Costs of migration
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General Discussion
ENDURANCE FLIGHT AND MIGRATION IN THE LABORATORY

Avian flapping flight is in terms of energy turnover rate arguably the most expensive behaviour known. The associated costs may appear on the short-term or may become apparent on a longer term. In this thesis, I investigated short-term costs of flight, in terms of energy, including the impact of body mass on flight costs, behaviour (e.g. wing beat frequency) and physiology (e.g. heart rate), and the adaptations and changes during prolonged flights. On the long-term scale, I explored effects of high workload during migration on seasonal changes in several physiological parameters and on subsequent reproductive success.

Migration is a challenging and demanding task. Birds need to find the right way, overcome ecological barriers like mountains, seas, or deserts, and have to bring along sufficient energy resources. On their way, they have to find suitable stopover sites to refuel. But predation risk often is high at stopover grounds (Lind and Cresswell 2006). On their long hauls birds may encounter new diseases and parasites. Juveniles have a particularly difficult time to successfully complete their first migration. It has been shown, e.g. in Light-bellied Brent Geese (*Branta bernicla hrota*), Barnacle Geese (*Branta leucopsis*), and Greater Snow Geese (*Chen caerulescens atlantica*), that about 35% of juveniles do not survive their first migration (reviewed in Newton 2006). Sillett and Holmes (2002) recorded survival rates in Black-throated Blue Warblers (*Dendroica caerulescens*) in their wintering and breeding grounds. They calculated that more than 85% of the annual mortality among all age classes occurred during migration.

For studying avian flight in the context of long-distance migration it is important to use prolonged flights of at least 1 h duration, as these are behaviourally and physiologically distinct from brief flight events as often realised in wind tunnels studies. Short flights are associated with high energetic costs, as shown e.g. in Zebra Finches (*Taeniopygia guttata*) and European Starlings (*Sturnus vulgaris*, Nudds and Bryant 2000, Hambly et al. 2004b). Flight costs expressed as multiples of basal metabolic rate (BMR) for these species were as high as 28 x and 25 x BMR, respectively. Short flights involve mainly take-off, ascent and descent flight, which all are executed at low flight speeds. According to aerodynamic theories, low flight speed increases flight costs (Nudds and Bryant 2000). Flight costs were observed to be much higher in European Starlings flying in cages at low speeds of 3.5 m s\(^{-1}\) compared to birds flying in the field at 10 m s\(^{-1}\) (Westerterp and Drent 1985). During longer flights, higher metabolic rates were measured during the first 15-20 min in Laughing Gulls (*Larus atricilla*) flying for about 30 min in a wind tunnel (Tucker 1972). Another indication that
birds reach a more stable and presumably less costly "steady state" flight after some time is the fact that core temperature reaches a steady level in flying European Starlings only after about 15 minutes in flight (Torre-Bueno 1976).

During the early phase of flight and thus also during short flights, birds metabolise mainly carbohydrates as energy source (Rothe et al. 1987, Nachtigall 1990), while endurance flights are mainly powered by fat (Jenni and Jenni-Eiermann 1998, Jenni-Eiermann et al. 2002, Landys et al. 2005) and a small but essential fraction of protein (Bauchinger and Biebach 2001, 2005, Landys et al. 2005). This gradual switch in substrate occurs during the first two hours of flight as shown e.g. in Pigeons (Columba livia) or Red Knots (Calidris canutus, Rothe et al. 1987, Schwilch et al. 1996, Jenni-Eiermann et al. 2002).

To make flights in the wind tunnel as comparable as possible to endurance flights during migration, it is therefore desirable to not restrict experiments to short flights of several seconds or a few minutes but to measure flights of several hours duration. Clearly, if we wish to study the consequences of real long-distance flight as during natural migration covering thousands of kilometres, such performance has to be imitated by many days or weeks of controlled wind tunnel flights.

In chapter 5, we investigated the effects of migratory workload on seasonal changes in a variety of physiological parameters and on subsequent reproductive performance. We manipulated flight activity without affecting food supply. This design allowed us to investigate the effect of flight activity on the birds' condition and fitness, but it does not quite simulate migration as under natural conditions. In the field, birds probably migrate for longer periods of time per day, while they "interrupt" migration for refuelling. Thus, periods of high workload associated with limited food supply may alternate with periods of lower workload and more favourable food conditions at the stopover sites. Although we have not precisely mimicked the temporal pattern of long-haul migration, the study presented in chapter 5 comes closer than any other wind tunnel study to simulate at least the full distance of 4700 km covered by Rose Coloured Starlings (Sturnus roseus) in natural migration.
FLYING FOR HOURS: SHORT-TERM EFFECTS

Energetic costs of flight

We showed in chapter 2 and 3 that flight costs and body mass are positively correlated within both Barn Swallows (*Hirundo rustica*) and Rose Coloured Starlings. It has now been revealed in three species flying for several hours with spontaneous changes in body mass, that flight cost increase with body mass to a lesser extent than previously thought. The scaling exponents measured in these intraspecific studies are 0.35 (Red Knot, Kvist et al. 2001), 0.58 (Barn Swallow, chapter 2), and 0.55 and 0.54 (Rose Coloured Starling, Engel et al. 2006 and chapter 3, respectively). These scaling exponents observed are lower than expected from aerodynamic theory or interspecific comparisons. Aerodynamic measurements and predictions result in scaling exponents ranging from 1.05 (Norberg 1990) to 1.59 (Rayner 1990; see chapter 2), while interspecific comparisons of direct measurements of energy expenditure during flight yield exponents ranging from 0.67 (Videler 2005) to 1.93 (Rayner 1990; see chapter 2). Among the three intraspecific studies, the slope of the scaling is lower within each species than across the three species (Figure 6.1 A). As Videler (2005) has emphasized, different species are not scale models of each other. Kvist et al (2001) have proposed that the reduced within-species slope in Red Knots is due to a seasonal increase in muscle efficiency along with the mass increase. Such a hypothesis would seem to predict that artificial loads would generate a steeper increase in costs than spontaneous weight changes. We have investigated this in chapter 3. Rose Coloured Starlings data turned out to follow the same regression of flight costs on to total mass regardless of whether the mass changes were spontaneous fuel stores or artificial loads. It made no difference, whether birds were already used to carrying an artificial load during nine days before the experimental flight or if the load was applied immediately before the flight. The birds thus neither needed time nor internal cues to “adjust” to the increased load. Our findings imply that carrying fuel loads is indeed cheaper than expected on the basis of prevalent aerodynamic theory. The findings are consistent with both of the previous wind tunnel studies on the effects of body mass on flight costs (Kvist et al. 2001, Engel et al. 2006).

Even if at a less steep slope, flight costs still increase with increasing mass, and birds still face trade-offs regarding the optimal fuel load. For this purpose the mass-specific flight costs, *i.e.* the flight costs per gram bird (W g⁻¹), may yield a proper measure. Mass-specific flight costs scale negatively with body mass even within a species (Figure 6.1 B), strengthening the observation that birds can transport an increased body mass in an economical way.
Figure 6.1

Flight costs in relation to body mass in three intraspecific studies. (A) Flight costs $e_f$ [W] and (B) mass-specific flight costs [W g$^{-1}$]. Solid lines refer to Barn Swallows (chapter 2), short dashed lines to Rose Coloured Starlings (chapter 3), and medium dashed lines to Red Knots (Kvist et al. 2001). The stippled regressions indicate the interspecific scaling as calculated from the three studies (A: $\log(e_f) = 0.12 + 0.98 \log(m)$, $R^2=0.99$; B: $\log($mass-specific $e_f)=0.14-0.06\log(m)$, $R^2=0.40$).
Wing beat frequency

Bird flight is a highly complex and greatly variable mode of locomotion. Modifiable parameters include wing beat frequency itself, but also mode, amount, and duration of gliding phases (such as undulating or bounding flight, with wings stretched out or flexed, respectively), stroke amplitude, wing area during up- and/or downstroke, or even arrangement of the primaries or the alula (Videler 2005). We analysed effective wing beat frequency (WBF) during flight, i.e. including periods of undulating or bounding flight, and observed that it increased with increasing body mass in Barn Swallows (chapter 2). In Rose Coloured Starlings, we detected a similar relationship in one study (chapter 3). Another experiment had too small a sample size to confirm this association (chapter 4). The observed scaling of WBF with body mass with an exponent of 0.38 corresponded well with the exponent of 0.5 in aerodynamic predictions (chapter 2; Pennycuick 1996). WBF did not change during flights of 6 h (Table 6.1; chapter 2 and 4, Engel et al. 2006), neither in Barn Swallows nor in Rose Coloured Starlings. It was not coupled to changes in body mass or the linear decrease in heart rate during these endurance flights (chapter 4).

Effects on energetics, physiology, and flight behaviour

The doubly labelled water (DLW) method is indispensable in yielding direct assessments of the energetic cost of flight. Yet, the method yields an average value integrated over the entire measurement period. To obtain insight into short-term changes during 6 h-flight bouts, we applied heart rate measurements. Heart rate appeared to be correlated with energy expenditure during flight (chapter 4). It reflected the positive relationship of body mass and flight costs as measured with the DLW method. The time resolution of the heart rate method allowed us to follow its development during the course of a flight. We observed a continuous decrease in heart rate over the flight time. This may be interpreted in two ways. The decrease may point (1) to a steady increase in flight efficiency or in oxygen pulse or (2) to the combustion of fuel causing a decrease of body mass resulting in a reduction of flight costs. On the basis of an association with the body mass drop during endurance flight (see Table 6.1) we used the decrease in heart rate to estimate the possible reduction of flight costs and carefully discussed the potential of the heart rate method to assess energetic costs on a short-term scale (see chapter 4).
In chapter 3, we presented data on the changes in breast muscle index observed during prolonged flights. Like body mass, the size of the breast muscle significantly decreased during such long flights (Table 6.1). Also total body water (TWB) decreased during endurance flight (Table 6.1 and chapter 3). Water efflux exceeded water influx as the birds' only water source was metabolic water. In contrast to the significant decrease in body mass, in breast muscle index, and in heart rate during endurance flights, wing beat frequency (WBF) did not change significantly over the time course of a flight (Table 6.1). WBF did not trace changes in body mass during those endurance flights, in spite of the fact that it is predicted to scale allometrically with body mass (e.g. Pennycuick 1996). WBF is not a fixed trait, but wing movements during flight can be modified in many ways. Among such modifications are the kind, frequency, and duration of gliding (such as undulating and bounding flight), amplitude of the wingbeat, and the effective wing area, i.e. the extent to which the wings are stretched out during the up- and downstroke. Since \( f_H \) systematically decreased during flights but WBF did not change demonstrates that these two parameters are not fixed with respect to each other.

Table 6.1
Effects of endurance flights of 6h on various parameters in Rose Coloured Starlings. Average values ± SD are presented.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>start / before flight</th>
<th>end / after flight</th>
<th>p</th>
<th>N</th>
<th>source</th>
</tr>
</thead>
<tbody>
<tr>
<td>body mass [g]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) 80.6 ± 9.9</td>
<td>75.0 ± 9.4</td>
<td>&lt;0.001</td>
<td>59</td>
<td></td>
<td>Chapter 3</td>
</tr>
<tr>
<td>(b) 85.6 ± 7.8</td>
<td>79.0 ± 7.2</td>
<td>&lt;0.001</td>
<td>15</td>
<td></td>
<td>Chapter 4</td>
</tr>
<tr>
<td>breast muscle index [mm]</td>
<td>5.34 ± 0.57</td>
<td>4.85 ± 0.60</td>
<td>&lt;0.001</td>
<td>35</td>
<td>Chapter 3</td>
</tr>
<tr>
<td>TBW [g]</td>
<td>45.1 ± 3.5</td>
<td>43.2 ± 3.4</td>
<td>&lt;0.001</td>
<td>59</td>
<td>Chapter 3</td>
</tr>
<tr>
<td>( f_H ) [Hz]</td>
<td>770.8 ± 20.7</td>
<td>710.4 ± 19.5</td>
<td>&lt;0.001</td>
<td>15</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>WBF [Hz]</td>
<td>8.9 ± 0.6</td>
<td>9.1 ± 0.5</td>
<td>n.s.</td>
<td>8</td>
<td>Chapter 4</td>
</tr>
<tr>
<td>main substrate</td>
<td>carbohydrate</td>
<td>lipids</td>
<td></td>
<td></td>
<td>Jenni-Eiermann et al. 2002</td>
</tr>
<tr>
<td>estimated flight costs [W]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>based on DLW</td>
<td>9.19</td>
<td>8.80</td>
<td>4</td>
<td></td>
<td>equation 3.3, chapter 3</td>
</tr>
<tr>
<td>based on ( f_H )</td>
<td>9.45</td>
<td>8.30</td>
<td>12</td>
<td></td>
<td>equation 4.3, chapter 4</td>
</tr>
</tbody>
</table>

\( a \) for the average body mass before and after experimental flights as measured in chapter 4 (see "body mass b")
FLYING FOR WEEKS: LONG-TERM EFFECTS AND CONSEQUENCES

Changes in body mass, physiology, and flight behaviour

During long migration hauls, birds do not only use fat stores, but they also combust protein from tissues like the breast muscle or leg muscle (Bauchinger and Biebach 1998, Gannes 2001, Schwilch et al. 2002). It has been shown that during migration birds may experience a reduction in almost all tissues, except for lungs and brain (Biebach 1998, Battley et al. 2000, Lindström et al. 2000, Battley et al. 2001, Biebach and Bauchinger 2003). A reduction of the gastrointestinal tract may serve as a strategy to save maintenance costs (e.g. in Garden Warblers (Sylvia borin), Biebach and Bauchinger 2003). Yet, a reduced gastrointestinal tract may be disadvantageous when a bird arrives at a stopover site. It would first have to rebuild the digestive tract before acquiring complete functionality and optimising fuelling rates and food utilisation. McWilliams and Karasov (2005) have suggested that the need to first rebuild the digestive system and activate digestive enzymes may influence the pace of migration.

Body mass and flight muscle may be reduced not only during migratory but also during shorter flights. In European Starlings, which performed take-off flights for 1 h per day, pectoral muscle was reduced parallel to body mass (Swaddle and Biewener 2000). The decrease in body mass and flight muscle in that study could not be explained by nutritional needs, as birds were fed ad libitum and had enough time to feed. The results of decreasing pectoral muscles in flying birds contradict the muscle use-disuse hypertrophy-atrophy hypothesis, which expects bigger flight muscles in birds using them (Swaddle and Biewener 2000). The authors suggested that body mass was reduced to save energetic costs during flight. We investigated the effect of daily workload on body mass, breast muscle size, and fat score (chapter 5). While we could not detect an effect on relative breast muscle size, body mass and fat scores were lower in birds flying every day for 3 h in the wind tunnel than in control birds. This workload effect was superimposed on profound endogenous seasonal changes. Body mass, fat score, and breast muscle size increased during the "migration" period. Birds of the experimental group underwent these seasonal changes on a lower level in body mass and fat score, but reached the same levels as control birds soon after the end of the experiment. These data support the idea that birds may not gain as much fuel resources as possible but "adjust" body mass to confine energetic flight costs.
Energy and time

It might be important for birds to either minimise time or energy expenditure during migration (Alerstam and Lindström 1990, Hedenström and Alerstam 1997, Weber et al. 1998, Weber et al. 1999). Birds may choose lower energy expenditure during migration if time is not important, while minimising overall duration of migration if early arrival like at the breeding ground is important. It has been observed, e.g. in Barn Swallows, that spring migration is faster than autumn migration (Suter 1985). The overall duration of migration depends on speed during migratory flights and on stopover duration. The ground speed of migratory flights is determined by flight velocity, but also by wind conditions. Birds can drastically increase ground speed by choosing tailwinds (Richardson 1990b, Green 2004). How much time birds spend at a stopover site is determined by food availability, fuel deposition rate, and departure fuel load. Competition at the stopover site and predation risk can further influence feeding rates and thus the length of a stay (Metcalfe and Furness 1984, Moore and Yong 1991, Fransson and Weber 1997). Birds may have to trade-off fuel deposition and avoiding predation (Weber et al. 1998). Optimal departure fuel load may be high if overall duration of migration is to be minimised while it may be lower if energetic costs are to be minimised (Hedenström and Alerstam 1997). High fuel loads are advantageous if birds have to overcome big distances. At the same time, predation risk (Bednekoff and Houston 1994), basal metabolic costs and cost of transport increase with increasing fuel load (Klaassen and Lindström 1996). Furthermore, the profit (in terms of coverable distance) per unit fuel deposited decreases with increasing fuel load due to higher flight costs (Lindström and Alerstam 1992). Lindström and Alerstam (1992) found that birds left stopover sites at lower fuel loads than predicted. We showed in two migratory species flying for several hours in the wind tunnel, that flight costs increased to a lesser extent than previously thought (chapter 2, 3 and 4). We propose that even smaller fuel stores than expected may be sufficient to cover respective flight ranges during migration.
The impact of "migration" on later annual phases

In preparation for reproduction, birds might allocate energy to (1) flight, (2) maintenance of tissues and development of gonads, or (3) a combination of both. The high workload during migration itself, however, had only little effect on the bird's condition, as we have seen in chapter 5. Parameters like body mass, fat score, breast muscle thickness, circulating testosterone, and colouration of bill and plumage changed during the "migration" period at virtually the same rates in "migrating" as in "non-migrating" starlings. Endogenous programs, probably triggered by changes in photoperiod, perhaps also to some extent based on endogenous circannual cycles, caused these changes. We also observed non-significantly higher plasma testosterone levels towards the end of the "migration" period in flying compared to control birds. Would the high workload during migration itself stimulate hormone production? This does not seem to be known so far. Earlier findings of a correlation of testosterone levels and activity have rather been interpreted reversely, as a stimulating effect of the hormone on behaviour (European Starling, Gwinner 1975; Canary Serinus canaria, Pohl 1994).

In bird studies during non-breeding, workload has been manipulated by rewarding for locomotion, i.e. simultaneously with food supply (Zebra Finches, Deerenberg et al. 1998, Deerenberg and Overkamp 1999, Wiersma and Verhulst 2005; European Starling, Wiersma et al. 2005). Without access to a wind tunnel or treadmill (applied in studies on energy expenditure in geese and penguins, e.g. Froget et al. 2001, Green et al. 2001, Ward et al. 2002) it is not possible to disentangle the effects of increased workload and of the manipulated food supply.

The study on the effects of migration on subsequent breeding in this thesis (chapter 5) demonstrated a total lack of interference of this large and prolonged increase of energy expenditure (DEE increased by 55% above sedentary levels maintained for 49 days) with annual changes in reproductive status. Physiological preparation for breeding and also the success of breeding after the long "migration" period showed no impact whatsoever of the sustained endurance flight. This attests in a remarkable way to the strength of the endogenous program preparing birds for the important phase of reproduction in the proper season. It is possible that the study does not precisely reflect the natural situation with regard to timing and food supply. For the "migrating" group of Rose Coloured Starlings, the total effort must have been closest to natural. The sedentary control group obviously has no natural counterpart, since all Rose Coloured Starlings perform this migration in the field as far as we know. It is thus...
these controls that are in a sense the experimental group. Viewed from that angle, one should perhaps conclude that suppressing the workload of long-haul migration does not in any sense modify the annual cycle of reproduction. This is apparently programmed for optimal timing and no force of natural selection elicits different timing in a bird prevented to migrate.

Eventually such studies in the lab should be augmented by research under field conditions. Assessing the effects of different migration distances or speeds within a species or on a population level is a big challenge. We know only little about the flexibility of migratory strategies within individuals. To fully understand the impact of migration and the tradeoffs between energetic costs of flight and wintering at the breeding grounds with high thermoregulatory costs and low food supply, one needs to study populations with polymorphisms in migration. In the absence of such field studies, the work in the wind tunnel has proved to be a highly valuable tools not only to study the aerodynamics and physiology of flight, but also to simulate true long-haul migration over thousands of kilometres.