

Fat stores and arrival on the breeding grounds: reproductive consequences for passerine migrants

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Migration is a period of exceptional energy demand (e.g. Berthold 1975, Blem 1980, Alerstam 1990). To meet this high demand, birds deposit substantial fat stores, which may reach 50% of total body mass among long-distance, intercontinental migrants (Blem 1980, 1990). The stores are depleted during migration, and birds are capable of replenishing fat stores at rates between 1–8% of their body mass per day (e.g. Dolnik and Blyumental 1967, Bairlein 1985, Biebach et al. 1986, Moore and Kerlinger 1987, Alerstam and Lindström 1990). If migrants are able to satisfy energetic demands and meet en route contingencies in a timely manner (cf. Alerstam and Lindström 1990), they may experience a successful migration. Whereas adequate fat stores are critical for surviving during migration, birds that arrive on their breeding grounds with fat stores may be better able to cope with energetic demands that arise during the onset of the breeding season and to 'offset' time constraints associated with the brief breeding season at, especially, high latitudes (e.g. Slagsvold 1976, Järvinen 1983, Ojanen 1984, Sandberg 1996).

It is well established that the pre-breeding nutritional condition of parents affects reproductive success (Drent and Daan 1980, Price et al. 1988, Rowe et al. 1994). Such an effect is most dramatic among some waterfowl that breed at high latitudes and rely almost exclusively on pre-stored fat stores to produce a complete clutch of eggs (reviewed by Alisauskas and Ankney 1992). Although it is unlikely that a small passerine would arrive at the breeding grounds with energy stores sufficient to produce a complete clutch of eggs (cf. Perrins 1970), experiments in which food has been supplemented prior to egg laying provide compelling evidence that parental condition is a determinant of clutch size and/or laying date in passerines (see reviews by Davies and Lundberg 1985, Arcese and Smith 1988, Daan et al. 1988). Hence, fat stores acquired during migration should improve

parental condition and influence reproductive success among passerine migrants.

Despite the intuitive appeal of the above argument, empirical support for it is lacking. King et al. (1963) speculated that substantial fat accumulation for spring migration in the white-crowned sparrow *Zonotrichia leucophrys gambelli* represents an adaptation for a faster migration and also for confronting inclement weather at the arrival on the breeding grounds. The arrival of female pied flycatchers *Ficedula hypoleuca* on the breeding grounds in northern Finland, with fat stores estimated at 14% of their body mass, prompted Ojanen (1984) to suggest that: "Arriving with plenty of reserves thus assists with energy requirements for competition over nest-holes and for a rapid onset of breeding activities". More recently, Sandberg (1996) reported that pied flycatchers, bluethroats *Luscinia svecica*, and willow warblers *Phylloscopus trochilus*, three intercontinental migrants, arrive on their breeding grounds in northern Sweden with substantial fat loads, depending on species and sex, individuals on average carried energy stores sufficient to allow non-stop flights for an extra 240 to 500 km, if they would have been inclined to continue migrating. Moreover, when females and males arrived on the breeding grounds simultaneously, females on average carried significantly more fat than did males.

Gudmundsson et al. (1991) hypothesized that "overloading" (i.e. to put on fat loads in excess of what is needed for the impending migration flight) at the last stopover site prior to arrival on the breeding grounds may confer an advantage during the breeding cycle. They predicted that it will be optimal to acquire extra energy stores at the penultimate stopover site as long as the fat deposition rate, devaluated by the concomitant flight costs, is greater than the expected rate of energy gain at the breeding destination.

In this paper, we advance four hypothesized benefits to passerine migrants who arrive on their breeding grounds with fat stores to spare, derive predictions based on the hypotheses, and finally, consider potential costs associated with carrying such energy stores to the breeding grounds. It should be recognized that the hypotheses we advance are not mutually exclusive.

Hypotheses and predictions

1. Breeding performance hypothesis: *Gamete production depends on pre-stored fat.* In preparation for the breeding season, birds' bodies change physiologically to initiate reproductive activities. Gonadal growth in both females and males contributes to breeding expenditures. While many passerines arrive on their breeding grounds with fully developed gonads, these birds do not carry sufficient fat stores to be able to meet the energy demands of migration and the start of egg production upon arrival on the breeding site at the same time. Production of eggs by the female requires a high expenditure of energy (Walsberg 1983). In passerines, 13–16% of the daily energy intake is transformed towards daily egg production (Perrins 1970, Ricklefs 1974). Although it is unlikely that a small songbird could accumulate energy stores sufficient to produce a complete clutch of eggs upon arrival to the breeding grounds (Perrins 1970), clutch size and timing of breeding, among other factors, are known to be constrained by parental condition (Drent and Daan 1980, Price et al. 1988, Rowe et al. 1994). Females in good condition (large fat reserves) typically produce both larger and earlier clutches (Lack 1968, Perrins 1970, Ankney and McInnes 1978, Pinowska 1979, Askenmo 1982, Winkler 1985, van Noordwijk and de Jong 1986). Since females invest relatively more into the production of gametes than do males, they should benefit more than males from the accumulation of fat stores prior to arrival on the breeding grounds if these stores are used to offset even a part of the energy expenditure of egg production. In fact, the amount of stored fat may well be decisive for the number of eggs/offspring that a female can produce (e.g. mediated by laying date, see Klomp 1970).

Prediction 1: Females that arrive at a certain date with surplus fat stores will produce larger clutches of eggs than will females that arrive at the same date but with depleted energy stores.

Prediction 2: Females that arrive with extra fat stores will begin breeding earlier than lean females. This prediction reflects a trade-off between the advantage of early breeding vs. the need to wait until the condition of the bird improves towards the level required for laying (cf. Perrins 1970, Rowe et al. 1994).

Prediction 3: Females that arrive on the breeding grounds with fat to spare, will lay larger and better quality eggs than will lean females (cf. Murphy 1986).

2. Time constraint hypothesis: *Individuals that arrive in the breeding area with surplus fat stores are better able to offset time constraints than those without such stores.* Fat stores permit the individual to devote more time to breeding activities, for example, song. To sing is an important factor in territory defence and for the attraction of females (e.g. Catchpole and Slater 1995). By singing, territorial males gain several advantages, including reduced risks of injury in fights. Rather than constantly chasing and fending off rivals, singing males are able to conserve valuable energy, which instead might be used to enhance reproductive success. Moreover, if females are selecting males by using song as an indicator of male and/or territory quality, then one cue may be the amount of singing that a male can produce (e.g. Payne and Payne 1977, Wasserman and Cigliano 1991). One way to increase output is to decrease inter-song intervals, but that entails a trade-off between foraging and singing activity (cf. Reid 1987). The more time spent feeding, the less time a male can afford to allocate to singing. One obvious consequence of this is that a male which arrives in better energetic condition, can afford to sing more. Pied flycatcher males that were provisioned with extra food sang at twice the rate as compared to controls, who spent more time searching for natural food and furthermore, provisioned males were paired with females before control males (see Gottlander 1987, Alatalo et al. 1990). Using the same argument, females carrying surplus energy stores will benefit during the mate-search and nest-building phases, since they are able to devote less time to foraging.

Prediction 1: Fat stores will be positively correlated with latitude. Migrants that breed at high latitudes have a shorter time available to perform both reproduction and moult before autumn migration begins (see Ojanen 1984, Sandberg 1996). Available evidence shows that northern bird populations start their breeding earlier with respect to vegetational phenology and air temperature than do more southerly populations (Slagsvold 1976, Järvinen 1983). This indicates that high latitude breeders are indeed more constrained than are their southern counterparts, being forced to commence breeding under relatively harsher environmental conditions (cf. Sandberg 1996). Hence, the shorter the time available for reproduction and moult is, the more valuable will fat stores at arrival be.

Prediction 2: Large fat stores at arrival will provide more time for breeding and moult by accelerating the start of reproduction (e.g. Davidson and Evans 1988). Individuals that arrive on the breeding grounds with fat

stores to spare will allocate more time to breeding activities such as territory establishment, mate attraction and nest building, and less time to foraging than a lean bird.

Prediction 3: The benefit of carrying surplus fat stores at arrival on the breeding grounds will be different for females and males, depending on sex-related differences in time budgets, reproductive costs and moult schedules. Because of sex-related differences, we expect that the most time constrained sex (mostly females, cf. above) will arrive with the largest fat stores.

3. Insurance hypothesis: *Fat stores will sustain the individual when environmental conditions upon arrival deteriorate.* Spring migration and arrival schedules have probably evolved to closely coincide with the average date when environmental conditions are favourable on the breeding grounds (cf. Hagan et al. 1991). Nevertheless, migrants sometimes find unfavourable conditions upon arrival, and fat stores accumulated during passage migration would suggest a mechanism to overcome the unpredictability in foraging conditions on the breeding grounds. Fat stores may also provide for retreat movements, awaiting improvement in environmental conditions in the breeding area, or alternatively, to enable a search for another breeding site.

Prediction 1: Individuals that arrive early will carry larger fat stores than those arriving later. The amount of fat stores will differ between females and males only if members of one sex arrive on the breeding grounds earlier than members of the other sex. This is because food supply is apt to be more scarce early in the breeding season (Perrins 1996).

Prediction 2: Birds breeding at high latitudes will carry larger fat stores at arrival than birds breeding at lower latitudes, because the degree of climatic variability is positively correlated with latitude in early spring (cf. Slagsvold 1982). Consequently, the risk of encountering harsh environmental conditions is greater at high latitudes.

Prediction 3: Intercontinental "calendar" migrants (endogenously controlled onset of migration; see review by Berthold 1975) will carry more fat at arrival than will shorter distance, so-called "weather" migrants because the latter category can more closely track environmental change (i.e., the advancement of spring and the concomitant increase in food supply; e.g. Hagan et al. 1991, Sandberg 1996).

Prediction 4: Species that can expect less predictable food resources on the breeding grounds will carry larger fat stores than birds with more reliable food resources (e.g. Rogers 1987, McNamara and Houston 1990, Sandberg 1996).

Prediction 5: Birds carrying fat stores will not benefit relative to lean individuals when environmental condi-

tions upon arrival are benign, if fat stores simply provide an insurance against the possibility of poor feeding conditions at arrival.

Prediction 6: Fat loads will gradually decrease through the season as environmental conditions become more predictably benign. If, however, fat stores are used to boost some specific aspect of breeding, such as territory establishment or egg-laying, then fat should be lost over a short period connected with that specific aspect.

4. Foraging shift hypothesis: *Fat stores 'buffer' the migrant's time budget in relation to the accumulation of limiting nutrients specific to breeding success.* During reproduction, the nutrient needs of laying birds include the nutrients required for maintenance of essential body components and those required for egg formation. The main components of avian eggs in addition to water are proteins, lipids and calcium (e.g. Walsberg 1983, Perrins 1996). Limited availability of any of these nutrients may inhibit egg production and/or compromise the health of the laying female (Graveland and Gijzen 1994). Hence, egg formation will depend not only on nutrient availability, but also on the time needed to identify and collect foods that meet these specific requirements (e.g. calcium, cf. Perrins 1996). The protein requirements for egg formation may be satisfied before the onset of egg production by depositing protein stores (see Davidson and Evans 1988, Alisauskas and Ankney 1992), directly from the diet during egg production (Ankney and Scott 1980), or possibly, after egg production by repletion of lost protein. Reliance on tissue stores is a less efficient way to offset the increased protein demand of egg synthesis than through the diet (Murphy 1994). Females that arrive with fat stores are able to devote more time towards the collection of protein or calcium-rich nutrients that are necessary for egg formation (e.g. Jones and Ward 1976, Fogden and Fogden 1979).

Prediction 1: Females will benefit more than males from having prestored energy since they have the responsibility for egg production.

Prediction 2: Females will shift their foraging to meet the specific nutrient needs entailed in egg formation.

Prediction 3: If females are constrained by finding specific food items necessary for egg production, there will be consequences tied to particular nutrients (e.g. calcium and egg-shell thinness, cf. Perrins 1996).

Fat stores upon arrival: possible costs

Although the benefits of stored fat are readily evident, the associated costs have received much less attention (e.g. Pond 1981, Witter and Cuthill 1993). However, the optimal fat load to carry should be viewed as a trade-

off between both benefits and costs of storage (see King 1972, Pond 1981, Gudmundsson et al. 1991).

1. Presumably the acquisition of fat stores beyond what is required to reach the next stopover site or the final destination ('overloading') may increase the vulnerability to predation during stopover (e.g. Lima 1986, McNamara and Houston 1990).
2. If time is devoted to the accumulation of extra fat stores, migrants may lose time and arrive (too) late in relation to the most opportune schedule at the breeding destination (e.g. high quality territories may already be occupied). Thus, time constraints associated with breeding biology will affect behavioural decisions of migrants during spring stopover. Intrasexual competition for breeding sites presumably confers a reproductive advantage to males that arrive on the breeding grounds as early as possible and may be a determinant of the differential timing of spring migration between the sexes (Francis and Cooke 1986).
3. Accumulation of excess fat stores will increase flight costs during passage migration. In addition, excessive fat probably impairs predator avoidance by reducing agility (e.g. Lima 1986, Norberg 1990, Hedenström 1992), and predator avoidance is essential not only during migration but also during the breeding period.
4. Although stored fat represents resources already 'on hand', conversions of incoming resources to a storable form and later used to provide energy for some activity, is a less efficient way to meet demands than directly through food metabolism (cf. Boggs 1992; see also Murphy 1994).
5. Older birds in migrant species tend to arrive on the breeding grounds earlier than younger birds (Francis and Cooke 1986). Young birds may pay the cost of inexperience in either of two ways: (1) yearlings arrive early enough to obtain breeding opportunities, but because of their inexperience in foraging and navigating en route towards the breeding area, they arrive with scant or no fat stores. Consequently, they have to delay the onset of breeding until their body condition improves. (2) Yearlings may arrive with adequate fat stores but later than adults, thereby jeopardizing their breeding attempt.

Conclusions

The annual cycle of birds is typically adapted to segregate the major demanding functions of moult, migration and reproduction (Helms 1968, King 1972). Separation of different functions during the annual cycle does not preclude the possibility that events occurring in one phase of the annual cycle influence survival and/or reproductive success in a subsequent phase. Migratory birds both gain benefits and suffer costs during the breeding season that, at least partly,

follow from behavioural acts in the previous migratory period. We would therefore like to emphasize the importance of studying bird migrants during the transition periods between the different phases of the annual cycle. Furthermore, to the extent that advantages accrue to individuals that arrive in the breeding area with surplus fat, we expect an increased selective pressure to find suitable (high quality) stopover sites and to make judicious decisions about when to leave a particular site, especially in relation to energetic gain and reproductive time schedules.

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