Staging studies of Knots *Calidris canutus islandica* in Iceland in the early 1970s: body mass patterns

J.R. Wilson & R.I.G. Morrison

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This paper provides an analysis of body weights of Knots *Calidris canutus islandica*, captured during their stopover in Iceland during the springs and autumns of 1970 - 1973. In May the average weights of captured Knots increased from about 140 g at the beginning to about 200 g at the end of the month. Individual Knots recaptured within May 1972 gained an average of 2.5 g/day, with heavy Knots at first capture showing a significantly smaller daily weight increase (1.4 g/day) than lighter Knots (3.3 g/day). In July and August average weights remained fairly constant over time, but two recaptured individuals showed daily weight gains of 2.0 and 3.6 g. Since the recapture rate of southbound Knots was also much lower than in spring, we conclude that the turnover rate in autumn is high. Assuming that the lightest birds captured are those that have just arrived from the breeding areas and the heaviest those that are about to depart to the wintering grounds, autumnal arrival weights in Iceland are estimated at 110 - 114 g, and the departure weights at 150 - 156 g implying staging periods between 6 and 17 days. It is discussed how differences in the timing and the weight of spring arrival in Iceland would affect the required rates of weight gain during the stopover period. Both the departure weights from Iceland and the arrival weights in Britain in autumn are lower than the weights during the return north in spring.

J.R. Wilson, Granveien 46, 1911 Flateby, Norway.
R.I.G. Morrison, Canadian Wildlife Service, National Wildlife Research Centre, 100 Gamelin Boulevard, Hull, Quebec, K1A 0H3, Canada.

INTRODUCTION

Iceland is an essential staging area for waders migrating along the East Atlantic Flyway between wintering areas in western Europe and Africa, and breeding grounds in Greenland and north-east Canada. Its importance arises because it lies between two major geographical barriers. In one direction is 1,000 km of sea between Iceland and the rest of Europe. In the other direction is 300 km of sea in the Denmark Strait and at least 700 km of the Greenland icecap between Iceland and west Greenland. The patterns of wader migration through Iceland and across the Greenland icecap have been described by Wilson (1981) and Alerstam *et al.* (1986).

Large numbers of Knots *Calidris canutus islandica* migrate across these barriers in autumn and spring, and use Iceland as a staging area between their wintering areas in Britain, France and the Wadden Sea, and their breeding areas in northern Greenland and Canada. The routes and migration timing for this population are now well established (see reviews by Meltofte 1985; Davidson & Wilson 1992), as is their migration phenology in Iceland (e.g. Wilson 1981; Morrison & Wilson 1992).

During studies of their migrations since the late 1960s large numbers of Knots have been caught and weighed in Britain, Germany and Iceland close to the times of their arrival and departure on migration. This paper summarizes the patterns of change in the weights of Knots staging during spring (chiefly May) and autumn (chiefly July/August) in south-west Iceland during the early 1970s, and compares these with known weights of Knots before and after their migrations through Iceland. Some preliminary results of the 1970s Iceland studies have been reported by Morrison & Wilson (1971); Morrison *et al.* (1971); Prater & Wilson (1972) and Morrison (1977). The results presented in this paper complement those of

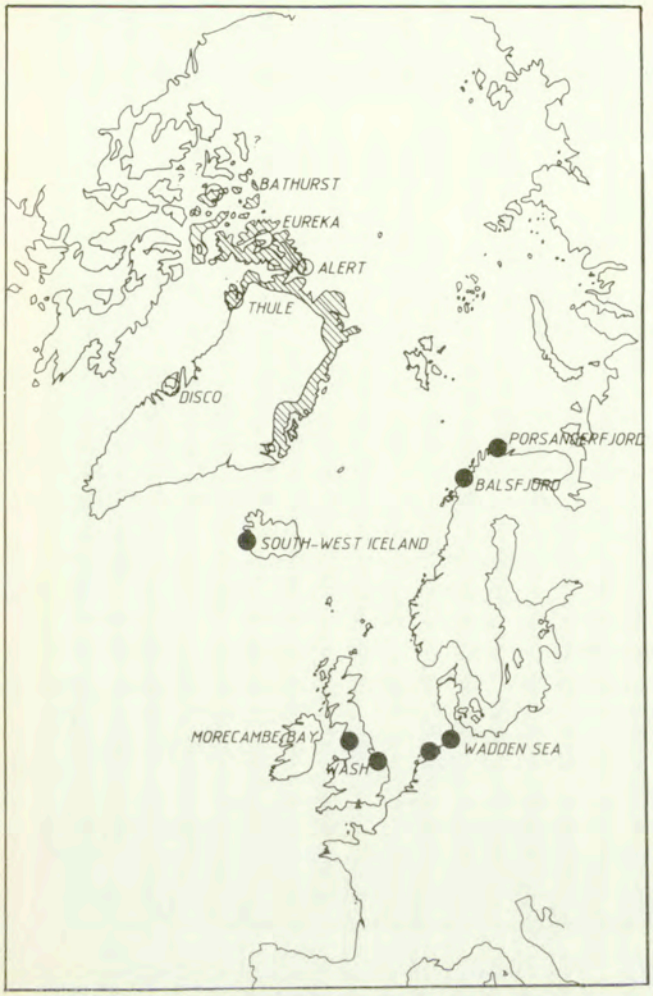

Figure 1. Main breeding areas (shown hatched) and early and late spring staging areas (filled circles) of Knots migrating in spring through Iceland and northern Norway.

recent studies reporting weights and migration phenology of high arctic waders in west Iceland (Gudmundsson & Alerstam 1992; Gudmundsson *et al.* 1991).

METHODS

Knots were caught in cannon-nets in south-west Iceland during May 1970, 1971 and 1972, and during August 1970 and July and August 1972. Birds were weighed to the nearest 1 g with a Pesola spring balance, and bill length (exposed culmen) was measured to the nearest 1 mm.

In addition, weights of 304 adult Knots in spring and 786 premoulting adult Knots in autumn in Britain were examined from Wader Study Group archive files. Since wing moult is known to start soon after the return of these birds to Britain it is probable that such premoulting birds had only recently arrived.

Data are from two large estuaries in Britain: Morecambe Bay in north-west England and the Wash in eastern England (Figure 1). These are amongst the major moulting areas for Knots in Britain.

Knots, in common with other waders, lose weight between their capture and when they are weighed (e.g. Wilson & Davidson 1982; Davidson 1984a). Although Knots caught in Iceland were usually weighed soon after their capture, data from each catch were examined for evidence of weight loss after capture using the method of Wilson & Davidson (1982). In the absence of information on the weight loss of individual birds, this compares the mean weights of sequentially-weighed groups of 30 birds.

In May 1971 and August 1972 the weight differences between the first and last group of 30 birds weighed were always less than 5 g. This is a very small difference in weight and so all weights from these periods are included in the analyses. On 12 August 1970 there was a difference of 10 g between the first and last groups weighed, so for this catch only

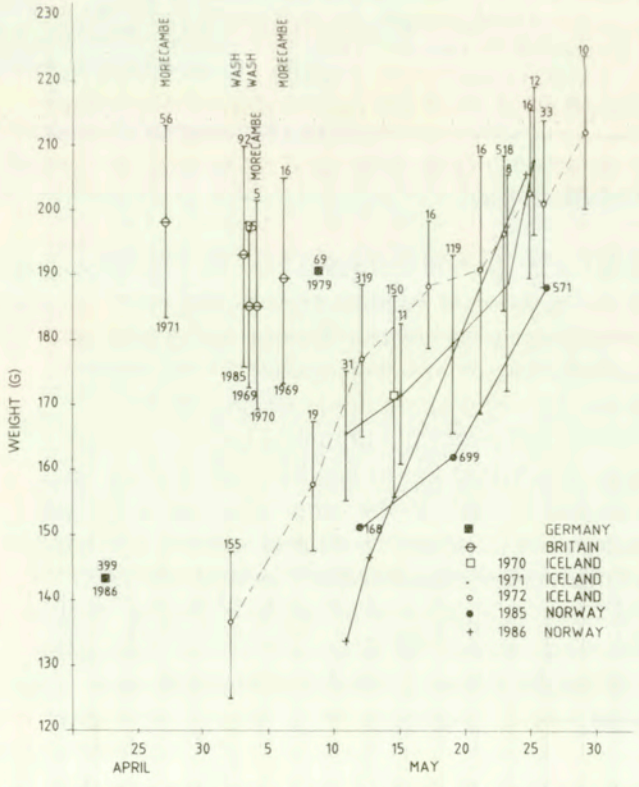

Figure 2. Weights of migrant adult *islandica* Knots in spring. Means ± 1 SD are shown, with the sample size above, and the year of capture below the symbol.

the weights of the first 30 birds are included. Weight losses in the 150 birds caught on 15 May 1970 cannot be assessed since the times of weighing after capture were not recorded. The mean weight for this catch may therefore be slightly lower than at capture. Only catches for which weight loss was less than 5 g have been used in the analyses of weights from Britain, but since weights of birds in Norway and Germany come from published sources no further adjustments for weight loss could be made for this data.

RESULTS

Spring weights in Britain and Germany

Spring weights of Knots are summarized in Figure 2. At the Wash in eastern Britain Knots begin increasing their weight in March from a late winter low of 135 g (Branson 1981). Many of these birds, however, may move to use the Wadden Sea as their early spring staging area. Some Knots do remain on the Wash, leaving as late as the first half of May. The mean weights of such birds, weighed on 3 May 1969 and 3 May 1980 were 182.8 g and 193.0 g respectively. These birds are unlikely to have used the Wadden Sea staging area, but probably migrated directly to the late spring staging areas of Iceland and north Norway (Davidson & Wilson 1992).

On Morecambe Bay in western England weights in early May, shortly before departure, were similar to those on the Wash. Mean weights were 197.8 g on the early date of 27 April 1971, 185.2 g on 4 May 1970 and 186.9 g on 6 May 1969 (Figure 2). At least some (and perhaps most) birds from Morecambe Bay are known to fly to late spring staging sites in Iceland. In the German Wadden Sea the mean weight on 9 May 1979, close to the date of departure, was 190.7 g (Prokosch 1988; Figure 2). This is similar to those in Britain.

Spring in Iceland

During May 1972 mean weights in Iceland increased steadily from 136.3 g on 2 May to 198.4 g on 26 May. Birds must have recently arrived on 2 May since there were few birds in the area in late April (Morrison & Wilson 1992).

Weights were lower during mid May in 1970 and 1971 than in 1972, but by 25 May 1971 were similar to those in 1972. By comparison, weights of Knots in May 1985 in Balsfjord in northern Norway, another major late spring staging area, were consistently lower for their dates than for any of the three years

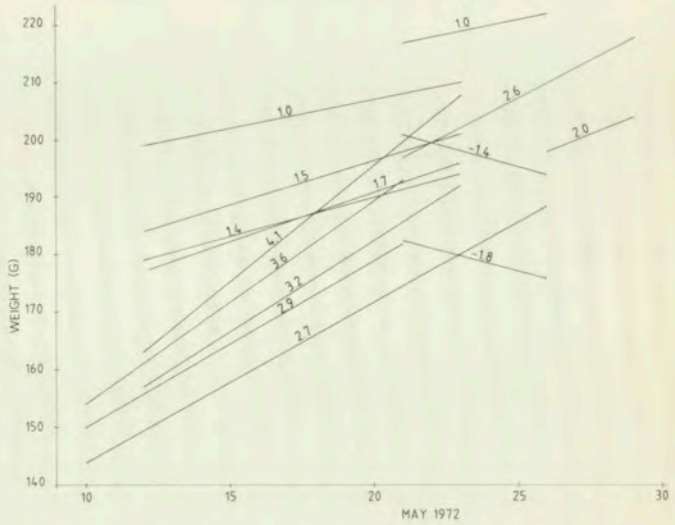

Figure 3. Weight changes of individual Knots captured twice in Iceland in May 1972. Numbers indicate the particular rates of weight gain (g/d).

in Iceland. At the departure time of 26 May, weights in Norway were 15 g lower than on 26 May 1972 in Iceland. Figure 2 shows that in early May 1986 weights in Balsfjord were again lower than those in Iceland, but that by the end of May weights in the two areas were similar (see Evans 1992 for further discussion of the weight patterns in Balsfjord).

Weights of individual Knots caught twice during May 1972 (Figure 3) show that birds which were relatively light (< 170 g) in early May gained weight significantly more rapidly than did relatively heavy birds (Student's t = 6.53, $P < 0.001$). Light birds averaged weight gains of 3.3 g/d ($n = 5$) with a maximum of 4.1 g/d. Heavy birds gained weight at an average of only 1.4 g/d ($n = 4$). This suggests that, as for the overall weight patterns in different years (Figure 2), weights were converging towards a similar departure weight. A similar pattern occurs for Turnstones *Arenaria interpres* in Iceland (unpubl. data).

At departure time mean weights in 1972 increased from 198.4 g on 26 May to 211.8 g on 28-30 May. The mean bill length of these latter birds was 35.4 mm ($n = 10$), over 3 mm longer than those of all birds caught before 27 May (32.4 mm, $n = 1,093$). Hence the apparent weight increase may arise largely from differences in body size. Interestingly such large birds are likely to be females, which have an average bill length of 34.4 mm (Cramp & Simmons 1983). This implies that the last birds to leave Iceland are females, although males and females normally arrive at the same time on their breeding grounds (Cramp & Simmons 1983).

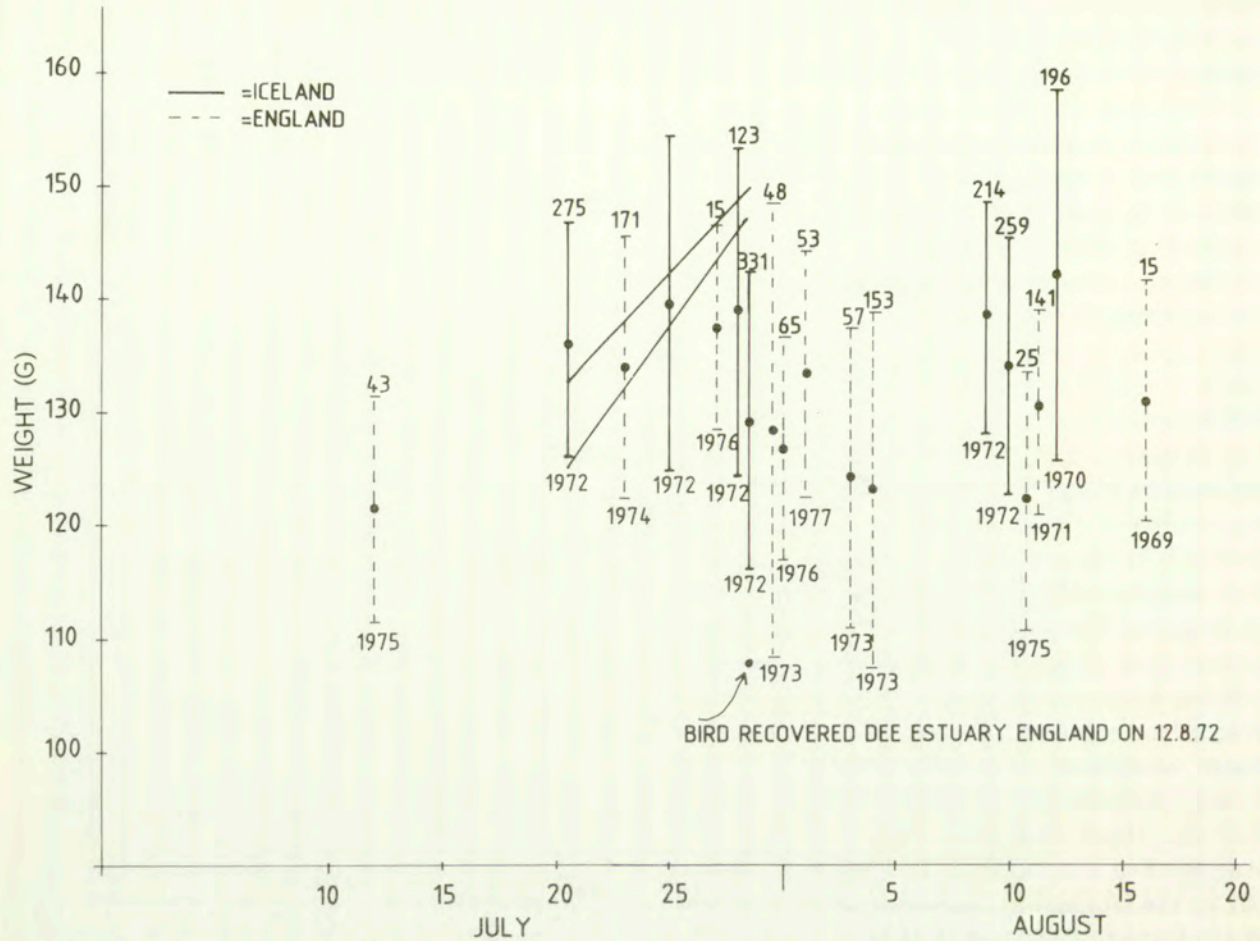

Figure 4. Weights of migrant adult *islandica* Knots in autumn in Iceland and England. Means ± 1 SD are shown, with the sample size above, and the year of capture below the symbol. Lines join the weights of individual birds captured twice during the same autumn.

Autumn in Iceland

The mean weight of each of the seven catches made in autumn in Iceland was similar, with individual catches averaging 128 - 141 g (Figure 4). These are lower than all but the first arrival weights of Knots in Iceland in spring (see Figure 2). If birds in autumn are accumulating weight in Iceland for onward migration, this pattern implies a constantly changing population. Each catch would contain both recent arrivals (with low weights) and birds nearing departure after storing fat (with high weights).

Evidence for such turnover of birds throughout the autumn staging period comes from birds caught at one location (Skogarnes) in autumn 1972. Two birds first caught on 21 July were recaptured on 28 July. When first caught their weights were lower than the mean, but they were amongst the heaviest birds on 28 July. During these seven days the weights of these birds had increased by 14 g and 25 g. The rates of weight gain (2.0 g/d and 3.6 g/d) are comparable with the rapid weight gains of light birds in spring (Figure 3). If these are typical rates of weight gain in autumn, all birds heavier than the mean weight on 21 July 1972 would have reached their likely departure weights and migrated before 28 July.

Other evidence also points to a more rapid and continuous turnover of birds in autumn than in spring. These two birds in July 1972 were the only ones captured twice during the same autumn, compared to 14 birds captured twice during their spring staging. This autumn recapture rate (0.14 birds recaptured per 100 birds caught) is a rate almost seven times lower than the spring recapture rate of 0.98 birds recaptured per 100 birds caught. Furthermore, no Knots were caught in July and recaptured later in August: at rates of weight gain similar to those during July, all birds caught on 21 July and 28 July would have reached departure weights before the next catch on 9 August. During this period the numbers of Knots present at any one time remained similar throughout, again implying

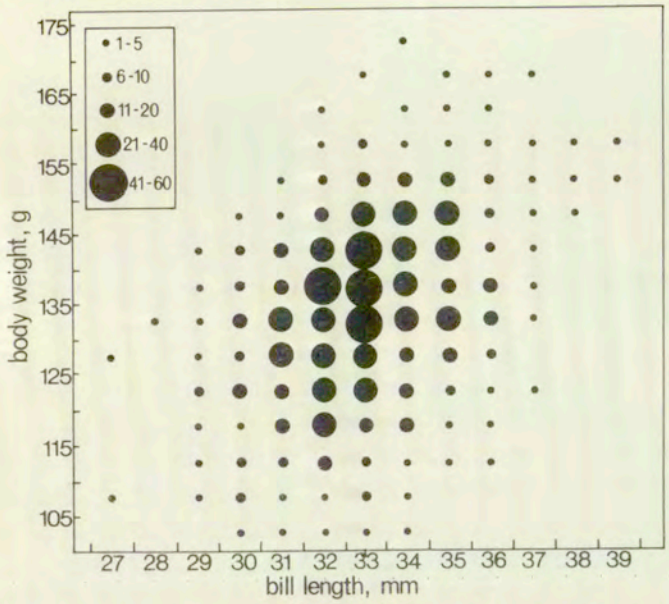

Figure 5. The relationship between bill length and weight for adult Knots caught in Iceland between 21 July and 10 August 1972. The total sample size is 1,204.

rapid turnover such that those departing were being replaced by similar numbers of new arivals.

Further evidence that birds moved on rapidly after capture comes from a bird ringed on 28 July 1972. This bird was recaptured on the Dee Estuary in western England on 12 August, only 15 days later. Assuming a flight speed of 70 km/h, this birds would have taken 23 hours to cover the direct distance of 1,600 km. Since all observed departures from Iceland were in the evening (see also Morrison & Wilson 1992) the latest this bird would have left Iceland was on 10 August. It was, however, one of the lightest birds when caught on 28 July, weighing only 108 g. It would therefore have needed to feed for several days to gain departure weight. This bird would seem to have spent between only one and two weeks staging in Iceland.

Arrival and departure weights cannot be estimated directly from the mean values of such a constantly changing population. The lowest and highest weights for a bird of a given size (measured by bill length), however, must represent minimum arrival weights and maximum departure weights. Figure 5 shows the relationship between weight and bill length for all birds caught in autumn 1972. This suggests that minimum arrival weights were 101 - 115 g depending on size, and that maximum departure weights were 136 - 155 g.

The data in Figure 5 can, however, be used to predict arrival and departure weights assuming different average staging periods, a constant turnover rate, and also that the lightest birds are arrivals and the heaviest are about to depart. For example, if the average duration of stay is 10 days, then the lightest 10% of birds will have just arrived and the heaviest 10% will be about to depart. Figure 6 shows these predicted mean arrival and departure weights for birds of average size (bill lengths of 32 and 33 mm). Calculated on this basis, average arrival weight varies from 114.8 g if birds are staying only 6 days to 109.7 g if birds stay 17 days. Average departure weights range from 150.1 g if birds stay 6 days to 155.8 g if the average stay is 17 days.

Figure 6 also show the rates of weight gain implied by these arrival and departure weights. If birds stayed only 6 days they would be gaining weight at

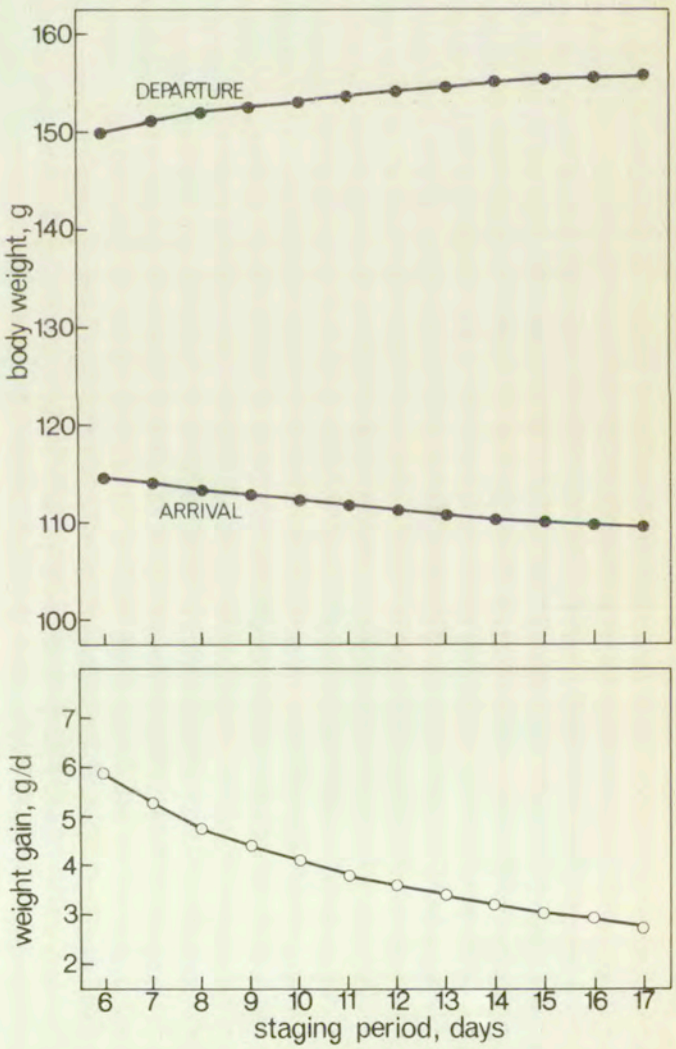

Figure 6. Estimated average arrival and departure weights and rates of weight gain for Knots staging in Iceland in autumn 1972, derived from data shown in Figure 5 (see text). The calculations are made only for birds of average body size, as measured by bill length (32-33 mm).

almost 6 g/d, and with an average stay of 17 days the rate of gain would be 2.7 g/d. The observed rates of weight gain by individuals of 3.0 - 2.6 g/d corresponds to an average staging duration of 12-15 days. Such birds would arrive weighing around 111 g and depart weighing 155 g.

Birds which leave the western areas of Iceland in autumn do not seem to stop for additional refuelling further south in Iceland. The south coast is mostly unsuitable for Knots, and numbers around the south-west (Reykjavik and Hvalfjördur) are too small (a few hundred birds) to account for the numbers in west Iceland (Morrison & Wilson 1992). Furthermore, the weights at Hafnarfjördur near Reykjavik on 25 July 1972 (139.6 g, n = 12) and in Hvalfjördur on 12 August 1970 (142.0 g, n = 196) were similar to those in west Iceland (Figure 4).

Autumn in Britain

Mean weights of pre-moulting birds from the Wash in mid July to mid August show little variation, and lie in the range 120 - 130 g, rather lower than in Iceland. 17% of all pre-moulting birds (n = 614) weighed less than 120 g. During this period, it appears that birds are arriving continuously.

The minimum flight distance on a great circle route from Iceland to the Wash is 1,750 km. Davidson's (1984b) flight range formulae for a Knot leaving Iceland weighing 155 g (see above) and flying at 70 km/h predicts a 27 g loss of weight during a still-air flight and an arrival weight on the Wash of 128 g. This falls within the observed range of mean weights of recently arrived birds on the Wash. Since there will almost certainly be some variation in arrival weight as a consequence of variation in departure weights from Iceland and in the extent of head winds encountered during the flight this range prediction fits very well with the observed weight patterns.

DISCUSSION

Spring migration

The mechanisms and timing of Knot migration through Iceland in spring can be described using a simple model (Figure 7). The following assumptions, based on the analyses above, are made:

1) departure from Britain and the Wadden Sea is in early May for most birds, and departure weight averages 190 g;
2) weight losses during migration will depend on wind conditions. Arrival weights in Iceland will vary as a consequence, but since precise arrival weights are difficult to establish, Davidson's (1984b) formula, with a flight speed of 70 km/h, is used to predict still-air flight;
3) Knots are capable of gaining weight at 4 g/d in Iceland;
4) Knots leave Iceland between 25 May and 30 May, with an average departure weight of 200 g. They must have reached departure weight by 25 May so as to exploit good weather conditions for their onward flight (see Alerstam *et al.* 1986).

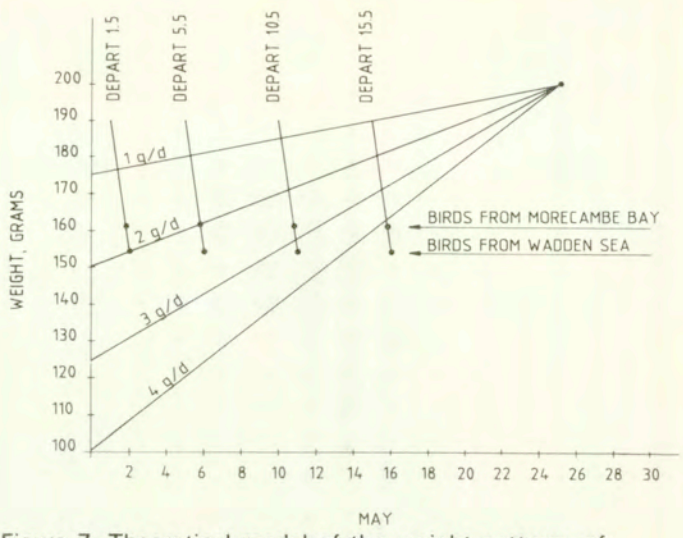

Figure 7. Theoretical model of the weight patterns of migrant Knots in spring. Lines show predicted weight loss during the flight from Morecambe Bay or the Wadden Sea to Iceland, and theoretical average weight gains in Iceland.

The model predicts that a Knot leaving Morecambe Bay (great circle distance to south-west Iceland is 1,560 km) on 1 May will have no difficulty in reaching departure weight in Iceland by 25 May. Such birds would need to gain weight at 2 g/d, much lower than some observed rates, and would have little risk even if they left their early spring staging areas weighing less than 190 g.

For Knots leaving Britain and the Wadden Sea as late as 10 May, the rate of weight gain in Iceland needs to be higher. To achieve departure weight by 25 May requires a weight gain of 3 g/d. If adverse wind conditions were encountered during the early spring migration, arrival weights in Iceland would be lower than predicted by this model. Such birds would face difficulty reaching departure weight by 25 May.

Leaving Britain as late as 15 May produces a definite risk that departure weight cannot be reached even after an migration made under still-air flight

conditions, and this risk would be much increased if adverse conditions affected the flight from Britain. Departure weights could still, however, be achieved if such late departing birds left Britain and the Wadden Sea heavier (200 - 210 g) than the early departing birds. Such high weights are achieved by some individuals in early spring (e.g. Prokosch 1988). Alternatively birds would have to gain weight in Iceland at rather more than 4 g/d, a rate higher than that recorded for any individual Knot in Iceland (see Figure 3).

In practice, direct observations of the timing of this spring migration to Iceland (Morrison & Wilson 1992) indicates that most birds fly to Iceland during the first ten days of May so that, if weather conditions during the flight are good, they need to gain weight at only the relatively low rate of 2-3 g/d. There is, therefore, considerable scope within their timing to cope with arrival at lower than usual weights. Such a situation could sometimes arise either if birds left Britain and the Wadden Sea at lower than usual weights, or if they used up more fat than usual during the flight to Iceland.

It is possible that birds might leave early spring staging areas earlier than usual, in late April, if they had reached departure weight earlier than usual as may have happened in Morecambe Bay in 1971 (see Figure 2), or if very favourable weather conditions arise before the completion of their usual weight gain. Such early departures may have occurred in 1972 (Prater & Wilson 1972). This may have led to the very low arrival weights in Iceland in 1972 and the earlier timing of the subsequent weight gain in comparison with 1970 and 1971 (Figure 2).

In spring there is some evidence that the timing of weight accumulation in Iceland differs between years. There may also be some differences in the timing of arrivals between Iceland and Norway, with birds apparently reaching Balsfjord a few days later than Iceland, and the subsequent weight gain schedule (see Figure 2). It is difficult to establish the validity of this interpretation, however, since the data for Iceland and Norway come from different years some 15 years apart. Such differences could therefore just represent year-to-year differences in migration schedule arising from other factors such as adverse weather during the earlier part of their migrations. Comparison of the more recent Iceland information with that collected in northern Norway (see e.g. Evans 1992; Gudmundsson & Alerstam 1992; Strann 1992) may help to elucidate these apparent differences.

Autumn migration

In autumn birds arrive in Iceland from widely scattered breeding areas where there may be differences in the timing of the breeding season depending on the timing of snowmelt. In addition, non-breeders and failed breeders are likely to return to Iceland earlier than successful breeders, and females which leave their young before fledging (Cramp & Simmons 1983) may return earlier than males. So, in contrast to spring migration, autumn migration is not highly synchronized and there is substantial turnover of birds throughout July and August.

Birds passing through Iceland in autumn are moving towards areas of milder weather, and both the departure weights from Iceland and the arrival weights in Britain in autumn are lower than the weights during the return north in spring. Birds moving south in autumn have little need for large body reserves since weather is mild and energy expenditure relatively low. In contrast, in spring Knots are known to use only part of their fat and protein reserves on their flight to late spring staging areas such as Norway and Iceland, and again to store more fat and muscle protein than is used for the flight to their breeding grounds (Davidson & Evans 1986, 1988; Morrison & Davidson 1990). These reserves seem to be used to buffer against food shortage during periods of high energy expenditure soon after the birds arrive on their breeding grounds (Davidson & Morrison 1992).

Once they have left Iceland in autumn Knots rapidly disperse throughout their moulting and wintering range. For example, Knots ringed in Iceland in July/-August 1972 were reported within two months from Denmark (1 bird), the Netherlands (1), the Dee Estuary in western England (1) and the Humber Estuary (1) and the Wash (3) in eastern England.

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