

## Why marathon migrants get away with high metabolic ceilings: towards an ecology of physiological restraint

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### Summary

**Animals usually are not willing to perform at levels, or for lengths of time, of which they should be maximally capable. In stating this, exercise performance and inferred capacity are gauged with respect to body size and the duration of particular levels of energy expenditure. In such relative terms, the long-term metabolic ceiling of ca. 7 times basal metabolic rate in challenged but energy-balanced individuals may be real and general, because greater performance over long periods requires larger metabolic machinery that is ever more expensive to maintain. Avian marathon migrants relying on stored fuel (and therefore not in energy balance) that work for 9 consecutive days at levels of 9–10 times basal metabolic rate are exceptional performers in terms of the ‘relative expenditure’ on ‘duration of a particular activity’ curve nevertheless. Here I argue that metabolic ceilings in all situations (energy balanced or not) have their origin in the fitness costs of high performance levels due to subsequently reduced survival, which then precludes the possibility of future reproduction. The limits to performance should therefore be studied relative to ecological context (which includes aspects such as pathogen pressure and risk of overheating), which determines the severity of the survival punishment of over-exertion. I conclude that many dimensions of ecology have determined at which performance levels (accounting for time) individual animals, including human athletes, begin to show physiological restraint. Using modern molecular techniques to assay wear and tear, in combination with manipulated work levels in different ecological contexts, might enable experimental verification of these ideas.**

Key words: athletes, BMR, disease ecology, endurance exercise, energetics, heat stress, life history decisions, metabolic rate, migration, trade-off, telomere shortening.

### Introduction

By the time the team of Robert Falcon Scott died on the way back from a successful attempt to reach the South Pole in the cold Antarctic summer of 1911/12 (it was also a failed attempt to be there first), they had been man-hauling sledges for some 159 consecutive days, of which the last 60 were in exceptionally bitter cold. They covered a total distance of 2500 km and expended an estimated total of 4.2 million kJ each. According to Noakes (Noakes, 2006; Noakes, 2007) this was ‘one of the greatest human performances of sustained physical endurance of all time’. Scott’s team, and other teams travelling across the Antarctic continent at the time (Noakes, 2006), certainly spent far more energy than endurance runners and cyclists during famous lower latitude sporting events. However, it was the long duration that made the polar exertions so physiologically and psychologically demanding.

For valid comparisons we have to recalculate performance levels over intervals of, for example, 1 day (Stroud, 1998). Table 1 makes clear that polar explorers, who expended 25–30 MJ per day, always incurred substantial energy deficits. They ate only 60–70% of their daily energy requirements and, not surprisingly, lost about a kilogram every 4 days. For this reason, Stroud (Stroud, 1987b) believes that starvation actually killed the men in Scott’s party. In fact, Stroud and Fiennes almost killed themselves during their attempt to ski across the whole of Antarctica in 1992/93 (Stroud, 2004). Before their eventual rescue they had lost over 20 kg each. Although humans can endure several days of heavy physical

exercise with limited food rations (Guezennec et al., 1994; Hoyt et al., 2006), by day 95 of the expedition Stroud and Fiennes showed considerable reductions in muscle power, reductions that were linked to marked decreases in cytoplasmic and mitochondrial enzyme activities (Stroud et al., 1997). Two other studies on endurance exercise levels that approach or exceed those of the Arctic explorers, on Tour de France cyclists (Westerterp et al., 1986) and Swedish cross-country skiers (Sjodin et al., 1994), respectively, show somewhat smaller deficits, or even complete energy balance. The data for the Swedish skiers (Table 1) suggest that an adult human male who expends 30 MJ per day must be close to his ‘metabolic ceiling’, i.e. the maximum energy output that can possibly be sustained by an organism that eats enough to stay in energy balance.

The energy expenditure of the sled dogs that in 1911/12 successfully pulled the team of Roald Amundsen from the Antarctic rim to the South Pole and back over a period of 97 days was reconstructed to be approximately 21 MJ day<sup>-1</sup> (Orr, 1966; Pugh, 1972; Campbell and Donaldson, 1981). Although this is a high level, Alaskan sled dogs racing for 70 h in bitter cold conditions expended twice that much [47 MJ day<sup>-1</sup> (Hinchcliff et al., 1997)]. This expenditure, however, comes with considerable costs, including the death of dogs during the races. The level of performance asked from these dogs, even when trained, has led to gastric ulcers and increased intestinal permeability (Davis et al., 2005; Davis et al., 2006), as well as some degree of muscle damage (Hinchcliff et al., 2004).

Table 1. Summary of human studies (male subjects only) on energy intake and expenditure per individual during prolonged intense exercise, and the extent to which energy intake during these periods could cover expenditure

Event	Duration (days)	Energy intake (MJ day <sup>-1</sup> )	Energy expenditure* (MJ day <sup>-1</sup> )	Deficit (MJ day <sup>-1</sup> )	Reference
Captain Scott's polar party	>150	ca. 18	ca. 25	7	Stroud, 1987b
South Pole expedition	70	21	25	4	Stroud, 1987a
North Pole expedition	48	19	30	11	Stroud et al., 1993
Trans-Antarctic expedition	First 50	20	32	12	Stroud et al., 1997
	Last 45	22	21	-1	
Tour de France	20	>25	34	<9	Westerterp et al., 1986
Military mountain training	11	13	21	8	Hoyt et al., 1991
Military Arctic training	10	>11	18	<7	Jones et al., 1993
Military jungle training	7	17	20	3	Forbes-Ewan et al., 1989
Cross-country skiing	7	31	30	-1	Sjodin et al., 1994
Sahara multi-marathon	7	15	27	12	Stroud, 1998

Expanded from Stroud (1998).

\*Most expenditure values are based on isotope dilution studies [see Speakman for the complete introduction (Speakman, 1997a)]. However, the value for the 70 day South Pole expedition is based on an energy balance evaluation. All values for Scott's party were estimated. In view of the uncertainties around each of the estimates, values presented are rounded to the nearest MJ. Human subjects tend to underreport their own food intake; where such effects were most obvious, reported energy intake estimates are minima.

Ever since Krogh (Krogh, 1916) started measuring metabolic rates of animals – that is, the metabolic rate of homeotherms under standardized conditions: inactive, in the thermoneutral temperature zone, and in the absence of digestion, growth, moult, ovulation or gestation – animal physiologists have used this strictly defined level of energy expenditure, the basal metabolic rate or BMR, as the yardstick for comparisons between different activity levels within and between species (King, 1974; McNab, 2002). In effect, the use of BMR as the yardstick for comparisons between individuals, species and ecological contexts (Piersma et al., 2003; McKechnie et al., 2006), as I will do repeatedly in this perspective, amounts to accounting allometrically for body size-related variation in the levels of energy expenditure under the assumption of identical slopes – on body size – of BMR and whatever expenditure level it is compared with [see Calder (Calder, 1984) and Peters (Peters, 1983) for two classic treatises using this approach, and Karasov and Martínez del Río (Karasov and Martínez del Río, 2007) for a modern review of the ideas].

Although BMR of humans varies widely as a function of size, sex and age (e.g. Henry, 2005; Froehle and Schoeninger, 2006; Wouters-Adriaans and Westerterp, 2006), and it may even vary within individuals (Johnstone et al., 2006), Henry's (Henry, 2005) compilation of 10,552 human BMR values suggests that for an athletic Caucasian man, a BMR of 6–7 MJ day<sup>-1</sup> would represent a fair estimate. On this basis, polar explorers would have lived at a level of ca. 4 times BMR (Table 1), whereas the well-fed athletes taking part in the Tour de France and cross-country skiing would have exceeded this level and probably come closer to 5 times BMR.

#### What do metabolic ceilings represent?

Realizing that maximal effort by hard-working animals may well reflect a compromise between physiological capacity (maximal physical output) and the 'willingness' to incur elevated mortality risks due to short- and long-term consequences of increased performance, Drent and Daan (Drent and Daan, 1980) introduced the concept of 'maximal sustained working levels', the aerobic capacity for work of animals limited by evolutionarily shaped physiological constraints (expressed as multiples of BMR; Fig. 1). In this concept, animals that ignore this 'physiological warning level' would lose body condition and face precipitous increases in

mortality risk. A similar evolutionary concept was earlier formulated by Royama (Royama, 1966). He called it the 'optimal working capacity', defined as the energetic performance level of parents beyond which they would suffer from increased risk due to physical fatigue, infection and predation. Summaries of the available literature following Drent and Daan (Drent and Daan, 1980) have confirmed that only a small proportion of the published ratios between sustained metabolic rate and BMR of birds and mammals, examined in situations where they work hard, are higher than 5 (Bryant and Tatner, 1991; Hammond and Diamond, 1997; Speakman, 2000). A 'sustained metabolic scope' of 5 may therefore represent a reasonable first guess at a maximal physiological working level of seriously challenged animals that still maintain energy balance.

Peterson and colleagues (Peterson et al., 1990) were the first to draw a representation of the empirical finding that the longer an

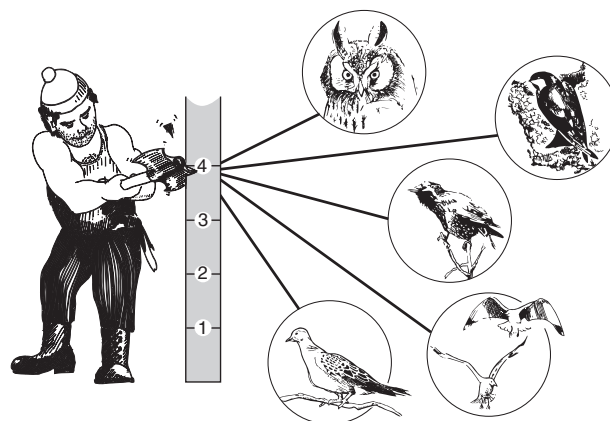


Fig. 1. Original version of the cartoon in which Drent and Daan (Drent and Daan, 1980) indicated that what they called 'maximum sustained working level' of parent birds tending nestlings usually approached values close to 4 times basal metabolic rate, a level also achieved by humans doing heavy labour such as lumberjacks (Brody, 1945). Their bird data referred to long-eared owls *Asio otis* (Wijnandts, 1984), house martins *Delichon urbica* (Bryant and Westerterp, 1980), starlings *Sturnus vulgaris*, glaucous gulls *Larus glaucescens* and turtle doves *Streptopelia risoria* (Brisbin, 1969). Cartoon reproduced with permission.

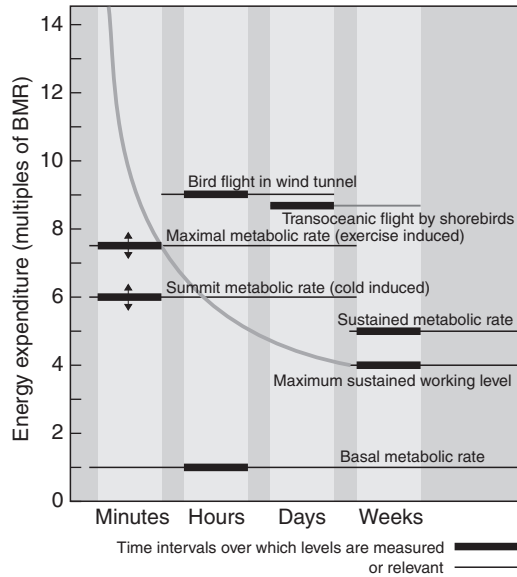


Fig. 2. Unlike basal metabolic rate, the power output of exercising animals is a negative function of the duration for which the particular activity level is maintained. Inspired by Peterson et al. (Peterson et al., 1990), the energy expenditure levels in this figure were compiled from Drent and Daan (Drent and Daan, 1980), Dawson and Marsh (Dawson and Marsh, 1989), Hammond and Diamond (Hammond and Diamond, 1997), Chappell et al. (Chappell et al., 1999; Chappell et al., 2003; Chappell et al., 2007), Videler (Videler, 2005), Vézina et al. (Vézina et al., 2006) and Gill et al. (Gill et al., 2005; Gill et al., 2009). Note that, in particular, cold-induced summit metabolic rate and exercise-induced maximal metabolic rate can vary a great deal among individuals, species and higher taxonomic levels.

activity is maintained, the lower the possible power output can be, with a decline towards some asymptotic value that is only a few times BMR (Fig. 2). [Note that what is done here, to enable comparisons between individuals, species and ecological contexts, is to account for the duration of a certain level of energy expenditure (in addition to body size, accounted for by BMR).] Relying on anaerobic metabolism, humans and other vertebrates can achieve energy expenditure levels up to 100 times BMR for a few seconds (Bennett and Ruben, 1979). This should just be enough to outrun or outfly a predator, which after all faces the same physiological problem: the build-up of 'toxic' levels of lactic acid during anaerobic ATP production. Still, exercise-trained animals may maintain energy expenditure levels of 20–30 times BMR for many minutes (Schmidt-Nielsen, 1984), though activity levels maintained for an hour or more rarely exceed 15 times BMR.

Exercise physiologists have developed different experimental procedures to assay metabolic peak performance. For example, they may expose animals to severe thermoregulatory demands until they show a decrease of core temperature (yielding a measure called summit metabolic rate) (e.g. Swanson, 1993; Chappell et al., 2003; Swanson and Liknes, 2006; Vézina et al., 2007; Wiersma et al., 2007) or they may chase them for several minutes on treadmills or in running wheels to the point of exhaustion while measuring oxygen consumption (a measure called maximal metabolic rate or  $\dot{V}_{O_{2,max}}$ ) (see Chappell et al., 1996; Chappell et al., 1999; Chappell et al., 2007; Bishop, 1999; Bundle et al., 1999; Hammond et al., 2000). In many such studies, BMR is measured in the same individuals, but even then factorial scopes (i.e. multiples of BMR) vary a lot. Averaged for different age or sex categories or species, summit and maximal metabolic rates usually fall between 5 and 10

times BMR (Fig. 2). Actually, these values seem rather low given the short intervals (minutes rather than hours) over which such peak performance measurements are made.

Another interesting point is that, although both exercise- and cold-induced metabolic rates strongly involve skeletal muscle work (in running and shivering, respectively), animals tend to have higher factorial scopes for exercise-induced power output than for cold-induced power output (Hinds et al., 1993). In birds, exercise-induced scopes are higher than cold-induced scopes (Dawson and Marsh, 1989; Hinds et al., 1993), but in some small mammals cold-induced factorial scope is higher than exercise-induced scope (Chappell et al., 2003). Although it is unlikely that differences between birds and mammals are due to them carrying different amounts of muscle for locomotion [in both groups skeletal muscle represents 40–45% of body mass; see p. 20 of Calder (Calder, 1984)], depending on the ratio between the great and small flight muscles (Piersma and Dietz, 2007) some species of birds may be able to have a higher shivering capacity than others (Hinds et al., 1993). However, mammals, but not birds, can use 'brown fat' to generate heat for thermogenesis (i.e. 'non-shivering thermogenesis') (see Cannon and Nedergaard, 2004; Morrison et al., 2008). With their two channels of heat generation, mammals achieve high cold-induced factorial scopes.

Experimental measurements of the cost of bird flight carried out in wind tunnels over many hours (Pennycuick et al., 1997; Kvist et al., 2001; Ward et al., 2004; Engel et al., 2006; Schmidt-Wellenburg et al., 2006; Schmidt-Wellenburg et al., 2008) also vary widely, but gravitate toward values around 9 times BMR (Videler, 2005). Migrating shorebirds have the capacity to process food and store fuel at fast rates (Kvist and Lindström, 2003) related to them usually being in a hurry and because they make such long-distance flights. They are in a hurry because they need to get to the Arctic breeding grounds in good time (Gudmundsson et al., 1991; Drent et al., 2003), or because getting back early to their southward staging areas or wintering grounds is beneficial (Zwarts et al., 1992; Alerstam, 2003). During long-distance flights of many thousands of kilometres, shorebirds spend the equivalent of 8–10 times BMR (Pennycuick and Battley, 2003; Gill et al., 2005). In the course of such non-stop flights shorebirds not only deplete much of their fat store but also lose protein, due to atrophy of organs in the body cavity and even the working flight muscles (Piersma and Jukema, 1990; Battley et al., 2000). Developments in satellite transmitter technology have recently made it possible to establish that such performance levels are maintained for at least 9 days in bar-tailed godwits *Limosa lapponica* (Gill et al., 2009). On the basis of reconstructed fat and protein losses during such flights, the godwits would be flying at energy expenditure levels of about 9 times BMR (Gill et al., 2005). This level is consistent with modern wind tunnel data, but still curiously high compared with the trendline (Fig. 2). It is almost double the long-term level for sustained metabolic rate in hard-working mammals and non-flying birds, yet takes place over similar lengths of time.

#### Proximate constraints on metabolic ceilings

Obviously, long-distance migrants are not in energy balance. They do not eat during the flight, but deplete the sizeable stores of fat and protein that are accrued before they take off (Piersma and Gill, 1998; Gill et al., 2005). Indeed, despite showing evidence of remarkable protein saving (Jenni and Jenni-Eiermann, 1998), such migrant shorebirds not only empty their abdominal and subcutaneous fat stores but, with the exception of lungs and brain, also burn up belly organs and other proteinaceous tissues in flight (Battley et al., 2000).

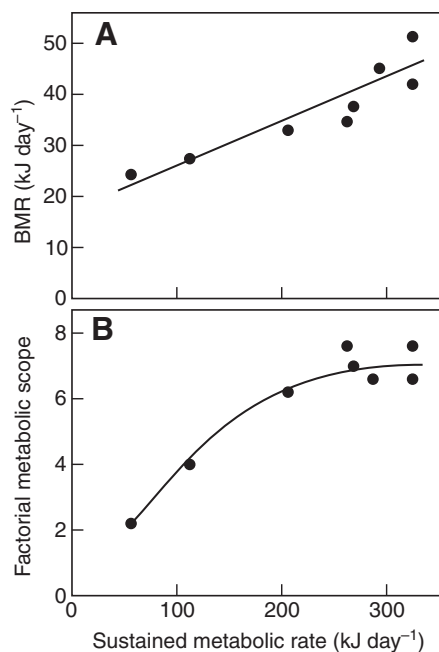


Fig. 3. How the laboratory mouse equivalent of basal metabolic rate (BMR) goes up with experimentally increased levels of energy expenditure due to hypertrophy of various organ groups (A), and how simultaneously the factorial scope of sustained energy expenditure on BMR reaches plateau levels of ca. 7 times BMR (B). Adapted from Hammond and Diamond (Hammond and Diamond, 1997).

When one builds bigger bodies to ingest, absorb, excrete and do work, the expanding machinery requires ever more energy for maintenance (Kersten and Piersma, 1987). Such increases in maintenance requirements will be reflected by increasing BMR levels (Piersma et al., 1996). A summary of the early studies on mice whose energy expenditure had been elevated in a variety of ways shows BMR to go up with sustained metabolic rate (Fig. 3A). This effect comes with an increase in body mass, due to hypertrophy of the liver, digestive tract and mammary glands (Hammond et al., 1994; Speakman and Johnson, 2000; Johnson et al., 2001). As a consequence of having put in place increasingly powerful machinery, factorial scope (the ratio between sustained energy expenditure and BMR) climbs to an asymptote of about 7 times BMR (Fig. 3B) (Hammond and Diamond, 1997), and there is no reason to think that this model would not hold for other animals, including (shore)birds. One reason that long-distance migrant shorebirds that are not in energy balance may exceed this level is that during flight their metabolic machinery for food processing and nutrient processing can be kept quite small (Piersma and Gill, 1998).

In the course of their study on metabolic ceilings in mice, Król and Speakman (Król and Speakman, 2003a; Król and Speakman, 2003b) concluded that performance in lactating mice must be limited by the capacity of female mice to dissipate heat, as under colder conditions – increased heat loss – milk production also went up and so did the mass of pups at weaning. They put this to the test by shaving some mice during lactation (Król et al., 2007): shaved mothers ate more and had heavier litters with heavier individual pups. That rates of heat loss best explain the limits to aerobic performance in lactating laboratory mice, which only push up their metabolic ceilings when it is cold enough or when insulation is poor enough, does not detract from the fact that mouse mothers can only

do this by building a bigger body, a bigger metabolic machine. Thus, they still face a maximum factorial scope of 7.

Król and Speakman recognized, and then garnered, a suite of empirical data to bear on their idea (Speakman and Król, 2010a; Speakman and Król, 2010b), that the problem of heat dissipation is probably rather general and is likely to constrain metabolic performance in many ecological contexts. Apart from the well-known link between high temperature, solar radiation and humidity and the reduction in milk production in dairy cattle (Thompson, 1973; King et al., 2006; Nassuna-Musoke et al., 2007), sheep *Ovis aries* (Abdalla et al., 1993) and pigs *Sus scrofa* (Black et al., 1993; Renaudeau and Noblet, 2001), heat dissipation limitations might help explain latitudinal and altitudinal trends in clutch sizes of birds (larger where it is colder) (Bohning-Gaese et al., 2000; Cooper et al., 2005) (but see McNamara et al., 2008). It could also provide a reason why humans, one of the few mammals that can sweat profusely, are able to outrun pretty much any running game in the midday heat (Heinrich, 2001). And it could help explain why long-distance migrant birds tend to fly in cool air at night (Klaassen, 1996), and why fuelling rates of migrant shorebirds are so low in the tropics (Battley et al., 2003; Piersma et al., 2005).

#### Protecting long-term fitness assets: the evolution of laziness

If animals are pushed hard, under some conditions (e.g. when enabling greater heat loss), they can raise the ceiling from working at 5 times BMR to working at 7 times BMR. As we have seen, human endurance athletes in energy balance can push their performance levels to 5 times BMR, but not further. We have also seen that free-living birds, except in the case of the marathon migrants, generally do not work harder than this either. The considerable gap between the maximum sustained working level of 4 or 5 times BMR that hard-working parent birds are prepared to give (Drent and Daan, 1980) and the physiological maxima of 7–10 times BMR that can be achieved under exceptional conditions makes evolutionary sense if working hard comes at a survival cost (Valencak et al., 2009). My reading of the literature suggests that any kind of hard work, perhaps above taxon- (or rather, ecology-) dependent thresholds (Speakman et al., 2002; Speakman, 2005; Furness and Speakman, 2008), comes with wear and tear. A precipitous increase in the likelihood of organ or performance failure, and mortality associated with increases in energy expenditure (Ricklefs, 2008), would explain why animals are reluctant to habitually spend as much as they are physiologically capable of (Valencak et al., 2009); that is, if such precipitous increases in the likelihood of death are not compensated for by increases in reproductive output (Williams, 1966; Lessells, 1991; Daan and Tinbergen, 1997). Evolutionary trade-offs would then select for animals that are not prepared to work harder than what we heuristically called the optimal working capacity (Fig. 4) (Royama, 1966). On the basis of field data on provisioning birds, optimal working capacity is seldom higher than 5 times BMR and is mostly lower (Drent and Daan, 1980; Bryant and Tatner, 1991; Tinbergen and Dietz, 1994). Speakman (Speakman, 1997b) found the same in small mammals, stating that these animals ‘routinely live their lives at well below their physiological capacities, in the same way that we drive our cars at well below their mechanical capacities’.

There seems abundant evidence that animals, even when confronted with challenges such as experimentally increased brood sizes that might gain them more offspring, are simply not prepared to work harder than 5 times BMR or, indeed, harder than necessary

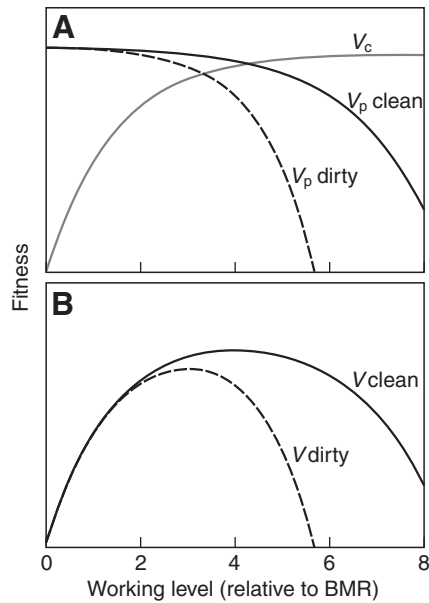


Fig. 4. The marginal value of work: Royama's (Royama, 1966) concept of an optimal working level during reproduction couched in terms of a simple optimality plot of (A) the two main fitness components (the residual reproductive value of the parent  $V_p$  and the reproductive value of the clutch  $V_c$ ) or (B) their sum as a function of the parent's relative metabolic rate. Two sorts of environment are distinguished: a 'clean' one in which the chance of catching a disease is small, and a 'dirty' one with a higher chance of becoming infected. Following Speakman and Król (Speakman and Król, 2010a) one could also speak about 'cold' and 'hot' environments, respectively. From Piersma and van Gils (Piersma and van Gils, 2011).

(Masman et al., 1988). Nevertheless, only a few experiments have demonstrated that 'increased daily work precipitates natural death'. An important example is the study by Daan and colleagues (Daan et al., 1996) with that very title, in which they analysed time till death of 63 free-living European kestrels *Falco tinnunculus* that had raised broods with manipulated sizes. They demonstrated that kestrels with larger broods incurred increased mortality the following winter compared with those with normal or reduced brood sizes (Fig. 5). This would explain why kestrels are quite unwilling to spend much more than  $500 \text{ kJ day}^{-1}$ , or 4 times BMR (Deerenberg et al., 1995).

Experiments with insects confirmed these trends. When honey bee workers *Apis mellifera* were forced to fly with extra loads and work really hard, they showed decreased life spans (Wolf and Schmid-Hempel, 1989). When house flies *Musca domestica* were prevented from flying by keeping them in small flasks, so that their energy expenditure decreased, they had increased life spans (Yan and Sohal, 2000). Interestingly, extra work load experiments on laboratory rats and various kinds of mice have yielded equivocal results (Holloszy and Smith, 1986; Navarro et al., 2004; Speakman et al., 2004; Selman et al., 2008; Vaanholt et al., 2009). Basically, experimentally elevated rates of daily energy expenditure did not shorten lifespan.

Whether or not enhanced energy expenditure has life-shortening effects, there is still evidence that these rodents prefer to work at lower than maximum levels with regard to their metabolic investments in reproduction. Lactating mouse mothers challenged to work for food make the 'decision' not to work above a certain level – or indeed, to increase body mass as required for maintaining

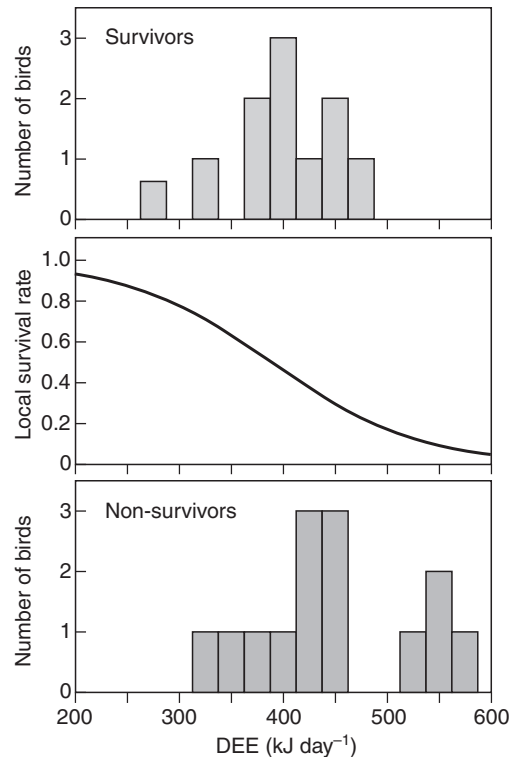


Fig. 5. Local survival rates of kestrels *Falco tinnunculus* in the northern Netherlands as a function of daily energy expenditure (DEE) during the raising of chicks. The upper and lower panels show the frequency distributions of experimental birds that were either recaptured (top) or not (bottom) in the study area during the next breeding season. The middle panel shows the logistic regression curve of survival on DEE ( $\chi^2=5.66$ , d.f.=1,  $P=0.02$ ). Compiled from Deerenberg et al. (Deerenberg et al., 1995).

metabolic machinery – even though this results in a decrease in milk energy output and thereby the biomass of weaned litters (Schubert et al., 2009). Perrigo (Perrigo, 1987) observed that two wild-type mouse species differed in their willingness to work in supporting their offspring. He attributed this to their different life history strategies. While *Mus musculus* are opportunistic breeders capable of maintaining fertility whenever food is available, *Peromyscus maniculatus* are strictly seasonal, and presumably face a higher opportunity cost of litter production. This species appeared more determined to save a smaller number of pups, even when this entailed working hard, when *Mus* mothers would already have abandoned their litters.

Earlier we encountered the elite cyclists who perform at very high levels during the three weeks of the Tour de France (Westerterp et al., 1986) (Table 1). Interestingly, in the Vuelta a España, a similarly demanding cycling race but a week shorter, total energy expenditure over the whole race was similar to that for the Tour de France (Lucia et al., 2003). This suggests that when expending energy, humans, and probably other animals, account for time. Animals are only prepared to deliver a certain level of effort over certain time periods, a phenomenon called 'pacing' in the world of sports (Foster et al., 2005). In the words of Tim Noakes (personal communication): 'Train hard when it is important, and rest when it is important. And don't confuse the two.' I suggest that the time spans over which the accounting of metabolic performance takes place in different animals could be a rich area of experimental biology.

### Towards an ecology of physiological constraint

Returning to marathon migrants, there should be good ecological reasons why bar-tailed godwits are prepared to work so hard for so long (note that their annual survival is also very high at >96%; P. F. Battley, personal communication). Gill and colleagues (Gill et al., 2009) proposed that, by making a non-stop trans-Pacific flight, godwits not only minimize the time and energy allocated to migration but also minimize the risk of mortality from predators, parasites and pathogens. Bar-tailed godwits and other shorebirds appear to have been selected to work routinely as hard, and for almost as long, as the Arctic explorers. They also deplete their bodies to the same extent. By making a living along the edges of our planet, so to speak, in places that some parasites, pathogens and predators have not been able to reach (e.g. Piersma, 1997; Piersma, 2003; Mendes et al., 2005), godwits may exploit ecological conditions that do not make them pay the price (of enhanced subsequent mortality) that usually comes with very hard work.

Free-living animals are resistant to experimental manipulations to increase their instantaneous work levels, for what we can now see (as explained at length above) are sound reasons. Unless some mechanistic shortcuts are found to the actual expenditure decision processes (e.g. Speakman and Król, 2005), it will be impossible to verify experimentally the optimality model of Fig. 4 along the whole range of work levels. Nevertheless, it seems likely that within taxa, the 'death on working level curves' would be determined by ecological conditions, e.g. the general environmental or social stress levels that have become known as 'allostatic loads' (McEwen and Wingfield, 2003; Wingfield, 2005; Rubenstein, 2007), food abundance (Lane et al., 2010), the levels of pathogens in the environment (Piersma, 1997), or the incidence of heat stress (Speakman and Król, 2010a; Speakman and Król, 2010b).

Such variations suggest that there is scope for studies in which relationships between energy expenditure levels and survival are studied, either in a strict comparative context (comparing relationships in groups with different environments) or in experimental contexts (by additionally manipulating aspects of the environments in which the expenditure-survival relationships are studied). During such endeavours it remains important to pay attention to constraints other than work level, especially time limitations, that may prevent animals from eating for long enough to keep up with the high energy expenditure (Tinbergen and Verhulst, 2000; Kvist and Lindström, 2000). When interpretable aspects of the ecological context can be linked to maximal performance, or rather to the relationships between experimentally manipulated work levels and both reproduction and survival (Fig. 4) [see Bouwhuis et al. for a possible field setting (Bouwhuis et al., 2009)], we may achieve deeper levels of understanding of the selection factors driving the height of metabolic ceilings.

As a first suggestion, and by way of example, if the shortening of telomeres (a molecular DNA-based marker of ageing cells) could be shown to reliably reflect the wear and tear that comes with working hard at an individual level (Epel et al., 2004; Hall et al., 2004; Haussmann et al., 2005; Salomons et al., 2009), differences in telomere-shortening rates between and within individuals (entertaining experimentally manipulated expenditure levels in different ecological contexts) should be measured. If telomere-shortening rates could then be brought in relation to fitness measurements, we would be working towards experimental verification of Royama's (Royama, 1966) concept of an optimal working level and the simple graphical incarnation of it (Fig. 4). It seems to me that such tests will provide nice bridges between ecology and physiology and evolution of the kind that

environmental physiologists have so desperately been searching for since the days of Feder and colleagues (Feder et al., 1987).

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### References

- Abdalla, E. B., Kotby, E. A. and Johnson, H. D. (1993). Physiological responses to heat-induced hyperthermia of pregnant and lactating ewes. *Small Rumin. Res.* **11**, 125-134.
- Alerstam, T. (2003). Bird migration speed. In *Avian Migration* (ed. P. Berthold, E. Gwinner and E. Sonnenschein), pp. 253-267. Berlin: Springer-Verlag.
- Battley, P. F., Piersma, T., Dietz, M. W., Tang, S., Dekinga, A. and Hulsman, K. (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proc. R. Soc. Lond. B. Biol. Sci.* **267**, 191-196.
- Battley, P. F., Rogers, D. I., Piersma, T. and Koolhaas, A. (2003). Behavioural evidence for heat-load problems in great knots in tropical Australia fuelling for long-distance flight. *Emu* **103**, 97-103.
- Bennett, A. F. and Ruben, J. A. (1979). Endothermy and activity in vertebrates. *Science* **206**, 649-654.
- Bishop, C. M. (1999). The maximum oxygen consumption and aerobic scope of birds and mammals: Getting to the heart of the matter. *Proc. R. Soc. Lond. B. Biol. Sci.* **266**, 2275-2281.
- Black, J. L., Mullan, B. P., Lorschy, M. L. and Giles, L. R. (1993). Lactation in the sow during heat-stress. *Livest. Prod. Sci.* **35**, 153-170.
- Bohning-Gaese, K., Halbe, B., Lemoine, N. and Oberrath, R. (2000). Factors influencing clutch size, number of broods and annual fecundity of North American and European land birds. *Evol. Ecol. Res.* **2**, 823-839.
- Bouwhuis, S., Sheldon, B. C., Verhulst, S. and Charmantier, A. (2009). Great tits growing old: Selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proc. R. Soc. Lond. B. Biol. Sci.* **276**, 2769-2777.
- Brisbin, I. L. (1969). Bioenergetics of the breeding cycle of the ring dove. *Auk* **86**, 54-74.
- Brody, S. (1945). *Bioenergetics and Growth*. New York: Reinhold.
- Bryant, D. M. and Tatner, P. (1991). Intraspecific variation in energy expenditure: Correlates and constraints. *Ibis* **133**, 236-245.
- Bryant, D. M. and Westerterp, K. R. (1980). The energy budget of the house martin (*Delichon urbica*). *Ardea* **68**, 91-102.
- Bundle, M. W., Hoppeler, H., Vock, R., Tester, J. M. and Weyand, P. G. (1999). High metabolic rates in running birds. *Nature* **397**, 31-32.
- Calder, W. A., III (1984). *Size, Function, and Life History*. Cambridge, MA: Harvard University Press.
- Campbell, I. T. and Donaldson, J. (1981). Energy requirements of Antarctic sledge dogs. *Brit. J. Nutr.* **45**, 95-98.
- Cannon, B. and Nedergaard, J. (2004). Brown adipose tissue: Function and physiological significance. *Physiol. Rev.* **84**, 277-359.
- Chappell, M. A., Zuk, M. and Johnsen, T. S. (1996). Repeatability of aerobic performance in red junglefowl: Effects of ontogeny and nematode infection. *Funct. Ecol.* **10**, 578-585.
- Chappell, M. A., Bech, C. and Buttemer, W. A. (1999). The relationship of central and peripheral organ masses to aerobic performance variation in house sparrows. *J. Exp. Biol.* **202**, 2269-2279.
- Chappell, M. A., Rezende, E. L. and Hammond, K. A. (2003). Age and aerobic performance of deer mice. *J. Exp. Biol.* **206**, 1221-1231.
- Chappell, M. A., Garland, T., Jr, Robertson, G. F. and Saltzman, W. (2007). Relationships among running performance, aerobic physiology and organ mass in male Mongolian gerbils. *J. Exp. Biol.* **210**, 4179-4197.
- Cooper, C. B., Hochachka, W. M., Butcher, G. and Dhondt, A. A. (2005). Seasonal and latitudinal trends in clutch size: thermal constraints during laying and incubation. *Ecology* **86**, 2018-2031.
- Daan, S. and Tinbergen, J. M. (1997). Adaptation in life histories. In *Behavioural Ecology: an Evolutionary Approach* (ed. J. R. Krebs and N. B. Davies), 4th edn, pp. 311-333. Oxford: Blackwell Science.
- Daan, S., Deerenberg, C. and Dijkstra, C. (1996). Increased daily work precipitates death in the kestrel. *J. Anim. Ecol.* **65**, 539-544.
- Davis, M. S., Willard, M. D., Williamson, K. K., Steiner, J. M. and Williams, D. A. (2005). Sustained strenuous exercise increases intestinal permeability in racing Alaskan sled dogs. *J. Vet. Int. Med.* **19**, 34-39.
- Davis, M. S., Willard, M. D., Williamson, K. K., Royer, C., Payton, M., Steiner, J. M., Hinchcliff, K., McKenzie, E. and Nelson, S., Jr (2006). Temporal relationship between gastrointestinal protein loss, gastric ulceration or erosion, and strenuous exercise in racing Alaskan sled dogs. *J. Vet. Int. Med.* **20**, 835-839.
- Dawson, W. R. and Marsh, R. L. (1989). Metabolic adaptations to cold and season in birds. In *Physiology of Cold Adaptation in Birds* (ed. C. Bech and R. E. Reinertsen), pp. 83-94. New York: Plenum Press.
- Deerenberg, C., Pen, I., Dijkstra, C., Arkies, B. J., Visser, G. H. and Daan, S. (1995). Parental energy expenditure in relation to manipulated brood size in the European kestrel *Falco tinnunculus*. *Zoology* **99**, 39-48.
- Drent, R. H. and Daan, S. (1980). The prudent parent: Energetic adjustments in avian breeding. *Ardea* **68**, 225-252.

- Drent, R., Both, C., Green, M., Madsen, J. and Piersma, T. (2003). Pay-offs and penalties of competing migratory schedules. *Oikos* **103**, 274-292.
- Engel, S., Biebach, H. and Visser, G. H. (2006). Metabolic costs of avian flight in relation to flight velocity: A study in rose coloured starlings (*Sturnus roseus*, Linnaeus). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **176**, 415-427.
- Epel, E. S., Blackburn, E. H., Lin, J., Dhabhar, F. S., Adler, N. E., Morrow, J. D. and Cawthon, R. M. (2004). Accelerated telomere shortening in response to life stress. *Proc. Natl. Acad. Sci. USA* **101**, 17312-17315.
- Feder, M. E., Bennett, A. F., Burggren, W. W. and Huey, R. B. (1987). *New Directions in Ecological Physiology*. Cambridge: Cambridge University Press.
- Forbes-Ewan, C. H., Morrissey, B. L. L., Gregg, G. C. and Waters, D. R. (1989). Use of the doubly labelled water technique in soldiers training for jungle warfare. *J. Appl. Physiol.* **67**, 14-18.
- Foster, C., Hoyos, J., Earnest, C. and Lucia, A. (2005). Regulation of energy expenditure during prolonged athletic competition. *Med. Sci. Sports Exerc.* **37**, 670-675.
- Froehle, A. W. and Schoeninger, M. J. (2006). Intraspecific variation in BMR does not affect estimates of early hominin total daily energy expenditure. *Am. J. Phys. Anthropol.* **131**, 552-559.
- Furness, L. J. and Speakman, J. R. (2008). Energetics and longevity in birds. *Age* **30**, 75-87.
- Gill, R. E., Jr, Piersma, T., Hufford, G., Servranckx, R. and Riegen, A. (2005). Crossing the ultimate ecological barrier: evidence for an 11 000-km-long nonstop flight from Alaska to New Zealand and eastern Australia by bar-tailed godwits. *Condor* **107**, 1-20.
- Gill, R. E., Jr, Tibbitts, T. L., Douglas, D. C., Mulcahy, D. M., Handel, C. M., Gottschalk, J. C., Warnock, N., McCaffery, B. J., Battley, P. F. and Piersma, T. (2009). Extreme endurance flights by landbirds crossing the Pacific Ocean: Ecological corridor rather than barrier? *Proc. R. Soc. Lond. B. Biol. Sci.* **276**, 447-457.
- Gudmundsson, G. A., Lindström, Å. and Alerstam, T. (1991). Optimal fat loads and long-distance flights by migrating knots, *Calidris canutus*, sanderlings, *C. alba*, and turnstones, *Arenaria interpres*. *Ibis* **133**, 140-152.
- Guezennec, C. Y., Satabin, P., Legrand, H. and Bigard, A. X. (1994). Physical performance and metabolic changes induced by combined prolonged exercise and different energy intakes in humans. *Eur. J. Appl. Physiol.* **68**, 525-530.
- Hall, M. E., Nasir, L., Daunt, F., Gault, E. A., Croxall, J. P., Wanless, S. and Monaghan, P. (2004). Telomere loss in relation to age and early environment in long-lived birds. *Proc. R. Soc. Lond. B. Biol. Sci.* **271**, 1571-1576.
- Hammond, K. A. and Diamond, J. M. (1997). Maximal sustained energy budgets in humans and animals. *Nature* **386**, 457-462.
- Hammond, K. A., Konarzewski, M., Torres, R. and Diamond, J. M. (1994). Metabolic ceilings under a combination of peak energy demands. *Physiol. Zool.* **67**, 1479-1506.
- Hammond, K. A., Chappell, M. A., Cardullo, R. A., Lin, R.-S. and Johnsen, T. S. (2000). The mechanistic basis of aerobic performance in red junglefowl. *J. Exp. Biol.* **203**, 2053-2064.
- Hausmann, M. F., Winkler, D. W. and Vleck, C. M. (2005). Longer telomeres associated with higher survival in birds. *Biol. Lett.* **1**, 212-214.
- Heinrich, B. (2001). *Racing the Antelope: What Animals Can Teach Us About Running and Life*. New York: HarperCollins.
- Henry, C. J. K. (2005). Basal metabolic rate studies in humans: Measurement and development of new equations. *Public Health Nutr.* **8**, 1133-1152.
- Hinchcliff, K. W., Reinhart, G. A., Burr, J. R., Schreier, C. J. and Swenson, R. A. (1997). Metabolizable energy intake and sustained energy expenditure of Alaskan sled dogs during heavy exertion in the cold. *Am. J. Vet. Res.* **58**, 1457-1462.
- Hinchcliff, K. W., Constable, P. D. and DiSilvestro, R. A. (2004). Muscle injury and antioxidant status in sled dogs competing in a long-distance sled dog race. *Equine Comp. Exerc. Physiol.* **1**, 81-85.
- Hinds, D. S., Baudinette, R. V., MacMillen, R. E. and Halpern, E. A. (1993). Maximum metabolism and the aerobic factorial scope of endotherms. *J. Exp. Biol.* **182**, 41-56.
- Holloszy, J. O. and Smith, E. K. (1986). Longevity of cold-exposed rats: a reevaluation of the 'rate-of-living theory'. *J. Appl. Physiol.* **61**, 1656-1660.
- Hoyt, R. W., Jones, T. E., Stein, T. P., McAnich, G. W., Lieberman, H. R., Askew, E. W. and Cymerman, A. (1991). Doubly labelled water measurement of human energy expenditure during strenuous exercise. *J. Appl. Physiol.* **71**, 16-22.
- Hoyt, R. W., Opstad, P. K., Haugen, A.-H., DeLany, J. P., Cymerman, A. and Friedl, K. E. (2006). Negative energy balance in male and female rangers: effects of 7 days of sustained exercise and food deprivation. *Am. J. Clin. Nutr.* **83**, 1068-1075.
- Jenni, L. and Jenni-Eiermann, S. (1998). Fuel supply and metabolic constraints in migrating birds. *J. Avian Biol.* **29**, 521-528.
- Johnson, M. S., Thomson, S. C. and Speakman, J. R. (2001). Limits to sustained intake. II. Interrelationships between resting metabolic rate, life-history traits and morphology in *Mus musculus*. *J. Exp. Biol.* **204**, 1937-1946.
- Johnstone, A. M., Rance, K. A., Murison, S. D., Duncan, J. S. and Speakman, J. R. (2006). Additional anthropometric measures may improve the predictability of basal metabolic rate in adult subjects. *Eur. J. Clin. Nutr.* **60**, 1437-1444.
- Jones, P. H., Jacobs, I., Morris, A. and Ducharme, M. B. (1993). Adequacy of food rations in soldiers during an arctic exercise measured by doubly labelled water. *J. Appl. Physiol.* **75**, 1790-1797.
- Karasov, W. H. and Martinez del Rio, C. (2007). *Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins*. Princeton, NJ: Princeton University Press.
- Kersten, M. and Piersma, T. (1987). High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* **75**, 175-187.
- King, J. M., Parsons, D. J., Turnpenny, J. R., Nyangaga, J., Bakari, P. and Wathes, C. M. (2006). Modelling energy metabolism of Friesians in Kenya smallholdings shows how heat stress and energy deficit constrain milk yield and cow replacement rate. *Anim. Sci.* **82**, 705-716.
- King, J. R. (1974). Seasonal allocation of time and energy resources in birds. In *Avian Energetics* (ed. R. A. Paynter, Jr), pp. 4-85. Cambridge, MA: Nuttall Ornithological Club.
- Klaassen, M. (1996). Metabolic constraints on long-distance migration in birds. *J. Exp. Biol.* **199**, 57-64.
- Krogh, A. (1916). *The Respiratory Exchange of Animals and Man*. London: Longmans-Green.
- Król, E. and Speakman, J. R. (2003a). Limits to sustained intake. VI. Energetics of lactation in laboratory mice at thermoneutrality. *J. Exp. Biol.* **206**, 4255-4266.
- Król, E. and Speakman, J. R. (2003b). Limits to sustained intake. VII. Milk energy output in laboratory mice at thermoneutrality. *J. Exp. Biol.* **206**, 4267-4281.
- Król, E., Murphy, M. and Speakman, J. R. (2007). Limits to sustained intake. X. Effects of fur removal on reproductive performance in laboratory mice. *J. Exp. Biol.* **210**, 4233-4243.
- Kvist, A. and Lindström, Å. (2000). Maximum daily energy intake: It takes time to lift the metabolic ceiling. *Physiol. Biochem. Zool.* **73**, 30-36.
- Kvist, A. and Lindström, Å. (2003). Gluttony in migratory waders – unprecedented energy assimilation rates in vertebrates. *Oikos* **103**, 397-402.
- Kvist, A., Lindström, Å., Green, M., Piersma, T. and Visser, G. H. (2001). Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**, 730-732.
- Lane, J. E., Boutin, S., Speakman, J. R. and Humphries, M. M. (2010). Energetic costs of male reproduction in a scramble competition mating system. *J. Anim. Ecol.* **79**, 27-34.
- Lessells, C. M. (1991). The evolution of life histories. In *Behavioural Ecology: an Evolutionary Approach*, 3rd edn (ed. J. R. Krebs and N. B. Davies), pp. 32-68. Oxford: Blackwell Science.
- Lucia, A., Hoyos, J., Santalla, A., Earnest, C. and Chicharro, J. L. (2003). Tour de France versus Vuelta a España: which is harder? *Med. Sci. Sports Exerc.* **35**, 872-878.
- Masman, D., Daan, S. and Dijkstra, C. (1988). Time allocation in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. *J. Anim. Ecol.* **57**, 411-432.
- McEwen, B. S. and Wingfield, J. C. (2003). The concept of allostasis in biology and biomedicine. *Horm. Behav.* **43**, 2-15.
- McKechnie, A. E., Freckleton, R. O. and Jetz, W. (2006). Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proc. R. Soc. Lond. B. Biol. Sci.* **273**, 931-937.
- McNab, B. K. (2002). *The Physiological Ecology of Vertebrates: a View from Energetics*. Ithaca: Cornell University Press.
- McNamara, J. M., Barta, Z., Wikelsi, M. and Houston, A. I. (2008). A theoretical investigation of the effect of latitude on avian life histories. *Am. Nat.* **172**, 331-345.
- Mendes, L., Piersma, T., Lecoq, M., Spaans, B. and Ricklefs, R. E. (2005). Disease-limited distributions? Contrasts in the prevalence of avian malaria in shorebird species using marine and freshwater habitats. *Oikos* **109**, 396-404.
- Morrison, S. F., Nakamura, K. and Madden, C. J. (2008). Central control of thermogenesis in mammals. *Exp. Physiol.* **93**, 773-797.
- Nassuna-Musoake, G. M., Kabasa, J. D. and King, M. J. (2007). Microclimate dynamics in smallholder Friesian dairies of the tropical warm-humid central Uganda. *J. Anim. Vet. Adv.* **6**, 907-911.
- Navarro, A., Gomez, C., Lopez-Cepero, J. M. and Boveris, A. (2004). Beneficial effects of moderate exercise on mice aging: survival, behavior, oxidative stress, and mitochondrial electron transfer. *Am. J. Physiol.* **286**, R505-R511.
- Noakes, T. D. (2006). The limits of endurance exercise. *Basic Res. Cardiol.* **101**, 408-417.
- Noakes, T. D. (2007). The limits of human endurance: what is the greatest endurance performance of all time? Which factors regulate performance at extreme altitude? In *Hypoxia and the Circulation* (ed. R. C. Roach), pp. 259-280. New York: Springer.
- Orr, N. W. M. (1966). The feeding of sledge dogs on Antarctic expeditions. *Brit. J. Nutr.* **20**, 1-12.
- Pennycook, C. J. and Battley, P. F. (2003). Burning the engine: A time-marching computation of fat and protein consumption in a 5420 km non-stop flight by great knots *Calidris tenuirostris*. *Oikos* **103**, 323-332.
- Pennycook, C. J., Alerstam, T. and Hedenström, A. (1997). A new low turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *J. Exp. Biol.* **200**, 1441-1449.
- Perrigo, G. (1987). Breeding and feeding strategies in deer mice and house mice when females are challenged to work for their food. *Anim. Behav.* **35**, 1298-1316.
- Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Peterson, C. C., Nagy, K. A. and Diamond, J. M. (1990). Sustained metabolic scope. *Proc. Natl. Acad. Sci. USA* **87**, 2324-2328.
- Piersma, T. (1997). Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* **80**, 623-631.
- Piersma, T. (2003). 'Coastal' versus 'inland' shorebird species: Interlinked fundamental dichotomies between their life- and demographic histories? *Wader Study Group Bull.* **100**, 5-9.
- Piersma, T. and Dietz, M. W. (2007). Twofold seasonal variation in the supposedly constant, species-specific, ratio of upstroke to downstroke flight muscles in red knots *Calidris canutus*. *J. Avian Biol.* **38**, 536-540.
- Piersma, T. and Gill, R. E., Jr (1998). Guts don't fly: Small digestive organs in obese bar-tailed godwits. *Auk* **115**, 196-203.
- Piersma, T. and Jukema, J. (1990). Budgeting the flight of a long-distance migrant: changes in nutrient reserve levels of bar-tailed godwits at successive spring staging sites. *Ardea* **78**, 315-337.
- Piersma, T. and van Gils, J. A. (2011). *The Flexible Phenotype: a Body-centred Integration of Ecology, Physiology, and Behaviour*. Oxford: Oxford University Press.
- Piersma, T., Bruinzeel, L., Drent, R., Kersten, M., van der Meer, J. and Wiersma, P. (1996). Variability in basal metabolic rate of a long-distance migrant shorebird (red knot, *Calidris canutus*) reflects shifts in organ sizes. *Physiol. Zool.* **69**, 191-217.
- Piersma, T., Lindström, Å., Drent, R., Tulp, I., Jukema, J., Morrison, R. I. G., Reneerkens, J., Schekkerman, H. and Visser, G. H. (2003). High daily energy

- expenditure of incubating shorebirds on High Arctic tundra: A circumpolar study. *Funct. Ecol.* **17**, 356-362.
- Piersma, T., Rogers, D. I., González, P. M., Zwarts, L., Niles, L. J., de Lima Serrano do Nascimento, I., Minton, C. D. T. and Baker, A. J.** (2005). Fuel storage rates in red knots worldwide: facing the severest ecological constraint in tropical intertidal conditions? In *Birds of Two Worlds: the Ecology and Evolution of Migratory Birds* (ed. R. Greenberg and P. P. Marra), pp. 262-274. Baltimore: Johns Hopkins University Press.
- Pugh, L. G.** (1972). The logistics of the polar journeys of Scott, Shackleton and Amundsen. *Proc. R. Soc. Med.* **65**, 42-47.
- Renaudeau, D. and Noblet, J.** (2001). Effects of exposure to high ambient temperature and dietary protein level on sow milk production and performance of piglets. *J. Anim. Sci.* **79**, 1540-1548.
- Ricklefs, R. E.** (2000). Intrinsic aging-related mortality in birds. *J. Avian Biol.* **31**, 103-111.
- Royama, T.** (1966). Factors governing feeding rate, food requirement and brood size of nesting great tits *Parus major*. *Ibis* **108**, 313-347.
- Rubenstein, D. M.** (2007). Stress hormones and sociality: integrating social and environmental stressors. *Proc. R. Soc. Lond. B. Biol. Sci.* **274**, 967-975.
- Salomons, H. M., Mulder, G. A., van de Zande, L., Haussmann, M. F., Linskens, M. H. K. and Verhulst, S.** (2009). Telomere shortening and survival in free-living corvids. *Proc. R. Soc. Lond. B. Biol. Sci.* **276**, 3157-3165.
- Schmidt-Nielsen, K.** (1984). *Scaling: Why is Animal Size so Important?* Cambridge: Cambridge University Press.
- Schmidt-Wellenburg, C. A., Biebach, H., Daan, S. and Visser, G. H.** (2006). Energy expenditure and wing beat frequency in relation to body mass in free flying swallows (*Hirundo rustica*). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **177**, 327-337.
- Schmidt-Wellenburg, C., Engel, S. and Visser, G. H.** (2008). Energy expenditure during flight in relation to body mass: effects of natural increases in mass and artificial load in rose coloured starlings. *J. Comp. Physiol. B* **178**, 767-777.
- Schubert, K. A., de Vries, G., Vaanholt, L. M., Meijer, H., Daan, S. and Verhulst, S.** (2009). Maternal energy allocation to offspring increases with environmental quality in house mice. *Am. Nat.* **173**, 831-840.
- Selman, C., McLaren, J. S., Collins, A. R., Duthie, G. G. and Speakman, J. R.** (2008). The impact of experimentally elevated energy expenditure on oxidative stress and lifespan in the short-tailed field vole *Microtus agrestis*. *Proc. R. Soc. Lond. B. Biol. Sci.* **275**, 1907-1916.
- Sjodin, A. M., Anderson, A. B., Hogberg, J. M. and Westerterp, K. R.** (1994). Energy balance in cross-country skiers: A study using doubly labelled water. *Med. Sci. Sports Exerc.* **26**, 720-724.
- Speakman, J. R.** (1997a). *Doubly Labelled Water: Theory and Practice*. London: Chapman and Hall.
- Speakman, J. R.** (1997b). Factors influencing the daily energy expenditure of small mammals. *Proc. Nutr. Soc.* **56**, 1119-1136.
- Speakman, J. R.** (2000). The cost of living: Field metabolic rates of small mammals. *Adv. Ecol. Res.* **30**, 177-297.
- Speakman, J. R.** (2005). Body size, energy metabolism and lifespan. *J. Exp. Biol.* **208**, 1717-1730.
- Speakman, J. R. and Johnson, M. S.** (2000). Relationships between resting metabolic rate and morphology in lactating mice: What tissues are the major contributors to resting metabolism? In *Living in the Cold*, Vol. 3 (ed. G. Heldmaier and M. Klingenspor), pp. 479-486. Berlin: Springer-Verlag.
- Speakman, J. R. and Król, E.** (2005). Limits to sustained intake. IX. A review of hypotheses. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **175**, 375-394.
- Speakman, J. R. and Król, E.** (2010a). Maximal heat dissipation capacity and hypothermia risk: neglected key factors in the ecology of endotherms. *J. Anim. Ecol.* **79**, 726-746.
- Speakman, J. R. and Król, E.** (2010b). The heat dissipation limit theory and evolution of life histories in endotherms – time to dispose of the disposable soma theory? *Integr. Comp. Biol.* (in press).
- Speakman, J. R., Selman, C., McLaren, J. and Harper, E. J.** (2002). Living fast, dying when? The link between aging and energetics. *J. Nutr.* **132**, 1583-1597.
- Speakman, J. R., Talbot, D. A., Selman, C., Snart, S., McLaren, J. S., Redman, P., Król, E., Jackson, D. M., Johnson, M. S. and Brand, M. D.** (2004). Uncoupling and surviving: Individual mice with higher metabolism have higher mitochondrial uncoupling and live longer. *Aging Cell* **3**, 87-95.
- Stroud, M. A.** (1987a). Nutrition and energy balance on the 'Footsteps of Scott' expedition 1984-86. *Human Nutr. Appl. Nutr.* **41A**, 426-433.
- Stroud, M. A.** (1987b). Did Scott simply starve? Lessons from 'The footsteps of the Scott Antarctic expedition'. *Proc. Nutr. Soc.* **46**, A129.
- Stroud, M.** (1998). The nutritional demands of very prolonged exercise in man. *Proc. Nutr. Soc.* **57**, 55-61.
- Stroud, M.** (2004). *Survival of the Fittest: Anatomy of Peak Physical Performance*. London: Vintage.
- Stroud, M. A., Coward, W. A. and Sawyer, M. B.** (1993). Measurements of energy expenditure using isotope-labelled water ( $^2\text{H}_2^{18}\text{O}$ ) during an Arctic expedition. *Eur. J. Appl. Physiol.* **67**, 375-379.
- Stroud, M. A., Ritz, P., Coward, W. A., Sawyer, M. B., Constantin-Teodosiu, D., Greenhaff, P. L. and Macdonald, I. A.** (1997). Energy expenditure using isotope-labelled water ( $^2\text{H}_2^{18}\text{O}$ ), exercise performance, skeletal muscle enzyme activities and plasma biochemical parameters in humans during 95 days of endurance exercise with inadequate energy intake. *Eur. J. Appl. Physiol.* **76**, 243-252.
- Swanson, D. L.** (1993). Cold tolerance and thermogenic capacity in dark-eyed juncos in winter: Geographic variation and comparison with American tree sparrows. *J. Therm. Biol.* **18**, 275-281.
- Swanson, D. L. and Liknes, E. T.** (2006). A comparative analysis of thermogenic capacity and cold tolerance in small birds. *J. Exp. Biol.* **209**, 466-474.
- Thompson, G. E.** (1973). Review of the progress of dairy sciences: Climatic physiology of cattle. *J. Dairy Res.* **40**, 441-473.
- Tinbergen, J. M. and Dietz, M. W.** (1994). Parental energy expenditure during brood rearing in the great tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **8**, 563-572.
- Tinbergen, J. M. and Verhulst, S.** (2000). A fixed energetic ceiling to parental effort in the great tit? *J. Anim. Ecol.* **69**, 323-334.
- Vaanholt, L. M., Daan, S., Schubert, K. A. and Visser, G. H.** (2009). Metabolism and aging: effects of cold exposure on metabolic rate, body composition and longevity in mice. *Physiol. Biochem. Zool.* **82**, 314-324.
- Valencak, T. G., Tataruch, F. and Ruf, T.** (2009). Peak energy turnover in lactating European hares: The role of fat reserves. *J. Exp. Biol.* **212**, 231-237.
- Vézina, F., Jalvingh, K. M., Dekinga, A. and Piersma, T.** (2006). Acclimation to different thermal conditions in a northerly wintering shorebird is driven by body mass-related changes in organ size. *J. Exp. Biol.* **209**, 3141-3154.
- Vézina, F., Jalvingh, K. M., Dekinga, A. and Piersma, T.** (2007). Thermogenic side-effects to migratory predisposition in shorebirds. *Am. J. Physiol.* **292**, R1287-R1297.
- Videler, J. J.** (2005). *Avian Flight*. Oxford: Oxford University Press.
- Ward, S., Moller, U., Rayner, J. M. V., Jackson, D. M., Nachtigall, W. and Speakman, J. R.** (2004). Metabolic power of European starlings *Sturnus vulgaris* during flight in a wind tunnel, estimated from heat transfer modelling, doubly labelled water and mask respirometry. *J. Exp. Biol.* **207**, 4291-4298.
- Westerterp, K. R., Saris, W. H. M., van Es, M. and ten Hoor, F.** (1986). Use of the doubly labeled water technique in humans during heavy sustained exercise. *J. Appl. Physiol.* **61**, 2162-2167.
- Wiersma, P., Muñoz-García, A., Walker, A. and Williams, J. B.** (2007). Tropical birds have a slow pace of life. *Proc. Natl. Acad. Sci. USA* **104**, 9340-9345.
- Wijnandts, H.** (1984). Ecological energetics of the long-eared owl (*Asio otus*). *Ardea* **72**, 1-92.
- Williams, G. C.** (1966). *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Wingfield, J. C.** (2005). The concept of allostasis: coping with a capricious environment. *J. Mammal.* **86**, 248-254.
- Wolf, T. J. and Schmid-Hempel, P.** (1989). Extra loads and foraging life span in honeybee workers. *J. Anim. Ecol.* **58**, 943-954.
- Wouters-Adriaans, M. P. E. and Westerterp, K. R.** (2006). Basal metabolic rate as a proxy for overnight energy expenditure: the effect of age. *Brit. J. Nutr.* **95**, 1166-1170.
- Yan, L. J. and Sohal, R. S.** (2000). Prevention of flight activity prolongs the life span of the housefly, *Musca domestica*, and attenuates the age-associated oxidative damage to specific mitochondrial proteins. *Free Radic. Biol. Med.* **29**, 1143-1150.
- Zwarts, L., Blomert, A.-M. and Wanink, J. H.** (1992). Annual and seasonal variation in the food supply harvestable by knot *Calidris canutus* staging in the Wadden Sea in late summer. *Mar. Ecol. Prog. Ser.* **83**, 129-139.