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Pay-offs and penalties of competing migratory schedules

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Drent, R., Both, C., Green, M., Madsen, J. and Piersma, T. 2003. Pay-offs and penalties of competing migratory schedules. – *Oikos* 103: 274–292.

We relate variation in the timing of arrival by migrating birds breeding at northerly latitudes to individual differences in the prior accumulation of energy stores. Balancing starvation risks early in the season against the almost universal declining trend in reproductive prospects with advancing date is seen as an individual decision with fitness consequences. We review three studies implicating events at the staging sites or in winter in setting the individual migratory schedule. Climate change influences the timetable of a pied flycatcher (*Ficedula hypoleuca*) population breeding in The Netherlands and wintering in West Africa, followed since 1960. Mean air temperature in the period mid April–mid May (arrival and laying) increased and laying date advanced by 10 days. Still, in recent years most birds did not lay early enough to maximise fitness (determined by recruitment and parental survival) whereas many parents achieved this goal in 1980–1985. As the flycatchers have not started to arrive earlier, some ecological constraint further upstream is postulated (possibly the hurdle of the crossing of Sahara and Mediterranean). The ability to follow individual migrants provides a second avenue to assess the fitness implications of migratory schedules. Thus, brightly coloured male bar-tailed godwits (*Limosa lapponica*) captured in the Dutch Wadden Sea (the intermediate staging site linking a West African wintering area with breeding sites in arctic Russia) and traced with miniature radio-transmitters did not depart early. The ‘best’ males (with bright breeding plumage) were picked up by the listening stations in Sweden 650 km further along the migratory route ten days later than the paler individuals. If early arrival confers the competitive advantage of prior occupancy but increases mortality, the ‘best’ males may be able to afford arriving later and thus avoid some of the survival costs. Return rate of the ‘bright’ males to the staging site in later seasons was indeed higher than for the ‘pale’, early males. Intensive observation of pink-footed geese (*Anser brachyrhynchus*) fitted with coded neck-collars substantiate the tight relationship between energy stores (fat) accumulated up to final departure from the final staging site (Vesterålen, N. Norway) en route to the nesting grounds (Spitsbergen) and subsequent success. The breeding outcome of individual parents (accompanied by juveniles or not) could be related to observations of body condition before departure (visual ‘abdominal profile index’). Recently, perceived conflicts with agriculture have resulted in widespread harassment by humans. The geese have: drastically shortened their stay on the Vesterålen, fail to achieve the body condition usual a decade ago and reproductive output has fallen. Although the geese are currently pioneering new staging sites, an adequate alternative has not materialised, underlining the critical role of the final take-off site.

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David Lack (1968) championed viewing avian migration from an evolutionary perspective, and emphasised that “its survival value at the present time...determines whether or not a migration is undertaken, and the routes followed”. Without detracting from descriptive studies or work on the proximate control of migration, Lack argued that appreciation of the evolutionary and ecological background is fundamental. The difficulty of taking the ideas put forward out of the realm of speculation was that “many...cannot be tested quantitatively in the field, few if any can be checked by experiments, and some depend on what happened in the unobservable past”. His plea has not gone unheeded, and nowadays the chain of decisions taken by the individual embodied in migratory behaviour has been elucidated by employing an optimality approach (Ens et al. 1994, Alerstam and Hedenström 1998, Weber et al. 1998). Admittedly opportunities for experimentation remain limited, but improvements in our ability to follow individual birds on their travels and relate migration schedules to breeding success serve to clarify the issues.

The basic conflict inherent in the timing of departure schedules is that individuals arriving early on the breeding grounds stand to benefit from a larger offspring production in the current year but at the expense of a survival cost of the parents upon early arrival when conditions are bad. The reasoning on optimal timing of migration is tightly linked with the notion of an optimal laying date for an individual, which depends on the seasonal change in reproductive value of the egg and the seasonal pattern of reproductive value of the parent. Data on the probability of offspring originating from eggs laid at different times of year becoming recruits in the next breeding generation, demonstrate a general declining trend for a variety of species (Daan et al. 1986), i.e. the earlier the better. The two best-documented witnesses of an experimental cost/benefit approach on laying date (European kestrel *Falco tinnunculus* and European coot *Fulica atra*) demonstrate that in general it is better to lay early, but that only individuals in good condition can afford to do so (Daan and Tinbergen 1997, Brinkhof et al. 2002). There are several reasons why individual parents may be unable to achieve an early lay date and thus harvest the maximal fitness bonanza (reviewed by Perrins 1996, Monaghan and Nager 1997) and the problem of completing spring migration is one of them, as we shall see.

Møller (1994a, b) considers the costs and benefits of early arrival in the barn swallow (*Hirundo rustica*) drawing on his extensive observations at a Danish colony. The benefits of early nesting follow from a seasonal decline in reproductive prospects, the swallows thus conforming to the pattern outlined above. The parental costs are represented most dramatically by mortality among early arriving males in some seasons. In these inclement seasons, the birds suffered from

snowstorms, leading to the dual threat of increased energy demand coupled with the absence of their insectivorous prey. Such catastrophic losses early in the season can exert a measurable selection pressure if losses hit some phenotypes more severely than others, as has been documented by Brown and Brown (1998, 1999) for the migrant cliff swallow (*Hirundo pyrrhonota*). Thus, the optimal arrival decision will depend on the quality of the individual, and Møller adduces evidence that the long-tailed males (wearing badges achieved during the previous moult and considered to be of ‘high quality’) indeed arrive earlier than shorter-tailed ones (Møller 1994b). In a follow-up study, Møller (2001) provides evidence that arrival date has a hereditary component, and argues that in the barn swallow the condition dependence influencing both tail length and migratory date has a genetic basis. Given the high heritability, arrival date could respond readily to selection (e.g. environmental change).

Kokko (1999) has further dissected this problem and emphasises that the essential distinction is not so much the difference in ‘inherent’ quality but rather the incremental cost to individuals of advancing arrival by a given time interval (say one day). Under difficult conditions (weatherwise ‘late’ springs, for example), poor quality individuals will be expected to be more disadvantaged than those of higher quality, hence the lag in time of arrival will be more pronounced. Indeed, Møller (1994b) showed that the ‘longtails’ achieved a relatively greater head start in seasons when the entire population arrived late (having presumably experienced tough conditions en route), whereas in early (‘easy’) seasons the timing gap was much less. On the other hand, if the cost curve for high quality birds declines more steeply with date than for the low quality ones, then the marginal cost of early arrival is higher for them and the low quality birds may be expected to follow the risky strategy and arrive earliest (Kokko 1999).

In contrast to laying date, the empirical evidence for the optimal timing of migration patterns is scarce, because of the logistical problem of following individuals over long distances and the paucity of experimental manipulation of the timing of migration. In this paper we review some well-studied examples in which we place the timing of migration in the larger context of optimal decision making during the annual cycle. It is our aim to understand why individuals vary in timing their migration, with attendant consequences on subsequent fitness. We deal here with the specific decision of the timing of departure from the penultimate staging site en route to northern breeding grounds in spring, and focus on long distance migrants. Our first step is to examine the flexibility of migratory schedules in the light of environmental change in The Netherlands over the past decades, and will then present individual-based histories of spring migration in geese and waders that

help to clarify the costs of migratory schedules. These birds typify the adage 'the earlier the better' as most populations of geese nest as early as secure nest sites become available (Sedinger et al. 1995). Indeed, the data to hand support the proposition that individuals in good condition before breeding, or who occupy good quality territories, breed earlier and produce more offspring. Since the individual trajectory of body condition impinges on the timetable of both migration and breeding we will clarify our notion on these relations by providing a diagram derived from Piersma and Baker (2000).

Dynamics of body stores during spring migration: a predictive model

In the model of Piersma and Baker (2000) high quality individuals achieve higher rates of accumulation of energy stores on the stopover sites (for example by excluding others from the better patches) and are thus expected to move on to the second stopover earlier (where the late arrivals will face prey depletion, Nolet and Drent 1998). The slopes may differ between sites reflecting differences in environmental constraints or even 'strategic' decisions (Fig. 1). In addition to differences in timing between high and low quality individuals, we expect these differences to extend to fuelling rates. Low quality individuals may then decide to 'cut the losses' by migrating earlier and taking the risk of meeting unfavourable conditions upon arrival in the far north. The individuals that lag far behind in accumulating stores do not have this compensatory but risky option and migrate last, if they depart to the breeding grounds at all. When reaching the breeding area (the still snow-bound tundra), we here assume low rates of energy accumulation. Only 'high quality' females will achieve sufficient energy stores to meet the minimal requirements in the narrow window of egg-laying opportunity. The best of the 'low quality' females has a sporting chance to breed successfully, either having the luck to arrive early and meeting favourable circumstances that year, or arriving late and laying at the twilight period of the breeding season. In strategic terms, individuals ensure success by breaking the double jackpot of energy maximisation at the stopover sites enabling quick travel onwards to the breeding areas (and hence achieving time minimisation) as well as sufficient stores when they get there as has been argued for the pectoral sandpiper (*Calidris melanotos*) by Farmer and Wiens (1999). Moments of increased risk are also shown in the diagram, and highlight the vicissitudes of avian migration. In the two species for which losses during migration can be considered separately (barnacle goose, Owen and Black 1989; black-throated blue warbler *Dendroica caerulescens*, Sillett and Holmes 2002), risks are much higher than during either breed-

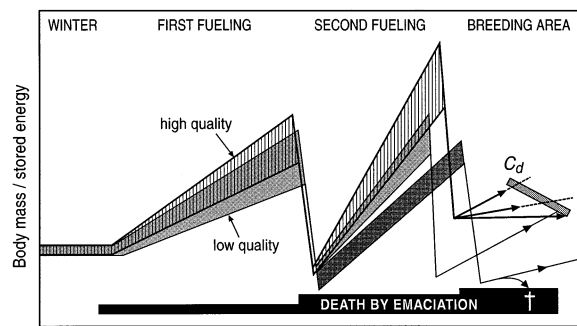


Fig. 1. Summary diagram of trajectories of body mass or energy stores during spring migration, adapted from Piersma and Baker (2000) with a threshold for laying (C_d) inserted based on data for swans and geese (see text).

ing or wintering, even in the complete absence of hunting.

To our knowledge there are no individual-based data that confirm this representation in detail for a migratory bird, but we can adduce strong evidence from a study on resident mute swans (*Cygnus olor*) where repeated assessment of body stores of individuals throughout the breeding cycle has proven possible (R. Ubels et al., unpubl.). A feral population with pinioned birds in the environs of Groningen (northern Netherlands) allowed capture at regular intervals. Whenever caught, the female swans were weighed, measured and the fat stores determined indirectly from deuterium injection (Groscolas et al. 1991, Speakman et al. 2001). When the data are plotted against calendar date (Fig. 2), the spread in extent of fat stores of females (all of which eventually breed) is striking, whereas the slopes representing improvement during the pre-egg stage do not differ sufficiently to allow the birds in poorest condition forty days before lay to catch up. The fat stores of the various females at the moment of egg laying thus span a range of nearly a kilogram, and these

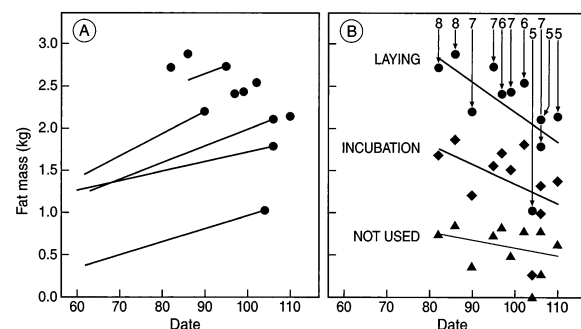


Fig. 2. A 50-day data set on total fat stores in individual pre-breeding female mute swans (A) sampled by deuterium injection in the field, in relation to calendar date (1 = 1 January). For these 11 females, fat mass at laying of first egg, start of incubation, and remaining at hatch ("not used") is shown in relation to laying date (B). Superscript figures denote clutch size achieved. From R. Ubels, pers. comm.

differences translate into the seasonal decline in clutch size familiar from so many studies (collated for waterfowl by Rohwer 1992). Individuals with highest fat stores lay earliest, produce the largest clutches, and retain the largest residues at hatch, despite having utilised more fat not only for the eggs but also during incubation. Clearly, the differences in individual breeding performance have their origin well before the first measurements in the breeding territories were undertaken. Equating measured fat stores to a declining condition threshold with advancing date for laying in the mute swan study substantiates the earlier model of Reynolds (1972), subsequently extended to birds in general (Drent and Daan 1980) and given elegant empirical support for the mallard (*Anas platyrhynchos*) by Krapu (1981). The current functional interpretation is that for females lagging behind in reserve accumulation their only option is to reduce the investment in the clutch in order to breed within the environmental window providing realistic options for survival of progeny and parents (Lepage et al. 2000 who marshal evidence for the snow goose, *Anser caerulescens atlanticus*). In our conception, the condition threshold may be viewed as the proximal calibration of the adjustment of reproductive effort to lay date (which ultimately depends on the survival outcomes of progeny and parents as pointed out above).

We can now insert this relation in the general scheme for dynamics of body mass or more specifically stored energy during spring migration in our diagram as a condition threshold for breeding, restricted to a brief window of opportunity and declining with date (Fig. 1). Including the costs of travel is here depicted by depletion of energy stores during two long-distance flight episodes. The most time-consuming phase of avian migration is clearly the accumulation of the energy stores needed to fuel flight (often in several cycles at different sites along the way) and subsequent breeding. The rate of accumulating stores (loosely referred to 'fattening' in the older literature but including protein as well) is subject to the physiological constraint of the digestive and metabolic machinery as has been elucidated by Kvist and Lindström (2000).

Armed with this framework we will examine (1) the repercussions of environmental amelioration at the breeding grounds for long-distance migrants where adequate response relies on shifting all preceding phases forward as well, (2) individual differences in the migratory timetable at the penultimate staging site to ascertain whether 'low quality' individuals depart earlier, not later and (3) the relevance of individual differences in accumulation of energy stores before take-off on the final flight step for subsequent breeding performance to confirm the 'condition hurdle' inserted in the diagram.

Results

Flexibility in adjusting laying and migration dates

Beintema et al. (1985) present an analysis of the Dutch ringing records on the timing of hatching for 5 species of waders, birds that traditionally have attracted ringers to the meadow landscape (Fig. 3). Between 1910 and 1975, hatching (and hence laying) advanced by as much as four weeks. Critical in evaluating this shift is the finding that young produced from early nesting were found to be more likely to survive and reproduce (Beintema and Drost 1986). Beintema et al. (1985) were impressed with the concomitant changes in agricultural practise in the years considered and depicted the mean mowing date as an index of change (itself triggered primarily by increased inputs of fertilisers and improved drainage). A more recent data analysis from the 25-yr period 1971–1995 comprising nest records for the British Isles (Crick et al. 1997), substantiates earlier laying in two of the species considered by Beintema and co-workers (oystercatcher *Haematopus ostralegus* and redshank *Tringa totanus*). These authors point out that over the past 11 years alone, the growing season for plants has advanced by roughly eight days at northern latitudes (Menzel and Fabian 1999).

The proximate trigger responsible for this shift in breeding schedule has not been elucidated by experiment, but the point we make is that a whole suite of migratory waders (four of the five being long-distance migrants) has shown a flexible response to a change in conditions on the breeding grounds. There is good

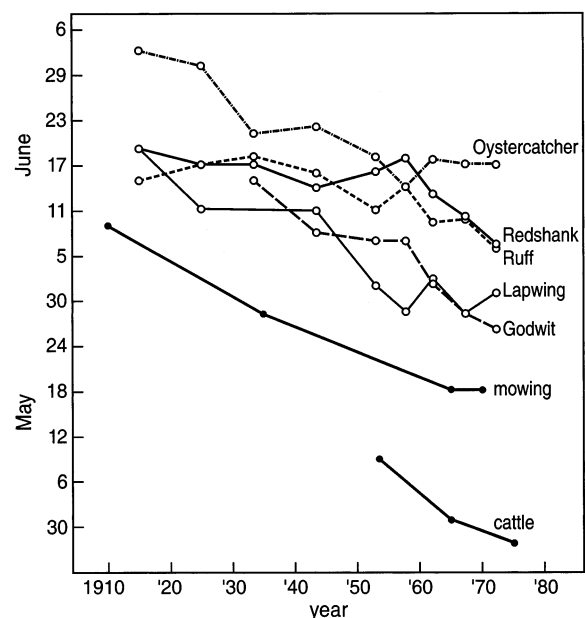


Fig. 3. Advancing laying date between 1910 and 1975 of five species of meadowbird (wader) in the Netherlands. After Beintema et al. (1985).

evidence that for the black-tailed godwit (*Limosa limosa*) at least (the Dutch breeders that winter in West Africa), arrival dates have also advanced (Lensink 1993), but in recent years the trend towards earlier hatch has flattened off (A. J. Beintema, pers. comm.). This is already hinted in the case of the lapwing (*Vanellus vanellus*) in Fig. 3. Further work on the energetics of laying will be called for to decide if laying date in waders is subject to a thermal constraint, as has been argued for the great tit (Stevenson and Bryant 2000). The interpretation that, alternatively or additionally, we are here up against a constraint imposed by migration timing can be argued from studies by Gill et al. (2001) concerning the black-tailed godwit population that winters in estuaries of the British Isles and breeds in Iceland. Over the past thirty years the overall wintering population in Britain has increased four-fold, and Gill and her co-workers ranked the estuaries according to the records of the number of godwits using each. Marked individuals wintering in estuaries long saturated in numbers (presumably the preferred sites), arrived in Iceland before those wintering in estuaries more recently settled and still experiencing strong growth in numbers (presumably the overflow, less preferred sites). These observed differences of 4–5 days in arrival date correlate with differences in foraging intake rates at the wintering sites (the early birds originating from estuaries providing better feeding conditions) suggesting that the early birds achieved migratory condition earlier, i.e. migratory departure is condition-dependent.

Pied flycatchers (*Ficedula hypoleuca*) colonised the central Netherlands 40 years ago. During the past 20 years, a nest-box population under study has reached plateau numbers and statistics can be presented without undue influence of density-dependent factors. As has been reported by Both and Visser (2001), laying date in this population has advanced by approximately 10 days over the past 20 years, tracking to some extent the warming trend in spring temperatures in the study area (presumably itself the proximate signal for laying, or closely correlated with it, e.g. via emergence times of the insect food relied on by the flycatchers). The critical question is whether the flycatchers have kept up with the shifting phenology through the years. To evaluate this we should know the fitness consequences accruing to lay date, and Both and Visser (2001) have demonstrated that the selection differential with respect to date has in fact become steeper since 1980 (i.e. selection for early laying has become stronger over the years, Fig. 4). In other words, despite shifting lay date ever earlier, the birds are still 'behind' the phenological schedule dictating survival and recruitment. This is elucidated in Fig. 5, contrasting female fitness in relation to laydate for the two time periods (1980–1985 and 1993–1998). Fitness is here measured as the sum of local recruits and adult females surviving to return to

the breeding area the next season. Clearly the dome-shaped fitness curve reflecting a match between environmental perspectives (for both adults and young) and lay date achieved early in the period, when mean laying date coincided with peak fitness has deteriorated to become a falling trend. Whereas in the early years the majority laid on time, in recent years only the very earliest birds achieve a maximal fitness. Although each female may still be reaching her individual fitness maximum, the population response represents a widening mismatch to current conditions. The clue for this incomplete adjustment can be found in the data for arrival in the Netherlands (Fig. 5). Despite the warming trend and the evidence for a selection differential in favour of advancing laydate, the flycatchers have not

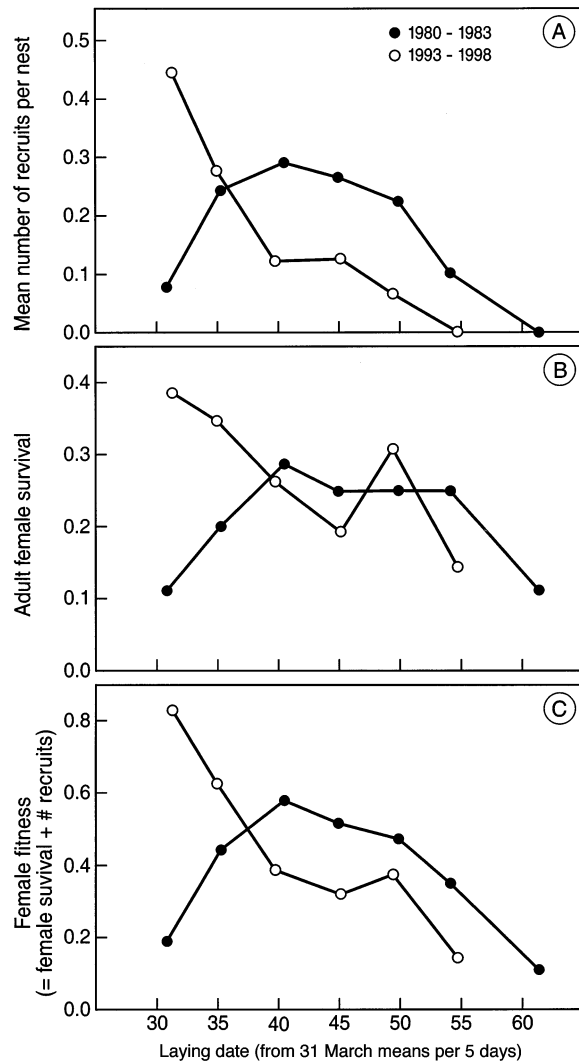
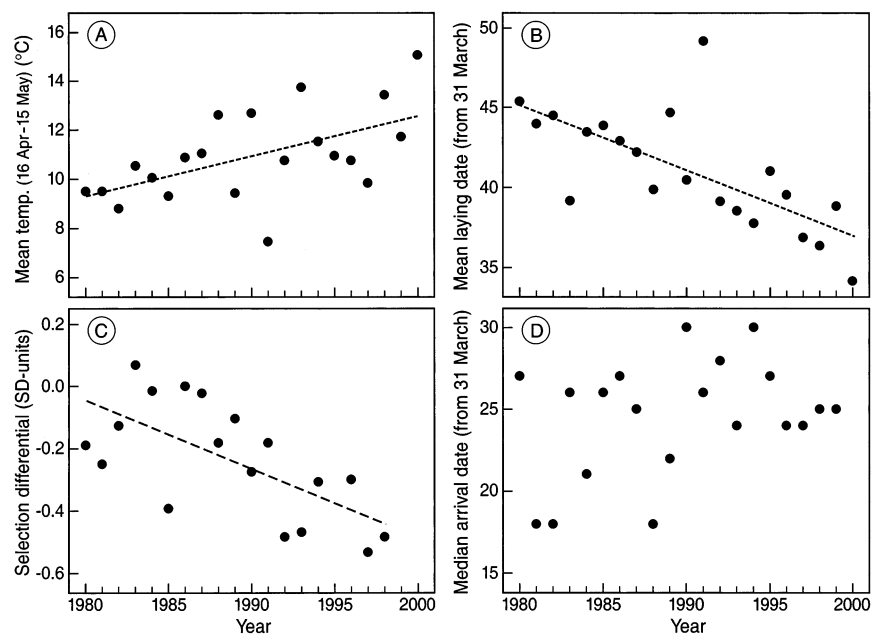


Fig. 4. Fitness performance measures in a pied flycatcher population on the Hoge Veluwe, the Netherlands in relation to laying date (1980–1998): (A) recruitment, (B) female survival, and (C) female fitness.

Fig. 5. Overview of the results of the Hoge Veluwe study on pied flycatchers (1980–1999): (A) mean spring temperature, (B) mean laying date, (C) selection differential (relatively early birds do better in the course of the years) and (D) median arrival date in the Netherlands (assembled from Both and Visser 2001)



responded by arriving earlier from their West African wintering quarters over the past 20 years. Both and Visser (2001) thus conclude that the birds are constrained by their migratory timetable, possibly because the proximate cue triggering spring departure from Africa has not altered. At first, the flycatchers responded to the increasing temperatures by reducing the interval between arrival and laying, but currently some individuals are laying within five days of arrival in the breeding area and a further reduction does not seem feasible.

Phenology data from central Sweden from 1941–1986 also fail to reveal a trend (Lundberg and Alatalo 1992) and the authors note ‘tropical migrants must have difficulties in forecasting the weather conditions at the breeding sites’. Limiting resource conditions somewhere upstream on the migratory pathway, such as fuelling requirements to surmount the double hurdle of the Sahara and Mediterranean, are another possible cause for the failure to adjust arrival date to changing conditions in the breeding area. For the spotted flycatcher (*Muscicapa striata*) another trans-Saharan migrant spanning the 10,000 km from the breeding area, Kok et al. (1991) emphasize the invariable departure date from the wintering area in South Africa in a 36-yr data set (1950–1986). In agreement with the departure data, the spotted flycatcher has not shown a statistically consistent trend towards earlier arrival in Britain (1890–1950, Huin and Sparks 2000; 1942–1991, Mason 1995) or Scotland (Jenkins and Watson 2000).

Forging a direct link between wintering and breeding localities is a tall order, but Marra and co-workers (Marra et al. 1998) have amassed circumstantial evidence strongly supporting the interpretation that male

American redstarts (*Setophaga ruticilla*) that secure the preferred winter territories in the West Indies, indeed return earlier to their North American breeding sites. These studies rely on removal experiments on the winter quarters (Marra et al. 1993, Marra 2000, Marra and Holmes 2001), substantiating the preferred status of mangrove thickets as contrasted with second-growth scrub. Indeed, males in the black mangroves had more favourable body mass gains and departed earlier. That they also arrived on the breeding grounds earlier hinges on an analysis of isotope signature (tissue of early arrivals matching the mangrove profile more closely than the late arrivals that resembled the scrub profile). To underline these close relations between the two key localities, the term ‘migratory connectivity’ has been coined (Webster et al. 2002).

Plumage quality, apparent survival and timing on migration

We have studied individual timing of migration of bar-tailed godwits, *Limosa lapponica* staging in the western Dutch Wadden Sea, enroute to their far northern breeding range. Spring captures (Piersma and Jukema 1993) revealed an association between plumage score and body mass, interpreted as equating the dark, heavy birds to ‘high quality males’ and the intensity of breeding plumage as an honest indicator of individual quality (in males as well as females). Another correlate reported was the incidence of a supplementary body moult that only occurred in birds with high plumage score (determined on a seven-point ‘red scale’ introduced by Piersma and Jukema 1993, Fig. 6) that were



Fig. 6. This assembly of male bar-tailed godwits captured in the Dutch Wadden Sea in mid May illustrates the variation in spring plumage scores attained (photo by J. Jukema).

also heavy. This was interpreted to mean that high quality individuals that were 'early on schedule' could afford to upgrade the quality of their plumage even more. Later work (Piersma et al. 2001) confirmed, at least for females, that birds with high plumage score and in active body moult were less liable to harbour 'demanding' endoparasites (Cestodes and Acanthocephalans) than birds with low plumage scores and not in active body moult. In a reanalysis of the data on parasites in Piersma et al. (2001) it can be shown that in adult males, birds with high plumage scores (i.e. 5, 6 and 7, $n = 49$) had a 12.2% incidence of infestation by Cestodes, whereas males with plumage score of 4 or lower ($n = 34$) suffered a 32.4% incidence (Pearson Chi-square = 4.98, $df = 1$, $P = 0.026$). In keeping with the 'individual quality hypothesis', males that were seen again in subsequent seasons were restricted to those with the highest breeding plumage scores, with a distribution of scores heavily skewed towards the top (red) end of the scale compared to all males captured at the study sites (Fig. 7).

In May 1999, 2000 and 2001 radio-transmitters were attached to samples of males and females in the Dutch Wadden Sea. Following release, birds were actively searched for using a hand-held antenna, to ascertain date of departure. In southernmost Sweden, 650 km further along the migratory pathway, an array of automatic radio-tracking stations (ARTS) was erected perpendicular to the migratory corridor (Green et al. 2002b), and this 'listening curtain' proved effective in picking up the radiotagged birds (75% in 2000). In the absence of evidence about subsequent stopover sites en route to the Siberian breeding grounds, passage at altitudes of 1–3 km over southern Sweden is taken to indicate long-distance flights onwards to the tundra breeding areas (Fig. 8). Scheiffarth et al. (2002) support

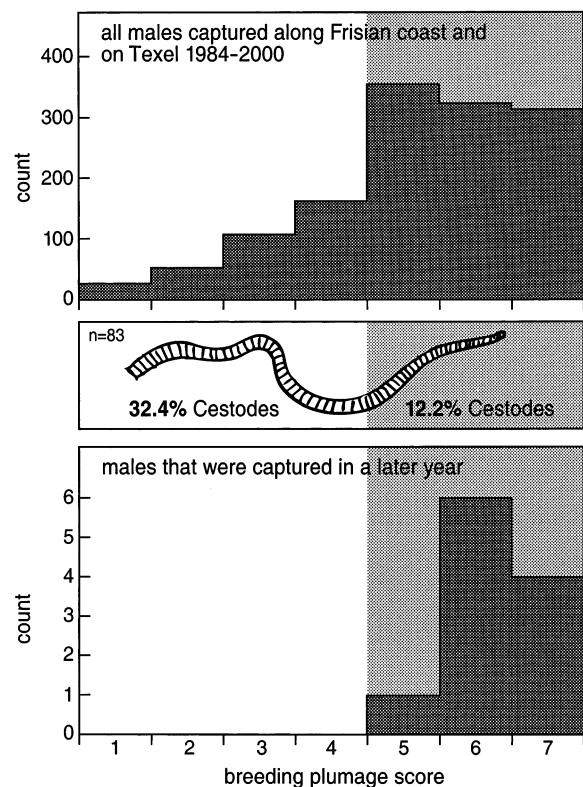
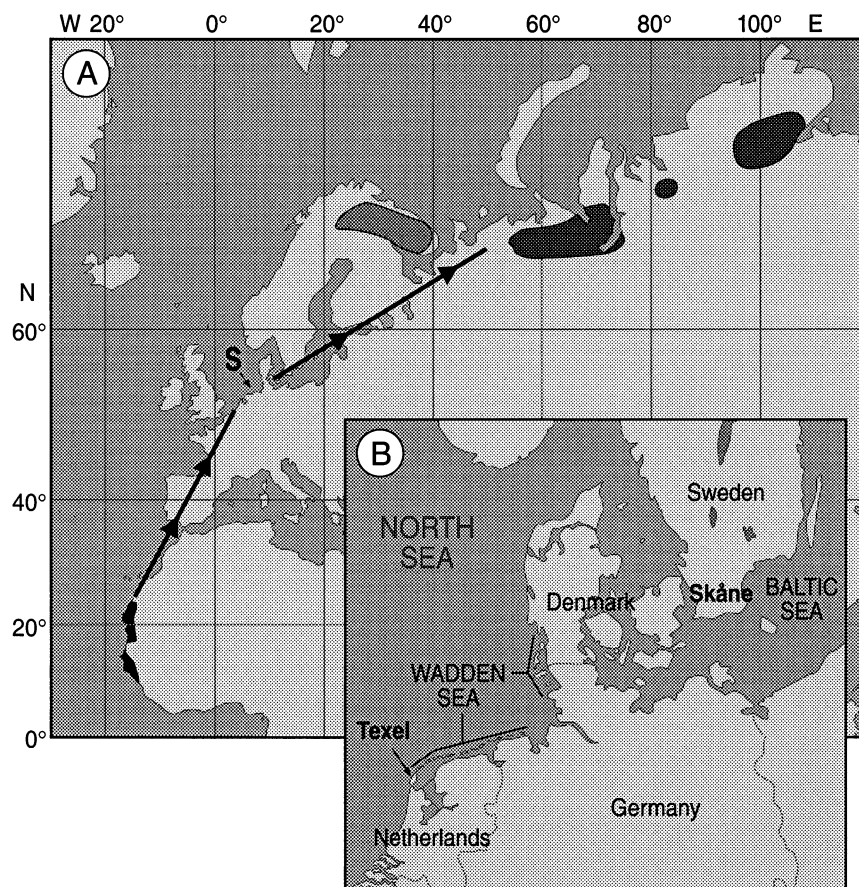


Fig. 7. Breeding plumage scores of adult male bar-tailed godwits captured in the Dutch Wadden Sea from 1984 to 2000 (top panel) and scores at first capture of individuals subsequently recaptured at the study sites (bottom panel) thus demonstrating both survival and site fidelity. Also shown (middle panel, from Piersma et al. 2001) is the incidence of cestode infestation.

Fig. 8. Migratory pathway of the bar-tailed godwit highlighting the sub-species *taymyrensis* heading for its breeding quarters from the Wadden Sea staging area in late May–early June after wintering in West Africa, and showing capture site (Texel) and the ‘listening curtain’ across southern Sweden (adapted from Green et al. 2002b). The breeding area of the nominate race *L. l. lapponica* (wintering in Europe), with which we are not concerned, is indicated by light shading.



the interpretation that this Afro-Siberian population during their stay in the Wadden Sea is following a strategy of maximising accumulation of body stores preparatory to the final leap.

The godwits (mainly males) were captured and marked in the period 18–24 May, and for our analysis of migratory timing we selected males captured from 18–20 May, individuals that would certainly still be in the refuelling phase (average body mass values of the staging population in the Wadden Sea reach a plateau after 20 May, T. Piersma, M. M. Landys-Ciannelli and J. Jukema, unpubl.). We also excluded the three males in active body moult that eventually passed southern Sweden late in the season (presumably they had to complete growth of the contour feathers before take-off; Piersma and Jukema 1993). At capture the males were weighed, measured and classified according to a seven-point plumage score (the ‘red scale’, Fig. 6). To date there is no evidence that these plumage scores undergo further change during stopover in May (regression of male plumage score against date, $n = 954$, slope non-significant, $P = 0.08$), and we assume that the classification represents the plumage with which the males will arrive on the breeding sites as far as 4300 km away. Recapture data provide no evidence that

plumage score improves with age (J. Jukema and T. Piersma, unpubl.).

Considering all male bar-tailed godwits captured between 1984 and 2000, birds with low breeding plumage score are lighter than those with high breeding plumage scores during the time of intense radio tagging (18–20 May) in 1999–2001 (Fig. 9 top panel). This difference between low and high score birds is maintained til the end of May (Fig. 9 bottom panel), although the effect is reduced. Light birds thus seem to be able to catch up to some extent. A first analysis of radio-tagged godwits, to our surprise, showed no correlation between the date of passage over southern Sweden (or the time between capture in the Dutch Wadden Sea and the flight to the breeding ground in view of the narrow range of marking dates) and body mass (Fig. 10). Also, it was unexpected that of the ‘early group’ of male godwits passing over southern Sweden in late May, most had rather weakly developed breeding plumage, with an average score of 4.4 points. The males passing after 1 June had significantly more reddish breeding plumages (average of 6.0 points), but the two groups showed no differences in body mass at all. Curiously, the data hint at a bimodality in the ‘late’ group, including both light and heavy individuals.

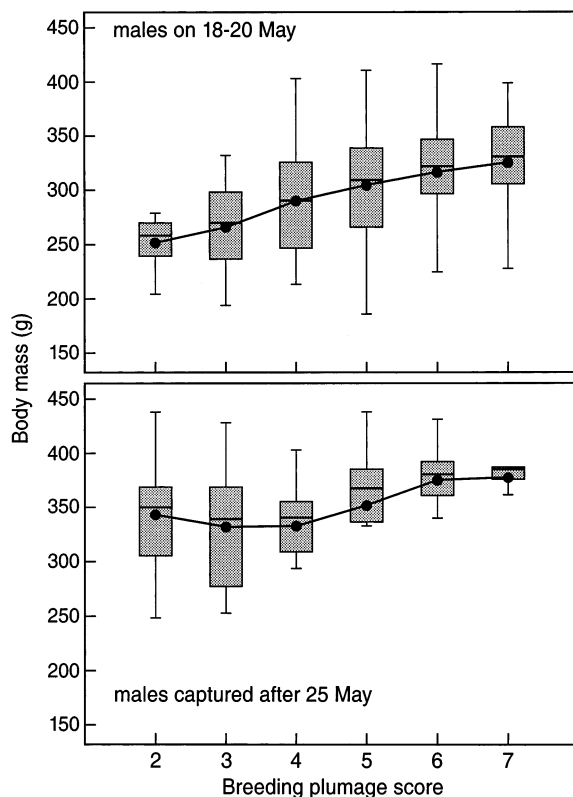


Fig. 9. Relation between body mass and breeding plumage score in adult bar-tailed godwits during stopover in the Dutch Wadden Sea (1984–2000) on 18–20 May (mid-stopover) and after 25 May (departure period) respectively. For the top panel the *n*-values are 6, 25, 32, 86, 107 and 188 (total = 374) and for the bottom panel 9, 7, 4, 11, 17 and 16 (total = 64).

For 13 individuals, exact departure times from Texel (the site of radio-tagging) are known, and all passed over southern Sweden within three days of departure, 5 individuals within 36 hours. The direct flight time between the sites is estimated at only 6 hours (Green et al. 2002b), so all godwits made intermediate stop(s), perhaps to sample wind conditions before the final leap that would carry them over Sweden. Following this up, we were unable to find any differences between the 'early' and 'late' birds in wind conditions experienced over Sweden, and both seemed to have attained equally favourable (following) winds.

Thus, there is a light-coloured group of males leaving early, and a dark-red plumaged group of birds that leaves late (Fig. 10). Such a dichotomy may reflect: (1) the presence on Texel of birds aiming for a breeding area (or even a stopover area) that becomes available rather early in the season and another group of birds aiming for a more easterly and northerly tundra breeding area (i.e. east of Yenisei River) that becomes available later in the season, or (2) different classes of male godwits using different strategies related to their success in developing a full breeding plumage and achieving

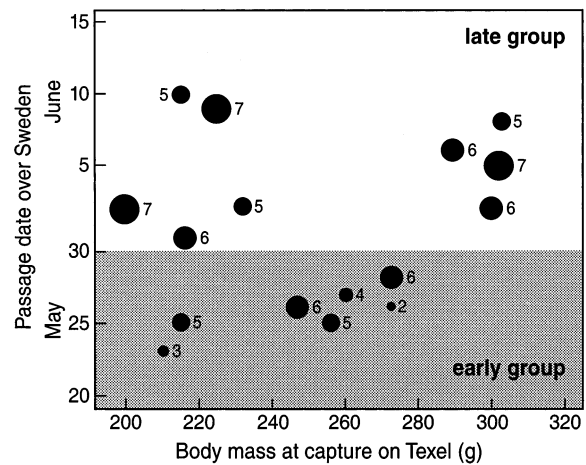


Fig. 10. Of the 16 male bar-tailed godwits without active body moult captured on 18–20 May 1999, 2000 and 2001 and equipped with individually coded radio transmitters, 7 individuals migrated over Sweden in late May and another 9 individuals in the first half of June (the demarcation in 'early' and 'late' coincides with the median passage date in the total material of Green et al. 2002b). Average body plumage score of the 'early group' was 4.4 points (SD = 1.5) and of the 'late group' 6.0 points (SD = 0.9) a significant difference (pooled variance Student's *t*-test, $t = -2.63$, $P = 0.020$). Average body mass at capture (ca 255 g) did not differ for the two groups.

high departure masses. P.S. Tomkovich (pers. comm.), after examining skin collections in the Zoological Museum of Moscow State University, has been unable to discern any geographical differences in the intensity of breeding plumage (the 'red scale') in birds from breeding areas west and east of the Yenisei. This makes the possibility of geographical 'types' unlikely, and calls for further comment.

Summarising, we find that the interpretation that bright red males are of high quality (Piersma and Jukema 1993) is supported by the overall data on body mass, incidence of endoparasites, and return rates to the spring staging sites. To harmonise these results with the radio-transmitter data, we hypothesise that the early group of light-plumaged males constitute 'desperates' whose best chance of breeding is to arrive quite a bit before the dark-plumaged, healthy males do and thus benefit from the advantage of 'prior occupation'. This 'early bird' tactic incurs a survival cost (inferred from the bias towards full breeding plumaged birds among those that were recaptured), as early arriving birds might find the tundra snow-covered for a long time and thus risk death by starvation (a likelihood enhanced by a greater incidence of infestation by costly endoparasites). Put in other terms, we suggest that for individuals in poor condition, the best option for breeding is to migrate early to the breeding grounds, and we will encounter this strategy among the arctic breeding geese as well (Prop et al. 2003). In our final example we will show that condition differences at the final stop-

over site indeed translate into differences in breeding success.

Spring migration strategies in pink-footed geese

Madsen (2001) has described the alternative strategies followed by individual pink-footed geese (*Anser brachyrhynchus*) of the Spitsbergen population in proceeding from their wintering quarters in the low countries via Denmark (D), mid-Norway (T = Trondheimfjord region) and northern Norway (V = Vesterålen) to the breeding grounds (localities and distances between stopover sites given in Fig. 11). This work relies on intensive observation of neck-banded birds (642 marked in Denmark since 1990) and traced on their spring travels. The salient advantage of working with geese is that individual fitness can be deduced from fall and winter sightings when the number of juveniles in the family can be ascertained. The Spitsbergen population has been estimated (from direct counts) at 33,000–38,000 in the period 1991–1998 with calculations from demographic parameters indicating stability in this period (Ganter and Madsen 2001). Our concern here is how to interpret the alternative spring migratory routines that have developed during recent years.

Traditionally, pink-footed geese left Denmark in early May and used only the Vesterålen as stopover site for approximately ten days before making the final flight to Spitsbergen (this is the D-V strategy, Fig. 11, top panel). Starting in the late 1980s, and gathering momentum in the late 1990s, Trondheimfjord has developed as a new stopover region intercalated between D and V, either for a relatively short period, followed by a brief stopover at the Vesterålen (D-T-V strategy, middle panel) or (by earlier departure from Denmark) for a much longer stay, with only a brief sojourn on the Vesterålen (bottom panel). The functional implications of these variations in pattern of spring migration can be deduced from observations on the rate of accumulation of body stores. Owen (1981) championed the use of what he termed the abdominal profile index (API), i.e. the visual estimate of the degree of curvature of the lower abdomen against a scale of previously agreed stages. Experienced observers, by referring to a set of drawings as they peer through their telescope (or in some cases comparing the profiles to models erected in the field of view), show surprising agreement and when calibrated against individual geese recently caught and weighed are able to reliably differentiate in steps of 10% of total mass (and when repeated measures are possible in even smaller steps).

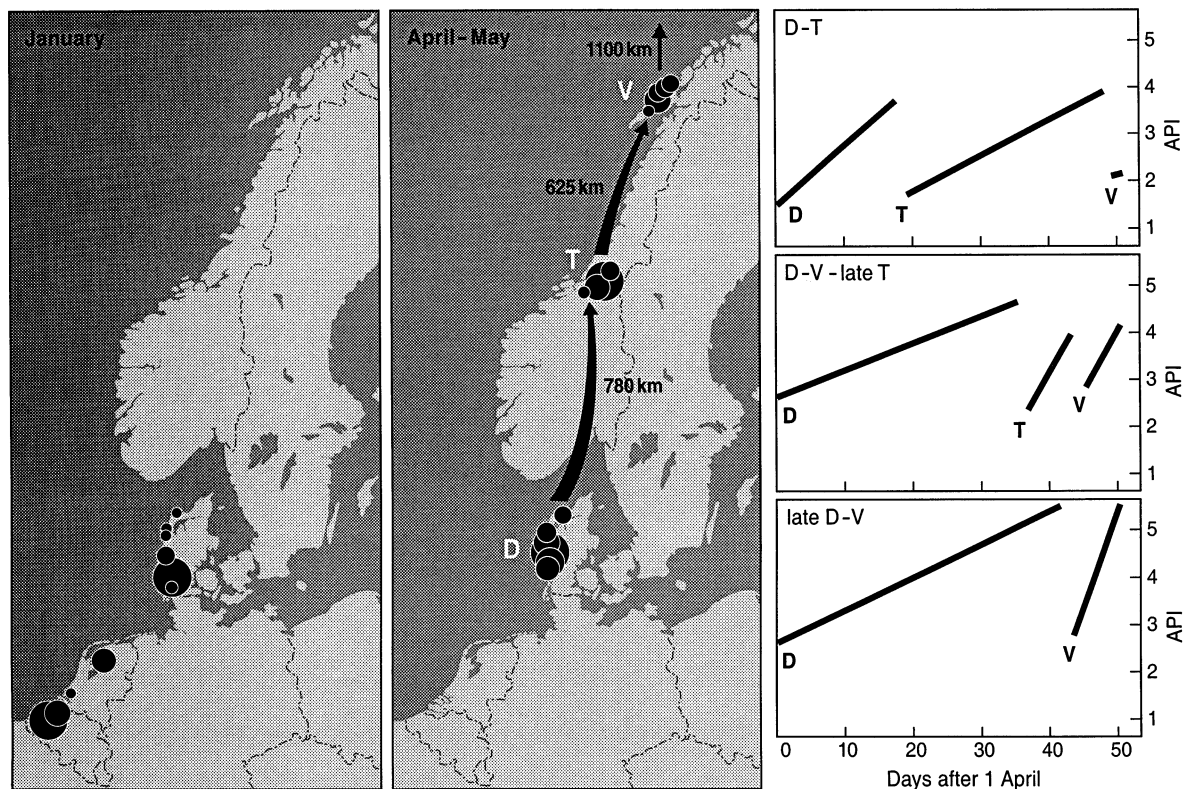


Fig. 11. Spring migratory routes of pink-footed geese with profile trajectories for individuals following three strategies (from top to bottom, D-T, D-V-late T, late D-V).

During the spring staging period, geese add some 30% to their body mass, and there is good evidence that females must achieve a defined threshold value of extra mass to enable successful breeding (Ebbinge and Spaans 1995 for black-bellied brent *Branta bernicla*; Alisauskas 2002 for lesser snow geese *Chen c. caerulescens*). Employment of the API method thus provides a powerful tool, and sample trajectories of body mass accumulation are shown in Fig. 11. To enable the conversion to energy budgets we need to calibrate the API scale against energy stores accumulated in the body. This, Madsen (unpubl.) has done by collecting individual pink-footed geese in the field after ascertaining the API. Subsequently energy content of the body has been determined following standard procedures of carcass analysis (such as described by Alisauskas 2002). Given the relation between body condition of the female and subsequent breeding success established in other Arctic goose species, we will confine our attention here to the female. We will be concerned with the costs of transport (95% of the energy required will be drawn from the combustion of fat, Battley et al. 2001) and subsequently with the costs of producing and incubating the eggs on the tundra, where the fat budget in geese depends heavily on supplies acquired on the spring staging grounds elsewhere (Meijer and Drent 1999). We realise that spring staging also involves building muscles and other protein stores, but since the evidence for implicating the derivation of protein in the eggs from the stores laid down previously (as against gathered locally at or near the breeding locale in the brief pre-egg stage characterised by frenzied foraging activity) is equivocal at best, we will focus on the fat budget. The calibration of fat stores (expressed in g) against abdominal profile index (API) in the female pink-footed goose allows a linear fit (Fig. 12) and confirms the ability of the trained observer to make subtle assessments of the fat stores of the individual.

Our next step is to provide a preliminary fat budget for the female pink-footed goose, to enable evaluation of the fitness implications of attaining specific levels of body stores during spring staging, expressed in API units. By assembling all observations fulfilling the requirement that an API value was taken within 1 day of departure from one site and obtained for the same individual at a subsequent site (again within 1 or 2 days of arrival), flight cost can be empirically estimated for the distance concerned (accepting shortest intervening distance in km). Determinations for 27 individual cases give a mean decrement of 1.26 units on the API scale per 1000 km traversed, and this converts to 170 g fat stores according to the calibration of Fig. 12. We consider this empirical value a reasonable first approximation, and can now estimate the flight cost from the penultimate staging site (Vesterålen) on to Spitsbergen (1100 km) at 180 g fat.

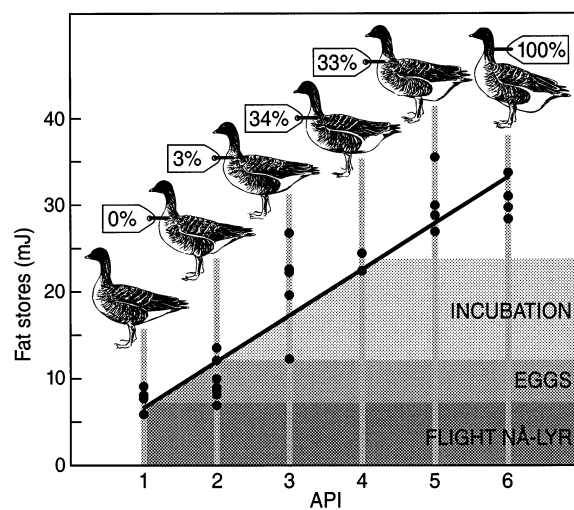


Fig. 12. Calibration of the fat stores of female pink-footed geese in relation to the abdominal profile index (API), with expected fat budget for breeding inserted (see text). Top panel shows breeding success in relation to API (data from 2000 and 2001, $n = 79$).

The next hurdle to be surmounted is the production of the eggs, and restricting ourselves to the contribution of fat, we arrive at a cost of 125 g fat input to a clutch of mean size 4.5 eggs (see Alisauskas and Ankney 1992 and appendix for calculations). Finally we must budget for the costs of incubation. Total cost can be estimated as equivalent to energy expenditure at the rate of 1 BMR (basal metabolic rate), accepting empirical work on respirometry of the sitting female eider ducks (*Somateria mollissima*) on Spitsbergen as a guide (Parker and Holm 1990, Gabrielsen et al. 1991). Part of these costs can be paid from the foraging intake gained during daily recesses from the clutch. Extrapolating on the basis of body mass from other goose species where intake has been measured (Prop and de Vries 1993), we provisionally accept that in the pinkfoot the female will be able to meet 1/3 of the cost from local forage, and thus will draw on her fat stores for 2/3 of the incubation cost. The fat budget of a female pinkfoot departing from Vesterålen with an API value of 4 units (equivalent to 630 g) as illustrated in Fig. 12 will thus allow a modest residue at hatch after subtracting the cost of travel to Spitsbergen and production and incubation of the clutch. Note that we here simplify the budget by assuming that feeding during the 7–10 day pre-egg stage on Spitsbergen will cover the daily energy cost at that time without measurable change to the fat stores. We will return to this point in the final discussion, as we lack critical data identifying the source of the fat deposited in the eggs of the pinkfeet.

On the basis of these considerations it seems clear that a female pinkfoot must attain an API value of 4 units or more to be able to breed with success. What do the observational data show? A sample of 79 neck-

collared females where both API (at departure from Vesterålen) and subsequent breeding success is known (as determined in Denmark and the Netherlands in the period October–November) is available from the 2000 and 2001 seasons to test this point. The results (Fig. 12) support the notion of a threshold value for breeding close to 25 MJoules (= 630 g fat), corresponding to the API value of 4.

Armed with this threshold value we can take a fresh look at the breeding prospects for geese adopting competing strategies. Individuals opting for use of the Trondheimsfjord as sole Norwegian staging site lagged behind in API scores at departure, and indeed had the lowest rate of breeding success. In most years, use of the Vesterålen site was rewarded as the best option for subsequent breeding success (Madsen 2001). These results pose two problems. How can migratory patterns attract followers if not rewarded by breeding success, and why is the most rewarding strategy being followed by a decreasing proportion of the population? The clue lies in the analysis of individual decisions from year to year. Individuals achieving an API score of 4 or more (the presumed threshold for breeding) at last sighting on the Vesterålen are less likely to change their migratory strategy than their less fortunate flock mates reaching only scores of API 2 or 3 (Madsen 2001).

The second complication that has arisen is related to a change in the attitude of the local farming community on the Vesterålen towards their spring guests with pink feet. Commencing around the mid 1990s (from 1993 on) the local farmers began systematically to discourage geese from using their agricultural grasslands that had become the major staging habitat (Madsen 1998, Mad-

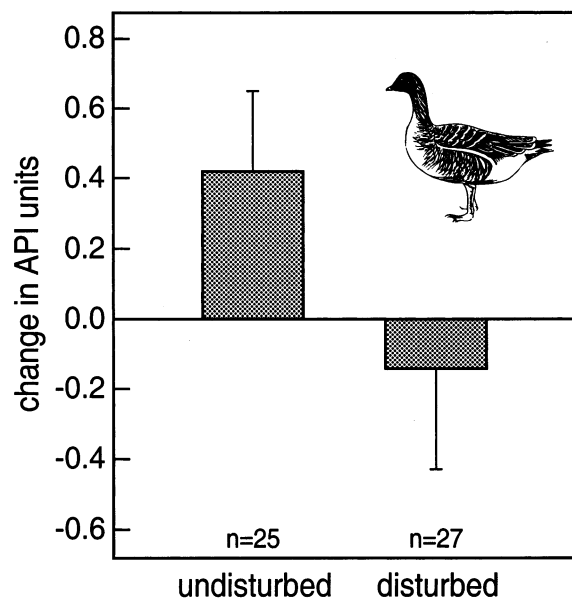


Fig. 13. Daily API increments in pink-footed geese in the Vesterålen in relation to disturbance.

sen et al. 1999). Observations on neck-collared birds confirmed that these forms of harassment effectively prevented the build-up of body condition, in sharp distinction to the high rates of fattening achieved by individual geese utilising pockets of suitable habitat undisturbed by man (Fig. 13). The changing trend of use of the Vesterålen as stopover site by pink-footed geese is illustrated in Fig. 14, where it is shown that a decreasing proportion of the population visited the islands (A, extending the sophisticated analysis of Frederiksen et al. (2001), who made this point by comparing 1996 with 1992), whereas those that did, stayed shorter (B) and failed to achieve as favourable an API index at final departure (C). Since over the years depicted (1991–2001) there is a steady decline in spring exploitation of the Vesterålen (as expressed in ‘goose-days’ for

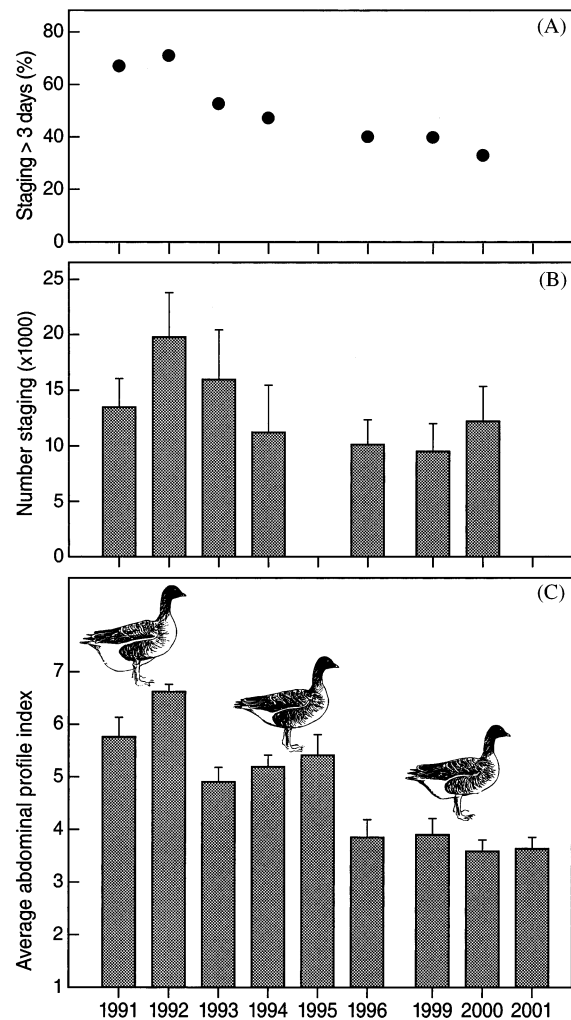


Fig. 14. Foreshortening of the Vesterålen stopover between 1991 and 2001 (A) with declining API (B), in relation to the total number of pink-footed geese passing through based on capture-recapture calculations (C).



Fig. 15. Landsat image of the eastern coast of Langøya, Vesterålen, northern Norway, 24 June 2001, showing agricultural fields (deep red) along the coastal fringe; for general location see Fig. 11, code V. Distance across image is 65 km.

example) and no evidence for a marked change in the total population of the Spitsbergen pink-footed geese, we cannot invoke some density-related process. Remarkably there has been no measurable trend of change in spring climate at this northern locality, so the human disturbance factor remains the most parsimonious explanation. Note that unfavourable experience in one season (with shortfall in the API index achieved) will

promote an individual shift in migratory strategy and hence quickly erode the Vesterålen tradition. The extreme patchiness of favourable goose foraging habitat in the archipelago, making the geese so vulnerable to disturbance, is illustrated in Fig. 15.

Table 1 collates the sightings of juveniles in the fall flocks, hinting that breeding success at the population level has indeed fallen off in the past few years. The

Table 1. Reproductive success in Spitsbergen pink-footed geese as measured by the percentages juveniles in the autumns of 1993–2001.

Year	Percentage juveniles	Total population size
1993	18.1	34,000
1994	12.4	33,000
1995	23.6	35,000
1996	18.4	33,000
1997		
1998	12.2	38,500
1999	12.0	37,000
2000	5.0	
2001	10.6	

Juvenile percentage is significantly higher in the years 1993–1996 compared to 1998–2001, Mann-Whitney U-test, $P < 0.02$

Norwegian authorities are aware of this problem, but a management programme ensuring undisturbed spring foraging of Spitsbergen pink-footed geese on the Vesterålen has yet to be implemented. This is not the only case of disrupted migratory routines in arctic goose populations, as we will note in the discussion under the heading ‘connectivity threatened’. A recent analysis of the resighting material on the pink-footed goose provides insights identifying the critical periods of the annual cycle marked by peaks in mortality (Madsen et al. 2002). The winter months represent a benign stage whereas the interval between last sightings on spring migration and return from the fall migration spans the period of major mortality in the annual cycle. Accepting the official bag statistics (there is an open season in fall both on Spitsbergen and in Norway–Denmark), it seems unlikely that hunting mortality is the problem. Mortality associated with migration or the interaction between migration and breeding is provisionally identified as the culprit (Madsen et al. 2002). Noteworthy in the context of the declining trend in body condition upon departure for the Arctic is the finding that adult mortality in the summer has increased markedly during the decade of study (1990–1999). For adult female pink-footed geese at the close of the 1990s, 13 out of 100 birds departing on spring migration will die before return (period 1 April–1 September) with 4 more deaths until 31 December (spanning the major hunting period), and only one further loss will occur up to the end of March in the next spring. Closing this observational gap to pinpoint where the added mortality occurs although logistically demanding obviously deserves high priority.

Discussion

Human disturbance at stopover sites: disrupting connectivity

Man as a provider or facilitator in today’s landscape

has another side, as emphasised in the project on pink-footed geese. The vulnerability of the geese to human disturbance, even in comparatively remote areas, may come as a surprise, but there is a growing body of evidence that waterfowl when in the migratory mode react drastically to human activities. Tracking of individuals has revealed how even apparently minor human disturbance can cause the birds to move on along the migratory pathway (Madsen and Fox 1997) and these observations warn against using simple before and after counts as a reliable index of vulnerability. Further evidence for the fragility of the spring staging phase comes from a massive experiment in North America. The recent implementation of a spring hunt to curb the population explosion of the snow goose in North America has resulted in a drastic downward spiral again underlining the vulnerability of prospective parents to disturbance during spring staging.

For the greater snows (*Chen (Anser) caerulescens atlanticus*), Mainguy et al. (2002) report on the repercussions of reinstating the spring ‘conservation’ hunt in Quebec in 1999 where the birds had enjoyed protection since 1917. The analysis hinges on the comparison of two non-hunting years with the first two years with spring hunting (1999 and 2000). A large sample of geese were caught on the breeding grounds (Bylot Island in Arctic Canada) and equipped with miniature radios mounted in the coded neck collars. Aerial search by aircraft facilitated locating these geese subsequently. In the non-hunting years, 85% of the geese identified on the spring staging areas on the St. Lawrence in Quebec ($n = 80$) were subsequently tracked on Bylot Island, where 56% actually nested. By contrast, only 28% of the geese radio-marked in the Arctic and using the St. Lawrence in the hunting years ($n = 80$) reached the nesting area on Bylot Island, and a mere 9% nested. This difference is not due simply to massive spring mortality as 66% of the ‘missing’ geese that had been located on the St. Lawrence but failed to reach the breeding area in the hunting years turned up again in the fall (in the non-hunting years 85% of the much smaller ‘missing’ contingent similarly were tracked in the fall). The authors conclude that the harassment associated with hunting interfered with accumulation of adequate energy stores, this shortfall disrupting normal migration and causing many geese to travel only as far as Baffin Island where they moulted without attempting breeding. A sample of female geese shot near the nest in the hunting years ($n = 34$) contained less abdominal fat than a sample from earlier years without the spring hunt ($n = 10$ from 1989 and 1990) and reconstruction of the clutch pointed to a decline in the hunting years. Egg laying in the colony as a whole was delayed one week in both hunting years compared to four ‘control’ years. Mainguy et al. (2002) reason that the disturbance accompanying the spring hunt affected body condition

of the birds surviving the hunt, and hence impinged on subsequent migratory performance and reproductive effort of laying geese.

The role of endogenous stores

That our general scheme is designed to elucidate events in a capital breeder (egg laying at the cost of endogenous reserves) raises the question how prevalent this pattern is. In his recent review, Klaassen (2002) points out that despite a wealth of observational studies direct evidence to ascertain the contribution of endogenous reserves to egg production is scarce. By application of the new techniques of stable isotope signatures Klaassen and his co-workers have confirmed the reality of considering the lesser snow goose from the Akamiski Island colony as a capital breeder (Klaassen 2002). The approach entails comparison of the isotope signature in natal down (produced from materials laid down in the egg) with that from juvenile feathers produced by the same individual geese later in the season (derived from nutrients ingested locally). The marked difference in these two samples indicates that the parent collected the nutrients put down in the egg from other than local sources, and must have acquired them during spring stopover further south. Isotopic signatures of the eggs and natal down from five species of waders collected in the Canadian arctic and n. e. Greenland resembled the signature from the juvenile feathers subsequently grown locally, but differed markedly from the signature from feathers of the parents that had moulted on the wintering grounds and/or en route to the breeding area. From these analyses, Klaassen et al. (2001) conclude that these waders (ranging in body mass with one order of magnitude, from 20 g to 250 g) must have followed the alternative strategy of paying as you go, typical for 'income' breeders. This does not mean that residual body stores that the parents bring with them to the breeding tundra are without significance for subsequent success, only that these endogenous nutrients cannot be traced in the eggs. As has been pointed out by Sandberg and Moore (1996) the contribution of the energy subsidy migrants bring with them deserves more quantitative study. Following this up, Smith and Moore (2003) obtained fat scores for the long-distance migrant American redstarts *Setophaga ruticilla* newly arrived in the breeding area (Michigan) and showed that females with more body fat at first capture have higher reproductive success (increased clutch size, egg volume and nestling mass). Tamisier et al. (1995) emphasise that the annual cycle in migratory ducks involves a chain of events interlocking the replenishment of nutrient stores following one migratory cycle with preparation for the next, and that we need to consider the role of endogenous stores on a year-round basis (McNamara et al. 1998).

Manipulating arrival date

So far we have built our story on correlations between spring schedules chosen by the birds themselves and subsequent events on the breeding grounds. Cristol (1995) hit upon the idea to delay the effective arrival of female red-winged blackbirds (*Agelaius phoeniceus*) to explore the repercussions of manipulating date independently of individual quality. Normally the females arrive on the breeding marshes quite early when the wetlands of the study area (Indiana) are still covered with ice and almost two months before nests are constructed. By baiting traps, Cristol captured newly arrived females and compared individuals released immediately (the controls) with those removed to an aviary and released at the capture site before the control females had commenced nest building. In this polygynous breeder, the late releases were subdominant to control females mated to the same male, and might suffer from less male helping behaviour later in the cycle. The delayed females ($n = 20$) nested on average more than one week later than controls ($n = 30$), a date effect expected from other work to reduce reproductive output (although this disadvantage of date was not established for the experiment on account of the small sample sizes). Cristol suggests that early arrival date confers a reproductive advantage via an enhancement of social dominance over late arriving birds, and when the early arrivals were removed from social contact they lost this prerogative. This appears a promising line to follow, and could conceivably be linked to experimental transport to bring individuals to the breeding areas early.

Individual quality differences: tactics for the underdog

The chain of correlations leading to the supposition that the intensity of red in the breeding plumage of the bar-tailed godwit is in fact a flag of individual quality is admittedly tenuous, but this interpretation is in line with work on other species where intensity differences in breeding plumage provide a similar scale. McGraw et al. (2001) have shown that male house finches (*Carpodacus mexicanus*) that paired with a female had redder plumage coloration, on average, than unpaired males, and among those males that paired, there was a significant relation between plumage redness and an early laying date of their partner (itself correlated with reproductive success). Laboratory experiments have shown that females prefer redder males when given a choice, and to cap this, the mean plumage redness was increased in the surviving male population following an epidemic of an avian disease. Hill (2000) calls attention to the energetic demand associated with achieving

maximal redness. The pattern in the bar-tailed godwits thus conforms to the model that an intensely red breeding plumage is a condition-dependent ornamental trait. We await with impatience the development of miniaturised satellite tracking devices allowing us to follow individual godwits from the Wadden Sea on to the breeding sites as has been done for brent (Green et al. 2002a).

The supposition that godwit males of low quality were aiming for early arrival at the breeding grounds, overcoming the disadvantage of their shabby plumage by staking out territory before their more gaudy competitors are on the scene and balancing this against the possible mortality costs, fits other work on individual quality. Forstmeier (2002) investigated arrival patterns in the long-distance migrant dusky warbler (*Phylloscopus fuscatus*) in the Russian far east. Some males defended fall territory the previous season and generally managed to pre-empt the best sites in the breeding season. In this group that try to compete for the best territories, the smallest males (body size by principal component scores) in fact arrived first, perhaps to compensate for presumably lower resource holding potential. Males that did not stake out a territory in the fall arrived still later, and ended up in the low quality territories for which there is little competition. Forstmeier thus concludes that competition between individual males drives arrival patterns. The idea that lower quality individuals arrive earlier but do so at the expense of a fitness cost is reminiscent of our finding that early nesting pied flycatcher hens have lower fitness than females nesting slightly later (Fig. 4). The role of body condition remains to be elucidated, since these measures were not obtained upon arrival, and we do not know if winter territories complicate the picture (Kelsey 1989, for this phenomenon in a long-distance migrant, the marsh warbler *Acrocephalus palustris*). In another study where events in one breeding season foreshadow those yet to come, Takaki et al. (2001) correlated growth bars on tail feathers with arrival and subsequent success in migrant male Styan's grasshopper warblers (*Locustella pleskei*) studied on breeding sites in Japan. Males with wider growth bars (indicative of good feeding conditions during the post-breeding moult the year before) arrived earlier and raised more fledglings, and enjoyed enhanced survival from one year to the next. Takaki et al. (2001) surmise that these individuals were able to maintain good body condition throughout the year, but whether female choice is date- or quality-driven is as yet unknown. Noteworthy is their finding that females laying either very early or very late suffered increased mortality. 'Be not the first nor yet the last' appears to be the motto, and underlines the narrow window of opportunity for successful breeding.

Optimal migratory scheduling: the way forward

Given the sophistication of the models marshalled by Kokko (1999) the empiricists must mount ambitious programs to achieve rigorous testing. We have emphasised two forms of connectivity that impinge on migratory routines. Geographic connectivity has been revealed by intensive work on individuals and implies that understanding of events at the breeding grounds is incomplete without information on prior wintering and stopover histories of the individuals concerned. At the least this demands keeping track of the individual migratory schedules, and to gain insight in the decision making implied one should ideally be able to ascertain body condition and how this changes enroute. Measuring fitness pay-offs associated with the migratory routines necessitates demographic studies that preferably enable partitioning mortality over the different phases of the annual cycle. This leads us to the temporal connectivity inherent between the life history events that form the units in the annual cycle. Thus selection for an earlier arrival on the breeding grounds entails a forward shift back down the chain at least as far as the wintering phase, and calls for adjustment of the temporal controls. At the level of mechanism this will involve phase adjustment of the endocrine system regulating the interlocking events that follow one another in an orderly sequence (Wingfield et al. 1999). Timing constraints may also involve seasonal changes in metabolism and organ size to balance maximisation of intake to accumulate body stores against the cost (in terms of energy and/or predation risk) of maintaining the machinery of the body in the acquisition mode (Piersma 2002). We hope to tie these threads together in the coming years.

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Appendix: Provisional spring energy budget for pink-footed goose

For converting fat mass at departure from northern Norway to breeding prospects on Spitsbergen we need to know:

1. Calibration abdominal profile index (API). Fat mass y (in g) is related to API by the formula $y = 5.36 \text{ API} + 1.31$ ($n = 27$ females, Fig. 10).
2. Flight cost – a sample of 34 birds whose abdominal profile index (API) was read before and after a migratory flight (Denmark to Trondheim/Vesterålen or Trondheim to Vesterålen) provide a mean estimate of 1.26 API units per 1000 km traversed. This converts to 6.758 MJ, or 171 g fat (taking the caloric equivalent of fat as 39.5 kJ/g) per 1000 km. The flight to Spitsbergen (1100 km from Vesterålen) would thus consume 180 g. Calculations with a modified version of the Pennycuik formula yield 145 g fat for 1000 km (P. Clausen, pers. comm.). Analysis of carcass fat in snow geese sampled before and after long flights provide roughly comparable estimates (77–104 g fat utilisation in female lesser snow geese for 1100 km Manitoba/Winisk, starting body mass 2400 g, Alisauskas 2002; 308 g fat utilisation in female greater snow geese for the 2900 km

journey from the St. Lawrence to the breeding site on Bylot Island, starting mass 2990 g, Gauthier et al. 1992).

3. Egg production – considering only the yolk, the depository of fat, this can be estimated as 50 g per egg with an energy value of 1009 kJ (egg mass of the pink-footed goose is 131 g, Owen 1980, and the yolk mass is related to egg mass by the formula given by Klaassen 2002 for waterfowl). If we calculate costs for a 4.5 clutch, and assume yolk fat is deposited at 75% efficiency, the female needs 4.875 MJ or the equivalent of 123 g fat.
4. Incubation cost – a female leaving Vesterålen at API 4 (and total body mass of 3000 g) would thus

commence incubation at approximately 2400 g, and the incubation midpoint mass is taken as 2200 g to derive and estimate of metabolic cost at the level of 1 BMR = 450 g fat if derived completely from body stores (BMR in waterfowl (Watts) = $0.039 M^{0.69}$ where M is in g). We assume that the female pink-footed geese could collect 1/3 of the requirement by feeding during recesses, hence the cost to the body stores equates to 300 g. According to this budget the total fat at departure (630 g) is expended as follows: 180 for flight, 123 for the eggs, and 300 for incubation, leaving a narrow margin at hatch providing the female remained in energy balance by local feeding during the pre-egg phase on Spitsbergen.