

PERSPECTIVE

Heat dissipation limit theory and the evolution of avian functional traits in a warming world

David Grémillet^{*,1,2}, Laurence Meslin³ and Amélie Lescroël⁴

¹Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, UMR5175, 1919 route de Mende, 34293 Cedex 05, Montpellier, France; ²Percy FitzPatrick Institute and DST/NRF Excellence Centre, University of Cape Town, 7701, Rondebosch, South Africa; ³Institut des Sciences de l'Evolution à Montpellier, CNRS, UMR5554(CNRS/UMII/IRD), Université Montpellier II, Place E. Bataillon, 34095 Montpellier cedex 5, France; and ⁴Biodiversité et Gestion des Territoires, URU420, Université de Rennes 1 – UMR 7204 Muséum National d'Histoire Naturelle, 263 avenue du Général Leclerc, CS 74205, 35042, Rennes Cedex, France

Summary

1. It is generally assumed that animal energy expenditure is limited by energy acquisition.
2. In a series of publications, Speakman, Król and colleagues argue that the capacity to dissipate metabolic heat may also limit maximum rates of energy expenditure in endotherms (heat dissipation limit theory – HDL theory).
3. The implications of the HDL theory for the evolution of avian functional traits are substantial and open fascinating research perspectives.
4. Notably, the HDL theory leads us to (i) link elevated bird body temperatures with their capacity to achieve higher rates of heat loss and of energy expenditure, (ii) reconsider the evolution of avian plumage patterns and speculate upon the capacity of white birds to achieve higher field metabolic rates than darker relatives, (iii) hypothesize that the avian brood patch also functions as a thermal window allowing birds to shed excess heat and (iv) revise our current view of the adaptive significance of limited plumage thermal insulation in great cormorants.
5. Such features have important implications for the capacity of birds to cope with global warming and for the design of mechanistic models of animal energetics aiming at predicting their responses to changing environmental conditions.

Key-words: allometry, animal energetics, bird body temperature, brood patch, great Cormorant, metabolic theory of ecology, plumage coloration, plumage insulation, seabirds

Introduction

Organisms are generally viewed as limited by their capacity to acquire matter and energy from the environment (Verhulst 1838). These resources serve growth, maintenance and reproduction and are hence thought to underpin population dynamics and ecosystem processes (Fisher 1930). Ecology has therefore often been regarded as primarily driven by environmental, extrinsic factors. Yet, the relative importance of environmental/extrinsic vs. biotic features is subject to enduring debates (McGill *et al.* 2006). For instance, work conducted over the last decades suggests that animals may also be limited by intrinsic, morphological and physiological traits (Fig. 1): (i) the functional materials that constitute a body require fixed proportions

of atoms, notably H, O, C, N, P, Na, Cl, S, Ca and K, which have to be acquired from the environment. This acquisition is highly selective because the natural occurrence rates of these elements strongly differ from their rates of use within an organism (Lotka 1925), and this generates an intrinsic limitation upon rates of energy expenditure. (ii) Although digestion has been thoroughly investigated by physiologists since the 19th century (Bernard 1856), its ecological implications have only been evaluated a century later. Drent & Daan (1980) anticipated the importance of digestion as an intrinsic limit to animal energetics and integrated this constraint in their 'central limitation hypothesis' (see also Weiner 1992). Further work by Karasov, Diamond and colleagues (Karasov & Diamond 1985; Diamond *et al.* 1986) demonstrated the occurrence of digestive bottlenecks in a series of species, notably hummingbirds (e.g. *Selasphorus rufus*). However, substantial digestive plasticity has been meanwhile demonstrated in

*Correspondence author. E-mail: david.gremillet@cefe.cnrs.fr

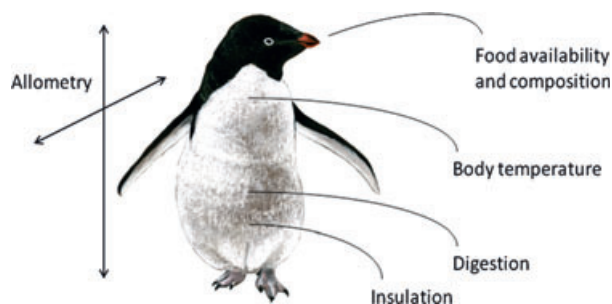


Fig. 1. In animals, maximum rates of energy expenditure are subject to not only the extrinsic constraint of food availability, but also a series of intrinsic constraints. The importance of thermal insulation as a constraint upon maximum rates of energy expenditure has been greatly underestimated and recently led Speakman & Król (2010) to formulate the heat dissipation limit theory (HDL theory) (©Laurence Meslin-CNRS 2012).

other bird species, tempering the overall relevance of digestive bottlenecks (Piersma, Koolhaas & Dekinga 1993; Caviedes-Vidal & Karasov 2007). (iii) Allometry also has long been recognized as a major driving force of bioenergetics (Kleiber 1932; Peters 1983), with metabolic rate (MR) increasing nonlinearly with body mass (BM), so that $MR = a BM^b$. West and colleagues calculated a scaling exponent b of 0.75 and proposed the fractal nature of biological surfaces and circulatory networks of organisms as explanatory characteristic (West, Brown & Enquist 1997). However, further meta-analyses revealed marked heterogeneity in b across taxa and functional groups, strongly suggesting variable allometric responses, and the absence of a universal b value (White, Blackburn & Seymour 2009). The maximum metabolic rate of single organisms is nevertheless related, to varying degrees, to their body mass, which sets an intrinsic limit to their energy expenditure, even if food resources are accessible *ad libitum*. (iv) Similarly, body temperature notably varies between taxonomic groups, potentially as a legacy of their respective evolutionary histories. Such body temperature levels condition biochemical processes responsible for energy production, thereby setting another intrinsic limit to maximum rates of energy expenditure (Clarke & Pörtner 2010).

On the basis of the three intrinsic constraints of allometry, body temperature and chemical composition of food, Brown and colleagues formulated the metabolic theory of Ecology (Brown *et al.* 2004) that aims at understanding the limits to animal energy expenditure using the first principles of physics and chemistry: living animals are thermodynamic machineries that exchange heat and matter with their environment at intrinsically fixed rates. This integrative framework has nonetheless been challenged both in theoretical and in empirical terms (Kozłowski & Konarzewski 2005; White, Blackburn & Seymour 2009).

More recently, new theoretical and empirical evidence suggested that the process of energy use may also limit overall energy expenditure (Speakman & Król 2010, 2011), and this 'heretic' notion generates a paradigm shift in our

approach to animal energetics. Specifically, Speakman and Król argue that it is the capacity of endothermic animals to shed heat generated by their metabolic activity that sets a limit to their rates of energy intake and expenditure. Evidence for a limit to endothermic animal energetics set by heat dissipation processes stems from work conducted in lactating rodents. In this study system, the metabolic capacity of the mammary gland has been shown to limit milk production (Hammond *et al.* 1994), and this initially led to formulating the 'peripheral limitation hypothesis' (Hammond, Lloyd & Diamond 1996) because this process was associated with rates of energy expenditure in peripheral organs. This initiated a series of sister-papers that focused on experimentally testing the limits to sustained energy intake in captive rodents (e.g. Johnson & Speakman 2001; Król & Speakman 2003; Speakman & Król 2005; Król, Murphy & Speakman 2007). Their key findings are that (i) lactating rodents for which heat dissipation has been artificially enhanced, either by exposing adults to lower temperatures or by removing some of their body pelage, have higher energy intake, milk production and litter size, strongly suggesting heat dissipation as a limiting factor, (ii) energy intake is not centrally limited in these study species, and hence, there is no apparent limit to sustained energy expenditure if the heat dissipation constraint is removed. This is particularly remarkable because maximum sustained energy expenditure is classically thought to reach a ceiling at four to seven times BMR (Drent & Daan 1980; Hammond & Diamond 1997). These findings have been partly contradicted by later investigations (Zhao & Cao 2009; Zhao 2011), yet they are calling for a reassessment of current views upon limits to energy expenditure.

Building upon this empirical evidence, Speakman & Król (2010, 2011) formulated the 'heat dissipation limit theory' (HDL theory) and demonstrated its general relevance using a theoretical model of heat exchange and a meta-analysis of field metabolic rates measured in mammals and birds using the doubly labelled water technique (Speakman 1997). The authors also discussed the far-ranging implications of their work for animal energetics and allometry, yet they admitted that 'there are many additional implications and predictions of this theory that we do not have space to elaborate here' (Speakman & Król 2010).

We therefore take this matter further and specifically discuss the implications of the heat dissipation limit theory for the evolution of avian functional traits, which are the morphological, physiological and behavioural characteristics that impact fitness indirectly via effects on growth, reproduction and survival (Violle *et al.* 2007). Indeed, we consider that these implications may be substantial.

HDL theory and the evolution of avian body temperatures

Ever since animal temperatures were measured, scientists have been wondering why birds have body temperatures 3–4 °C higher than mammals (Eydoux & Souleyet 1838). A

variety of potential explanations have been put forward, including the idea that elevated bird temperatures are linked with the higher net rates of energy expenditure required for flying (Feduccia 1999).

The magnitude of heat exchange between the body of an animal and the surrounding media depends upon the physical, insulating characteristics of the interface, the conditions prevailing at this interface (e.g. turbulent/laminar flow) and the temperature differential across the interface. Crucially, radiative heat exchange increases in a cubic manner with the temperature differential between the two compartments. Hence, because of their elevated internal temperature, heat loss is theoretically higher in birds than in mammals of equivalent size and insulation experiencing the same ambient conditions. This is usually regarded as a handicap, triggering higher energy demand and food consumption in birds. The HDL theory throws a new light onto this apparent paradox. Indeed, under this framework, we can predict avian tolerance towards higher body temperatures to allow for an improved capacity to release metabolic heat and therefore also for a higher sustained energy expenditure when food resources are not limiting. This strategy is facilitated by the fact that bird body temperatures are not only higher than in mammals (on average 2.43 °C higher when active), but also far more labile, with a average range of >5 °C between resting and high activity levels (Prinzinger, Pressmar & Schleucher 1991). This is far beyond short-term body temperature plasticity recorded in mammals outside torpor and hibernation

(McNab 2002). In this context, the actual relevance of the HDL theory could be tested by exposing birds fed *ad libitum* to varying environmental temperatures while measuring their internal temperatures and exercising them to their maximum rates of energy expenditure (Fig. 2a). This would allow testing the prediction that birds will modulate their body temperatures according to environmental temperatures, so as to maximize the temperature differential between their bodies and their surroundings, to achieve highest possible heat losses and rates of energy expenditure.

HDL theory and the evolution of avian plumage coloration

Aristophanes (414 BC) already reported upon the diversity of avian plumage coloration, and ever since Darwin's work (1872), there have been intense debates about the adaptive significance of bird plumage colour and its fitness consequences. Plumage coloration has for instance been shown to affect individual recognition and social ranking (Whitfield 1987), mate choice (Hill 1991), territory defence (Marchetti 1993), predator avoidance (Gotmark 1997) and parental care (Linville, Breitwisch & Schilling 1998). Darker plumage also has higher heat gain from solar radiation than lighter plumage, and this can help darker birds acquire heat from their environment or lead them to overheating (Hochscheid *et al.* 2002), even if overheating via dark plumage might be substantially tempered by strong

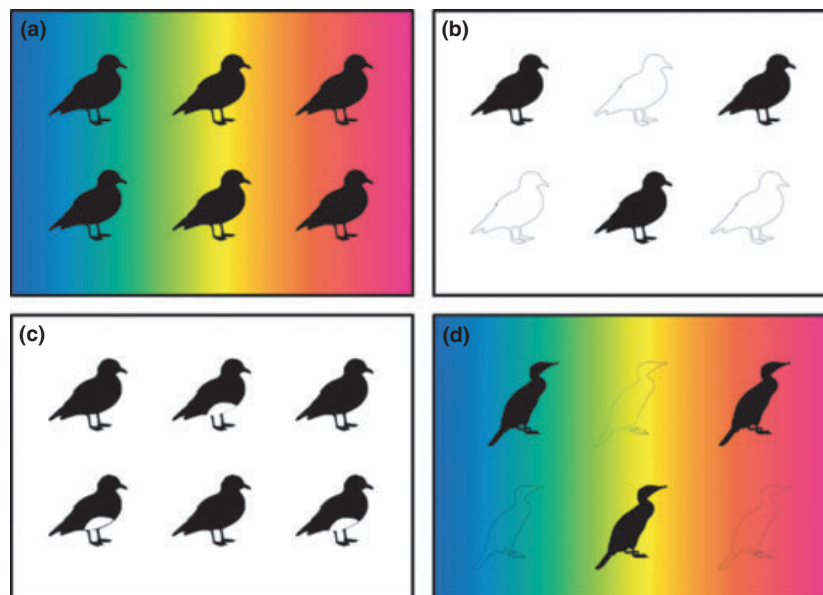


Fig. 2. Heat dissipation limit theory (HDL theory) could be evaluated by testing the hypothesis that individuals exposed to elevated temperatures increase their body temperatures, thereby allowing higher heat dissipation and higher rates of energy expenditure (a). Plumage coloration could also be manipulated, to test the hypothesis that white morphs absorb less solar radiation and have higher rates of energy expenditure (b). Comparing birds with different brood patch sizes could also allow testing the hypothesis that birds with reduced body insulation achieve higher rates of energy expenditure (c). Finally, in great cormorants, plumage characteristics, environmental temperatures and food availability could be manipulated to test the hypothesis that this species evolved towards maximum rates of energy expenditure, rather than towards an energy-saving strategy. Adjustments of body temperature, plumage colour and body insulation are mutually nonexclusive, and joint adaptation of these traits could funnel towards maximum heat dissipation.

winds, for example, in flying birds (Walsberg, Campbell & King 1978).

Under the HDL theory, we may therefore hypothesize that different plumage colorations might significantly influence the capacity of birds to loose radiative heat, and this greatly modifies the adaptive significance of this functional trait. Specifically, we might speculate that white bird plumages actually evolved to avoid heat gain from solar radiation and allow higher field metabolic rates (FMR), as well as a faster pace of life. Obviously, the HDL theory is only one within a series of evolutionary constraints that potentially act on plumage coloration, yet this new pathway opens fascinating research perspectives. For instance, statistical analyses could make use of available data sets (e.g. White *et al.* 2007), to assess linkages between plumage coloration, climate and metabolic rate. Beyond such correlative studies, plumage coloration could be manipulated using nonpermanent, biocompatible dyes, to test the prediction that experimentally darkened, breeding birds fed *ad libitum* will have lower maximum rates of energy expenditure and/or higher body temperatures than a control group of white conspecifics (Fig. 2b).

HDL theory and the evolution of avian body insulation

Heat dissipation in birds might not only be modified via changes in body temperature and plumage coloration, but also by variation in plumage cover and insulating properties. In a provocative manner, Speakman & Król (2010) therefore ask why breeding birds do not shed their plumage entirely and fly naked to ensure maximum heat dissipation while foraging for their offspring. They admit that heat dissipation is not the only factor driving the evolution of avian plumage and that birds rather have to adjust plumage characteristics according to a variety of constraints. They conclude that bird plumage is indeed useful insulation yet that some way to reduce this insulation is beneficial when birds work hardest and food is not limited, for example, during the breeding season. We think that

such a feature does exist: it is the brood patch. Brood patches occur in a majority of breeding birds as an area of bare skin on the ventral side. Its primary function is to ease heat conduction towards the egg, yet, under the HDL theory, it seems the perfect interface to shed excess heat in foraging birds.

One spectacular example is found in king penguins (*Aptenodytes patagonicus*): these athletes of the Southern Ocean routinely dive to depths of >200m in 4 °C water. Yet, instead of maximizing heat conservation at all times, they seem capable of losing vast amounts of heat to cold water via their brood patch. King penguins have been shown to drop their abdominal temperature by 10–20 °C during the deepest, longest dives, a likely oxygen-saving strategy (Handrich *et al.* 1997). However, further temperature measurements performed in different body regions showed that, contrarily to the internal abdomen, the brood patch retained high temperatures (38 °C) at the sea surface and episodically warmed up during the descent to depth (Schmidt, Alard & Handrich 2006). This result might seem puzzling because it does not fit with the prediction that penguin body temperatures should decrease from the inside of the body towards the outside, to maximize energy savings. However, according to the HDL theory, these measurements simply mean that energy acquisition is probably not the limiting factor for foraging king penguins, but rather the dissipation of muscle heat that they efficiently shed to the water via the brood patch (Fig. 3). This area is not only bare, but also highly vascularized. It is therefore a far better interface for heat transfer than flippers and feet. In our opinion, the king penguin example therefore provides support to the HDL theory, and these speculations could be tested via further field measurements of king penguin energetics and temperature regulation.

The idea that brood patches might be used for heat dissipation also stems from observations in further bird species. For instance, black-billed gulls (*Chroicocephalus bulleri*) have three brood patches but only lay two eggs, little auks (*Alle alle*) have two brood patches but only lay one egg, and in American kestrel (*Falco sparverius*), there



Fig. 3. Temperature recordings performed in free-ranging king penguins foraging at sea (Schmidt, Alard & Handrich 2006) strongly suggest that this species actively sheds excess heat through the brood patch while diving and at the water surface (©Laurence Meslin-CNRS 2012). Red tones on the y-axis indicate depths at which an increase in brood patch temperature has been recorded in foraging king penguins (Schmidt, Alard & Handrich 2006).

is no direct correspondence between clutch size and the number and size of brood patches; overall patch size rather significantly increases with female body mass, suggesting a link between metabolic rate and the capacity to dissipate heat (Wiebe & Bortolotti 1993).

The relevance of the brood patch for heat dissipation could be tested by studying birds with different brood patch sizes when fed *ad libitum* (Fig. 2c). Artificially enlarging brood patches would be the optimal solution, yet we admit that it is probably both technically and ethically challenging.

HDL theory and the great cormorant model

Finally, the HDL theory leads us to rethink some of our own work on metabolic rates and plumage characteristics in great cormorants (*Phalacrocorax carbo*). This species has a unique, partially permeable plumage, which allows birds to minimize buoyancy and is viewed as an adaptation to diving in shallow, warm subtropical waters (Grémillet *et al.* 2005a). Yet, this plumage also provides extremely limited thermal insulation, and when great cormorants forage in very cold water as in Greenland, they were observed to substantially increase their rates of energy expenditure and their foraging efficiency, and to reduce time spent in water (Grémillet *et al.* 2001; White *et al.* 2011). This strategy has generally been interpreted as energetically conservative and the partly permeable great cormorant plumage as a handicap in cold environments. Yet, under the HDL theory, we might hypothesize that a wettable plumage is actually advantageous because it allows cormorants to dissipate metabolic heat, to achieve higher rates of energy expenditure than better-insulated diving endotherms and to pursue a faster pace of life. This might well explain why great cormorants maintain elevated body temperatures even when wintering in Arctic Greenland (Grémillet *et al.* 2005b), raise up to five chicks, far more than most seabirds of their body size, and show exponential population growth when fish resources are abundant (Behrens, Rauschmayer & Wittmer 2008). The implications of the HDL theory for great cormorant energetics clearly deserve specific testing, using existing information on their body temperature, metabolic rates, predatory and reproductive performances, as well as complementary field and laboratory trials manipulating food availability and environmental temperature (Fig. 2d).

Conclusions

Speakman and Król's heat dissipation limit theory may initially seem extravagant, yet the authors and their co-workers provided theoretical and empirical evidence supporting their hypothesis. They initially developed the HDL theory while working on the energetics of small rodents during the lactating period and then expanded their findings to a wide range of mammals and birds, using heat dissipation models and measurements of

field metabolic rates performed with the doubly labelled water method. The HDL theory does open a series of fascinating perspectives for animal energetics, yet it is essential to keep in mind that it only functions when food resources are not limiting, something that does not always occur under field conditions (as acknowledged by Speakman & Król 2010). With respect to avian energetics, we have shown that the HDL theory leads us to rethink the evolution of bird body temperatures, plumage coloration and plumage insulating performance. We also speculate that the brood patch does not only serve the purpose of incubating eggs, but also as a thermal window potentially allowing modulated heat loss, higher avian metabolic rates and reproductive performance. These considerations lead us to designing a series of experiments, which could be performed to test the pertinence of the HDL theory in birds (Fig. 2). Indeed, tests of the HDL theory have so far mainly been performed under laboratory conditions, and some results were challenged by later investigations (Zhao & Cao 2009; Zhao 2011). This clearly calls for further tests in different taxa and under field conditions.

Such experiments are required, not only in theoretical terms, but also for understanding how birds will cope with global warming. Indeed, there have been much discussions about the indirect impact of anthropogenic warming upon the biosphere, mainly through modifications of species ranges and trophic interactions (Parmesan 2006), yet warming also has a direct impact on the energy balance of birds (e.g. Oswald *et al.* 2011). According to the HDL theory, higher environmental temperatures will decrease the temperature differential between the birds' bodies and their surroundings, as well as their capacity to dissipate heat, and their maximum rates of energy expenditure. This potential additional handicap of birds exposed to global warming has yet not been taken into account. Birds might further modulate their body temperatures and the insulating properties of their outer shell to compensate for warming, and these physiological and morphological adjustments correspond to phenotypic plasticity and microevolution. Such evolutionary processes clearly have to be taken into account in mechanistic models used to assess the capacity of organisms to cope with global warming.

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References

- Aristophanes. (1987) (414 BC) Birds. *The Comedies of Aristophanes* Vol. 6. (ed A.H. Sommerstein), Aris and Phillips, Warminster.

- Behrens, V., Rauschmayer, F. & Wittmer, H. (2008) Managing international 'problem' species: why pan-European cormorant management is so difficult. *Environmental Conservation*, **35**, 55–63.
- Bernard, C. (1856) *Mémoire sur le Pancréas et sur le Rôle du suc Pancréatique Dans les Phénomènes Digestifs, Particulièrement Dans la Digestion des Matières Grasses*. J.-B. Baillière, Paris.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. & West, G.B. (2004) Towards a metabolic theory of ecology. *Ecology*, **85**, 1771–1789.
- Caviedes-Vidal, E. & Karasov, W.H. (2007) Digestive plasticity in birds: Mechanisms and ecological consequences. *Comparative Biochemistry and Physiology A*, **148**, S132–S132.
- Clarke, A. & Pörtner, H.-O. (2010) Temperature, metabolic power and the evolution of endothermy. *Biological Reviews*, **85**, 703–727.
- Darwin, C. (1872) *The Origin of Species*. John Murray, London.
- Diamond, J.M., Karasov, W.H., Phan, D. & Carpenter, F.L. (1986) Digestive physiology is a determinant of foraging bout frequency in hummingbirds. *Nature*, **320**, 62–63.
- Drent, R.H. & Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, **68**, 225–252.
- Eydoux, F. & Souleyet, L.F.A. (1838) Sur la température des hommes et des oiseaux. *Comptes Rendus de l'Académie des Sciences de Paris*, **6**, 456–458.
- Feduccia, A. (1999) *The Origin and Evolution of Birds*. Yale University Press, New Haven and London.
- Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford UK.
- Gotmark, F. (1997) Bright plumage in the magpie: does it increase or decrease risk of predation? *Behavioral Ecology and Sociobiology*, **40**, 41–49.
- Grémillet, D., Wanless, S., Carss, D.N., Linton, D., Harris, M.P., Speakman, J.R. & Le Maho, Y. (2001) Foraging energetics of arctic cormorants and the evolution of diving birds. *Ecology Letters*, **4**, 180–184.
- Grémillet, D., Chauvin, C., Wilson, R.P., Le Maho, Y. & Wanless, S. (2005a) Unusual feather structure allows partial plumage wettability in diving great cormorants. *Journal of Avian Biology*, **36**, 1–7.
- Grémillet, D., Kuntz, G., Woakes, A.J., Gilbert, C., Robin, J.-P., Le Maho, Y. & Butler, P.J. (2005b) Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *Journal of Experimental Biology*, **208**, 4231–4241.
- Hammond, K.A. & Diamond, J.M. (1997) Maximal sustained energy budgets in humans and animals. *Nature*, **386**, 457–462.
- Hammond, K.A., Lloyd, K.C.K. & Diamond, J.M. (1996) Is mammary output capacity limiting to lactational performance in mice? *Journal of Experimental Biology*, **199**, 337–349.
- Hammond, K.A., Konarzewski, M., Torres, R.M. & Diamond, J.M. (1994) Metabolic ceilings under a combination of peak energy demands. *Physiological Zoology*, **67**, 1479–1506.
- Handrich, H., Bevan, R.M., Charrassin, J.-B., Butler, P.J., Pütz, K., Woakes, A.J., Lage, J. & Le Maho, Y. (1997) Hypothermia in foraging king penguins. *Nature*, **388**, 64–67.
- Hill, G.E. (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature*, **350**, 337–339.
- Hochscheid, S., Grémillet, D., Wanless, S. & Du Plessis, M.A. (2002) Black and white under the South African sun: are juvenile Cape Gannets heat stressed? *Journal of Thermal Biology*, **27**, 325–332.
- Johnson, M.S. & Speakman, J.R. (2001) Limits to sustained energy intake V. Effects of cold-exposure during lactation in *Mus musculus*. *Journal of Experimental Biology*, **204**, 1967–1977.
- Karasov, W.H. & Diamond, J.M. (1985) Digestive adaptations for fuelling the cost of endothermy. *Science*, **228**, 202–204.
- Kleiber, M. (1932) Body size and metabolism. *Hilgardia*, **6**, 315–353.
- Kozłowski, J. & Konarzewski, M. (2005) West, Brown and Enquist's model of allometric scaling again: the same questions remain. *Functional Ecology*, **19**, 739–743.
- Król, E., Murphy, M. & Speakman, J.R. (2007) Limits to sustained energy intake. X. Effects of fur removal on reproductive performance in laboratory mice. *Journal of Experimental Biology*, **210**, 4233–4243.
- Król, E. & Speakman, J.R. (2003) Limits to sustained energy intake. VI. Energetics of lactation in laboratory mice at thermoneutrality. *Journal of Experimental Biology*, **206**, 4225–4266.
- Linville, S.U., Breitwisch, R. & Schilling, A.J. (1998) Plumage brightness as an indicator of parental care in northern cardinals. *Animal Behaviour*, **55**, 119–127.
- Lotka, A.J. (1925) *Elements of Physical Biology*. Williams and Wilkins, Baltimore, Maryland, USA.
- Marchetti, K. (1993) Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, **362**, 149–152.
- McGill, B., Enquist, B.J., Westoby, M. & Weiher, E. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–184.
- McNab, B.K. (2002) *The Physiological Ecology of Vertebrates – A View From Energetics*. Comstock, Cornell.
- Oswald, S.A., Huntley, B., Russell, D.J., Anderson, B., Arnold, J.M., Furness, R.W. & Hamer, K.C. (2011) Physiological effects of climate on distributions of endothermic species. *Journal of Biogeography*, **38**, 430–438.
- Parnesian, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Reviews in Ecology Evolution and Systematics*, **37**, 637–669.
- Peters, R.H. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Piersma, T., Koolhaas, A. & Dekinga, A. (1993) Interactions between stomach structure and diet choice in shorebirds. *Auk*, **110**, 552–564.
- Prinzinger, R., Pressmar, A. & Schleucher, E. (1991) Body temperature in birds. *Comparative Biochemistry and Physiology A*, **99**, 499–506.
- Schmidt, A., Alard, F. & Handrich, Y. (2006) Changes in body temperature in king penguins at sea: the result of fine adjustments in peripheral heat loss? *American Journal of Physiology*, **291**, R608–R618.
- Speakman, J.R. (1997) *Doubly Labelled Water: Theory and Practice*. Chapman & Hall, London, UK.
- Speakman, J.R. & Król, E. (2005) Limits to sustained energy intake IX: a review of hypotheses. *Journal of Comparative Physiology B*, **175**, 375–394.
- Speakman, J.R. & Król, E. (2010) Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, **79**, 726–746.
- Speakman, J.R. & Król, E. (2011) Limits to sustained energy intake. XII. Recent progress and future perspectives. *Journal of Experimental Biology*, **214**, 230–241.
- Verhulst, P.-F. (1838) Notice sur la loi que la population poursuit dans son accroissement. *Correspondance mathématique et physique*, **10**, 113–121.
- Vielle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional. *Oikos*, **116**, 882–892.
- Walsberg, G.E., Campbell, G.S. & King, J.R. (1978) Animal coat color and radiative heat gain: a re-evaluation. *Journal of Comparative Physiology*, **126**, 211–222.
- Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals – ecological implications. *Trends in Ecology & Evolution*, **7**, 384–388.
- West, G.B., Brown, J.H. & Enquist, B.J. (1997) A general model for the origin of allometric scaling laws in biology. *Science*, **276**, 122–126.
- White, C.R., Blackburn, T.M. & Seymour, R.S. (2009) Phylogenetically informed analysis of the allometry of mammalian basal metabolic rate supports neither geometric nor quarter-power scaling. *Evolution*, **63**, 2658–2667.
- White, C.R., Blackburn, T.M., Martin, G.R. & Butler, P.J. (2007) Basal metabolic rate of birds is associated with habitat temperature and precipitation, not primary productivity. *Proceedings of the Royal Society B*, **274**, 287–293.
- White, C.R., Grémillet, D., Green, J.A., Martin, G.R. & Butler, P.J. (2011) Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in Great Cormorants. *Ecology*, **92**, 475–486.
- Whitfield, D.P. (1987) Plumage variability, status signalling and individual recognition in avian flocks. *Trends in Ecology and Evolution*, **2**, 13–18.
- Wiebe, K.L. & Bortolotti, G.R. (1993) Brood patches of American Kestrels: an ecological and evolutionary perspective. *Ornis Scandinavica*, **24**, 197–204.
- Zhao, Z.-J. (2011) Milk energy output in Swiss mice throughout the first, second, third and fourth lactation events. *Journal of Experimental Biology*, **214**, 2919–2926.
- Zhao, Z.-J. & Cao, J. (2009) Effect of fur removal on the thermal conductance and energy budget of lactating Swiss mice. *Journal of Experimental Biology*, **212**, 2541–2549.

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