the flight, it is assumed that the waders have used up all their fat and that the fat-free mass is 10% below the fat-free mass in the tropical winter (Piersma & Jukema 1990).

Flight time (3) Flight time is predicted from two models (Fig. 14). The first model (Summers & Waltner 1978) is based on initial body mass only, while the second (Castro & Myers 1989) also takes wing length (Table 1) into account. Compared to the first model, the second model 'predicts' that flying is cheaper for the smaller wader species and more expensive for the larger ones. We modify the assumption of both models that the mass loss during flight is of fat only, because our data indicate that the migratory reserve consists of 60% fat and 40% protein.

The estimates of departure mass (Fig. 9) can now be transformed into flight time. According to the model of Summers & Waltner (1978) flight time increases with body mass from 35 h in the Little Stint to 65 h in the Whimbrel *Numenius phaeopus*. If wing length is included (Castro & Myers 1989), body mass has no effect and all waders have enough fuel to fly ca. 30-35 h. On theoretical grounds the estimates incorporating wing measurements are probably better (Masman & Klaassen 1987, Castro & Myers 1988), so we will use those estimates (but see Piersma & Jukema 1990 who discuss the problems with these and other models).

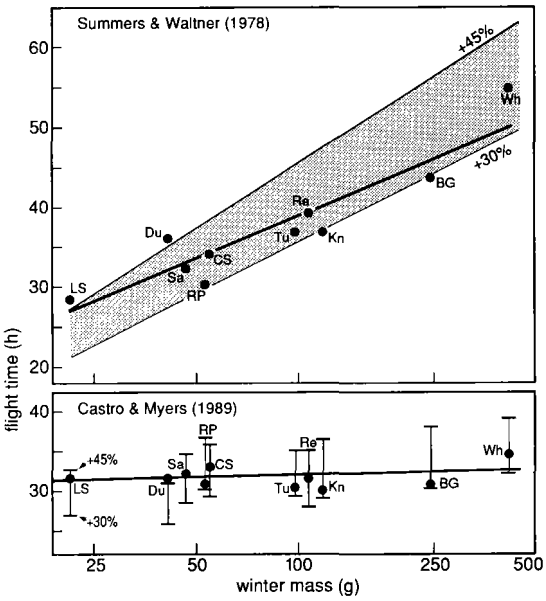

Fig. 14. Predicted travel time for waders departing from the Banc d'Arguin as a function of body mass, given the estimated energy reserve (see Fig. 9, 13 and text) and the flight costs according to two models (Summers & Waltner 1978 and Castro & Myers 1989). The predicted flight range according to Summers and Waltner, given a departure mass of 1.30 or 1.45 x winter mass, is indicated in grey. The same predictions according to Castro & Myers are given with lines. Species are indicated by a two-letter code (see Table 1).

Flight speed (4) Travel time is converted into flight distance from flight speed, estimated by radar. Unfortunately, the estimates vary greatly. Grimes (1974) recorded flight speeds between 55 and 92 km h^{-1}, although most lay between 65 and 84 km h^{-1}. Richardson (1979) gave an average speed of 74 km h^{-1}. Williams (1985) and Williams & Williams (1988) corrected flight speeds for wind and all such 'air speed' measurements fall between 40 and 100 km h^{-1} and averaged 75 and 60 km h^{-1}, respectively. T. Alerstam (pers. comm.) found an average air speed of 57 km h^{-1} in godwits and Lane & Jessop (1985) 50-60 km h^{-1} in a variety of waders.

How much of this variation is due to interspe-

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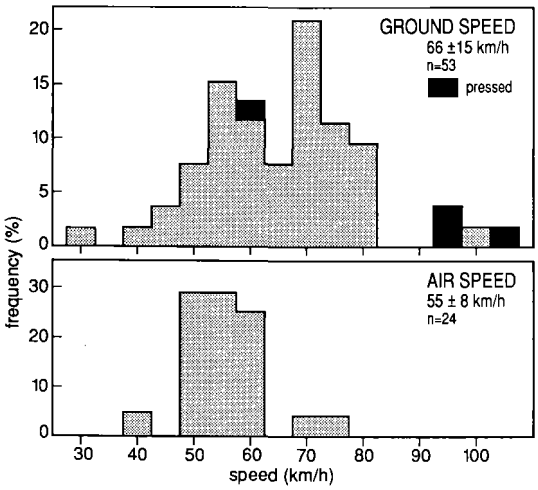

Fig. 15. Frequency distribution of measured flight speed in 38 wader species. Ground speeds (upper panel) are taken from Longstreet (1930), Cooke (1933), Meinertzhagen (1955) and McNeil (1970). Waders which were pressed by a plane or car, are indicated separately, since they probably represent maximum flight speed. Air speeds (lower panel) are taken from Tucker & Schmidt-Koenig (1971), Schnell & Hellack (1978), Noer (1979), Alerstam *et al.* (1990) and Piersma & Bruggemann (own obs.).

cific differences in flying speeds? A positive relation between mass and flight speed was expected. Greenewalt (1975) predicted that the speed at which flight power has its minimum value increases with body mass. In his shorebird model flight costs are minimal at 25 km h^{-1} for a wader of 50 g, and at 40 km h^{-1} for a wader of 1000 g. Likewise Rayner (1990) predicted that the speed at which the energy expended to fly a given distance is minimized, and flight range therefore maximized, increased from 25 km h^{-1} for a bird with a body mass of 50 g to 45 km h^{-1} for a bird with a body mass of 1000 g. Figure 15 summarizes measurements of flight speed in 47 wader species. There appears to be a negative correlation between year of publication and the flight speed (r = -0.22, n = 77, p < 0.05), probably because only recent publications gave 'air speed' rather than 'ground speed'. Some of the earlier measurements also concern birds which may have been harried, or pressed, by car, train or plane to fly at above normal speeds (indicated, where known, separately in Fig. 15). Excluding these cases and combining air and ground speeds produced a negative correlation between body mass and speed (r = -0.27, n = 73, p = 0.02). However, the effect of mass disappears if only the air speed measurements are used (r = -0.15, n = 24, p = 0.47). Pending more data, it is therefore assumed that waders of different sizes all fly at the same speed. Since under those assumptions the estimated flight times do not differ much (Fig. 14), the predicted flight distances for the species leaving the Banc d'Arguin must all be about the same.

Wind conditions 'en route' (5) With a flight time of 30-35 h and an air speed of 60-70 km h^{-1}, the predicted flight distance in still air is 1800-2500 km. However, Piersma & Jukema (1990) suggest that Bar-tailed Godwits departing from the Banc d'Arguin to fly to the Wadden Sea in late April must make use of tail winds. If they fly at altitudes with the most favourable winds, the average tail wind (calculated over four different years) would be 10-35 km h^{-1} (Piersma & Jukema 1990: Table 3). This increases the predicted maximum flight ranges to between 2100 km and 3500 km.

Problems with flight range equations

Most estimates of flight range are based on the equations given by McNeil & Cadieux (1972), Summers & Waltner (1978), Davidson (1984a) and Castro & Myers (1989). Two arguments suggest that many of the resulting estimates are too low. First, waders may adjust their flight altitude to find advantageous winds (Piersma & Jukema 1990), and this has never before been taken into account. Second, waders fly in flocks which might be cheaper than flying alone (references in Piersma & Jukema 1990).

However, the flight distances may also be overestimated, for three reasons. First, flight speed is assumed to be 75 km h^{-1}, or even 106 km h^{-1} (e.g. Johnson *et al.* 1989), whereas a better estimate may be 60-70 km h^{-1} (see Fig. 15). Second, the migratory reserve is assumed to be 100% fat, whereas the real value may be only 60-90% (Table 6). Finally, the flight cost of the large wader species may have been underestimated in papers using the earlier

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flight range equations (compare Fig. 14A with Fig. 14B).

Do the overestimations and underestimations cancel each other out? The predictive value of the flight range equations can very occasionally be checked against real measurements of flight distances flown by birds of known mass at departure (Davidson 1984a). Dunn *et al.* (1988) reported a Semipalmated Sandpiper which was weighed and banded in Maine (USA) and recovered two days later in Guyana. This bird had covered a distance twice as large as predicted by the flight-range equation of McNeil & Cadieux (1972), and 1.5 times as large as that predicted by the formulae of Summers & Waltner (1978) or Castro & Myers (1989). Unless the bird had benefited from strong tail wind during the whole flight ,which is unknown though likely (see Stoddard *et al.* 1983), the predictions are thus clearly too low.

Flight range of waders departing from the Banc d'Arguin

Before discussing the wader species that migrate along the East Atlantic Flyway, some comments need to be made on those species that follow a more easterly course along the Mediterranean Flyway. Without doubt, Little Stints and Curlew Sandpipers cross the Sahara and the Mediterranean (Wymenga *et al.* 1990) to reach their northern breeding grounds. There are also indications that Curlews wintering in W. Africa follow the Mediterranean Flyway since field estimates of bill length (Zwarts 1988) suggest they originate from Asian breeding grounds (M. Engelmoer pers. comm.). Waders flying over Italy may profit from tail-winds more than waders passing over Spain (Piersma pers. obs.). If Little Stints, Curlew Sandpipers and Curlews, assumed to take this Mediterranean Flyway, deposit as much mass as species of the same size that follow the East Atlantic coast (Figs. 9 & 14), their stopover site could be situated as far as the Wadden Sea. This would bring the Black Sea within the range of one flight.

It all depends on the validity of the claim that the majority of the waders departing from the Banc d'Arguin in late April fly directly to the NW. European estuaries. There can be no doubt that more direct determinations of flight range are to be preferred over contrived calculations starting from departure mass, which itself has to be estimated along tortuous routes. The short time between departure from the Banc d'Arguin and arrival in NW. Europe suggests that Bar-tailed Godwits (Piersma & Jukema 1990) and Whimbrels (Zwarts 1990) are able to fly directly from the Banc d'Arguin to NW. Europe (4300 km) without refuelling. If it is accepted that many Bar-tailed Godwits and Whimbrels are able to fly this distance and if it is accepted that flight ranges do not differ greatly among species (Fig. 14B), it must be concluded that many individuals of the other species leaving the Banc d'Arguin at the end of April are able to fly 4300 km as well. Is there any evidence that the other species indeed fly directly from Africa to NW. Europe?

Waders were dye-marked on the Banc d'Arguin during spring, but unfortunately there were not enough sightings to describe the return migration in detail (Ens *et al.* 1989). Ruff *Philomachus pugnax*, colour-marked in Senegal, appeared to fly directly from W. Africa to NW. Europe (OAG Münster 1989). Several problems stop us from comparing the time of departure to the time of arrival in NW. Europa, as derived from series of wader counts, for species other than Bar-tailed Godwits (Piersma & Jukema 1990) and Whimbrels (Zwarts 1990). First, though many counts have been done, they have not yet been analysed. Second, the counts which were available have not been done frequently enough to indicate the exact date of arrival. Third, in some species conspecifics wintering in Europe already migrate in March and April (e.g. Grey Plover: Evans & Pienkowski 1984; Knot and Bar-tailed Godwit: Prokosch 1988; Dunlin: Goede *et al.* 1990). This necessitates either the estimation of the turnover of the different populations with methods described by Kersten & Smit (1984), i.e. combining counts of all birds present with counts of marked birds (see Moser & Carrier 1883, Goede *et al* 1990) or the study of the departure of waders marked individually (Evans & Pienkowski 1984, Metcalfe & Furness, 1985).

Counts on stopover sites between the Banc

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d'Arguin and NW. Europa might give a direct indication of the numbers using these staging areas. If the ca. 200 000 waders following a more easterly course and the ca. 300 000 waders remaining to summer (van Dijk *et al.* 1990) are subtracted from the number wintering on the Banc d'Arguin (Engelmoer *et al.* 1984), a total of 1 750 000 migrants remains. The vast majority of these birds leave the Banc d'Arguin in the last weeks of April and the first weeks of May (Piersma *et al.* 1990 or in this paper: Fig. 5). If the waders departing from the Banc d'Arguin cannot fly directly to the NW. European estuaries, they should visit the coasts along these countries. The number of migrants involved is so enormous that one should even be able to detect their passage from series of counts at very short intervals (e.g. Dominguez & Rabuñal 1989). It is possible that small estuaries along the route serve as emergency sites, harbouring highly variable numbers of waders in different years, depending on the meteorological conditions encountered during the flight (Dick *et al.* 1987, Smit & Piersma 1989). If few birds are counted in a long run of years it would prove our suggestion that most waders fly directly to the NW. European estuaries.

We found no evidence that different species follow different strategies when they depart from the Banc d'Arguin by the end of April, or in early May, apparently contradicting the earlier suggestion of Piersma (1987). However, the few early leaving Dunlin deposit less mass than conspecifics later in the season (Kersten 1989, Table 3). These early birds must use Moroccan and S. European sites as the next stopover sites (Kersten & Smit 1984). In general, the different migration strategies of Piersma (1987), may apply more to different individuals within a species, than to species as a whole.

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SAMENVATTING

De meeste steltlopers verlaten rond eind april de Banc d'Arguin. In de 4-6 weken daarvoor nemen ze gemiddeld met zo'n 40% in gewicht toe. Vergelijking met andere wadgebieden leert dat de gemiddelde gewichtstoename varieert tussen 20 tot 80% en de toename per dag tussen 0.1 and 4%; op de Banc d'Arguin is deze 1.0-1.2 %/dag. De opvetsnelheid blijkt voor een groot deel af te hangen van de totale gewichttoename. Het lijkt erop dat opvetperiode minder dan een maand bedraagt en iets langer is als de steltlopers zich klaarmaken voor de voorjaarstrek vanaf de wintergebieden. De gewichtstoename op de Banc d'Arguin blijkt synchroon te lopen met de overgang van winter naar zomerkleed. Vogels die hun lichaamsrui onderbreken zijn zwaarder dan hun ruiende soortgenoten, zodat we aannemen dat de niet-ruiende steltlopers die minstens in overgangskleed zijn, klaar zijn voor vertrek.

Deze schatting is te laag, omdat ook overzomerende vogels met een laag gewicht dit stadium bereiken. Bovendien blijven de gewichten toenemen als steltlopers, wat kleed betreft, een voorlopig eindstadium hebben bereikt. Voor drie soorten konden we een vergelijking maken met wat het gemiddelde gewicht zou moeten zijn van de vertrekkende vogels, als alleen de zwaarste vogels zouden verdwijnen. Op grond daarvan vermoeden we dat de onderschatting 30% is.

Gebruik makend van de verzamelde gegevens en modellen waarmee we de vliegkosten schatten, concluderen we dat de steltlopers vanaf de Banc d'Arguin ruim 4000 km kunnen vliegen. Zij kunnen dus de Waddenzee of ZO. Europa halen. Het lijkt er op dat de bestaande modellen de vliegafstand onderschatten, ook als rekening wordt gehouden met het feit dat steltlopers gebruik maken van rugwinden op grote hoogte.

RÉSUMÉ

La plupart des limicoles quittent le Banc d'Arguin vers la fin avril. Dans les 4 à 6 semaines qui précèdent leur poids corporel s'accroît en moyenne de 40% environ. Une comparaison avec d'autres vasières nous apprend que la croissance pondérale moyenne varie entre 20 et 80% et que la croissance s'élève entre 0,1 et 4% par jour; sur le Banc d'Arguin elle est de 1,0 1,2 % par jour. On a constaté que la vitesse dont ils constituent leur réserve de graisse dépend pour une grande partie de la croissance pondérale totale. Il semble que la période où ils constituent leur réserve dure moins d'un mois et est un peu longue quand les limicoles se préparent pour quitter les zones d'hivernage et partir en migration printanière. La croissance pondérale sur le Banc d'Arguin s'avère synchrone au passage du plumage hivernal en plumage nuptial. Vu le fait que les oiseaux qui interrompent leur mue de corps pèsent davantage que leurs congénères muants, nous supposons que la moitié la plus lourde des limicoles non-muants recouvert d'un plumage mi-hivernal mi-

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nuptial, est prête à partir. Nous étions à même de contrôler cette supposition en calculant quel devrait être le poids moyen si seuls les oiseaux les plus lourds partiraient. Profitant des données recueillies et de modèles estimant les frais de vol, nous tirons la conclusion que les limicoles peuvent voler plus de 4000 kilomètres à partir du Banc d'Arguin et sont donc capables d'atteindre la Mer des Wadden et l'Europe du Sud-Est.

The late Ely ould Elemine, Marcel Kersten, Pierre Campredon and Cheikhna ould M'Baré preparing the cannon net on the sebkha bordering the Baie d'Aouatif (photo Bruno Ens).

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