Chapter 10

Working for a living: physiological and behavioural trade-offs in birds facing hard work

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Cost of reproduction

Experimental data generate a picture that birds are reluctant to increase energy expenditure (Wiersma & Tinbergen 2003: Chapter 5; Wiersma & Verhulst 2003a: Chapter 2; Wiersma et al. 2003a: Chapter 4). By decreasing night-time energy expenditure, body mass, flight costs or non-foraging activity birds are able to achieve appreciable savings on their daily energy budget. Apparently, spending more energy entails disadvantages. To find out what these are, one can look for effects of experimentally induced increases in work levels. The most widely used experimental avenue to achieve this is by manipulating brood size. By reducing or enlarging broods parent birds are ‘provoked’ to adjust the energy they put into food provisioning. The advantage of manipulating parental effort is that fitness costs can relatively easily be measured through their current, and additionally, future reproductive success. Although detrimental effects of increased parental effort on adult survival have been shown, the nature of the mechanisms involved remains elusive. The immune system is potentially an important mediator in the costs of reproduction (Sheldon & Verhulst 1996). To what extent energy plays a role in a trade-off with the immune system was the focus of Chapter 7 (Verhulst et al. 2003). We also explored a novel potential candidate that might play an important role in mediating costs of reproduction, namely the production of oxygen free radicals and associated molecules in energy metabolism processes (Wiersma et al. 2003b: Chapter 8). In addition to these factors we have examined an aspect of competition for time (Komdeur et al. 2002: Chapter 9).

Time reallocation as a cost of reproduction

In addition to the physiological trade-offs, such as those with immunological and antioxidant processes, time also has to be allocated between different activities. Time invested in parental effort cannot be spent on other activities, including social behaviour. Activities that may become affected are, for example, vigilance, increasing the risk of predation (Magnhagen 1991), or preening, increasing the risk of damage to feathers and infestation with parasites. Also the time devoted to conspecifics may be affected. Birds of (facultative) polygynous species, that spend more time on incubation, brooding or food provisioning, will have less time left for extra-pair liaisons and for mate guarding. The trade-off between pursuing extra-pair fertilisations and caring for the current clutch or brood will be affected by the size of the clutch and brood, because that is expected to affect how the clutch or brood is valued (in terms of fitness) by the parents (Delehanty & Oring 1993). Males attending large clutches or broods may have relatively less to gain from pursuing extra-pair copulations or attracting additional mates than males with small clutches or broods (Wright & Cuthill 1990; Whittingham 1993; Magrath & Elgar 1997; Magrath & Komdeur 2003).

As we expected, we found that the male starlings’ *Sturnus vulgaris* pursuit for additional mates was negatively related to manipulated clutch size (Komdeur et al. 2002:
Chapter 9). Paired starling males trying to attract an additional mate must first occupy another nestbox. They usually sing very close to or in this nestbox, using ‘wing-waving’ displays (Feare 1984; Eens et al. 1990) and carry green plant material into the nestbox when females are nearby (Gwinner 1997; Brouwer & Komdeur, submitted manuscript). The frequency of male singing close to an empty nestbox during incubation of the first clutch is positively associated with the acquisition of a secondary mate (Pinxten & Eens 1998). We found that when we had enlarged a clutch the males indeed spend more time incubating, while spending less time singing near and bringing green plant material to an adjacent empty nest box. This resulted in a negative relationship between clutch size and the probability of getting an additional female.

Immunosuppression as a cost of reproduction

It has been repeatedly shown that challenging the immune system with antigens leads to a reduction in parental effort. Råberg et al. (2000) showed that blue tits Parus caeruleus immunised with diphtheria-tetanus vaccine (DPT) reduced nestling feeding rate. DPT vaccinated pied flycatchers Ficedula hypoleuca had reduced breeding success (Ilmonen et al. 2000). House sparrows Passer domesticus injected with lipopolysaccharide were more likely to desert their nest, and those that continued breeding raised fewer fledglings (Bonneaud et al. 2003). Apparently, when challenged, resources that were earlier expended on brood provisioning are channelled into immune processes to eradicate the alien substances.

Conversely, parental effort has also been shown to suppress immune responses, further underlining the conclusion that reproductive effort and immune responses compete for the same resources. Nordling et al. (1998) and Cichoń et al. (1998) manipulated reproductive effort of collared flycatchers Ficedula albicollis and found a reduced response to Newcastle disease virus vaccine and sheep red blood cells (SRBC) antigens, respectively. Moreover, Nordling et al. (1998) also found an increased intensity of Haemoproteus infections in collared flycatchers when reproductive effort was increased, and this was associated with higher mortality rates.

Although it is often assumed that mounting an immune response is energetically costly, actually measuring this is difficult due to the many confounding effects (changes in behaviour, food intake, etc.). Lochmiller & Deerenberg (2000) conclude from the data available in the literature that the associated energetic costs of mild immune challenges represent increments of 15-30% of resting metabolic rate. Measurements of the basal metabolic rate (BMR) after immunisation showed a 9% increase in free-living great tits Parus major challenged with SRBC (Ots et al. 2001), 29% of RMR in house sparrows challenged with a cellular immune response eliciting mitogen (PHA) (Martin et al. 2003) and 27% of RMR in laboratory mice Mus musculus challenged with the antigen keyhole limpet hemocyanin (Demas et al. 1997). However, Svensson et al. (1998) did not find a significant BMR increase in captive blue tits challenged with DPT, nor did Henken & Brandsma (1982) challenging domestic chickens Gallus gallus and Hörak et al. (2003) challenging greenfinches Carduelis chloris with SRBC. We measured the...
energetic costs of a humoral immune response in zebra finches *Taeniopygia guttata* (Verhulst et al. 2003: Chapter 7). The birds were immunised with either SRBC, a novel antigen, or injected with a physiological salt (PBS) as a control. The metabolic rate was not affected by the antigen immunisation around the time when maximum antibody numbers circulate in the body, which is ca. 6 days after injection (Verhulst et al. 2003: Chapter 7). However, earlier, immediately after immunisation there was an effect on metabolic rate, although not in the expected direction (Figure 10.1). We found a reduction in metabolic rate that was greatest during the hour immediately following the immunisation (10%) and vanished during the following 9 h. Recently, a decrease in metabolic rate after immunisation has also been found in ruffs *Philomachus pugnax* (Luisa Mendes, personal communication). As far as we are aware, similar results have not been published before, but reductions in metabolic rate may also have remained undetected due to the rapid disappearance of the effect.

The decrease in metabolic rate after immunisation that we measured does not fit the assumption that the formation of antibodies is energetically costly. A reduction in energy expenditure, however, agrees with the often reported reduction in locomotory activity as an effect of an immune challenge (Bonneaud et al. 2003; Hőrak et al. 2003). This might be linked to the reduction in food intake which is also a typical effect of an immune challenge (Lochmiller & Deerenberg 2000). We did not detect an effect of immunisation on the zebra finches’ activity, though. The conflicting results of the effect of immunisation on metabolism as presented above, may be due to the differences in antigens used, dosage, health or condition of the animals, behavioural reaction to the immunisation, etc. It is important to bear in mind that energy will not be the only resource the immune system is drawing upon. The demand for proteins may be

![Figure 10.1](image-url)  
*Figure 10.1* Changes in metabolic rate (in W/bird) of control and immunised birds at different times after immunisation. On the x-axis time since immunisation is indicated, showing data separately for the afternoon (A), night (N), and morning (M). Data shown are mean differences (±SE) between the measurement at the indicated time, and the control measurement prior to immunisation.
high, since nitrogen balance during an immune reaction is usually negative (Lochmiller & Deerenberg 2000). In addition, immune reactions are accompanied by high levels of reactive oxygen species (ROS), such as free oxygen radicals, that are damaging to DNA, proteins and fat (von Schantz et al. 1999).

Although the formation of antibodies has been suggested to be costly (Fair et al. 1999; Williams et al. 1999), high costs may also arise from maintenance of the immune response generating system. In that case it could be expected that the immune system would be downsized when it is not expected to be needed or when other processes drawing from the same resources gain priority. Then, instead of being the result of direct competition for resources between antibody production and parental effort, the reproductive trade-off with immune function, as has been found in birds (Nordling et al. 1998), could also be an effect of a downsized, low-capacity, immune system.

We tested whether reproductive effort resulted in an immune system with a smaller capacity. Assuming that if a brood size manipulation led to changes in the size or physiological make-up of the antibody-producing system, we expected that the effect of the manipulation on antibody production would not immediately disappear when the birds suddenly did not have to take care of a brood anymore. Indeed, the reduction in immune activity lingered after experimentally relieving the birds from parental duties (Figure 10.2). This was not an effect of body mass, since, at the time of immunisation, this was not related to manipulated brood size. The relationship of the immune response with brood size that we found was very similar to that found by Deerenberg et al. (1997) who had immunised zebra finches with SRBC while still provisioning their brood (Figure 10.2). The suggested flexibility of the size of the immune system is supported by the variation found in spleen mass, and the associated cell-mediated immune activity, between the breeding and non-breeding season in various bird species (Møller et al. 2003). Possibly, the immune system possesses the same adaptive flexibility as many other organs, in particular the nutritional organs and the ‘exercise’ organs (e.g. heart, muscles), that vary in size according to their need (Piersma 2002; Biebach & Bauchinger 2003).

**Oxidative stress as a cost of reproduction**

In addition to immunosuppression, as a component of maintenance and repair processes that are traded-off with reproductive effort, we studied protection against oxidative damage. Reactive oxygen species (ROS), i.e. molecules containing or generating oxygen free radicals, cause damage to fat, protein and DNA molecules, thereby impairing the functioning of cells. The damaging potential of ROS is termed oxidative stress. Because all metabolic processes that use oxygen, including the immune and detoxification systems, are continuously producing ROS (von Schantz et al. 1999; Finkel & Holbrook 2000), oxidative stress is inescapable. Fortunately, the effects of oxidative stress can be alleviated by a suite of endogenous and dietary anti-oxidants that scavenge for these noxious molecules (Ahmad 1995). In parallel with immunosuppression, we
hypothesised that endogenous antioxidant activity might be suppressed when reproductive effort increases, due to the costs involved in producing the antioxidants. This then could result in a decline in future reproductive output. Experimentally increasing parental effort generally results in a decline in future reproductive potential. Interpreting this decline as due to an acceleration of senescence (Gustafsson & Pärt 1990; Kirkwood & Austad 2000), links the studies on ageing with those on reproductive costs.

Oxidative stress has been extensively studied in the context of ageing and degenerative diseases (Ahmad 1995; Austad 1997), mostly using a proximate approach, or, when in an evolutionary context, usually on an interspecific level (see Box). However, the interaction with physical effort, and more particular parental effort, may make it an essential component of life-history evolution and hence life-history decisions of individuals. We showed that captive zebra finches rearing experimentally created large broods showed lower relative activities of the antioxidant enzymes SOD and GPx than zebra finches with small broods (Wiersma et al. 2003b: Chapter 8). The antioxidant activity was expressed relative to the oxygen consumption rate, because that determines, at least in part, the rate at which ROS are produced. This implies that a higher reproductive effort incurs the cost of less protection against oxidative damage, leading to more damage to DNA, proteins and fats. However, changes in only one component of the oxidative stress complex are difficult to interpret. To assess the potential rate at which damage might occur information on the ROS formation rate is needed as well. We measured 2 of the 3 antioxidant enzymes, but other, mostly exogenous, antioxidant agents exist (Clarkson & Thompson 2000). Therefore, measurements on the actual oxidative damage will be essential for the interpretation of experimental results.

Figure 10.2 Proportion (± SE) of birds with SRBC-antibodies six days after immunisation (sexes pooled). Open dot: Proportion responders when parents were immunised after the young were removed (for brood size 2, 4, 6, n = 34, 31, 32 respectively). Immunisation took place one day after the young were removed, closed dot: Proportion responders when young remained present shown for comparison (from Deerenberg et al. 1997).
**BOX: The disposable soma theory**

Senescence is a decline in the state of the organism with age that is manifested through a reduction in the rate of survival and a decline in reproductive output rate (Partridge & Barton 1996). Theories formulated to explain variation in senescence, and presumably rates of oxidative damage, are mostly of a proximate nature. The disposable soma theory, formulated by Kirkwood (1977; Kirkwood & Holliday 1979), intends to explain the variation in ageing rates in evolutionary terms. It states that there is a trade-off between resources allocated to reproduction and to damage prevention and repair processes, and that this trade-off is mediated through extrinsic mortality rates. For example, when rates of extrinsic mortality are high, spending a great deal of resources on maintenance and repair would be a waste, because death will strike soon anyway. If more resources would have been spent on reproduction instead, fitness would have been higher. The disposable soma theory also supports comparative results by giving a functional explanation for the low rates of ageing and long life spans of species that have to some extent succeeded in escaping predators, namely birds and bats (Austad 1993). Birds have a four times longer maximum life spans than mammals with the same BMR or body mass (Austad & Fischer 1991).

**Energy management under demanding conditions**

If energy is a limiting resource for important life-history traits, it is advantageous to manage energy as economically as possible. In this view it is worthwhile to measure energy budgets, because this may give insights into the behavioural decisions that animals make. A good example of the use of an energy budget in explaining behavioural decisions and limitations is given by de Leeuw’s (1997) study on diving ducks wintering in the (Lake) IJsselmeer. By quantifying the costs for diving, flying and maintenance he defines limits to distances between roost and foraging sites. Another good example is the study on kestrels *Falco tinnunculus* by Masman *et al.* (1988), quantifying the energy budget throughout the annual cycle and approximating the energetic consequences of changes in the annual timing. In general, knowledge on energy budgets makes it possible to consider behavioural alternatives, both on a daily and annual scale, to make statements about optimisation of behaviour (i.e. diet, time budgets, reproduction, etc.) and maximisation of fitness.

To balance their daily energy budget animals have to gather food during their active period to cover the energy expenditure of the whole day and to store energy to cover the energy expenditure during the inactive period. The most straightforward way to balance the energy budget in demanding periods (e.g. when food availability is low, at low temperatures, or during build up of energy stores) is by extension of the foraging time or reduction of energy expenditure during the inactive period (McNab 2002).
Extension of the foraging time to increase the daily energy intake is limited by the available foraging time and the rate at which food can be processed (Kirkwood 1983; Weiner 1989; Lindström 1991; Kersten & Visser 1996). Increasing the food processing rate requires that the digestive system is modified to cope with the higher processing rates. Remarkable examples of the flexibility of the digestive system have been found in a range of species (Piersma & Lindström 1997). Because BMR partly reflects the size of metabolically active organ systems (the ‘metabolic machinery’), a size increase of the digestive system will usually manifest itself by a BMR increase (Piersma 2002).

This process of adapting to (or even anticipating) periods of demanding conditions by enlarging particular organ systems seems to contrast with processes in animals that reduce their metabolic rate when they encounter demanding conditions. Reducing BMR by hypothermia when thermoregulatory demands are high, is well documented and seemingly quite common in small birds (Reinertsen 1989; McKechnie & Lovegrove 2002). But other energetically demanding conditions, for example when facing high foraging costs or when caring for a brood, have not received much attention when it comes to physiological adjustments. Among the few reported cases are reductions in nocturnal energy expenditure after a reduction in foraging success in hummingbird Trochilidae species (Tiebout 1991; López-Calleja et al. 1997), birds renowned for their hypothermia abilities (Krüger et al. 1982; McNab 2002). Yet, mass, and concurrent, BMR reductions that are not likely to be completely explained by hypothermia have been found in starlings (Bautista et al. 1998; Wiersma et al. 2003a: Chapter 4) and zebra finches (Deerenberg et al. 1998; Nudds & Bryant 2001; Wiersma & Verhulst 2003a: Chapter 2) when forced to increase the daily flight time. This suggests that BMR reductions (whether or not resulting from body composition changes) in response to high energetic demands are more wide-spread than was earlier taken into consideration.

Moreover, the reductions in energy expenditure as shown in zebra finches and starlings are not restricted to the night: in response to a reduction of the foraging reward rate, the energy expended during the entire day (DEE) may be economised as well (Deerenberg et al. 1998; Bautista et al. 1998; Wiersma & Verhulst 2003a: Chapter 2). That animals, forced to work harder for their food, reduce their total energy expenditure is a startling result, and makes one wonder whether the flexibility in the energy budget has been appreciated to its true extent. Many mammals and birds spend more than 60% of their active period at rest (Herbers 1981), and therefore changes in metabolism during this period have a potential for appreciable savings.

**Joint effects of work on BMR and DEE**

To study the effects of varying work levels on the energy budget of individual animals, partitions of this budget have to be measured simultaneously at different work loads. This, however, is a rare amalgamation. Often DEE is measured under different conditions, while BMR is estimated from allometric relationships or from prior measurements. When effects on BMR are measured, often DEE is not of direct interest. DEE values from experimental studies where work levels were manipulated, either by fora-
gging reward rate or parental demand, and where the effects on both DEE and BMR (or SMR) and on body mass were measured are shown in Figure 10.3. The figure shows that when birds increase the time spent flying and foraging, DEE does not necessarily increase too. In some cases DEE actually decreases with increases in work levels (st1, zf1-3). Work and DEE are therefore not interchangeable terms. Comparing the DEE data with a large number of field measurements assembled by Bryant & Tatner (1991) shows that the energy expenditure levels are not particularly high (Figure 10.4). Only the zebra finches (zf3) and our starlings (st2), both flying for food, had reasonably high energy expenditure rates. Our starling data also happen to represent the largest DEE increase of the data set and actually the starling was the only species that showed an increase in the mass-specific DEE (not shown).

Figure 10.5A-C shows the concurrent changes in body mass, mass-specific BMR (i.e. BMR divided by body mass), BMR and DEE in response to an increase in work level. To account for between-experiment differences between overall work levels and for between-species differences, the changes in DEE are shown in percentages instead of absolute values. Changes in (mass-specific) BMR are also expressed in percentages, to allow for between-species comparisons. Body mass often decreased; and in one starling study it did plummet quite dramatically (st1; Figure 10.5A). DEE and body mass were not associated in a straightforward way: changes in mass and DEE seem to be related according to a quadratic relationship. Clearly, there is a great deal of flexibility in both DEE and (mass-specific) BMR, and they can change in either direction with increasing work levels (Figure 10.5B, C). The positive association between changes in mass-specific BMR and DEE borders significance. The changes in mass-specific BMR are most likely

![Figure 10.3](image-url)

**Figure 10.3** Daily energy expenditure of birds at different manipulated work levels. zf: zebra finches, zf1: Wiersma & Verhulst 2003a: Chapter 2, zf2: own unpublished results from manipulation of foraging reward rate by mixing chaff through seeds, zf3: Deerenberg et al. 1998, st: starling, st1: Bautista et al. 1998, st2: changes from low to intermediate and intermediate to high foraging reward rates (Wiersma et al. 2003a: Chapter 4), gt: great tit (Wiersma & Tinbergen 2003: Chapter 5), mt: marsh tit (Nilsson 2002).
due to body composition or body temperature changes. In most experiments BMR of the birds decreased and the marsh tit \textit{Parus palustris} (mt) was the only species that increased BMR (Nilsson 2002). The association between BMR and DEE changes seems to be positive, confirming the generally reported positive relationships between BMR and DEE (Daan et al. 1991; Koteja 1991; but see Ricklefs et al. 1996). Nudds & Bryant (2001) also measured a reduction in BMR in zebra finches that were stimulated to increase their daily flight time. Unfortunately they did not measure DEE of these birds.

When analysing the association between BMR and DEE there might be a problem of inherent dependency due to the fact that BMR is incorporated in DEE (Ricklefs et al. 1996). To compare independent parameters, BMR (in kJ/d) can be subtracted from DEE, resulting in the energy expenditure of activity (ACT). The resulting data are shown in Figure 5D. ACT has no apparent association with BMR, suggesting that DEE and BMR are affected independently. Whether this is the appropriate combination to consider depends on how BMR and DEE are functionally related. One option is that DEE is ‘generated’ by an intensification of the maintenance processes that make up BMR (‘shared pathways model’ in Ricklefs et al.’s (1996) terminology). Alternatively, DEE is the summation of BMR and ACT, where BMR and ACT use separate metabolic pathways (‘parti-
tioned pathways model’). Ricklefs et al. (1996) warn that in the second situation BMR and DEE are statistically dependent (an increase in BMR inevitably results in an increase in DEE), while in the first situation this would not be the case. Unfortunately, Ricklefs et al. (1996) do not specify which physiological and biochemical mechanisms might be involved in creating ‘different physiological states’ for active and resting animals.

Suggested mechanisms resulting in a shared pathway are the make-up and size of the organs that constitute the metabolic machinery of an organism (Daan et al. 1990; Piersma et al. 1996a; Piersma 2002). In this view, the make-up and size of the organs are related to their minimum and sustained metabolic output, reflected in BMR and DEE. This scenario of a shared pathway results from a multiplicative model, where DEE can be considered an ‘inflated BMR’ with the extent of inflation depending on the initial size of the ‘BMR-balloon’. In this multiplicative scenario, that could be termed a ‘shared sources model’, BMR and DEE are dependent, as in the additive ‘partitioned pathways model’. Both scenarios make a case for analysing the association between BMR and ACT instead of DEE (Figure 10.5D). A ‘shared sources model’ is compatible with the ‘aerobic capacity’ hypothesis (Bennett & Ruben 1979), stating that variation

\[ r = -0.85, P = 0.017, \text{DEE and mass-specific BMR: } r = 0.66, P = 0.077, \text{DEE and BMR: } r = 0.58, P = 0.14, \text{ACT and BMR: } r = 0.18, P = 0.67. \]
in maximum sustained metabolic rates corresponds with the capacity of underlying metabolic and physiological systems and is therefore functionally linked with BMR (Drent & Daan 1980; Peterson et al. 1990; Daan et al. 1991). This link would be caused by the relatively high metabolic rates of some organs (in particular heart, kidney, liver and intestines) that vary in size in keeping with long-term energetic demands (Daan et al. 1990; Piersma et al. 1996a; Piersma 2002).

Explaining the pattern(s) in Figure 10.5 is complicated by the mixture of different experimental systems used that may have led to different food intake rates. First, there is a difference in the type of work: brood food provisioning or foraging. The birds caring for a brood tend not to decrease BMR and body mass with increased work levels, while the birds working for food do decrease BMR and body mass with increased work levels (Figure 10.5A, C), although this difference is not apparent in mass-specific BMR (Figure 10.5B). Second, when foraging involves mainly flying, foraging decisions can have large consequences for the energy expenditure, and hence food intake may differ from birds foraging with cheaper locomotory means. In the experiments where the birds had to fly for food (zf3, st1 and st2), DEE had increased most, while mass tended to decrease most (Figure 10.5). Third, the presence or absence of variation in the foraging reward rates can have important consequences (Fotheringham 1998), as will be discussed below.

Because a large brood size is associated with a high parental effort, we hypothesised that having large exercise organs could be beneficial for raising successful nestlings. Because of the link between BMR and the size of the exercise organs (Piersma 2002), we measured whether birds with a high BMR would have a high reproductive output (Wiersma & Verhulst 2003b: Chapter 6). (Because the measurement temperature was slightly below the lower critical temperature, we refer to these measurements as SMR, not BMR.) In both sexes, SMR and manipulated brood size were not correlated. Also the change in SMR from just before nest building to brood provisioning was not affected by manipulated brood size, nor was SMR before nesting correlated with original clutch size. Nilsson (2002) reported an increase in BMR in marsh tits with experimentally enlarged broods and we did not find such an effect in great tits (Wiersma & Tinbergen 2003: Chapter 5; Figure 10.5C). It is possible that the increases in parental effort in zebra finches and great tits were not strong enough to necessitate an enlargement of exercise organs, but on the other hand the marsh tits had a similar increase in DEE than the great tit (Figure 10.3). Birds that rely stronger on flight during food provisioning (e.g. many kestrels Falco spec. and swallows Hirundo spec.) might show more pronounced effects of brood size on body composition and BMR.

Decisions concerning energy management may differ between the reproductive and the non-reproductive season. This might explain why BMR of the birds working for their own food decreased their BMR while BMR did not change in the free-living great tits studied by us (Wiersma & Tinbergen 2003: Chapter 5) and increased in the marsh tits studied by Nilsson (2002) at elevated levels of parental effort (Figure 10.5C). One could argue that the increase in work levels that was achieved by enlarging the brood size may have been modest, perhaps not necessitating the saving of energy during the night. However, a BMR increase, as measured in the marsh tits, would then not be
expected. Energy savings may bear a direct fitness cost, because suppressing DEE would not enhance the nestlings’ growth and condition, while the potential gain in the future reproductive output is unlikely to outweigh the costs incurred by the current brood, even more so, given that there is a risk of not having a next brood at all.

**Variability in the foraging reward rate**

Fotheringham (1998) studied starlings in cages where they had to collect food by flying back and forth between two perches. By manipulating the number of flights needed to receive food he could change the food reward rate (i.e. foraging efficiency) and measure the consequences for daily food intake, body mass, activity patterns and more. He also manipulated the variability of the food reward rates by adding random variation to the average number of flights needed to obtain food. This revealed major effects: when the foraging reward rate was fixed (without variation and thus entirely predictable) a decrease in the reward rate resulted in a decrease in daily food consumption and body mass, while using variable food reward rates (random but with fixed mean value), daily food consumption and body mass were not reduced. The difference is explained in terms of cognitive processes: although the average intake rate while foraging would have been identical, a variable success rate seems to offer a preferred stimulus to forage. It may in some way be related to differences in memorising fixed versus variable time intervals, as hypothesised by the scalar expectance theory (Giraldeau 1997). The difference between fixed and variable reward rates was actually already a research topic fifty years ago in the psychology tradition typified by application of the ‘Skinner Box’ (Ferster & Skinner 1957).

Whatever the mechanism behind the effect of variability, it is likely that variable foraging reward rates are the norm under natural conditions, while experiments are typically conducted using fixed reward rates (Table 10.1). This makes it important to find out whether nocturnal and/or day-time energy expenditure reductions also occur under more natural foraging conditions. We compared energy budgets from Bautista *et al.*’s (1998) starling experiment, who applied fixed reward rates, with those of our starlings that experienced variable reward rates (Wiersma *et al.* 2003a: Chapter 4). From Fotheringham’s (1998) results we expected that, because of the variable reward rates, DEE would not decrease with a decreasing reward rate, as was the case in Bautista *et al.*’s (1998) study. Actually, DEE increased from 154 to 220 kJ/d with a decreasing reward rate (Figure 10.6, and ‘st2’ in Figure 10.5). Our starlings further showed a major decrease in body mass (Figure 10.5A), probably largely due to reduced fat reserves and partly due to reduction of the flight muscle size (Wiersma *et al.* 2003a: Chapter 4). The starlings in the study of Bautista *et al.* (1998) also strongly decreased their body mass and reached levels that must have been close to their starvation mass. At the same time mass-specific BMR decreased with decreasing fixed reward rates, while this remained constant in our starlings (Figure 10.5B). Apparently, in these two studies the birds had different body compositions at the high work levels. The starlings kept with variable reward rates also achieved higher working levels (3.7xBMR) than the birds in the other studies. It seems that with fixed reward rates the starlings are
merely starving while with variable reward rates the birds adjust to the higher demands. Because Bautista et al.’s (1998) starlings had an average DEE of 144 kJ/d, which is quite similar to Wiersma et al.’s (2003a: Chapter 4) starlings, differences in overall work levels in the two experiments seem not to be responsible for the different results. Note, however, that the experimental effects of work on DEE have shown that ‘work’ and DEE are not synonymous (Figure 10.3).

The opposite effect on DEE and on body mass in our starlings compared to the results from experiments using fixed reward rates in zebra finches, starlings and two hummingbird species (Tiebout 1991; Deerenberg et al. 1998; Bautista et al. 1998; Figure 10.5C) support Fotheringham’s (1998) conclusions. However, two experiments with zebra finches, manipulating foraging reward rate, also applied variable reward rates (by mixing chaff through seeds), while DEE and body mass decreased with decreasing foraging reward rate (zf1 and zf2 in Figure 10.5). Clearly, the presence or absence of variability in the food reward rate is not an adequate explanation for the variation in the effect of foraging reward rates on DEE in all situations.

Table 10.1 Summary of DEE measurements from experiments with birds or mammals in which foraging reward rate was manipulated in a closed economy system. The responses to a decrease in foraging reward rate are shown. DEE may have been inferred from daily food intake measurements. Reward rates could either be fixed (without variation) or variable (with variation but with fixed mean). Increases and decreases are depicted with ‘+’ and ‘-‘, while ‘0’ means no change.

<table>
<thead>
<tr>
<th>species/dietary style</th>
<th>reward rate</th>
<th>DEE</th>
<th>source</th>
</tr>
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<tbody>
<tr>
<td>starling, <em>Sturnus vulgaris</em></td>
<td>variable</td>
<td>+</td>
<td>Wiersma et al. (2003a):Chapter 4</td>
</tr>
<tr>
<td>starling, <em>Sturnus vulgaris</em></td>
<td>variable</td>
<td>0</td>
<td>Fotheringham (1998)</td>
</tr>
<tr>
<td>zebra finch, <em>Taeniopygia guttata</em></td>
<td>variable</td>
<td>0</td>
<td>Lemon &amp; Barth (1992)</td>
</tr>
<tr>
<td>starling, <em>Sturnus vulgaris</em></td>
<td>fixed</td>
<td>-</td>
<td>Bautista et al. (1998)</td>
</tr>
<tr>
<td>zebra finch, <em>Taeniopygia guttata</em></td>
<td>fixed</td>
<td>-</td>
<td>Deerenberg et al. (1998)</td>
</tr>
<tr>
<td>fork-tailed emerald, <em>Chlorostilbon canivetii</em></td>
<td>fixed</td>
<td>-</td>
<td>Tiebout (1991)</td>
</tr>
<tr>
<td>house mouse, <em>Mus domesticus</em></td>
<td>fixed</td>
<td>-</td>
<td>Perrigo (1987)</td>
</tr>
<tr>
<td>deer mouse, <em>Peromyscus maniculatus</em></td>
<td>fixed</td>
<td>-</td>
<td>Perrigo (1987)</td>
</tr>
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</table>
Energy saving mechanisms

Although the increase in DEE with a lowering of the food reward rate in our starlings does not reveal energy saving measures, this is far from the truth. Savings have actually been achieved in key components of the energy budget, but they have become obscured in the energy budget’s total. With the detailed measurements on the time-energy budget of the starlings (Figure 10.6) we are able to calculate alternative scenario’s. We reconstructed the energy budget of a starling working for food under poor conditions, while it would have retained the body mass actually measured under the rich regime. Because the higher body mass results in a higher BMR and in higher flight costs, the energy budget would rise significantly. Without the savings the energy budget under poor conditions would increase not be 220, but 353 kJ/d, which equals ca. 4.7xBMR (Figure 10.6, rightmost bar). Partly, this predicted increase would be due to the higher resting metabolic rate (including BMR), but above all, most extra energy is spent in flight. This is the result of the greatly extended foraging time in combination with the higher flight costs, resulting from the higher body mass (Wiersma et al. 2003a: Chapter 4). The increase in energy expenditure will amplify energy expenditure further, because this demands an additional increase in foraging time.

Figure 10.6 Daily energy budget and flight time of captive starlings at different foraging reward rates. Seven birds were kept alternately in a rich, intermediate or poor environment where they had to fly, respectively, 2, 4 or ±6 times back-and-forth between perches that were 5 m apart to obtain food. E_fly is the energy spent during flight, BMR_night the energy spent during the 10-h night on a BMR level, while E_night is what is spent in total during the night. E_nonfly is the energy spent during day-time while not flying. The rightmost bar represents the predicted energy budget of a bird under poor conditions that has retained the same mass, BMR and flight costs as a bird under rich conditions. Also its predicted flight time is shown. See Wiersma et al. (2003a: Chapter 4) for more details.
Zebra finches foraging at different reward rates showed a small but significant decrease in DEE with increasing work levels (Figure 10.7, zf1 and zf2 in Figure 10.5). These birds did not have to fly large distances for their food, but were searching for seeds between large quantities of chaff. Therefore, foraging was not as energetically laborious as in the case of the starlings. Body mass of the birds was not affected by food reward rate, and presumably, lowering body mass would have had no significant effect on the foraging costs. BMR and mass-specific BMR were not related to food reward rate either. Foraging time increases considerably with decreasing foraging reward rates, as did the energy spent on foraging, but total energy expenditure during daytime nevertheless decreased (Figure 10.7). Although BMR did not vary with food reward rate, the total energy expenditure during the night decreased with decreasing reward rate. At temperatures below the thermoneutral zone, SMR and mass-specific SMR decreased with decreasing reward rate too, implying that the birds might have lowered their body temperature. The energy expenditure during the day is mainly adjusted by the energy spent on other activities (labelled ‘remainder’ in Figure 10.7). This was confirmed by activity measurements using infrared sensors.

An overview of mechanisms that can be used to control energy expenditure is given in Table 10.2. Several of these methods have been shown to be used by birds that were pressed to perform. Reducing time spent on costly activities has the greatest potential for economising energy expenditure, especially when the bird can cut back on flight time. A reduction in body mass is often shown when foraging reward rates decrease. This can have a considerable impact on flight costs. By lowering body mass, resting metabolism may be reduced significantly too, but this depends on the nature of the

Figure 10.7 Energy budgets (bars) and foraging times (dots: means ±SE) of zebra finches during the 10-h day-time period. The birds were foraging for seeds that were offered ad libitum, or mixed with chaff according to chaff/seed mass-ratios of 1 or 3 to manipulate foraging reward rates. Energy expenditure was measured by respirometry at 22°C. Average BMR was 0.216 W and independent of foraging reward rate. The partition of the energy budget labelled ‘remainder’ is made up of the energy expenditure not accounted for by resting or foraging. See Wiersma & Verhulst (2003a: Chapter 2) for details.
mass loss. If only stores are usurped, that mainly consist of fat with a very low metabolism (Scott & Evans 1992), BMR will not be affected. Size reductions of reserves (muscle tissue) and of the ‘metabolic machinery’ are necessary to reduce BMR, but these obviously may comprise major consequences for the animal. In addition, the mass-specific metabolism of the ‘metabolic machinery’ may be altered (Weber & Piersma 1996), but probably, the achieved saving would be negligible. Hypothermia is regularly used in some bird species (McKechnie & Lovegrove 2002), and seems to be an effective way of reducing energy expenditure during the resting phase. It also seems to be mainly restricted to small birds, presumably because they can increase their body temperature quicker than large-sized birds. We have some indications that birds in our foraging experiments might have reduced night-time body temperature to some degree (Wiersma & Verhulst 2003a: Chapter 2; Wiersma et al. 2003a: Chapter 4), but we are lacking actual measurements.

In this thesis I restricted myself to a proximate view of the costs of reproduction, sometimes even outside a reproductive setting. We studied how energetic constraints might affect different trade-offs, and hypothesise how this could affect life-history traits. Nevertheless, although fitness is the currency by which we ultimately have to explain animal physiology and behaviour, without knowledge of how various resources are divided between physiological processes and behavioural activities, a real understanding of life-history theory will not emerge. In this thesis I have touched upon the changes in energy management and a few critical, physiological trade-offs under different conditions, to learn about the role of energy in ‘physiological decisions’. The substantial variability in the energy budget that emerged has to be considered when making predictions about animal behaviour. But unfortunately we often do not understand the variation we see, such as that in Figure 10.5. Will a bird economise when it is forced to work harder for its food? Perhaps even to such an extent that DEE decreases? The answer is still not evident. Fortunately, progress might be expected with fairly basic experiments, such as studying a single species’ foraging intensity and daily energy budget while manipulating along the various axes that make up the environment.

Table 10.2 Animals working hard for a living: overview of measures to economise energy expenditure. The targets between brackets are only weakly affected by the particular method of saving.

<table>
<thead>
<tr>
<th>Saving measures</th>
<th>Saving targets</th>
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<tbody>
<tr>
<td>reduce time spent on costly activities (e.g. foraging)</td>
<td>DEE</td>
</tr>
<tr>
<td>reduce size of stores (e.g. subcutaneous fat)</td>
<td>locomotory costs; BMR</td>
</tr>
<tr>
<td>reduce size of reserves (e.g. pectoral muscles)</td>
<td>locomotory costs; BMR</td>
</tr>
<tr>
<td>reduce body temperature</td>
<td>BMR</td>
</tr>
<tr>
<td>reduce size of ‘metabolic machinery’ (e.g. intestines, liver)</td>
<td>BMR; (locomotory costs)</td>
</tr>
<tr>
<td>reduce mass-specific metabolism of ‘metabolic machinery’ (e.g. liver, kidneys)</td>
<td>BMR</td>
</tr>
</tbody>
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