Centuries ago, people observed that birds disappeared from their breeding grounds in autumn. But where would they go? Aristotle assumed that redstarts transformed into robins during winter and back into redstarts in summer. Swallows, which roost in huge flocks in the reeds in autumn, were thought to hibernate in the mud at the bottom of ponds. Even Carl von Linné had been committed to that theory (Nachtigall 1987). Migration of small passerines as an explanation seems to have been unthinkable not only in the antiquities but until the 18th century. Even today, as we know that birds do not hibernate or metamorphose but migrate, such migratory flights of over hundreds and thousands of kilometres still are a fascinating phenomenon.

Migrants have to face diverse challenges: they have to follow the right route, find favourable conditions during migration such as tailwinds, and well-time migration with regard to other phases of a circannual life. Furthermore, as avian flight is associated with high energetic costs, birds have to provide sufficient fuel resources to overcome long distances and cope with ecological barriers. Hence, most migrants increase their body mass in preparation for migratory flights, which is associated with changes in the size and physiology of most organs and tissues. During migration, birds are challenged by the costs of high energy turnover during endurance flight. In addition, effects of such high energetic costs may carry-over into subsequent life-history stages such as reproduction. In my thesis, I investigated both short- and long-term consequences of endurance flights. Those endurance flights were performed under standardised conditions in the wind tunnel of the Max Planck Institute for Ornithology in Seewiesen, Germany.

Energetic costs of flight have been measured in a variety of species and with diverse approaches. Species investigated range from small-sized birds such as hummingbirds to large birds like albatrosses. Energetic costs have been assessed from aerodynamic measurements as well as from direct and indirect calorimetry, and have been measured both in the field and in the laboratory, respectively in flight chambers and wind tunnels. Most of these measurements, however, have been restricted to short flights of less than one hour. Regarding migratory flights, it is of great importance to not only measure flight costs during endurance flights but also to quantify the effects of fuel stores on flight cost. So far, there have been only two studies available measuring flight costs in relation to body mass during prolonged flights within a species (Kvist et al. 2001, Engel et al. 2006).
The effects of spontaneous changes in body mass on flight costs during flights of six hours are investigated in chapter 2 on a small-sized species, the Barn Swallow (*Hirundo rustica*), and in chapter 3 on a larger species, the Rose Coloured Starling (*Sturnus roseus*). Both studies showed, that energy expenditure during flight was allometrically related with body mass to a lesser extent than predicted from aerodynamic theory or interspecific comparisons. The allometric scaling exponents measured were 0.58 and 0.57 (equation 2.3 and 3.1, respectively), while they range from 1.05 to 1.59 in aerodynamic calculations and from 0.67 to 1.93 in interspecific comparisons (chapter 2). My results support the intraspecific measurements on Red Knots (*Calidris canutus*, Kvist et al. 2001) and on Rose Coloured Starlings (Engel et al. 2006), which also observed low exponents (0.35 and 0.55, respectively). Hence, flight costs appear to increase with increasing fuel stores to a lesser extent than generally assumed. In consequence, predictions of migratory strategies or flight range have to be applied carefully.

Other authors have proposed that changes in flight efficiency may allow birds to fly with fuel loads at lower costs than previously thought. Such changes could include modifications of the flight style as well as physiological adjustments. We investigated flight style in terms of wing beat frequency in relation to body mass in Barn Swallows (chapter 2) and in Rose Coloured Starlings (chapter 3 and 4). While wing beat frequency scaled mostly positively with body mass (equation 2.4 and 3.4). It was not detectably correlated with energy expenditure during flight. We cannot rule out that flight behaviour was altered not only in terms of wing beat frequency but also with regard to stroke amplitude or effective wing area. We further investigated possible underlying mechanisms of the shallow increase of flight costs with body mass in chapter 3. For this purpose, we measured endurance flights of Rose Coloured Starlings, with individuals flying repeatedly with natural variations in body mass and one of the following treatments: unrestrained; with a light control harness; or with an artificial load in the harness, which was either applied immediately or at least nine days before an experimental flight. We expected flight costs in "loaded" flights to increase with body mass to either the same extent as in unrestrained or control flights, or to a higher extent in case the birds needed internal cues and/or time to "adjust" to the higher mass. Concerning the loaded harnesses flight costs were the same for both treatments, indicating that birds did not need time to "adjust" to an increased load. Also breast muscle size was not dependent on when the loaded harness had been applied. With regard to natural and artificial
increases in mass, we found the same increase in flight costs in all treatments. A natural increase in mass of 7.4% resulted in a raise in flight costs of 3.4%, while an artificial load of 7.4% resulted in a raise of 4.2%. Consequently, flight costs could best be explained by the actually transported mass (i.e. body mass plus mass of the harness; equation 3.3), irrespective of the experimental situation. Also wing beat frequency was not affected by the different treatments. These results indicate that the relatively low costs at a high body mass are a consequence of immediate adjustments in either physiology and/or flight behaviour and not a long-term adaptation to a certain body mass.

Flight costs in the studies mentioned before were measured with the doubly labelled water (DLW) method. DLW is enriched in heavy hydrogen ($^2$H) and oxygen ($^{18}$O) isotopes. Hydrogen leaves the body mainly in form of water, while oxygen is lost as water and as carbon dioxide. Basically, the DLW method makes use of these different turnover rates to estimate carbon dioxide production and consequently energy expenditure. Although it is possible to measure energy consumption during unrestrained, natural behaviours, this method bears the disadvantage of measuring energy expenditure during long time intervals of several hours or even days. For some research questions it is desirable to measure energy expenditure with a higher time resolution. In chapter 4, we validated heart rate recordings as an estimate of energy expenditure in Rose Coloured Starlings flying for six hours under controlled conditions with natural variations in body mass. Heart rate was higher in heavier birds and proved to be a good predictor of flight costs. We observed a continuous decline of heart rate during endurance flights by 8%. Body mass decreased to the same extent (by 8%) during experimental flights. Thus, the decrease in heart rate is likely to be associated with a reduction in body mass. Such a decrease in mass may well result in lower flight costs at the end of an endurance flight compared to the beginning of a flight. To quantify the possible reduction of flight cost during flight, we employed both the intraspecific scaling of flight costs and body mass (equation 3.3) and the decline in heart rate. For an average Rose Coloured Starling of ~ 87 g, we predict a decrease of flight costs by 4 - 12% during a six hour flight in the wind tunnel.

Not only are migratory flights associated with high energetic costs and physiological changes, they might also trade-off with other demands such as organisation of the circannual cycle or subsequent life-history stages. As
reported in chapter 5, we had Rose Coloured Starlings "migrate" in the wind tunnel and investigated effects on the birds’ condition and on their successive reproductive performance. A group of males covered a distance of more than 4700 km during seven weeks and was compared to "sedentary" controls. Energy expenditure was increased by 55% in the "migrating" compared to the "sedentary" birds. During the "migration" period, we observed significant increases in body mass, fat stores, and in breast muscle size. Colouration of the bills and of the mantle feathers (which probably act as sexual signals) became more rose-coloured during that time. Even in the absence of nesting sites and females, circulating plasma testosterone levels significantly increased during the migration period, indicating a progressive development of the testes. Most of these changes in body condition observed were not in any way altered by the high workload applied. The strong seasonal changes during the "migration" period are probably endogenously programmed. After the "migration" period, males of both groups were directly competing for nest boxes and mates in one common aviary. They easily accepted the "breeding site", and immediately started to sing and to build nests. Males of both groups were to the same extent engaged in song and other courtship behaviours. Also aggressiveness towards other males did not differ between the groups, and "migrating" males performed as well as "sedentary" ones in these aggressive interactions.

Thus, we failed to find a trade-off between the high workload during long flight and seasonal changes, the development of traits in preparation for breeding, or reproductive performance. A possible treatment effect might have been obscured by the unrestricted food supply. Alternatively, birds might have been able to compensate for the workload.

We know only little about the flexibility of migratory strategies within individuals. Fuel stores have a significant impact on flight costs, consequently on the migratory distances, and on speed of migration. We also saw that as long as birds can match the energetic demands during migration, they might not be impaired by the high workload during migration, neither with regard to circannual changes in condition nor to reproductive performance. In contrast, birds might have to pay later for energetically expensive migratory flights and suffer from reduced life-time fitness.

Although by now we know a lot more than Aristotle, the phenomena of bird migration still require further research before (and if ever) they may be fully understood.