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## Travelling to breed

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**Abstract** Traditionally, investigation of the dynamics of avian migration has been heavily biased towards the autumn return trip to the wintering quarters. Since the migratory prelude to breeding has direct fitness consequences, the European Science Foundation recently redressed the balance and sponsored a workshop on spring travels. We here survey the findings elucidating the complications arising during migration directed towards the breeding quarters. The evidence that early nesting confers advantage is overwhelming, hence demands of reproduction pose a constraint on both time and energy resources during spring. Both during migration and upon arrival there must therefore be strong selection in favour of saving time. Experimental results (e.g. using supplementary feeding) show that the date of laying is generally proximately constrained by the inability of the female to find sufficient nutrients. A key question thus concerns the implementation of the ‘capital’ strategy for breeding, the female accumulating nutrient stores along the way to bridge periods of shortage upon arrival on the breeding grounds. Eight studies on waterfowl (geese and eiders) and shorebirds (turnstones and knots) nesting in the arctic combine tracking of individuals (satellite telemetry) with direct observation (marked birds) and reconstruction of the

origin of nutrients laid down in the eggs or in the form of body stores of the female parent (stable isotope signatures of tissues compared to potential food sources). The consensus emerges that in most cases a mixed strategy prevails, with nutrients garnered locally supplementing ‘imported’ body stores. The species concerned face a shortage of feeding time during incubation and suffer an energy deficit. Successful breeding thus depends on adequate fat depots that form part of the ‘capital’ the parents bring with them. Some headway has been made in predicting the extent of dependence on body stores for breeding in relation to body mass and length of migration from rates of fat deposition during stopover and fat consumption during flight for waterfowl. This work poses a challenge to refine field studies accordingly. The pressure to save time en route highlights the need to effectively exploit rich food resources. Several case studies underline the crucial significance of a very limited set of stopover sites, each with a narrow time window of optimal harvest. The influence of man at such sites often verges on the disastrous, and ongoing climate change may unhinge the finely tuned timing long-distance migrants depend on. There is a real need to extend this work to provide the scientific basis to underpin adequate conservation actions.

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### Introduction

The differences between spring and autumn migration regarding timing in relation to the annual cycle, rate of travel and routes followed have long been a source of fascination (Alerstam 2006). The question posed at the European Science Foundation conference we summarize here was the extent to which these differences can be understood as adaptations to optimize avian spring

travel in relation to breeding (bearing in mind constraints of date and energetics). The emphasis of the contributions was thus the elucidation of the ecology of spring migration, but we started with revisiting the fundamental concept advanced by Perrins (1970) that physiological constraints operating on the female might delimit the ability to adjust the laying date to environmental conditions (Drent 2006). Perrins reasoned from the survival data on progeny hatched at various times in a variety of species, both resident and migratory, that the earliest enjoyed the best prospects. More surprisingly, he also showed from his extensive studies on the great tit, *Parus major*, that the majority of the parent birds were in fact laying too late and thus missed the optimal timing. In fact, as confirmed by the tabulation of Rohwer (1992), in the vast majority of avian species late hatch lowers subsequent survival.

The major insight in Perrins (1970) concept was that he postulated that the female laid as soon as her nutritional state allowed. In other words, the laying date was set by 'proximate controls' each season, each individual female laying as soon as physiologically possible. As rephrased by Perrins (1996), 'the assumption must be that the females cannot find sufficient food for themselves to breed at the most opportune time'. This idea generated field experiments to test the prediction that individual females if provided with supplementary food would indeed lay earlier. As shown in Nager's (2006) overview covering 60 studies in 37 species, the majority of field tests indeed resulted in earlier laying by the fed birds; excluding colonial seabirds where feeding of individuals seems to be overruled by the synchrony of the colony as a whole, 21/32 species advanced laying in 35/52 studies. Nevertheless, in most cases the advancement in laying date was rather modest. We conclude that there is general support for the notion that birds are often prevented from laying earlier in the season by some nutritional bottleneck as postulated by Perrins. Given the limited scale of reaction measured in days of advancement there must be additional timing factors involved, and it is but a short step to implicate the endogenous circannual rhythmicity well documented for birds by Gwinner and coworkers (Gwinner and Helm 2003). This accounts for the mechanism but not for the selective pressure behind conservatism in laying date. The missing ingredient in the original formulations on breeding times concerns the fitness consequences of early laying for the laying female herself. A variety of ingenious experiments also reviewed by Nager (2006) make clear that there is a cost in laying early, as evidenced in increased parental mortality. A well documented case is shown in Fig. 1 for the kestrel, *Falco tinnunculus*, where survival prospects for parents and offspring in relation to date of laying do not coincide and the optimal laying date is a compromise where fitness for the combination is maximized.

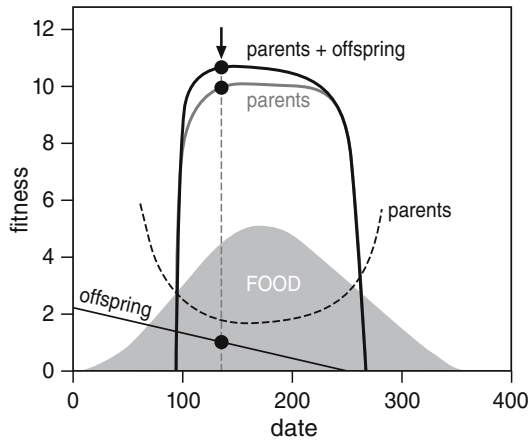
In many bird species, clutch size declines with date, and this requires explanation. Reynolds (1972) introduced the idea that there is a threshold value of 'body

condition' (in its simplest form, body mass) that triggers the date of laying, and that this threshold declines with season. For the mute swans, *Cygnus olor*, that Reynolds was dealing with, early in the season the minimal condition to trigger egg laying would thus be higher than at a later date, and these early females would go on to lay a large clutch. In resident species, the trajectory of 'personal body condition' of the female would be a reliable predictor of local environmental richness for the coming season, and 'decisions' on family size taken accordingly. Drent and Daan (1980) formalized these ideas and emphasized that long-distance migrants facing the trade-off between early breeding but high cost of the larger clutch against a later date at lower nutritional cost (see Bety et al. 2003) might well opt to bring nutrients for egg formation with them in the form of body stores. Females bringing the nutrients with them to the breeding grounds were described as 'capital breeders' as distinct from 'income breeders' procuring egg ingredients locally after arrival. This specific problem received a lot of attention at our conference.

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### Distinguishing between capital and income strategies

Several avenues allow identification of where the nutrients originate that are incorporated in the egg, or in the wider definition in the hypertrophy of the reproductive organs that precede this, and the costs of incubation that will follow. The most direct method is to determine exactly where the female birds are feeding in the days identified as embracing the period of rapid follicular development. In geese, for example, this process takes about 12 days (Ely and Raveling 1984) and the whereabouts of birds at this time was determined in several studies employing tracking methods plus visual observation of marked individuals at the nesting site. For the pink-footed goose, *Anser brachyrhynchus*, breeding on Svalbard and wintering in NW Europe, Glahder et al. (2006) showed convincingly from travel itineraries that manufacture of the eggs commenced at the spring stopover in arctic Norway. Madsen and his team (J. Madsen, M. Klaassen, in preparation) demonstrated in addition that the level of fat stores accumulated by the time individuals left this Norwegian stopover predicted not only the prospects of successful breeding but also survival until return in the autumn. For the barnacle goose, *Branta leucopsis*, breeding in Russia, Eichhorn et al. (2006) similarly determined that the majority of the individuals tracked commenced rapid follicular growth at various staging sites along the arctic coast before arriving at the nesting site only 1–4 days before laying the first egg. This population winters in coastal Germany and the Netherlands and migrates into the White Sea 18–20 days before arrival at the nesting colony. The majority of the individuals tracked proceeded from Wadden Sea staging sites directly without making more than very brief stops en route in the Baltic. Efforts aimed at estimating the rate of accumulation of nutrients along



**Fig. 1** Solution of optimal date of egg laying depending on the trade-off between the decline in fitness (prospects for later breeding) of offspring with advancing date against the cost in parental fitness for feeding the chicks (depending in turn on the yield curve for food availability in the environment). The optimal date is earlier than the food peak (from Daan and Tinbergen 1997, based on work with the kestrel, *Falco tinnunculus*, in the Netherlands and its food supply, the common vole)

the way include the use of a visual index of the rounding of the abdomen revealing fat stores (Madsen and Klaassen 2005). These studies indicate that the geese are moving in accordance with the phenology of their food plants (Van der Graaf et al. 2006; Klaassen et al. 2005;

**Fig. 2** Successive seasonal peaks in the food supply of the barnacle goose, *Branta leucopsis*, along its flyway between the Netherlands and arctic Russia as represented by gram nitrogen per square meter in the forage, with timing of usage shown. Drop lines indicate the average departure date in the Wadden Sea area and at the Baltic coast, respectively. Arrows indicate peak hatch date at the Baltic Sea and the Russian breeding grounds, respectively (Van der Graaf et al. 2006)

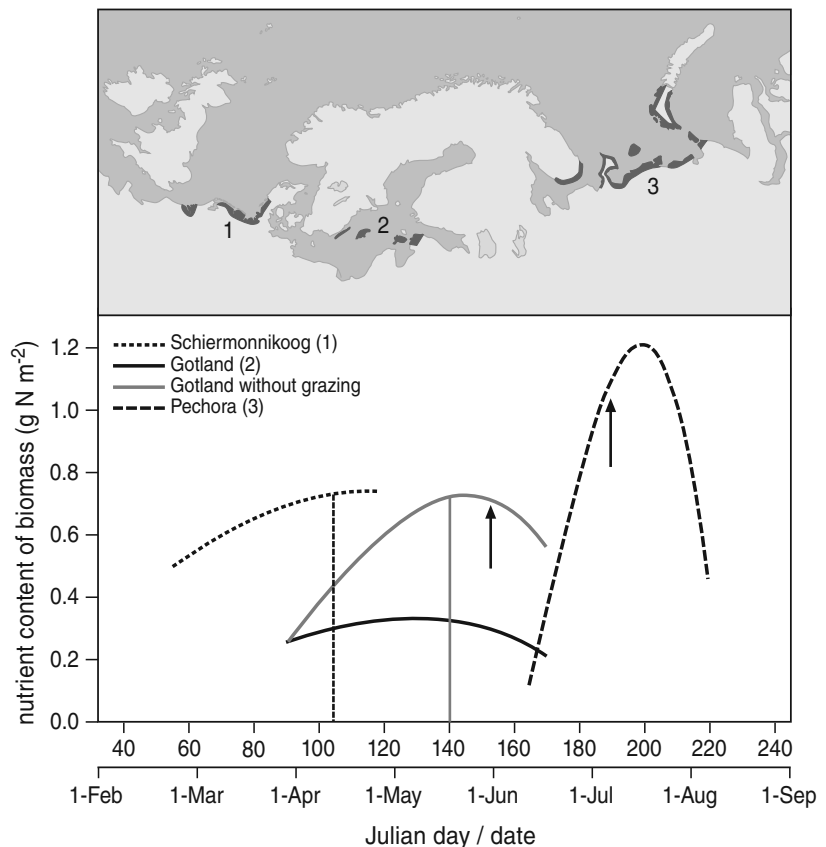
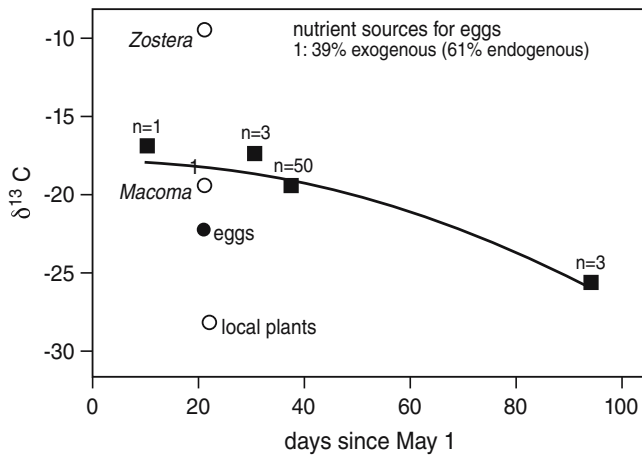


Fig. 2). Migratory timing is fine-tuned to enable a switch to a better site when the current site is beyond the local peak in potential spring harvest (Hübner 2006). Satellite tracking of eiders, *Somateria mollissima*, of the *borealis* subspecies wintering off west Greenland and Canada during the spring migration to the high arctic nesting areas revealed a movement pattern allowing extensive foraging en route, and at some sites females arrived only shortly before presumed dates of egg laying (Mosbech et al. 2006).

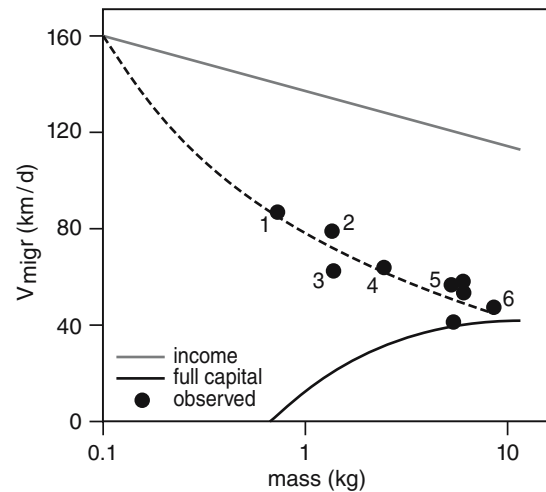
A second avenue to determine the origin of nutrients deposited in the eggs and required to subsidize the process of incubation relies on identification by means of the isotopic signature. Concentrations of stable isotopes (expressed as ratios  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$ ) in avian foods differ, and this 'isotopic signature' can be used to identify the origin of the nutrients incorporated in body tissues and reproductive products such as eggs (Hobson 1999, 2006). Gauthier et al. (2003) successfully employed this technique to show that greater snow geese, *Chen caerulescens atlanticus*, are not pure capital breeders but incorporate local foods in components of the egg. The long-distance migrants, emperor goose, *Anser canagicus*, and brent goose, *Branta bernicla*, studied by Schmutz and co-workers in Alaska (Schmutz et al. 2006) are especially suitable for this technique on account of the switch from marine foods (*Macoma* and *Zostera*, respectively) to terrestrial plants upon arrival at the breeding grounds. As displayed in Fig. 3, the isotope



**Fig. 3** Source of nutrients in breeding of the emperor goose, *Anser canagicus*, in Alaska revealed by stable isotope values (carbon 13) in eggs (filled dots) and blood plasma (squares) of nesting female geese in relation to food sources (open dots) at spring staging sites (bivalves, *Macoma*) contrasted to terrestrial plants from breeding area, plotted against date (from Schmutz et al. 2006). Note that a marine plant, *Zostera* (utilized by brent geese) also has a distinctive isotopic signature

values in eggs and blood plasma reveal a marine signature. Calculations on the exact proportions of 'endogenous' versus 'exogenous' sources are complex and depend on assumptions in an isotope mixing model, but Schmutz et al. (2006) conclude that emperor geese used nutrients garnered on spring staging areas to contribute at least half of the nutrients in eggs and fuel virtually all of their own maintenance during incubation. Preliminary analyses from other studies discussed at our meeting (M. Klaassen et al. 2006) indicate that this mixed strategy is most likely the dominant pattern in arctic geese. Differences within seasons in isotopic data for the blood of nesting shorebirds in the arctic (Morrison and Hobson 2004; Hobson 2006) suggest that early birds are using 'transported nutrients' hence a 'capital' input in achieving breeding condition, although this may not always be discernable in the eggs (Klaassen et al. 2001; Klaassen 2003).

Incubation is a period of near-starvation in geese and swans breeding in the far north, and energy requirements to cover both egg production and incubation can be cast in an allometric framework. Nolet (2006) has related these allometric predictions to the energy stores available at arrival on the breeding stations (correcting stores accumulated at the stopover sites by subtracting estimated travel costs). These considerations yield a prediction of the potential for capital breeding for swans, ducks and geese (Fig. 4). A further theoretical insight is that large birds have less leeway in the time they may devote to migration in their annual cycle (Hedenström 2006) underlining the reality of constraints operating in favour of capital breeding in these species. Farmer and Wiens (1999) documented the accumulation of fat stores in the course of spring migration in the pectoral sandpiper, *Calidris malanotos*, moving



**Fig. 4** Prediction of reliance on capital as contrasted to income sources for breeding in waterfowl in relation to body mass, resulting from the overall rate of spring migration achieved (km per day). Ducks of 100 g are predicted to be entirely income breeders, swans at 10 kg entirely capital breeders. The empirical data on travel rates (1 pintail, *Anas acuta*, 2, 3 brent goose, *Branta bernicla*, 4 greater white-fronted goose *Anser albifrons*, 5 tundra swan *Cygnus columbianus bewickii*, 6 whooper swan *Cygnus cygnus*) indicate a gradual shift of increasing dependence on 'imported nutrients' in heavier (and slower) birds (from Nolet 2006)

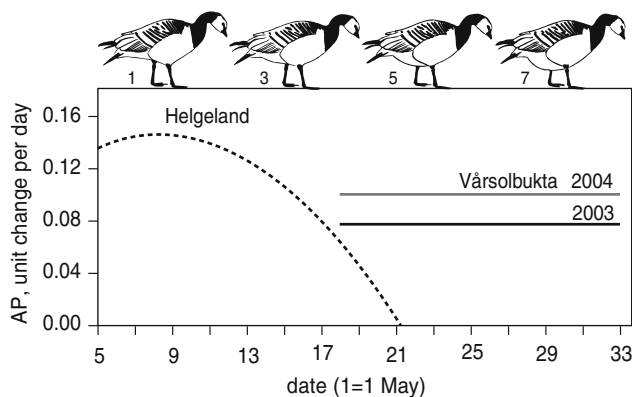
through Texas, Missouri and Nebraska en route to Alaska. They then estimated residual fat stores in females caught on the nest in Alaska during incubation and discovered that the fattest individuals had laid the largest eggs, resulting in the heaviest hatchlings with presumed enhanced survival prospects. Farmer and Wiens (1999) conclude that females aim 'to arrive on the breeding grounds as early as possible and with excess energy reserves' enabling them to lay and hatch out eggs of superior quality. This specific aspect of a capital breeding strategy deserves following up, especially now we are informed about the energetic costs facing the female during incubation. In keeping with the extremely high determinations of daily energy expenditure by means of doubly-labelled water in incubating shorebirds (nine species, see Piersma et al. 2003; Piersma and Morrison 1994), Cresswell et al. (2004) found that pectoral sandpipers during the incubation phase had a power output equivalent to 6 times basal metabolic rate ( $n=24$  female birds by DLW). Remarkably, Cresswell et al. reported that these high costs are chiefly associated with off-the-nest activities and not directly in energy needed to warm the eggs. In their view, body stores of the nesting female allow higher egg attendance and hence lower daily energetic costs. Just why foraging absences are so expensive remains to be elucidated (DLW readings for males at this time would be revealing although technically demanding). In any case, the incubation phase is energetically expensive in shorebirds (for the peak values known for birds so far, see Tinbergen and Williams 2002) underlining the adaptive value of fat stores at this time.



There is no substitute for direct observation of these potential capital breeders upon arrival in the arctic and several studies at this phase were facilitated by modern logistics. Visual assessment of the abdominal index (a reliable clue of fat stores in geese; Madsen and Klaassen 2005) by repeated observation of marked individuals confirmed that even in the first days after arrival at a staging site on the west coast of Svalbard barnacle geese were capable of adding to their stores (Hübner 2006). Confirming the assumptions from modelling the progression of spring migration (Klaassen et al. 2005; Bauer et al. 2006) the daily rate of accumulation of fat stores at the Svalbard site exceeded that measured at the last known stopover site used by the barnacle geese in the far north of Norway by that date (the rate at that site shows a decline with date; see Prop et al. 2003; Fig. 5). The larger pink-footed goose, *A. brachyrhynchus*, also accumulated fat stores on arrival in Svalbard, despite the lack of above ground primary productivity at that time (Fox et al. 2006). The reliance of this species on below ground over-wintering storage organs of specific plants and their availability with respect to inter-annual variability in patterns of substrate thaw confirms the delicate interplay between goose arrival dates, soil temperature and reproductive output in a given year and the susceptibility to perturbations through climate change.

### Migratory connectivity and conservation

Since the energetic and nutrient requirements for successful breeding come hard on the heels of the costs of migration, the critical role that spring stopover sites play in the annual cycle has become a focus of investigation (Webster et al. 2002; Drent et al. 2003; review Webster and Marra 2005). Morrison (2006) reported on a 30-year



**Fig. 5** Rate of accumulation of fat stores as revealed by daily increments of the abdominal profile index (*API*, a seven-step scale selectively displayed across the top of the figure) in individually marked barnacle geese, *Branta leucopsis*, observed at the last stopover in Norway (Helgeland) and upon arrival at the pre-nesting staging site in Svalbard (Vårsol Bukta) plotted against date. A longer stay in Norway would not be profitable (Prop et al. 2003; Hübner 2006, combined)

ringing and recapture study based on Iceland that serves as a springboard for red knots, *Calidris canutus*, en route to high arctic Canada from their wintering range in NW Europe. He showed that poor condition (low fat supplies) at capture during the spring stopover not only prejudiced breeding, but affected survival and paraphrased the function of Iceland to enable the birds to 'survive to breed'. Gunnarsson et al. (2005b) described the double buffer system operating on the black-tailed godwit, *Limosa limosa*, population breeding in Iceland that has experienced a remarkable expansion in recent decades. These birds winter over a wide arc of sites in coastal Europe, and the crux of the study is the ability to pinpoint marked individuals at this time and relate foraging conditions in these estuaries to prospects for successful breeding in Iceland. Individuals at sites providing high intake rates depart earlier and settle in prime breeding habitat in Iceland (Gill et al. 2001), and the supposition is that competition occurs at both ends of the migratory pathway, excluding less dominant individuals from the preferred habitat by the process originally described as the 'buffer effect' (Kluijver and Tinbergen 1953). At our conference, it was emphasized that long-distance migrants using a chain of stopovers in fact face 'multiple buffers'. Since these sites provide nutrients crucial for completing the journey and breeding afterwards, the well-being of the population may well rely on the integrity of multiple spring stopover sites. Support for this emphasis on the spring sites, even though they may be used for only a few days each season, as 'weak links' in the migratory chain was forthcoming from the ongoing studies on the deleterious impact of disturbance at spring stopovers in arctic-nesting geese (the Svalbard population of the pink-footed goose, Klaassen et al. 2005; Tombre et al. 2005; the population of greater snow geese nesting in the high arctic of Canada, Béchet et al. 2004; Reed et al. 2004). Effects of human disturbance (deliberate or otherwise) at restricted spring stopovers is having an impact at the population level and is a major complication in management aimed at setting defined limits on goose numbers (Calvert and Gauthier 2005). Evidence that the temporal and spatial pattern of grazing by geese at spring stopovers may have positive effects on their own food supply on the short-term (Fox et al. 1998; Van der Graaf et al. 2005, 2006) underlines the vulnerability of this 'fine-tuning' to external disturbance or other agents of change such as climate trends (Prop et al. 1998; Tøttrup et al. 2006, for an extensive overview see Møller et al. 2004).

A parallel case exists for long-distance migrating shorebirds. Van Gils et al. (2005a, b, 2006) have argued that, during the spring migration, the red knot, which at that time of year relies on crushing shellfish that are swallowed whole, makes special demands on the stopover sites. Despite the potentially phenotypic flexible response of the muscular gizzard to expand, and hence increase the volume of ingested shell matter that can be processed in a given time in order to compensate for

poor quality prey (cf. McWilliams and Karasov 2001; Karasov and McWilliams 2005; Piersma and Drent 2003), the red knot is in spring virtually restricted to sites with most profitable prey on offer (high flesh to shell ratios). This is because the overall rate of travel of a knot with a 'lean' gizzard saves a full week, which is presumed to confer advantage. The implication of this work is that, for the populations undertaking very long spring migrations (15,000 km), the red knot depends on a very restricted number of sites that provide high-quality forage at the critical time (often tied in with the life history of the prey). There is already evidence from at least one of these crucial spring stopovers (Delaware Bay, critical for the subspecies *rufa*) that declines in the key prey species on account of habitat loss and overexploitation by man has led to a decline in the red knot at a population level (Baker et al. 2004). These case histories depend on intensive studies of foraging ecology in situ, and R. Klaassen et al. (2006) sketched recent advances in the modelling of movement rules that elucidate patch use in migratory swans, incorporating social enhancement. Study of individual wintering strategies in great cormorants, *Phalacrocorax carbo sinensis*, breeding in Denmark, based on an intensive ring-reading campaign covering the entire reproductive lifespan (Bregnballe and Gregersen 2006), emphasized the repercussions for the males. Life time reproductive success of males wintering at an intermediate distance from the nesting colony (300–900 km) was lower than that of individuals wintering locally or further away (up to 2,500 km), but how individuals make these choices of wintering locale is unexplained. The origin of individual migratory routines in great skuas, *Stercorarius skua*, was reconstructed from tracking data, supplemented by sampling of stable isotopes from feathers formed in August–December but obtained from the marked birds upon their return to the breeding site (Furness et al. 2006). There is suggestive evidence that newly discovered wintering areas off West Africa are an opportunistic response to exploiting discards from the demersal fishing industry that has developed recently in this area. How these changes impinge on breeding performance is being actively investigated.

Evidence for how conditions on spring stopovers impact breeding in long-distance migrant passerines is so far based on correlative studies, but is convincing nonetheless and of eminent conservation importance (Hutto 2000). Szép and Møller (2005) made imaginative use of normalized difference vegetation index (NDVI) data for the African continent and related variations in this index over the period 1984–2001 to breeding parameters of the barn swallow, *Hirundo rustica*, in two intensively studied breeding populations in Europe (study sites in Denmark and Hungary). Ringing data in conjunction with sophisticated analyses of adult survival allowed identification of areas in Africa of presumed importance during spring migration for these two populations. For the Danish data, arrival dates and adult male survival showed tight correlations with the spring

NDVI values for Algeria (in 17 years). In a comparable study on another trans-Saharan migrant Both et al. (2006), drawing on data from 17 population studies on pied flycatchers, *Ficedula hypoleuca*, in Europe, demonstrated that populations with an early breeding date bred earlier in years with more vegetation in the northern African and Sahel regions. By contrast, late-breeding populations (high altitude, N and E Europe) were more sensitive to conditions en route within Europe. Breeding date thus depends partly on conditions encountered during travel. For a Swedish population of this species, Sandberg (in Moore et al. 2005) managed to capture and mark females upon arrival, and showed not only that early arrivers also laid early, but that these early layers arrived with more fat in the body ( $n=49$ ). The fattest birds also managed the highest hatching success. Ahola et al. (2004) offer a further Finnish perspective in this well-studied species. They found that pied flycatchers heading for breeding sites in SW Finland have speeded up their migration in recent years in response to rising spring temperatures along the migration route, but have not advanced the time of breeding because temperatures at the breeding site after arrival have not changed. This population has thus extended the interval between arrival and laying by almost 5 days in the past 30 years.

Table 1 lists documented cases of carry-over effects from wintering or spring stopovers impacting breeding in avian migrants, based both on individually marked birds as well as population sampling. This listing is doubtless incomplete, but stresses the ubiquity of the phenomenon.

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### Evolutionary roots

Although still the subject of a debate of at least two millennia standing (going back to Aristotle) the origin of avian migration in one view with many adherents (Rappole and Jones 2002) identifies the tropics as the original 'home' of the majority of long-distance migrants utilizing temperate breeding stations. If we accept this view, "travelling to breed" assumes a major role in building a scenario on how the migratory strategy arose, building on a universal template (Piersma et al. 2005). Arctic-breeding shorebirds offer scope for such speculations. Reconstructing 'palaeo-flyways' of the red knot, by combining the dating of population divergence based on molecular technology with what is known about the distribution of suitable habitat at the time, reverses common wisdom on how this system spanning the polar region today actually arose (Buehler et al. 2006). Divergence dates are recent (20 thousand years ago and less) and the evidence points to the migration linking the breeding stations of *C. c. islandica* in the high arctic of Canada to maritime W European wintering areas as a recent 'engineering feat' originating from an eastward expansion from the New World. This subspecies (the only representative electing to winter in temperate rather than tropical regions) represents a recent 'innovation'

**Table 1** Carry-over effects from wintering or spring stopovers impacting breeding in avian migrants

Species	Linkage	References
Little egret <i>Egretta garzetta</i>	Variable influx to Camargue breeding sites depending on drought in Spain	Hafner et al. (1994) and H. Hafner, personal communication
Purple heron <i>Ardea purpurea</i>	Fewer return to breed from W African wintering areas following drought	Den Held (1981), Cavé (1983)
White stork <i>Ciconia ciconia</i>	Breeding success in W Europe related to locust numbers in W Africa	Dallinga and Schoenmakers (1987)
White stork <i>Ciconia ciconia</i>	Breeding success in NW Germany related to Sahelian rainfall	Bairlein and Henneberg (2000)
White ibis <i>Eudocimus albus</i>	Dry winters followed by reduced breeding	Bildstein (1993)
Tundra swan <sup>a</sup> <i>Cygnus columbianus</i>	Early users of Baltic and White Sea stopovers gain body stores more rapidly and have higher breeding success (Pechora)	Nolet and Drent (1998), Rees and Bowler (1991), Beekman (2005)
Whooper swan <i>Cygnus cygnus</i>	Breeding more successful following mild winters	Nilsson (1979)
Pink-footed goose <sup>a</sup> <i>Anser brachyrhynchus</i>	Spring body mass and fat stores N Norway/breeding success Spitsbergen	Madsen and Klaassen ms
Barnacle goose <sup>a</sup> <i>Branta leucopsis</i>	Spring fat stores N Norway/breeding success Spitsbergen	Prop and Black (1998), Prop et al. (2003)
Brent goose <sup>a</sup> <i>Branta bernicla</i>	Spring mass Netherlands/breeding success Siberia	Ebbinge and Spaans (1995)
Greater snow goose <sup>a</sup> <i>Chen c. atlanticus</i>	Spring body fat Quebec/breeding propensity Bylot Id	Reed et al. (2004)
Lesser snow goose <i>Chen c. caerulescens</i>	Drought at spring stopovers/breeding propensity Hudson Bay	Davies and Cooke (1983)
Canvasback <i>Aythya valisineria</i>	Spring body condition predicts fall ad/immature ratios	Alisauskas (2002)
Lesser scaup <i>Aythya affinis</i>	Females nesting in Manitoba depend on fat stores accumulated at prior stopovers	Barzen and Serie (1990)
Spectacled eider <i>Somateria fischer</i>	Declines spring stopover nutrient reserves predict breeding failure	Anteau and Afion (2004)
Red knot <sup>a</sup> <i>Calidris c. canutus</i>	Females nesting in Alaska (Y-K delta) depend on body stores acquired at as yet undiscovered spring stopovers after leaving wintering sites in Bering Sea	Lovvorn et al. (2003)
Black-tailed godwit <sup>a</sup> <i>Limosa l. islandica</i>	Spring mass Iceland/breeding success Arctic Canada	Morrison (2006)
Barn swallow <i>Hirundo rustica</i>	Users of saline estuarine habitats during late winter NW Europe arrive Iceland earlier and occupy most productive breeding habitat	Gill et al. (2001), Gunnarsson et al. (2005a)
American redstart <i>Setophaga ruticilla</i>	NDVI African wintering areas/breeding in Italy ('green' winters/early arrival, higher fledging success)	Saino et al. (2004)
Pied flycatcher <i>Ficedula hypoleuca</i>	Users of mangroves and lowland forest in Caribbean depart earlier and lay earlier in Ontario with higher fledging success compared to arid scrub winterers	Marra and Holmes (2001), Norris et al. (2004)
	Spring temperature at North African staging sites identified from ringing affect arrival and breeding times in the Netherlands	Both et al. (2005)

<sup>a</sup>Studies relying on individually marked birds

and the molecular data rule out a close relationship to the *C. c. canutus* population with which it shares use of the Wadden Sea nowadays (*canutus* travelling on to winter on tropical African shores).

In a biogeographic analysis covering 30 arctic shorebird species from ten contrasting wintering communities in both hemispheres, Henningsson and Alerstam (2006) sought clues on the observed degree of differentiation in subspecies. They expected the number of subspecies per species to be associated with the diversity of overwintering regions occupied. In fact, both the size of breeding and winter ranges are correlated with this differentiation measure. Migratory distances along current flyways did not help to solve the conundrum, and further progress is likely to depend on further exploration of dating of divergence using the 'molecular clock'.

As most of the conference contributions dealt with species with synchronized pulsed annual breeding seasons, it was important to remember that "travelling to breed" for some bird populations is neither regular in time nor space. Newton (2006), in a wide-ranging overview, argued that irruptive movements foreshadow 'regular' migratory movements, and pointed out that, depending on the predictability of its food supply, the same species may behave as a resident or regular migrant in one part of its range, and as an 'irruptive migrant' in another. Roshier et al. (2006) used lightweight satellite transmitters to follow grey teal, *Anas gracilis*, in southern Australia. This species had been known as the ultimate nomad since the pioneering research of Frith (1967, revised 1982) who described the species to 'wander over the continent in an erratic manner' in what he termed 'explosive random dispersals'. The year-long tracking data by Roshier et al. documenting yearly travels of more than 2,000 km bear this out (the individual with the longest tracking duration travelled 2,037 km in 451 days), but do not solve the puzzle of how these super opportunists succeed in locating ephemeral waterbodies (often of restricted dimensions) after prolonged nocturnal flights over most unpromising terrain.

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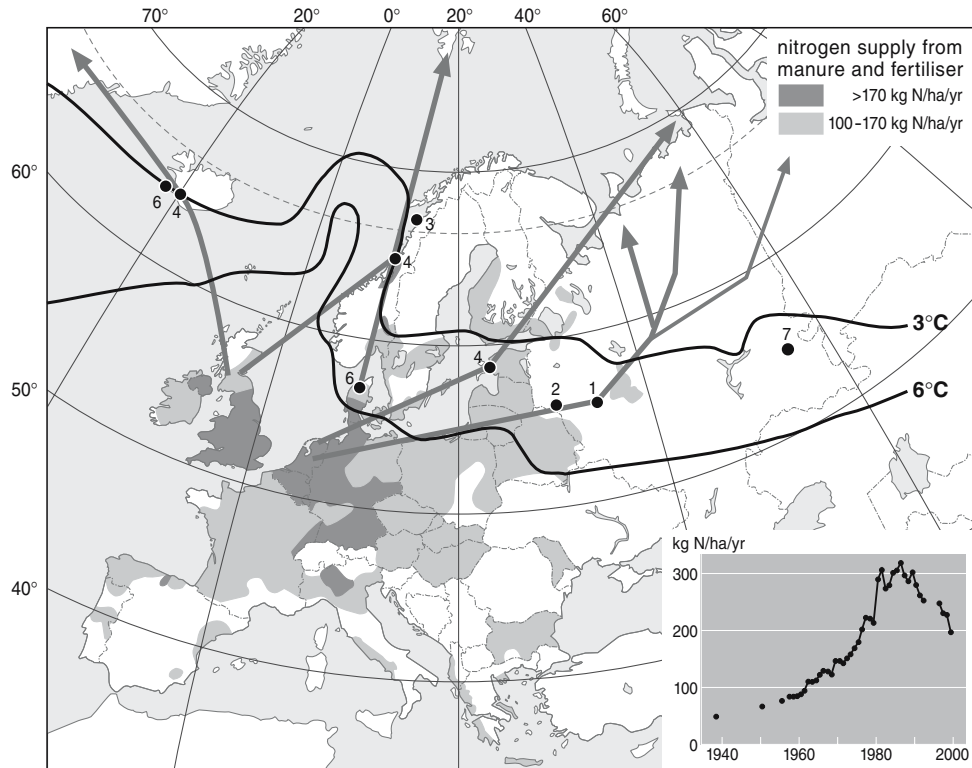
## Discussion

We accept the validity of the Perrins' hypothesis that, among birds, breeding times are proximately controlled by nutrient shortage constraining egg formation. This implies that the quantification of the energetic and nutrient requirements for breeding is a high priority to interpret repercussions for spring migration routines. This is only possible by combining relatively new sophisticated techniques which are only now enjoying wide applicability. Ideally, studies should cover both the synthesis of eggs and include the energy balance of the parent(s) during incubation. Impressive strides have been made employing stable isotopes to track the specific sources of energy and nutrients to their ultimate

investment (Hobson 1999, 2006). Knowledge of the diet and movements of the female before egg laying maximizes the information that can be gleaned from comparing the isotopic signature of potential foods with the egg constituents and parental body stores. Interpretation of how energy and nutrients are mobilized to allow hypertrophy of the gonads and oviduct is so far limited to captive studies (Williams and Vézina 2001), but enough is known to emphasize the high metabolic costs. Parental energetics during incubation can be assessed by using doubly-labelled water (Speakman 1997; Tinbergen and Williams 2002) requiring capture and recapture of the incubating parent(s). In waterfowl, the female is generally the sole incubator and she faces a period of near starvation since she has little time for feeding and fresh plant growth is usually sparse. If the sitting bird can be captured periodically, deuterium injections can be used to estimate the fat deposits in the body and how these decline through incubation (Speakman 2001). So far, this arsenal of techniques (see also Klaassen 1999) has not been brought to bear on a single study system, but we already know enough to reject simple dichotomies between 'capital' and 'income' breeding. The task ahead is to apportion the share of 'imported' nutrients as contrasted to those obtained locally. This is likely to vary between seasons, with the date within the season, and with the geographical area within the species range.

The time minimization strategy during spring migration to ensure early nesting with enhanced survival prospects of progeny and parents must therefore be combined with the ability to transport a buffer supply of body stores to the breeding grounds. This added requirement puts limits on the stopover sites used in spring. Not only is a strategic placement needed to minimize transport cost (Alerstam et al. 2003) but the forage on offer must allow rapid replenishment of the body stores (Scheiffarth et al. 2002; Nolet and Klaassen 2005). As studies on long-distance migrating shorebirds and waterfowl have shown, these spring 'hot spots' may in fact be quite restricted, putting the migratory system at risk when faced with global change. Although climate change justly claims attention as the timing of the availability of food resources along the route may be disrupted, the influence of man should not be ignored. Many geese and swans nesting in remote areas of the arctic are now entirely or largely dependent on man-dominated landscapes for their spring feeding (Fig. 6). Modern agriculture has transformed the original vegetation in the far north of Norway as well as the extreme northerly coastline of Iceland, areas traditionally vital as spring staging sites for migrating geese. The barnacle goose passing through both areas (Black et al. 1991; Percival and Percival 1997) is now largely dependent on agricultural land (improved grasslands). The Greenland white-fronted, greylag and pink-footed geese staging in Iceland en route to local and (in the case of white-fronted geese) Greenland nesting sites have all shifted their spring staging from natural and semi-natural habitats to increasingly intensively managed agricultural





**Fig. 6** Goose flyways in Europe connected to the High Arctic via spring staging sites (dots) used in late April–May (1 greater white-fronted goose, 2 tundra bean goose *Anser fabalis rossicus*, 3 pink-footed goose, 4 barnacle goose, 5 dark-bellied goose *Branta b. bernicla*, 6 light-bellied brent goose *B.b. hrota*, 7 red-breasted goose *B. ruficollis*). Most sites fall within the 3–6°C April isotherms defining the advent of graminoid growth (from Prop 2004). The continental flyways for barnacle and brent geese following the coast of the Baltic and White Sea as well as the inland route used by

populations 1 and 2 are depicted. Flyways to Svalbard (3,4,6) as well as Greenland (4,6) are also shown schematically. Note the large differences in amounts of nitrogen added to farmland in Europe (coding shown), the richest core area coinciding with the major wintering sites (Ireland England, low countries, NW Germany). The spring staging sites are generally located in enriched areas. The inset shows nitrogen applied to grasslands (kg per ha per year) in the Netherlands 1940–2000, note decline in recent years (adapted from Van Eerden et al. 2005)

landscapes (Fox et al. 2000, 2005). Here, as is the case elsewhere in the far north, the association with marginal agriculture courts conflict. Semi-natural habitats are abandoned for farmland as more intensive cultivation attracts foraging geese, concentrating wildlife conflict. Such conflicts between farmers and spring foraging pinkfeet in arctic Norway have only partially been resolved (Tombre et al. 2005), and as the economics of agriculture on its very outer reaches become less attractive, it seems that, without protection mechanisms, agriculture may be abandoned in such areas. On a wider continental scale, the reductions on fertilizer inputs currently underway are liable to have a profound effect on spring staging sites for many goose populations using the continental flyway in the western Palaearctic (Van Eerden et al. 2005) and will challenge the flexibility of the migratory systems to accommodate these sweeping changes (Sutherland 1998).

Now more than ever before, we see goose populations reliant on networks of agricultural production through which to accumulate body stores and travel to ultimate breeding sites to reproduce. Yet the nature and future of these northern agricultural systems have never been so uncertain in the face of cheaper food production in more

favourable climates. Amongst the shorebirds, there has never been such comprehensive coverage of protected reserves covering intertidal and wetland sites, yet rarely is any attempt made to create a cohesive network of sites along a flyway with the specific aim of ensuring the survival of a given population. Delingat et al. (2006) showed how long distance passerines such as the wheatear, *Oenanthe oenanthe*, are also time limited spring migrants, moving in short hops by night and feeding by day, dependent upon the existent of suitable refuelling habitats to maintain progress. As the workshop ably demonstrated, we are making great strides in our understanding of how different populations travel to breed and the factors that affect their vital rates along the way. Above all, work to date clearly underlines the need for detailed studies at the individual level if we are to understand how birds win the race to survive and breed. In the face of threats from human induced landscape and climate change, populations can no longer rely upon staging posts of sufficient quality and interval to support their annual migrations. It is ever more essential that conservation managers collaborate closely with biologists to shape political mechanisms to perpetuate networks of such staging posts and to ensure

that sound science underpins conservation actions for long distance migratory populations.

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## Zusammenfassung

Unterwegs ins Brutgebiet

Traditionellerweise richten sich Untersuchungen zur Dynamik des Vogelzuges stark auf den herbstlichen Rückzug in die Wintergebiete. Da das dem Brutgeschäft vorangehende Zugeschehen direkte Fitnesskonsequenzen hat, bemühte sich die ESF kürzlich um eine Wiederherstellung des Forschungsgleichgewichtes und finanzierte einen Workshop zum Frühjahrszug. Wir geben hier eine Übersicht der Schwierigkeiten, die sich während des Zuges in die Brutgebiete ergeben. Die Beweislast, dass frühes Brüten Vorteile birgt, ist überwältigend, und es ergeben sich aus den Anforderungen des bevorstehenden Brutgeschehens deutliche Beschränkungen für Zeit- und Energievorräte im Frühjahr. Sowohl während des Zuges als auch bei Ankunft ist daher ein starker Selektionsdruck hinsichtlich einer Zeitersparnis zu erwarten. Experimente (z.B. Zusatzfütterungen) zeigen, dass das Legedatum im allgemeinen unmittelbar durch das Unvermögen des Weibchens beschränkt wird, in ausreichendem Masse Nährstoffe zu finden. Eine Kernfrage richtet sich daher auf die Umsetzung der sog. Kapital-Brutstrategie, die besagt, dass das Weibchen schon während des Zuges Nährstoffreserven anlegt und dieses "Kapital" nach Ankunft im Brutgebiet zur Überbrückung von Mangelperioden einsetzt. Acht Studien zu Wasservögeln (Gänse und Eiderenten) und Watvögeln (Steinwälzer und Knutt), die in der Arktis brüten, verbinden Satellitentelemetrie mit direkten Beobachtungen von beringten Einzeltieren und rekonstruieren die Herkunft der Nährstoffe in Eiern oder in den Körperreserven der weiblichen Elterntiere (Signaturen stabiler Isotope aus Körpergewebe werden mit Signaturen potentieller Nahrung verglichen). Es besteht weitgehende Übereinstimmung, dass in den meisten Fällen eine sog. "gemischte" Strategie vorherrscht: das "importierte" Brutkapital wird durch bei Ankunft im Brutgebiet verfügbare Nahrung ergänzt. Die betroffenen Arten sehen sich mit einer starken Limitierung der Fresszeit während der Inkubationsperiode konfrontiert und leiden daher unter Energiedefiziten. Der Erfolg des Brütens hängt daher ganz entscheidend davon ab, ob adäquate Fettdepots als Brutkapital von den Eltern bereits ins Brutgebiet mitgebracht werden. Inzwischen ist es mit Einschränkungen möglich, die Abhängigkeit von mitgebrachten Körperreserven in Relation zum Körpergewicht und der Zuglänge für Wasservögel vorauszusagen, wenn man die Fettdepositionsraten in den Zwischenstoppgebieten und den Fettverbrauch während des Fluges kennt. Diese Arbeiten fordern geradezu die Verfeinerung unserer Freilandstudien heraus. Der Druck, während des Zuges Zeit zu sparen, weist auf die Notwendigkeit hin, reiche

Nahrungsreserven effizient zu nutzen. Einige Fallstudien unterstreichen die grundlegende Bedeutung, wenige Zwischenstoppgebiete während kurzer, genau definierter Zeitperioden zu nutzen, die eine optimale Nahrungsausbeute sichern. Der Einfluss des Menschen in solchen Zwischenstoppgebieten ist häufig desaströs, und Klimaänderungen können die präzise zeitliche Abstimmung des Langstreckenzuges empfindlich stören. Es gibt eine starke Notwendigkeit, diese Forschung auszubauen, um geeignete Schutzmassnahmen mit einer wissenschaftlichen Basis zu unterstützen und zu begründen.

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