CHAPTER 5

Energy gain and use during animal migration

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5.1 Introduction

Despite its widespread occurrence, long-distance migration is potentially a risky process because it commonly involves fasting periods, elevated metabolic costs, feeding on exotic diets and movement through unfamiliar environments. It is therefore not surprising that mortality rates have been estimated to be far greater during migration than during any other period of the year (Owen and Black 1991; Sillett and Holmes 2002; Strandberg *et al*. 2009, Guillemain *et al*. 2010). How can migrants prepare for, and react to, hazardous environmental circumstances encountered en route in order to alleviate the risks of migration? Animals may control their movements, such as their speed of progression and time of departure (Chapters 4 and 6). Another way to mitigate some of the perils of migration is for the animal to manage its energy budget throughout the journey. A balance of energy gain and use is needed during migration to safeguard against starvation and to minimize costs of becoming overloaded with energy stores (Chapter 4). How this is achieved is the subject of the present chapter.

Animal migration may be divided into four distinct stages; preparatory, movement, stopovers and arrival (Ramenofsky *et al*. 1999). During the preparatory stage, the animal may prepare for the expected journey using a suite of behavioural (e.g., increased food consumption), physiological (e.g., fat loading) and navigational (e.g., compass calibration) processes. After departure, the animal may divide its journey into several, and sometime numerous, movement periods, interspersed by stopovers. Stopover periods can last from several hours to several weeks, during which the animal rests, and may gain energy through feeding. An entire migration journey may take place with only a single stopover, for example Alaskan bar-tailed godwits (*Limosa lapponica*) stop over in the Alaskan coastal areas that are located close to, or even within, the breeding area (Gill *et al*. 2009).

During the preparatory and stopover stages, many migrating animals load their body with large fuel deposits (mainly fat but also protein) that are used throughout the journey. The ability of the animal to deposit fuel may be limited ecologically (i.e., by the abundance of food) or physiologically (i.e., by its ability to process food when food is unlimited; Lindström 1991). Physiological factors such as the transport of the fuel and its oxidation may limit the use of stored fuel during migratory movements (Jenni and Jenni-Eiermann 1998). Various environmental factors (e.g., air turbulence; Bowlin and Wikelski 2008) may affect energy expenditure during different migratory stages. Moreover, the properties of the animal, such as its mode of locomotion (e.g., passive vs. powered movement; Sapir 2009) and its size (Lindström 1991; Hedenström 1993) may govern animal energy gain and use (Chapter 4). Consequently, this chapter will deal with the following questions:

- What is the extent of fuel loading and how are its dynamics determined by different environmental factors?
- How is energy use affected by environmental factors during long-distance movement?
- How do the specific needs of the animal during distinct migratory phases affect fuel loading and energy expenditure?
- What are the methods that can be applied to answer questions related to energy gain and use by migrating animals?

We will first describe the dynamics of fuel storing and discuss factors that have been found to influence them. Second, we will describe how the migrating animal expends energy during different stages of migration. The chapter largely draws on avian examples, which reflects the dearth of studies on other taxonomic groups. However we draw parallels where possible.

5.2 Fuel storage for migration

5.2.1 Why store fuel and how?

In order to meet the high metabolic demands associated with movement between two distant geographical regions, the animal must gain energy that is later used for two purposes. First, energy is supplied to muscles to fuel their operation during movement (Pennycuick 1998). Second, energy is used to maintain body homeostasis during periods of movement when feeding cannot be conducted (e.g. Gill *et al*. 2009) or when alighting in environments scarce in food en route (e.g., Moreau 1972; Biebach *et al*. 1986). In these cases, energy stores are utilized to offset energetic costs related to the basal metabolism of the body, maintenance of the animal's body temperature under ambient temperatures outside its thermoneutral zone, foraging that involves movement, and for supporting other body systems, such as the immune system. Fat loading has been describe in many migratory taxa, including migrating insects (e.g., monarch butterfly *Danaus plexippus*; Brower *et al*. 2006), fish (e.g., European eel *Anguilla anguilla*; Svedang and Wickstrom 1997), reptiles (e.g., green turtle, *Chelonia mydas*; Kwan 1994), mammals (e.g., humpback whales *Megaptera novaeangliae*; Boyd 2004), and numerous bird species.

To measure how much fat a migrating animal is carrying and the rate of fat deposition, one can visually inspect fat deposits in some species and assess their level (e.g., visible subcutaneous fat in passerines; Sapir *et al*. 2004b), measure lean body mass of the animal in question (e.g., Piersma *et al*. 2003), or use blood measurements of fatty acids, specifically triglyceride (Jenni-Eirmann and Jenni 1994; Smith and McWilliams 2010). The advantage of the last method is that the rate of fat deposition can be estimated from a single measurement of the individual, whereas in the other two methods the animal must be captured twice. In cases where these methods cannot be applied, fat must be extracted from the animal, for example, when studying fat storage in migrating butterflies (Brower *et al*. 2006; Dudley and Srygley 2008).

5.2.2 Fuel storage in relation to migratory stages and overall migratory strategy

The extent of fuel loading can be substantial during preparation for the journey and stopover, but it has also been suggested that the rate of fuel loading may be important. Maximizing the speed of migration has been argued to be an optimal strategy for migrating birds (Alerstam and Lindström 1990) and other taxa (Hedenström 2009; Chapter 4), and this may be achieved by maximizing the rate of fuel deposition. Hence, it is not only important to load enough fuel to meet the energetic requirements of the journey, it is also advantageous to do it quickly. To store fuel, let alone at a high rate, the animal has to consume more energy than it expends during the preparatory and stopover stages (Fig. 5.1) and this may be achieved in a number of ways. First, the animal may increase its daily food intake by increasing its intake rate (Karasov and Pinshow 2000) or by extending the period devoted to feeding during the day (Kvist and Lindström 2000). Second, the animal may change its diet in order to consume food resources that are more abundant in its environment. A diet switch may also enable the animal to consume food combinations that are better suited as fuel for muscle function during the subsequent movement stage (Bairlein and Gwinner 1994; Bairlein 1998; Lepczyk *et al*. 2000). Third, the animal may assimilate the consumed food at higher efficiency through the enhancement of biochemical absorption of food in the intestine (Hume and Biebach 1996). All these changes require a highly developed digestive system that is capable of processing large amounts of food during the preparatory and stopover stages (Bairlein and Gwinner 1994; Karasov and Pinshow 2000; Gannes 2002; McWilliams *et al*. 2002; van Gils *et al*. 2006).

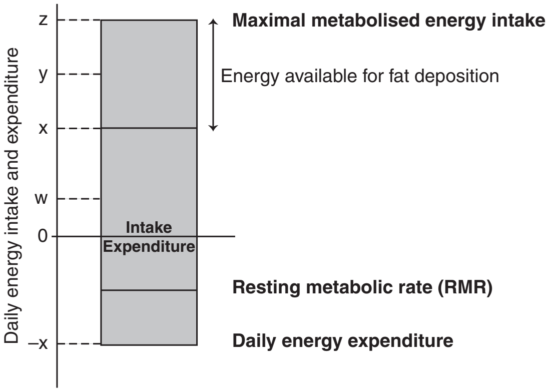

Figure 5.1 Daily energy expenditure and intake of a staging migratory animal in relation to migratory phase and ecology, following Lindström (1991). Resting metabolic rate (RMR) and the additional energy costs resulting from different behaviours of the bird other than resting comprise the daily energy expenditure with an absolute value of *x*, with a negative *x* also shown. During staging when conditions do not permit any energy intake, fat stores are used for maintenance, resulting in a decrease of fat loads. If daily energy intake equals *w*, which is defined as $0 < w < x$, then the bird must use some stored fat to compensate for its daily energy expenditure. This situation is typical of staging in poor stopover sites where food is meagre. If daily energy intake during staging equals *x*, then daily energy needs are exactly compensated by energy intake, resulting in constant fat levels. If the bird's daily energy intake equals *y*, which is defined as $x < y < z$, then energy intake is greater than energy expenditure, allowing for fat deposition. Fat deposition is limited in this case by food abundance and/or by the animal's foraging abilities. If bird daily energy intake during staging equals *z*, which is defined as the maximal metabolizable energy intake, fat is deposited at the maximal rate. Fat deposition is not limited in this case by food intake but instead by the capacity of the digestive system to process the food. Note that RMR, daily energy expenditure and maximal metabolizable energy intake are assumed to be constant over time (cf. Fig. 5.2).

Attaining a highly developed digestive system may be extremely beneficial when energy gain is desirable, but this same system may become a burden during flight. This is because high body mass increases the energetic cost of transport, especially for flapping flyers that must exert a power proportional to their body mass in order to remain airborne.

Maintaining a highly developed digestive system may thus trade off with energy saving during movement. There are different solutions for this conflict, depending on the strategy of the migrant (Piersma 1998).

One solution, common in many migratory flapping birds that engage in flights of several days duration, is to decrease the digestive system during flight and to build it up again during stopovers (Weber and Hedenström 2001). However, this process takes time, usually in the order of several days (Karasov and Pinshow 2000), and therefore migrants that degrade their digestive system before takeoff to lower their cost of transport may hamper their ability to process high quantities of food during stopovers. A decrease in fat accumulation several days before takeoff has been documented in several species of staging passerines (Fransson 1998; Bayly 2006; Bayly 2007), indicating that the birds started to degrade their digestive system well before takeoff. An example of the dynamics of fat storage of a flapping flyer during stopover is illustrated in Fig. 5.2. An extreme example of this strategy is the population of bar-tailed godwits that may fly nonstop for about eight days over 11 000 km from Alaska to over-winter in New Zealand (Piersma and Gill 1998; Gill *et al.* 2009). Godwits departing from Alaska have very small digestive systems and very large fat deposits that account for 55% of their body mass (Piersma and Gill 1998).

A different solution, used by animals that feed on the move or that are involved in short duration movement, is to bear the metabolic costs of transporting an enlarged digestive system in order to maintain at least some if not all of its digestive capabilities. For example, *Catharus* thrushes migrating over the Midwestern US move at night and feed during the day (Cochran and Wikelski 2005). Presumably, these birds do not usually degrade their digestive system and deposit modest fat stores that are used for night time flights. Intermediate strategies are also likely to exist in addition to the two extremes described above.

Overall, the strategy of migrants is probably influenced by ecological factors (e.g., food abundance) and by the location of staging sites in relation to ecological barriers along the route (e.g., digestive system atrophy is likely in a warbler that

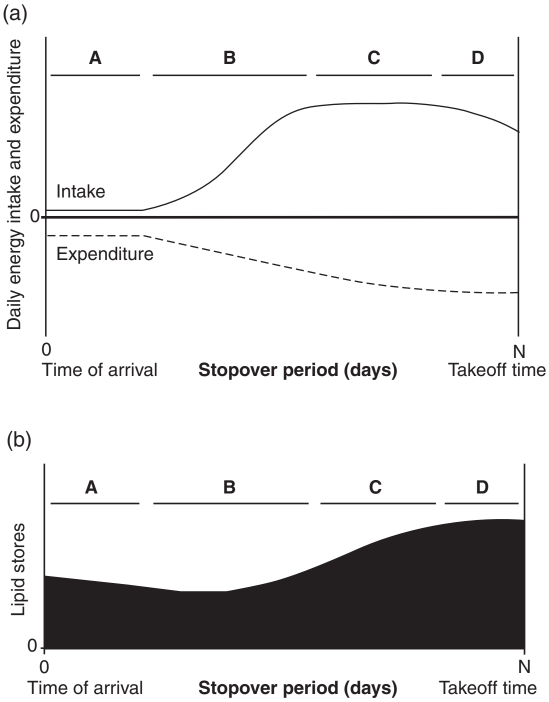

Figure 5.2 (a) Dynamics of daily energy intake and expenditure of a typical migratory bird throughout its stopover period. Daily energy intake is depicted by a solid line, while daily energy expenditure is illustrated by a hatched line. Horizontal lines are used to distinguish between stopover stages, as follows. A: Search and settlement time and the time required for building up the bird's digestive system. During this stage, feeding is substantially limited by the ability of the bird to locate food in its unfamiliar surroundings, as well as by its digestive capacity. This stage may last 1–3 days. B: Steep increase in energy intake with time due to adjustments of the digestive tract towards processing larger food quantities and better knowledge about food distribution in the stopover site. During this stage, energy expenditure increases due to intense foraging and because of an increase in fat tissue that is maintained by the body. C: High and constant energy intake, with the digestive system fully functional for processing high quantities of food. During this stage, energy expenditure further increases due to the increase in the mass of the adipose tissue that must be maintained by the body. D: Decrease in energy intake resulting from atrophy of the digestive system towards take-off for migratory flight that may last 1–3 days. During this stage, energy expenditure levels off due to a decrease in foraging activity towards the end of the stopover period. (b) Dynamics of fat stores due to changes in energy intake and expenditure of a typical migratory bird throughout its stopover period. The daily energy available for fat deposition is calculated by subtracting the daily energy expenditure from the daily energy intake (see Fig. 5.2(a)) and the actual energy (fat) deposited is this surplus energy times a conversion coefficient. A: Decrease in fat stores due to impaired food intake during search and settling and due to limited digestive capacity. B: Increase in fat stores following better foraging and better performance of the digestive tract. Note that if energy expenditure increases during this period, fat stores may increase to a lesser extent. C: High and constant increase in fat stores. D: Fat storage levels off before take-off for migratory flight.

is about to cross a wide sea where no feeding can be carried out). In addition, the type of motion may also affect fat storage strategies. For example, soaring birds that do not exert power for flapping, but rather stretch out their wings when soaring over thermal updrafts, expend much less energy than their flapping counterparts (Pennycuick 1972; Bevan *et al.*; 1995, Sapir 2009). Consequently, their fat stores are expected to be rather modest, and this has been demonstrated in white storks (*Ciconia ciconia*) that had lower fat stores during migration relative to their mid-winter stores (Berthold *et al.* 2001).

5.2.3 Ecological effects on fuel loading: food and water availability, competition and predation risk

When food is plentiful, the rate at which fuel is deposited may be constrained by the capacity of the digestive system to process and assimilate food. Under such a situation, fuel deposition is physiologically rather than ecologically constrained (Zwartz and Dirksen 1990; Kvist and Lindström 2000; Dierschke *et al.* 2003; Kvist and Lindström 2003). The capacity of the digestive system to process and assimilate food varies depending on the system's acclimation to feeding conditions (Karasov 1990). So, a staging migrant may be physiologically limited at first, but later on, when the capacity of its digestive system to process food increases, its food intake may be limited by ecological factors such as food abundance. There are only a handful of examples of birds being physiologically constrained, since ecological factors commonly limit food intake, and it is thus likely that birds rarely reach their physiological maximal fuel deposition rate in the field (Lindström 1991).

The distribution in space and time of different food types available for consumption is a key ecological factor limiting the ability of migrating animals to fuel up. For example, in the Mediterranean scrub, bird diet varies greatly depending on the season. Bird-dispersed fruits are abundant during autumn and are readily consumed by a large number of omnivorous passerine migrants that stop over in this region. Edible fruits are largely absent in this area during spring, at which time staging migrants are compelled to feed on invertebrates (Izhaki and Safriel 1985). Owing to the between-season difference in food abundance, staging migrants may be able to load fuel much faster in autumn compared with spring. However, evidence is still lacking for such a difference. Moreover, this difference may imply that autumn migrants need a certain set of physiological adjustments to facilitate rapid fuelling on large quantities of fruit, while on their northward journey, these same birds may require a different set of capabilities for detecting, handling and processing invertebrates.

In addition to food, water availability can also limit fuel loading. Water availability facilitates fuel loading in autumn migrating blackcaps (*Sylvia atricapilla*; Sapir *et al.* 2004b, Tsurim *et al.* 2008) feeding on fruits of the Mt Atlas gum tree *Pistacia atlantica*. The fruit's pulp contains only 35% water and lipids make up over 50% of its dry matter. If their water requirements are met, the birds are able to boost their fat deposition by consuming these fruits rather than insects. If not, they may deposit low amounts of fat or even lose fat. Therefore, fuel loading in blackcaps may be impeded throughout many desert and Mediterranean-type areas due to lack of drinking water. Interestingly, this effect was not found in a congeneric species, the lesser whitethroat (*S. curruca*; Sapir *et al.* 2004b).

Other biotic interactions may limit foraging and consequently fat deposition even if food is ample and water is available. Competitors may hamper feeding either by direct interference and food resources monopolization (Rappole and Warner 1976; Lindström *et al.* 1990; Carpenter *et al.* 1993) or through reduction in food availability due to exploitation (Moore and Yong 1991; Kelly *et al.* 2002). Predation risk may also reduce food intake by shortening foraging duration (Fransson and Weber 1997) and this effect may be more severe for migrants loaded with large lipid depots that are more vulnerable to predation (Cimprich and Moore 2006). Predation risk may result in preference for food-poor but relatively risk-free habitats and microhabitats (Lindström 1990; Sapir *et al.* 2004a; Cimprich *et al.* 2005), which may vary by individual depending on body mass. Under such a scenario, food-rich but dangerous habitats may be occupied by relatively lean birds, and fatter birds may sacrifice food intake for safety by inhabiting food-poor but safer sites (Ydenberg *et al.* 2002). Overall, predation risk could have a significant effect on fuel loading in staging migrants, although direct evidence for this effect is quite rare (Piersma *et al.* 2003, but see Schmaljohann and Dierschke 2005).

5.2.4 Variation by age and sex

There are many documented examples of differences in fat stores between different age groups with similar lean body mass (e.g., Ellegren 1991; Woodrey and Moore 1997; Yong *et al.* 1998). These studies found that first-year birds have lower fat reserves than those of older birds (but see Arizaga *et al.* 2008). Lower fat reserves in first-year birds may result from lower intake rates, attributed to either lower foraging success due to lack of experience, or competition with adult birds that are more successful in winning disputes over food resources. For example, Menu *et al.* (2005), who studied migratory greater snow geese (*Chen caerulescens atlantica*), reported mortality of juvenile geese under harsh environmental conditions. These conditions impaired foraging and increased thermoregulatory costs, leading to mortality of individuals that had failed to accumulate the required fat to overcome the energetic requirements of migration under severe environmental conditions. Carpenter *et al.* (1993) described the consequences of stopover territoriality on feeding in migratory rufous hummingbirds (*Selasphorus rufus*) during autumn. They found that different age and sex classes had different successes in monopolizing food resources (flowers), thereby directly affecting the birds' fuel storage. Consequently, adult females that were more successful in obtaining nectar than young females had higher fuel stores.

In general, age is a significant factor explaining inter-individual variation in fuel loading during autumn, whereas sex-related differences have been usually reported during spring. Spring-migrating males are characterized by higher fuel loads or fuel deposition rates (Hedenström and Pettersson 1986; Morris *et al.* 1996; Woodrey and Moore 1997; Yong *et al.* 1998; Lyons *et al.* 2008), and since higher rates of fuel deposition enable higher speed of migration (Alerstam and Lindström 1990; Hedenström and Alerstam 1997), males that travel at faster rates may benefit from early arrival at breeding grounds. This may allow them to occupy high-quality territories where food can be delivered to the brood at a higher rate. Dierschke *et al.* (2005), who studied fuelling dynamics in Greenlandic/Icelandic northern wheatears (*Oenanthe oenanthe*) stopping over in a Baltic Sea island and about to cross the North Sea, reported that males had overall higher fuel loads at departure compared with females. Yet, Scandinavian northern wheatears at the same location, which is much nearer their destination than that of the Greenlandic/Icelandic birds, had lower fuel loads regardless of sex. Sex may thus affect fuel loading depending on the strategy of the animals and the position of the staging site in relation to ecological barriers en route.

5.2.5 The effect of geomagnetism on fuel loading

The extent of fuel deposition may be affected by geomagnetic fields. In the thrush nightingale (*Luscinia luscinia*), a long-distance migrant that moves between Sweden, Egypt and sub-Saharan Africa, fuel loading is low in high latitudes (Sweden) and high in low latitudes (Egypt) where the birds must store large fuel depots for crossing the 1800-km wide Sahara Desert. The upper limits of fuel loading in Sweden and Egypt are correlated with the local geomagnetic field, demonstrating that the spatial information provided by the Earth's geomagnetic field may enable the animals to overcome extensive ecological barriers that are located within their migration routes (Fransson *et al.* 2001). Similarly, the response of the robin (*Erithacus rubecula*) exposed to a simulated geomagnetic field characterizing the end point of its medium distance journey, was a decrease in fuel loading (Kullberg *et al.* 2007). These studies suggest that the local geomagnetic field has a key influence on fat storage. Consequently, studies that investigate the mechanisms responsible for spatial variation in fuel loading should consider this effect.

While not much is known about fuel loading of migratory insects, there have been a few studies focusing on butterflies. Brower *et al.* (2006) summarized extensive data on fuel loading in the monarch butterfly. Butterflies that hatch in eastern and central

N. America during summer migrate towards central Mexico during the autumn. At the beginning of their migration they deposit only small amounts of fat, while much higher lipid levels were found in migrating individuals staging in Texas and northern and central Mexico during late autumn. These lipids are used during their entire over-wintering period in Mexico in which they do not feed, and possibly also during their roughly 2000-km return migration in the following spring. A peculiarity of this migration system is that after about 2000 km of a return migration, the butterflies reproduce. Their offspring and later on their offspring's offspring continue to migrate to eastern and central N. America where the population existed in the previous summer. The entire annual cycle of this migratory population is therefore composed of several butterfly generations. This study suggested that the butterflies underwent a behavioural shift to hyperphagia (increased food consumption) at lower latitudes before the start of their extended over-wintering period. The equivalent pattern of an increase in fat deposition at low latitudes during the migratory journey in both the monarch butterfly and the thrush nightingale (Fransson *et al.* 2001) may suggest that a similar process controls fat loading in these two species.

5.2.6 The effect of feather moult on fat deposition

The effects of moult on migratory fuel deposition have been studied so far only very rarely. In migratory passerines, most of the adults moult after breeding and also need to migrate sometime during this period. Consequently, there may be some conflict between the timing and energy demands of the moult and of migration (Lindström *et al.* 1994). In most cases, migration usually starts after the moult is completed. Otherwise, moult is suspended or arrested and may be completed only after the completion of the entire migratory journey. In many waterfowl species, a complete moult of the wing feathers occurs after breeding to the extent that the birds endure an extended, several weeks long, flightless period. Waterfowl moulting is characterized by body mass reduction due to elevated energetic demands and decreased energy intake even when food is plentiful (Portugal *et al.* 2007). This decrease in food intake presumably evolved to reduce exposure to predation risk when the birds' escape capabilities are severely hampered. In these species, the allocation of energy to fuel storage in preparation for migration is postponed until feather growth is completed and may depend on food availability at particular sites where the required food can be consumed during both moulting and the subsequent pre-migration period (Loonen *et al.* 1991).

5.2.7 The effect of fuel loading on flight performance

There are three possible effects of fuel loading on flying migrants. First, the higher energy demands of the added fat tissue must be met. Thus, the metabolic rate of the animal is expected to increase as a function of the added fuel deposits. Second, since fat is deposited subcutaneously it may change the body's streamlining and consequently cause higher drag (Chapter 4). Third, the energy cost of lifting and transporting a body of higher mass may result in higher investment being needed for the locomotory machinery of the body. For swimming migrants, the cost of increased mass is probably negligible, since they do not need to lift themselves in the water. In addition, for soaring animals that are carried by atmospheric up currents, this latter cost may be smaller and be independent of body mass (or even decrease with body mass; Hedenström 1993).

Aerodynamic theory predicts that changes in body mass have consequences on optimal flight speed. For example, higher body mass of a migrant flying by flapping flight would invariably result in higher flight speed (Pennycuick 1969; Hedenström 1993). Dudley *et al.* (2002), who studied diurnal flapping flights of the migratory neotropical moth (*Urania fulges*) over Lake Gatún, Panama, found no relationship between the size, mass and fat content of moths and their airspeed in individuals with a fat content of 4–38% of their body mass. By contrast, Dudley and Srygley (2008), who studied ten migratory butterfly species with fat content averaging 4.5–15.6% of their body mass in the same location, found a positive relationship between fat load and air speed in all the species with sufficiently large sample sizes, supporting the predictions made by models of optimal flapping flight speed. An inter-seasonal difference in flight speed was similarly attributed to body mass in Brent geese (*Branta bernicla*) migrating over southern Sweden and studied by tracking radar (Green and Alerstam 2000). This study suggested that spring migrating Brent geese flew significantly faster than autumn migrating geese, due to an average 20% increase in their body mass.

Aerodynamic theory further predicts that an animal's rate of climb during migratory flights is negatively related to body mass; therefore, animals loaded with large fuel stores will not be able to climb as fast as individuals with lower fuel stores. Hedenström and Alerstam (1992) tested this prediction by comparing climb rates of dunlins (*Calidris alpine*) in Sweden during autumn and in Mauritania during spring, with average fuel loads accounting for 17 and 50% of their body mass, respectively. Dunlins migrating during spring in Mauritania had an average rate of climb of 0.6 m s^{-1}, almost three times lower than those migrating during autumn in Sweden, with a climb rate of 1.7 m s^{-1}, consistent with the predictions of aerodynamic theory. Similarly, Green and Alerstam (2000) observed that heavier Brent geese migrating during spring showed lower climb rates than lighter birds during the autumn migration, but differences in climbing rates (0.46 and 0.62 m s^{-1}) between the seasons were quite small in this study. These findings from the field are supported by laboratory studies in which birds with different fuel levels were exposed to a predator in order to simulate a controlled escape flight. In these studies, take-off angle and take-off speed were negatively related to fuel load (Kullberg *et al.* 1996; Lind *et al.* 1999).

5.2.8 Fuel use during flight

Only rarely have researchers studied fuel use in wind tunnels during 1–12 hours long, continuous flight (Klaassen *et al.* 2000; Jenni-Eiermman *et al.* 2002; Schmidt-Wellenburg *et al.* 2008). These studies reveal that protein provides about 10% of the catabolized fuel mass during flight. Also, there was apparently no shift between fat and protein as a metabolic substrate under different levels of exercise and the ratio between protein and fat use remained constant for at least ten hours during flight (Jenni-Eiermman *et al.* 2002). Studying fuel consumption in wild ranging birds during cross-country flights is challenging, and consequently most studies on fuel use rely on data from birds alighting at different locations relative to their departure site (e.g., Biebach 1998), or when birds unfortunately hit erected man-made structures such as lighthouses, communication towers and wind turbines (e.g. Piersma and Gill 1998). To assess fuel use during migratory flight in the field, nocturnal migrating passerines were trapped in a mountain pass and their blood metabolites were sampled. This approach allowed comparison between different species, and between migratory flight and other activities carried out by the birds during migration, such as rest and foraging during stopover. High levels of triglyceride as well as evidence for protein breakdown were found, and differences between species were quantified and partially explained by the migratory strategies of the birds (Jenni and Jenni-Eiermann 1992).

5.2.9 Physiological constraints on lipid oxidation

Animals can obtain energy from any one or from a mixture of three metabolic substrates; carbohydrates, fats or proteins. Dehydrated fats provide approximately twice as much energy as dehydrated carbohydrates or proteins but, as stored lipids are almost completely dry whereas carbohydrates and proteins are not, the difference is as much as 8–10 times on a wet mass basis (McQuire and Guglielmo 2009). Yet, both the supply and oxidation of lipids from adipose tissues to the muscles may be limited. It is believed that to overcome these potential constraints, birds have developed mechanisms to enhance the transport of fatty acids from the adipose tissue to the muscle, and to increase their aerobic capacity, possibly through the modification of enzymatic processes (Jenni and Jenni-Eirmann 1998).

Lipids are largely used by the oxidative fibres in the locomotor muscles during sustained exercise. In fish, the oxidative muscle fibres are located in two bands running the length of each side of the body

(Butler 1986), while the flight muscles of migratory birds consist mainly of oxidative fibres (Butler and Bishop 2000). However, the locomotor muscles of mammals tend to consist of mixtures of muscle fibres with the oxidative fibres being used primarily during relatively low intensity exercise and the glycolytic (anaerobic) fibres being recruited at higher intensity exercise (Armstrong and Laughlin 1985). Thus, in most species of mammals, there tends to be a decreasing reliance on lipids and an increasing use of carbohydrates (glycogen) as exercise intensity increases (see Fig. 2 in McClelland 2004). As metabolic rate is particularly high during forward flapping flight in birds and at least twice as high as that in running mammals of similar body mass (Butler 1982), it would be predicted from the mammalian data that carbohydrates would fuel migratory flight in birds, but this is not the case. In fact, migratory fish and birds have the ability to store large amounts of lipids for use by their oxidative muscle fibres during migration (Blem 1980).

The main reason why the use of lipids is restricted in most species of mammals is their inability to transport lipids sufficiently rapidly across the plasma membrane and into the mitochondria. Membrane-bound and cytosolic fatty acid binding proteins (FABPs), plus specific enzymes on the mitochondrial membranes, serve this function and migrating birds have substantially more FABPs in their flight muscles than mammals have in their locomotor muscles (McQuire and Guglielmo 2009). There is some evidence that bats use lipids as the primary fuel during flight, but whether or not they store fat for migration is not known for certain. Most species of bats for which fat stores have been determined during migration also hibernate, so it has not been possible to conclude that the lipids were accumulated specifically as fuel for migration. There may be little point in any species of mammal storing lipids for migration if it is unable to transport them sufficiently rapidly across the muscle and mitochondrial membranes. This issue is currently being investigated in migrating and non-migrating hoary bats, *Lasiurus cinereus*, (McQuire and Guglielmo 2009) but to the authors' knowledge, it has not been studied in any other species of migratory mammal.

Fatty acid binding proteins have been characterized in oxidative muscles of fish, as well as in the flight muscles of birds, and of insects, which are known to use lipids during sustained exercise, such as migration (Weber 2009). Whether or not the lipid stores of marine mammals or reptiles are used specifically for migration has not been investigated, although a number of studies seem to have incorporated the use of lipid stores during migrations to breeding areas as part of the metabolic cost of reproduction (Biuw *et al.* 2007; Southwood and Avens 2010). Examples of this are migratory cetaceans such as right whales (*Eubalaena glacialis*) and humpback whales (*Megaptera novaeangliae*) which seem to accumulate large blubber reserves during the summer when they inhabit polar seas that are rich in food resources. During winter, however, they are often found in sub-tropical waters where they breed but where relatively little feeding takes place (Boyd 2004).

5.2.10 Capital versus income breeding in migratory animals

Whether animals carry the nutrients needed for reproduction from the wintering or stopover areas to their breeding grounds (capital breeding), or whether they obtain them entirely at the breeding areas (income breeding) is a question that relates to the level of fuel carried by the migrant on arrival. Having fuel stores at the end of the journey may enable the individual to survive in the potentially harsh environment of the breeding grounds early in the season, and may help in providing for the demanding physiological processes involved in egg production and the feeding of young (Smith and Moore 2003). Yet, the amount of fat stored before breeding does not always have a positive effect on reproductive output, for example in tree swallows *Tachycineta bicolor* (Winkler and Allen 1996). Indeed, the relatively rich literature on capital vs. income breeding in Arctic waders and geese is controversial (Klaassen *et al.* 2001; Clausen *et al.* 2003; Alerstam 2006; Hedenström 2006), and the general picture is not well understood. Nevertheless, in their review, Drent *et al.* (2006) suggested that the prevailing strategy is a mixture between the two options, where fuel, acquired at stopover sites, is carried to breeding grounds and then supplemented by local resources for building up the reproductive system.

Capital breeding has also been documented in the migratory European eel, *Anguilla anguilla* (Svedang and Wickstrom 1997; van Ginneken and van den Thillart 2000; van Ginneken *et al.* 2005). Eels move to breeding grounds where they produce eggs from lipid stores that have been deposited before the start of the journey, representing an example of capital breeding in an ecological context similar to that of arctic-breeding birds.

Capital breeding considerations may have far-reaching consequences for migration strategy. For example, bar-tailed godwits that migrate during spring from New Zealand to Alaska, divide their journey into at least two different movement legs: from New Zealand to China's Yellow Sea (10 000 km), and from there to Alaska (6500 km); therefore they need to load themselves with substantial amount of lipids twice during their migration. The reasons for this bi-phasic springtime voyage are unclear. One possible explanation relates to capital breeding considerations, as a shorter pre-arrival flight from the last staging site may allow the birds to allocate the fuel deposits remaining after the termination of the journey to reproduction.

To evaluate fully the effects of different parameters on female reproductive strategy, Houston *et al.* (2007) modelled the effects of factors such as length of gestation, offspring metabolism, efficiency of energy transfer from parent to offspring, and the rates of energy intake by females with and without offspring. They suggested that the most important factor determining reproductive strategy was the cost associated with carrying accumulated energy stores, and therefore the elevated energetic demands when transporting a higher body mass during flight to springtime breeding sites may have far reaching consequences for animal life histories.

5.2.11 Conservation implications of energy gain in migratory animals

Migratory performance (e.g. overall migration speed) is determined to a large extent by the fuelling possibilities. Therefore, if suitable stopover habitats or sites are destroyed or become less profitable, the speed of migration and the time of arrival to over-wintering and breeding sites may be affected. For example, if the phenology of the emergence of insects varies due to underlying climate change, tropical wintering birds may encounter reduce fuelling rates during spring migration (Marra *et al.* 2005). In turn, this may affect the timing of arrival with consequences for the animal's fitness. Furthermore, the consequences of similar phenological changes in insect emergence that are the outcome of warming at the breeding grounds may be particularly severe for long-distance migrants. This may be because these animals cannot adjust their arrival time to coincide with the emergence of the insects due to numerous constraints operating in several geographical areas. Consequently, global warming may have severe fitness consequences for long-distance migrants (Both and Visser 2001).

Changes in the quality of individual staging points can have a dramatic effect on migratory performance. Delaware Bay is used by a population of spring migrating red knots *Calidris canutus rufa* on their northbound journey to Arctic Canada from their over-wintering area at Tierra del Fuego. The knots feed there on the eggs of spawning horseshoe crabs *Limulus polyphemus* but, due to commercial fishing for horseshoe crabs in combination with erosion of beaches, this food source has declined dramatically in recent years (Baker *et al.* 2004). The consequence is that knots cannot gain mass as fast as before in order to reach the breeding area in good condition. This knot population has declined dramatically, probably as a consequence of deterioration of this single stopover site during its spring migration (Baker *et al.* 2004). The lesson from this example is that migratory animals may be vulnerable to changes in habitats used en route during their migrations, and that conservation strategies should include the entire migration route (Chapter 11).

5.3 Energy use during migration

5.3.1 Energetic estimates of migratory movements

How animal performance and morphology affect fitness is a central question in organismal biology (Arnold 1983). Quantifying the metabolic consequences of behavioural, morphological and physiological attributes of animal migration may provide insights into their effect on the fitness of the organism. Estimation of metabolic rates during migration is, however, a challenge, since migratory organisms are difficult to track throughout their migratory journeys. Moreover, the collection of physiological data from wide-ranging animals is usually logistically limited (Cooke *et al.* 2004; Goldstein and Pinshow 2006). Currently, there is only a handful of field studies in which animal metabolism has been estimated during migratory movements.

Wikelski *et al.* (2003) estimated energy expenditure in migrating Swainson's *(Catharus ustulatus*) and hermit (*C. guttatus*) thrushes over the Midwestern US using the doubly-labelled water technique. They provided the first empirical support for the theoretical prediction of Hedenström and Alerstam (1997) that the energy expended during flight makes up only about one third of the total energy used during migration, with the other two thirds spent during stopover periods. Bowlin *et al.* (2005), and Bowlin and Wikelski (2008) tracked Swainson's thrushes (*Catharus ustulatus*) using radio-telemetry while recording their heart beat frequency (f_H) continuously during flight. The relationships between f_H and metabolic rates at rest and in flight in this species were established using respirometry chambers and doubly-labelled water techniques (Bowlin, Meijer and Wikelski, unpublished data). Bowlin and Wikelski (2008) examined the effect of several factors on f_H throughout entire migratory cross-country flights, from departure to landing. They revealed that individuals with relatively sharply pointed wingtips and higher wingload (higher ratio of body weight to wing area) were characterized by elevated f_H, suggesting that morphology and body mass have an important effect on bird energy expenditure during flight. Additional findings from this study suggest that when cruising birds encountered strong winds (regardless of wind direction) and more turbulent air, they expended more energy than during calm conditions. Mandel *et al.* (2008) studied a migratory turkey vulture (*Cathartes aura*) over North America using an f_H logger, and similarly found that the vulture's f_H increased under conditions of high vertical air speed and above rugged terrain where the structure and availability of hot air thermals may impair their use by soaring-gliding birds, presumably forcing the birds to flap their wings.

Sapir (2009), studying migrating European bee-eaters (*Merops apiaster*) in southern Israel using radio-telemetry, found that bird flight mode had a substantial effect on bird f_H, with f_H during powered flapping flight being about 2.5 times higher than f_H during soaring–gliding flight. Moreover, the birds' f_H during soaring–gliding was similar to their resting f_H, suggesting that soaring–gliding may be particularly cheap. This finding suggests that flight mode-related differences in metabolism may be substantial and may explain the propensity of European bee-eaters to migrate using soaring–gliding, when meteorological conditions permit the use of this flight mode. The ability of these birds to time their flight in accordance with environmental conditions, permitting soaring over hot air thermals, may lead to considerable energy savings throughout their entire migratory route. Similarly, the propensity of migrating monarch butterflies to use soaring flight over flapping flight was proposed to reflect energy economy consideration (Gibo and Pallet 1979). Owing to practical limitations in estimating flight metabolism in butterflies, no empirical findings are available to test this suggestion.

5.3.2 Energetics of migrating barnacle geese

Butler *et al.* (1998) combined satellite telemetry and f_H loggers in barnacle geese (*Branta leucopsis*) migrating in autumn from Svalbard to Scotland over 2500 km. Since it has not been possible to calibrate f_H against rate of oxygen consumption ($\dot{V}O_2$) accurately, at least for the autumn migration of wild barnacle geese (Bishop *et al.* 2002), Butler *et al.* (1998) used an allometric approach based on recorded f_H and mass loss to estimate the metabolic rate of the wild barnacle geese throughout their autumn migration (Bishop and Butler 1995). Butler *et al.* (1998) found that, contrary to the conclusions of earlier studies (Owen and Gullestad 1984), the barnacle geese they studied did not fly non-stop in 30–40 h from the Arctic to southern Scotland. Instead, they flew along the Norwegian coast (Fig. 5.3), making frequent stops along the way. The total duration of the journey was between 4 and 39 days, with the longest non-stop flight being 18.6 h

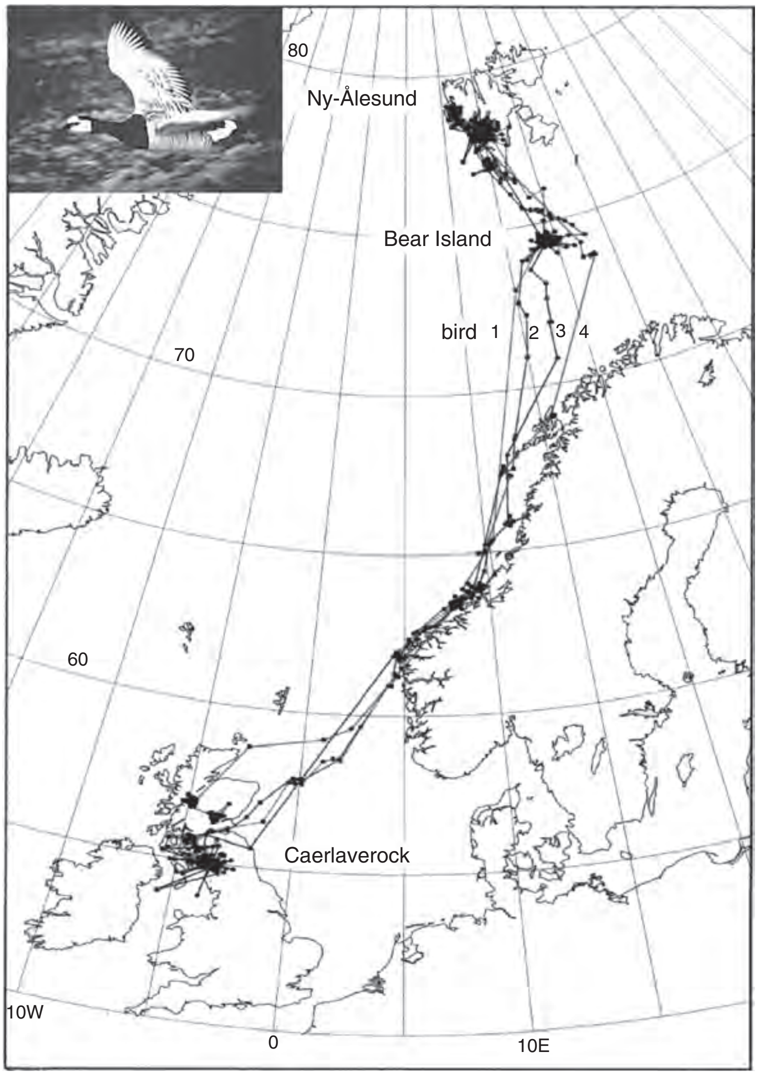

Figure 5.3 Southerly (autumn) routes of four barnacle geese, *Branta leucopsis*, fitted with satellite transmitters. Note that they all flew (and stopped) along the Norwegian coast (Butler *et al.* 1998). An individual in flight is shown in the inset (Photo: Patrick Butler).

(mean for 10 birds, 13.5 h). Despite the large variability in the total duration of the migration, the total time spent flying was reasonably consistent (range 46.5–85.2 h, mean 61 h), which means that most of the variation in total duration is due to individuals spending different lengths of time at stopover sites. The duration of stopovers was so variable because the birds presumably waited for tailwind assistance to aid their flight under the overall unfavourable (headwind) weather conditions that prevail in this region during this time of the year. For example, one bird spent 23 days in south-western Norway before leaving the Norwegian coast for Scotland. During most of this period, strong southerly winds (mean velocity 10 m s^{-1}) prevailed.

The most intriguing data from the study of migrating barnacle geese are the f_H during migratory flight. Heart rate during the autumn migratory flight was around 300 beats min^{-1} at the beginning, gradually decreasing to a low of 225 beats min^{-1} at

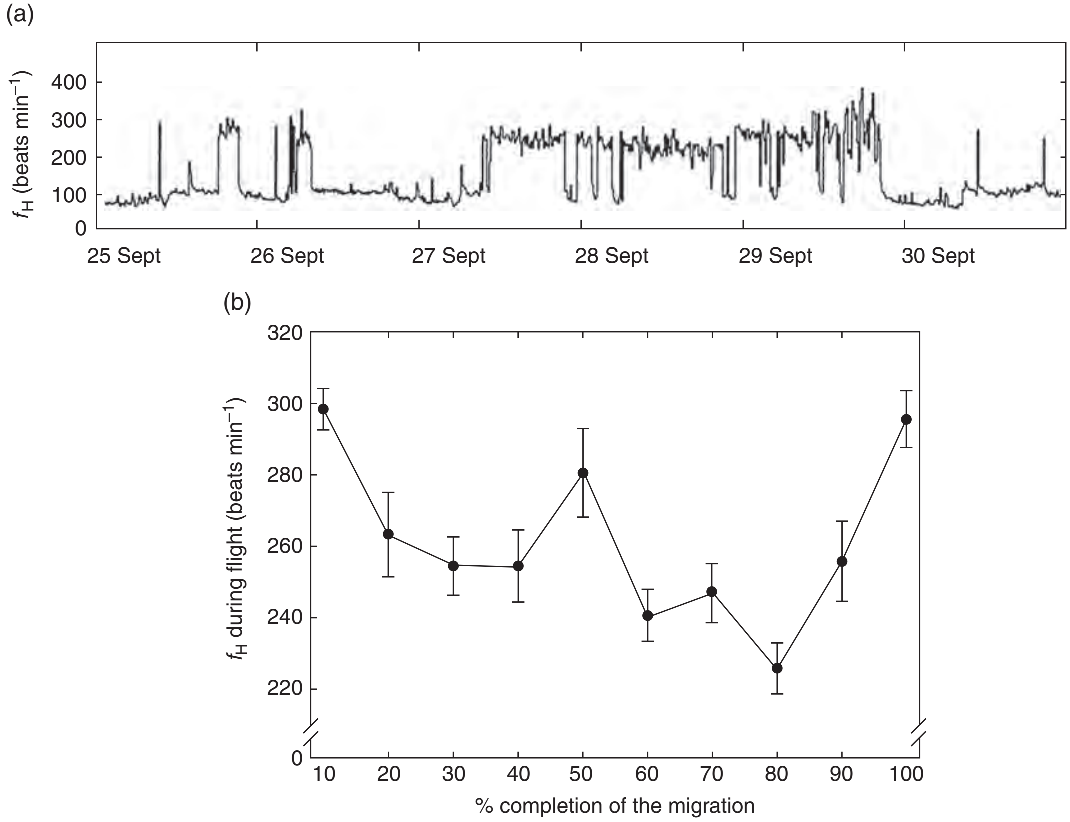

Figure 5.4 Heart beat frequency (f_H) during migration. (a) Trace of f_H during autumn migration of a male barnacle goose, *Branta leucopsis* (1.98 kg). The bird was flying when f_H was high (Butler *et al.* 1998). (b) Mean (± SEM) values of f_H while flying from ten barnacle geese as a proportion of the total flight time during migration (P. J. Butler and A. J. Woakes, unpublished data).

about 70% through the migration (Fig. 5.4). These values are lower than the lowest obtained from captive barnacle geese flying in a wind tunnel (about 350 beats min^{-1}) and within the range of the same birds running on a treadmill (about 130 beats min^{-1} to 330 beats min^{-1}; Ward *et al.* 2002). However, in the last 30% of the migratory journey, there was a steady increase in f_H during flight, which coincided with the birds leaving the Norwegian coast and heading towards Scotland. Consequently, by the end of the migration, f_H during flight was almost back to the value recorded at the beginning of the journey. One possible reason for the progressive decrease in f_H during the middle phase of the migration could have been the progressive loss of body mass (see Fig. 5.2, Part B.), but why the overall frequency was lower during this phase than at the end of migration, and even than when running, is not so obvious. It could be that the birds were benefiting from vertical air currents as they flew along the Norwegian coast, which is possible since this species is capable of slope soaring (Butler and Woakes 1980) and could, therefore, make use of updrafts created when winds hit cliffs located on shore-lines within the bird's migratory flyway. Support for this explanation is provided by the fact that during wind-tunnel flight both f_H and $\dot{V}O_2$ fell when the trainer's presence created an updraft (Fig. 5.5).

Interestingly, at the beginning of the spring migration, f_H during flight was over 400 beats min^{-1} (P.J. Butler and A.J. Woakes, unpublished data), which is similar to that obtained for captive birds flying in a wind tunnel (Ward *et al.* 2002), although it did decrease throughout the migratory period.

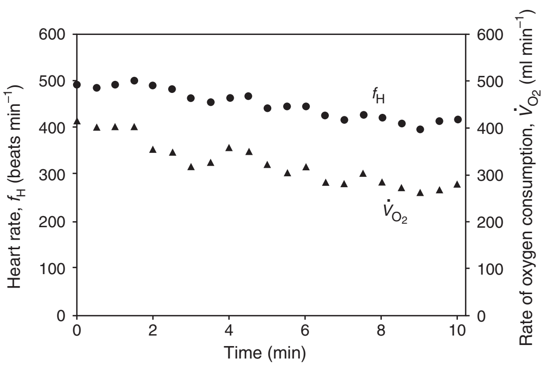

Figure 5.5 Heart rate (f_H) and rate of oxygen consumption ($\dot{V}O_2$) during a 10-minute flight in a wind tunnel by a barnacle goose, *Branta leucopsis*. During this flight, the bird flew progressively closer to the trainer (Ward *et al.* 2002).

This would suggest that during these flights the birds were not being assisted by vertical air currents. Also, as f_H during spring migratory flights and during flights of captive birds in a wind tunnel were similar, the calibration of $f_H$against $\dot{V}O_2$ obtained by Ward *et al.* (2002) on captive birds is most likely to be applicable to the spring migratory flights of wild barnacle geese.

Taking an average f_H during the autumn migration of 254 beats min^{-1} and using the allometric method of Bishop and Butler (1995), gives an average $\dot{V}O_2$ during migration of approximately 120 ml min^{-1}kg^{-1} (Butler *et al.* 1998) and mass loss data give a value of approximately 160 ml min^{-1} kg^{-1} (Bishop *et al.* 2002). These values, therefore, seem to be reasonable estimates of the energy cost of the autumn migratory flights of barnacle geese, and are 13–18 times the night time resting value for this species (Portugal *et al.* 2007). These high metabolic demands of flapping flight compared with resting metabolism are in line with allometric relationships of bird physiology and flight mechanics, suggesting that flight metabolism increases disproportionately with body mass, leading to very large power inputs in large bodied flapping flyers (Pennycuick 1969).

Another intriguing observation concerning the study of migrating barnacle geese is that, during the autumn migration, the body temperature of wild geese did not increase during the periods of flight, which could be for many hours, whereas when flying in a wind tunnel, even for only 20 minutes, the body temperature of captive birds increased by almost 1°C, which is consistent with previous studies of birds flying in wind tunnels in temperatures as low as 0°C (Butler 1991; Torre-Bueno 1976). Reasons for this difference remain elusive. This finding and the difference in f_H mentioned above (see also Bishop *et al.* 2002) suggests that flight in wind tunnels may differ from some migratory flights to a greater extent than previously assumed.

5.3.3 Use of accelerometry to determine behaviour of migrating animals: moving towards estimation of behaviour-specific metabolic rates

Present knowledge of migratory animal energetics is still limited to the very few examples provided above, therefore currently it is not possible to give a year-round estimation of the energetics of migrating species. This means that we are unable to deduce the potential effect of variation in energy use throughout the life cycle of migrating animals on their fitness. Since different behaviours have unique metabolic rates (e.g., Bevan *et al.* 1995; Ward *et al.* 2002), a first, necessary, step in estimating the energetics of migrating animals throughout different periods of the year is to document their activity time budget. The technology of three-axial accelerometry that has been applied recently in several studies of non-migratory species (e.g., Wilson *et al.* 2006; Green *et al.* 2009; Holland *et al.* 2009) can potentially overcome the practical challenge of registering animal behaviour over extended routes throughout the entire migratory period, and even throughout the entire life cycle of a migratory animal. For example, this technology, in combination with GPS telemetry, has been recently applied to study year-round movements and activity time budgets of common cranes (*Grus grus*). Cranes are studied during over-wintering in the Hula Valley in Israel and possibly also in Ethiopia, during breeding in northern Russia, as well as during migration between these localities, allowing researchers to assess how environmental conditions affect bird behaviour throughout their annual routine. Crane flight mode and wing flap rate could be measured using this technology en route over Lebanon after a springtime takeoff from the over-wintering site in the Hula Valley (Fig. 5.6).

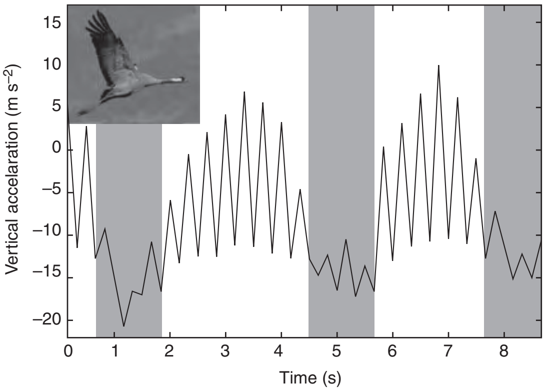

Figure 5.6 Wing flap rate registered by accelerometry of a crane (*Grus grus*) during migratory cross-country flight over Lebanon. The crane was flying 20 km away from its over-wintering area in the Hula Valley in Israel at an altitude of 800 m above the ground on 7th March 2009. Later the bird reversed its flight course and returned to the Hula Valley. Wing flap rate was registered by the body's vertical acceleration in an 18-Hz sampling rate. Crane wing flap rate is about 3.5 Hz. Shaded areas depict pauses in wing flaps (I. Shanni, N. Sapir, M. Wikelski and R. Nathan, unpublished data). An individual in flight is shown in the inset (Photo: Udi Maman).

Moving towards estimation of behaviour-specific metabolic rate and ultimately estimating the energetics of migrating animals throughout their annual cycle using accelerometry is a challenge. First, this technology could be combined with behaviour-specific measurements of metabolic rate (Green *et al.* 2009). This should be done in the laboratory and also in the field but it is extremely difficult to obtain accurate data on metabolic rate during specific activities, for example during flapping flight of birds in the field. Also, accelerometry will not be able to provide exact information on other factors known to affect animal's metabolic rate. For example, it will not always be known if an animal is feeding and/or if it is exposed to temperatures outside its thermally neutral zone. Consequently, we are not likely to have accurate values of metabolic rates for a whole range of different behaviours. Having information on the behaviour of an animal so that any measurements of metabolic rate can be related to specific behaviours (e.g., bird flight modes) would be a huge advance. We propose that a long term aim must be to use techniques such as accelerometry to provide behavioural data to go alongside real-time estimates of metabolic rate, e.g. from measurements of heart rate. This would enable the energetics of different migratory stages and different periods of the year to be determined and thus lead to substantial improvements in our understanding of the causes, mechanisms, patterns and consequences of animal migration.

5.4 Concluding remarks

The extent and dynamics of fuel gain and its use throughout long-distance migratory routes is determined by a number of behavioural, physiological, aerodynamical and environmental factors. Some of these factors are more pronounced at certain stages of the migration and at particular points along the way (e.g., near an ecological barrier), and some trade-off with others. Consequently, the migratory animal must manage its fuel loads and energy expenditure in an optimal manner (Alerstam and Lindström 1990; Weber and Hedenström 2001).

Over the last two decades many studies, especially in birds, have documented the dynamics of fuel loading and the environmental factors affecting them, but due to practical difficulties in obtaining physiological measurements from animals that are on the move, how energy is used during migration is poorly known. There are only a few examples of studies that investigated energy expenditure at different stages of the voyage and under different environmental scenarios. Insights gained from these studies are unmatched by any other study conducted on migratory animals in the laboratory, and demonstrate the capability of such methods in resolving long-standing issues in the field of animal migration, such as the effect of loaded fuel on flapping flight performance, and the allocation of energy between stopover and movement phases during migration journeys. The combined use of techniques such as three-axis accelerometry and heart rate can help overcome the practical challenges of measuring metabolic rate in the field and relating it to specific behaviours. To explore how global climate change may affect important outcomes of animal migration, such as ecosystem services, agricultural productivity and the spread of pathogens, it is essential to further study how the environment affects animal physiology during migration and how animal physiology may influence the timing, scheduling and extent of animal migration. Moreover, quantifying the food requirements of migratory species and securing these requirements in habitats located throughout migratory corridors may aid the conservation of migratory animals for years to come (Wikelski and Cooke 2006; Wikelski *et al.* 2007).