

RESEARCH ARTICLE

What determines the basal rate of metabolism?

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ABSTRACT

The basal rate of metabolism (BMR) is the most reported estimate of energy expenditure in endotherms. Its principal determinant is body mass, but BMR also correlates with a variety of behavioral and ecological factors that do not determine basal rate: they are byproducts of the mechanisms that are its determinate. In mammals, mass-independent BMR increases when muscle mass is >40% of total body mass and BMR is then $\geq 100\%$ of the value expected from body mass. Mammals with muscle masses <30% of body mass have lower BMRs, a diminished capacity to regulate body temperature and often have reduced activity levels. At muscle masses <42% of body mass, birds have body temperatures and basal rates higher than mammals with the same muscle mass. Their high basal rates derive from fast blood flow and increased mitochondrial density in their pectoral muscles. These enhancements also occur in the flight muscles of bats. Oxygen transport to the pectoral muscles of birds is facilitated by an increase in heart mass and hematocrit. This arrangement avoids transporting a large muscle mass to fuel flight, thereby reducing the cost of flight. Pectoral muscle masses <9% of body mass correlate with a flightless condition in kiwis, rails and ducks but some fruit pigeons have BMRs as low as those measured in kiwis, while remaining volant. The mass-independent BMRs of endotherms principally reflect changes of muscle activity and mass. An increase in muscle mass may have contributed to the evolution of endothermy.

KEY WORDS: BMR, Capillary volume, Flightless birds, Migration, Mitochondrial density, Muscle mass, Sedentary lifestyle

INTRODUCTION

A common measure of performance in endotherms is the basal rate of metabolism (BMR). It has been measured in >1400 species, including a collection of mammals (McNab, 2008; Sieg et al., 2009), birds (McNab, 2009) and numerous species reported after these surveys. The value of studying BMR is that it correlates with many aspects of the life history of endotherms, including their food habits, distribution, thermal biology, reproductive output and field energy expenditures (McNab, 2012). Energetics is at a pivotal point in the life of endotherms, which need to balance energy expenditure and performance with energy acquisition.

A limited capacity for temperature regulation correlates with low BMRs in mammals, so the cost of precise thermoregulation is often given as the basis for their high rates. Of interest in this context is the inverse concern: ‘How low can you go?’ (Swanson et al., 2017). With reference to high BMRs, the answer was: ‘High BMR ... represents elevated maintenance costs required to support energy

demanding lifestyles, including living in harsh environments...’ (Swanson et al., 2017, p. 1039). Yet, some harsh environments require a depressed BMR, as when facing xeric conditions (Mueller and Diamond, 2001; Tieleman et al., 2002; McNab, 2019). Here, I address the identity of the mechanisms that determine the rate of metabolism, the secondary consequences of which are correlatives of basal rate. Correlatives themselves do not influence basal rate, but are a guide to the mechanisms that determine energy expenditure.

MATERIALS AND METHODS

The analyses are based on data collected from the literature. BMRs and corresponding body masses were obtained from a collection of mammals (McNab, 2008) and birds (McNab, 2009). Body muscle masses of mammals were obtained from Chivers and Hladick (1980), Raichlen et al. (2010) and Muchlinski et al. (2012). Body muscle masses, heart masses and pectoral muscle masses of birds were found in Hartman (1961) and Wright et al. (2016); the same data on bats were obtained from Hartman (1963). All factors that correlate with mass as a power function are indicated as mass-independent values derived from dividing the measured values by those expected from mass in the appropriate scaling relationship. These dimensionless ratios are expressed as percentages of the ‘expected’ value, which are simply dimensionless ratios multiplied by 100. The curves were fitted using ANCOVA.

RESULTS

Body composition directly impacts energy expenditure, as demonstrated in mammals by Wang et al. (2001), in primates by Muchlinski et al. (2012) and Raichlen et al. (2010) and in birds by Daan et al. (1990), Wiersma et al. (2012), and McNab (1994, 2003a, 2015). Mass-independent BMR in eutherian mammals is proportional to muscle mass when it is >40% of body mass (Fig. 1). These mammals are active, have BMRs $\geq 100\%$ of that expected from a mammalian scaling curve (McNab, 2008) and precisely regulate body temperature.

Mammals with muscle masses between 20 and 40% of body mass have mass-independent BMRs that are between 50 and 80% of that expected from body mass (Fig. 1). When muscle mass is <30%, they have flexible body temperatures and often a ‘slow’ lifestyle. This restriction is found in a small marsupial (*Marmosa robinsoni*), some small primates (*Loris tardigradus*, *Nycticebus coucang*, *Tarsius syrichta*, *Perodicticus potto*) and tree sloths (*Bradypus variegatus* and *Choloepus hoffmanni*). In spite of their larger mass, sloths have variable body temperatures reflecting small mass-independent muscle masses (23 and 26% of body mass, respectively; Grand, 1977) and low mass-independent BMRs (50 and 55%, respectively; McNab, 2008) (Fig. 1). The principal determinant of BMR in mammals is the combination of body mass and the proportion of mass that is muscle tissue. What determines the BMR in birds?

To compare the mass-independent BMRs of birds with those of mammals requires the use of the same standard, in this case the mammalian scaling curve (McNab, 2008). The mass-independent BMRs of birds are also independent of muscle masses between 20

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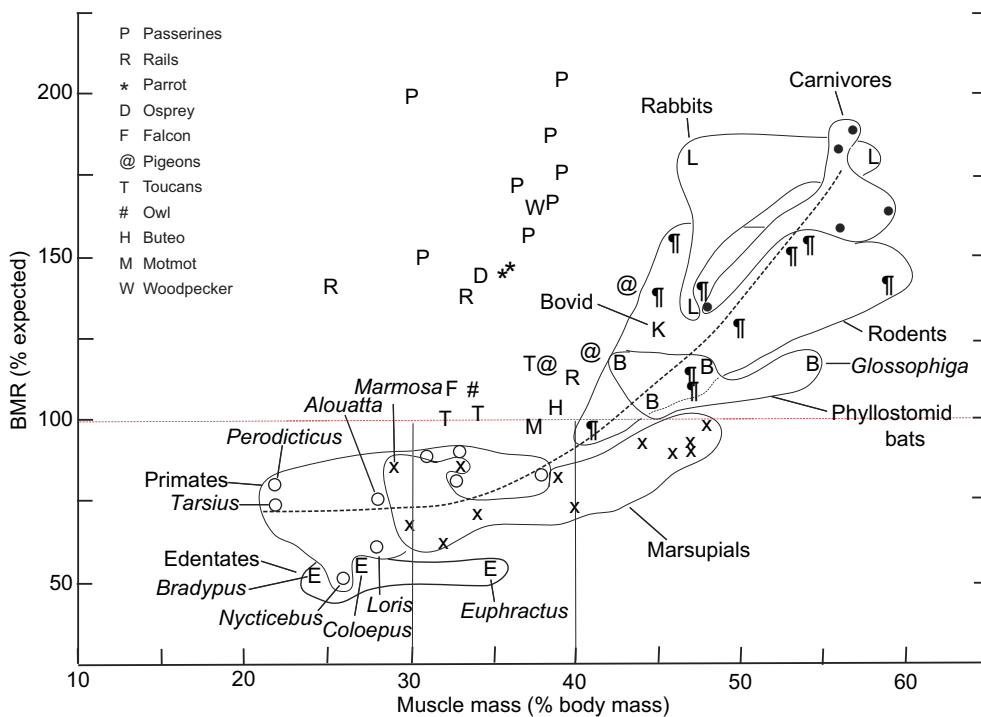


Fig. 1. Basal rate of metabolism (BMR; % of expected from a mammalian scaling curve) as a function of muscle mass (% of body mass) in mammals and birds. Data on muscle mass of mammals are from Chivers and Hladik (1980), Raichlen et al. (2010) and Muchlinski et al. (2012). Muscle masses of birds are derived from Hartman (1961). Basal rates of birds are compared with a mammalian scaling curve (McNab, 2008) to use the same standard as in mammals. Dashed black curve indicates a BMR equal to 100% of the value expected from mass. Horizontal red dotted line indicates the standard rate of metabolism (100%) against which the metabolic rates of species are compared. Vertical solid lines at 30 and 40% muscle mass distinguish the species at <30% body mass, which have low basal rates and often have poor temperature regulation, and those in which basal rate increases with mass at >40% body mass.

and 42% of body mass with great variation (Fig. 1). They are higher than those of mammals in this mass range ($F=581.9$, $P<0.0001$; $t=7.37$, $P<0.0001$). The higher BMRs in birds correlate with their higher body temperatures over the same range in muscle mass (Fig. 2). Much of the variation in the BMR of birds correlates with the intensity and frequency of flight, with high rates in most ducks, parrots, pigeons and passerines. Low rates are found in species with low intensity and frequency of flight, e.g. motmot, goatsucker, owl, soaring hawks and toucans. The increase in BMR with muscle masses >40% in eutherian mammals leads to mass-independent BMRs equivalent to those of birds, as seen in rabbits, carnivores, a bovid and some rodents (Fig. 1). Notice that

mass-independent BMRs in marsupials only show a modest increase with muscle mass, but do not exceed the mammal scaling curve (McNab, 2012).

How can birds have high BMRs without having large muscles? The answer reflects the intensity of muscle activity, which depends on their structure, specifically capillary length and mitochondrial density. These structures are much greater in avian pectoral muscles than in the soleus (leg) muscles of cursorial mammals, the muscles principally responsible for locomotion in birds and terrestrial mammals, respectively. For example, pectoral muscles in finches have capillary length/fiber volume and mitochondrial density/fiber volume that are four times those in the finch leg and the rat soleus (Hepple et al., 1998). High densities of capillaries and mitochondria are found in the pectoral muscles of hummingbirds (Mathieu-Costello et al., 1992a). The very high BMRs and commitment to endothermy at very small masses in shrews are facilitated by a large capillary volume and mitochondrial density in their diaphragms, which are as high as they are in the flight muscles of birds (Mathieu-Costello et al., 2002).

Phyllostomid bats have capillary volumes and mitochondrial densities in their flight muscles that are twice those in the bat hind limb and five times that in the rat soleus (Mathieu-Costello et al., 1992b), but phyllostomids also have larger flight muscles than birds (Fig. 1). The largest occurs in *Glossophaga soricina*, a hovering nectarivore. Phyllostomid bats that regulate body temperature (McNab, 2003b) with muscle masses >40% of body mass (Hartman, 1963) have BMRs similar to those of birds with low intensity flight (Fig. 1). The cost of flight in bats is less than the cost in birds (Winter and von Helversen, 1998).

A large oxygen flux occurs from the capillaries to mitochondria, where oxygen acts as the terminal electron acceptor. The large capillary volumes and mitochondrial densities in the flight muscles of birds and bats provide the energy expenditures required for flight. This accounts for the high BMRs in birds and to a limited extent in endothermic bats. (This pattern occurs in some phyllostomids because they are the only microchiropterans committed to continuous

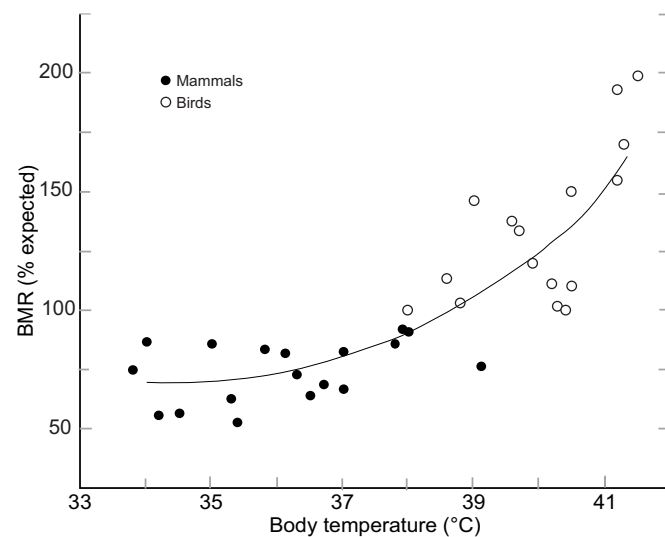


Fig. 2. Body temperature (°C) as a function of BMR (% of the value expected from mass) in birds and mammals. These data are from species with BMR between 20 and 42% of muscle mass (% body mass) indicated in Fig. 1.

endothermy. High oxygen flux in insectivorous bats is not correlated with BMR because these bats do not maintain a constant body temperature and therefore do not have a basal rate that can be defined.) The presence of augmented blood flow and mitochondrial density in birds avoids transporting large pectoral muscles to pay the cost of flight.

The dependence of flight on a high oxygen flux in birds requires an adequate blood supply, which is facilitated by large hearts. An examination of 143 species demonstrates that mass-independent heart mass, expressed as a percentage of body mass, correlates ($F=0.170$, $P<0.0001$; $t=6.71$, $P<0.0001$) with mass-independent pectoral muscle mass (Fig. 3), with great variation (data from Hartman, 1961). This variation reflects the diversity in flight, including soaring, powered flight, gliding and hovering, resulting in an R^2 value of only 0.246. The variation in pectoral mass accounts for only 24.6% of the variation in heart mass. Hummingbirds have very large hearts (2.1 to 2.5% of body mass), as to be expected from the intensity of their hovering flight. Others with large hearts (1.3 to 1.7%) and swift flight include shorebirds, parrots and finches. Accipiters, especially buteos, caprimulgids, tinamous and a motmot, as expected from their form of flight, have small hearts.

Furthermore, the transport of oxygen to flight muscles depends on the hematocrit content of blood. That increases with body temperature (Gillooly and Zenil-Ferguson, 2014). Endotherms have higher hematocrits than reptiles, amphibians and fish. Most birds have higher hematocrits than most mammals do because birds generally have higher body temperatures, which contributes to the higher BMR of birds.

If this analysis is correct, the BMRs of birds should correlate with heart mass, which they do ($F=388.68$, $P=0.0033$; $t=3.16$, $P=0.0033$), again reflecting variation in the level of activity. This correlation occurs in the 36 species of the 143 that have BMRs available (Fig. 4). Because of their diverse range of behaviors, R^2 equals only 0.221, which is similar to that found between heart mass and pectoral mass. In spite of its very large heart, a hummingbird

does not have a high BMR (Fig. 4), presumably reflecting the inverse relationship of BMR and entrance into torpor; a pattern that is widespread in endotherms (McNab, 2008, 2009). Migratory ducks have BMRs that are 2.5-times those of caprimulgids with the same heart mass, which illustrates the complexity of factor interactions.

Vertebrate-eating carnivores have higher BMRs than carnivores committed to varying degrees of herbivory (McNab, 2000b). The higher BMRs of the meat-eating species was suggested to reflect a high mitochondrial density in their muscles and that their muscles were designed for endurance rather than power output (Muñoz-García and Williams, 2005). Konarzewski and Książek (2013) also emphasized the importance of cellular and tissue mitochondrial activity in setting energy expenditure.

Another possible contribution to the high rates of the meat-eaters is a large muscle mass. Unfortunately, few data are available on the body composition of carnivores. Schoenemann (2004) had data from two felids, three mustelids and the raccoon (*Procyon lotor*). Muscle masses of the meat-eaters varied from 55.5 to 57.1% of body mass, whereas that of the mixed-diet raccoon was 48.4%. The cats and mustelids have a plant-free diet, but plants are 26.5% of the diet in the raccoon, the remainder of its diet being invertebrates (McNab, 1995; McDonald et al., 2000; Muñoz-García and Williams, 2005; Larivière and Jennings, 2009).

Mass-independent BMRs decrease as plants in the diet increase (Fig. 5), or put another way, BMRs in carnivores with a mixed diet increase as vertebrates in the diet increase (McNab, 1995). Data are unavailable on the muscle mass of carnivores with a nearly complete commitment to a plant diet. Sloths and two primates have mass-independent BMRs similar to those of carnivores that have diets that consist only of plants (Fig. 5). They have muscle masses that are between 23 and 31% of body mass. This raises the question as to whether carnivores with similar diets have similar muscle masses. These data can be used to estimate the relationship between muscle mass and diet, which suggests that species with a largely plant-based diet have small muscle masses, which is why they have low BMRs

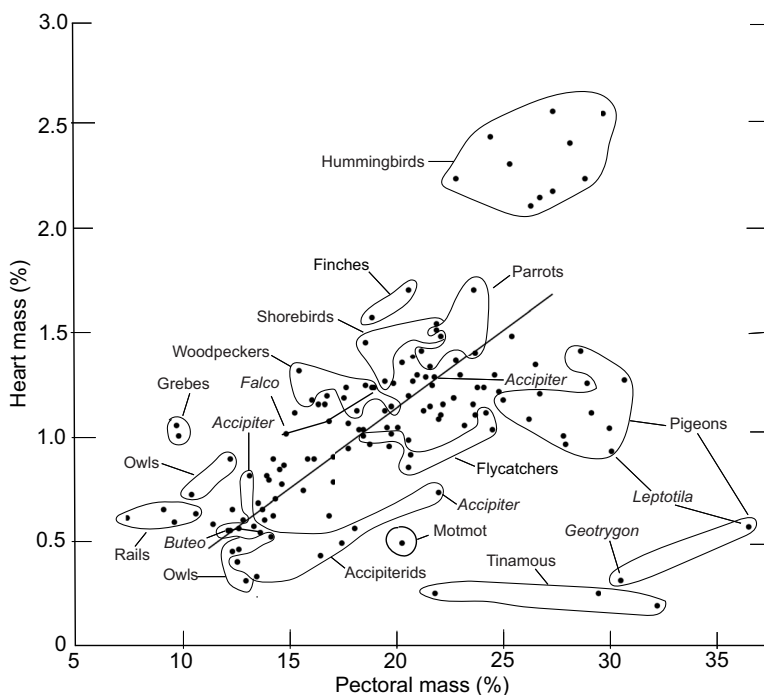


Fig. 3. Avian heart muscle mass (% body mass) as a function of the sum of the pectoral and supracoracoideus muscle masses. The sum of the pectoral and supracoracoideus muscle masses is referred to here as the pectoral muscle mass. These data are derived from Hartman (1961).

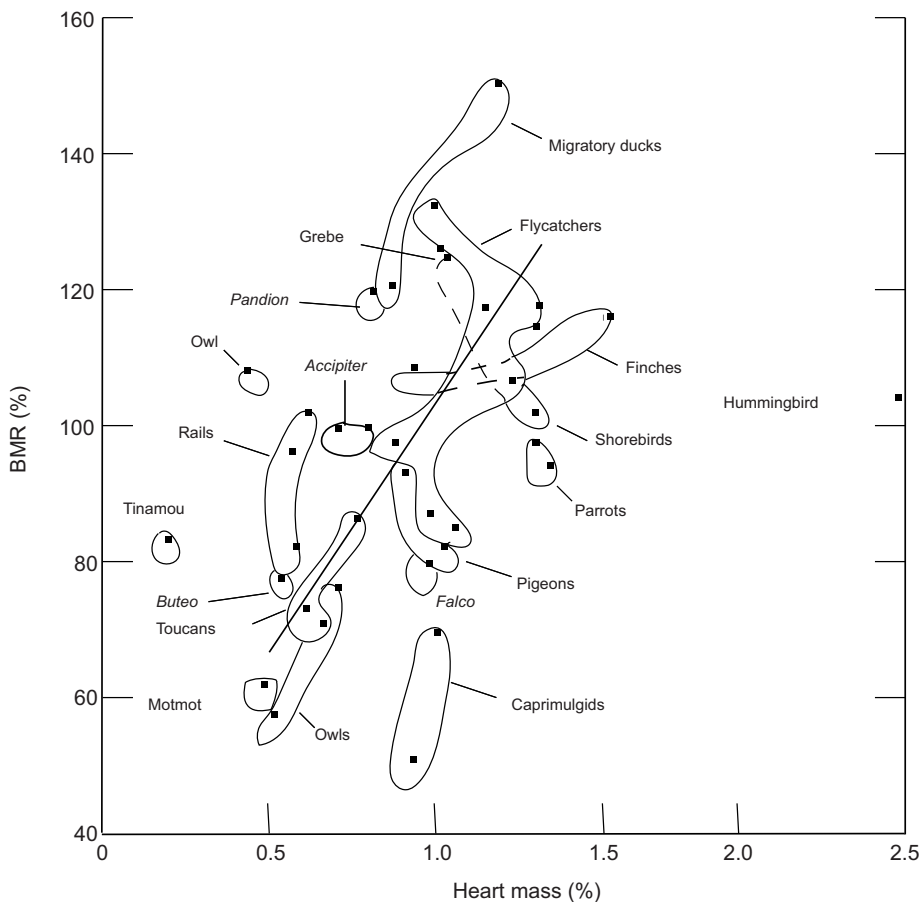


Fig. 4. BMR (% expected from mass from an avian scaling curve) as a function of heart mass (% of body mass). Data from McNab (2009), Hartman (1961) and Larivière and Jennings (2009).

(Fig. 5). From personal experience, this is likely to be the case in the frugivorous binturong (*Arctictus binturong*), which has the lowest mass-independent BMR (36%) of all carnivores and is sluggish.

A relevant observation is found in two cats that are close relatives, the ocelot (*Leopardus pardalis*) and the margay (*Leopardus wiedii*). The ocelot, like most cats, has a high BMR (123% of the value expected from mass), whereas the margay has a low BMR (79%) (McNab, 2000b). Both are committed to a vertebrate diet. Unfortunately, there are no data on the body composition of these species, but they appear to be quite different in that the ocelot is a muscular, terrestrial species. Sunquist and Sunquist (2009, p. 145) state that the margay is ‘A small, lightly built cat...’. My experience with the margay confirms its lean body. The difference in their BMRs likely reflects body composition, with a small muscle mass in the margay that is potentially a response to its arboreal habits.

How is a particular correlation of energy expenditure with behavior and the environment attained? Consider, for example, the correlation of BMR with food habits in carnivores. Vertebrates are a high-quality prey. They (usually) are readily available and their tissues are packed with water, proteins, minerals, calories and fats, and permit the mass-independent BMR of the predator to increase through an increase in muscle mass. A specialization on fruit diet, however, involves a variable supply that principally consists of water and sugar. Frugivorous carnivores have low BMRs, e.g. *Potos*, *Arctogalidia*, *Nandinia* and *Arctictus* (Fig. 5). The depression of BMR in these species appears to be implemented by a decrease in muscle mass. This pattern leads to the correlation of BMR with food habits, which is a byproduct of modification of body muscle mass: large muscles in carnivorous species and small muscles in frugivorous species. The correlation of BMR with food habits in

carnivores therefore is an indirect reflection of a change in the body composition of consumers in response to energy availability, as associated with the characteristics of food. Food habits do not directly influence the BMR of the consumers, but do so indirectly through their nutritional characteristics.

Examples from flightless and island species

The wide variability in the energy expenditure of ducks is independent of pectoral muscle mass when this is between 10 and 20% of body mass (Fig. 6). Here, BMRs are 80–100% of the value expected in birds from body mass; the independence potentially accomplished by the adjustment of pectoral muscle mass activity. Most of these species are sedentary (note that volant ducks in New Zealand are also sedentary) or make short-distance movements (McNab, 2003a). However, at pectoral muscle masses near 20%, most long-distant migrants have BMRs that are between 110 and 200% of the BMRs expected from mass in birds (Fig. 6). But some exceptions appear, including the green-winged teal (*Anas crecca*), tufted duck (*Aythya fuligula*) and lesser scaup (*Aythya affinis*). Why that is the case is unknown.

Ducks that are long-distance migrants have much of their breeding range at high latitudes in the northern hemisphere, which requires them to migrate long distances seasonally. They have pectoral muscle masses between 19 and 28% of body mass and large hearts, which represent 1.0–1.5% of body mass (Hartman, 1961). Many sandpipers (Scolopacidae) also breed at high latitudes in the subarctic, which requires them to be long-distant migrants. A sandpiper belonging to the genus *Tringa* has a BMR equal to 122% of that expected from mass, pectoral muscles 22.2% of body mass, and a heart mass of 1.1% of body mass (Fig. 6).

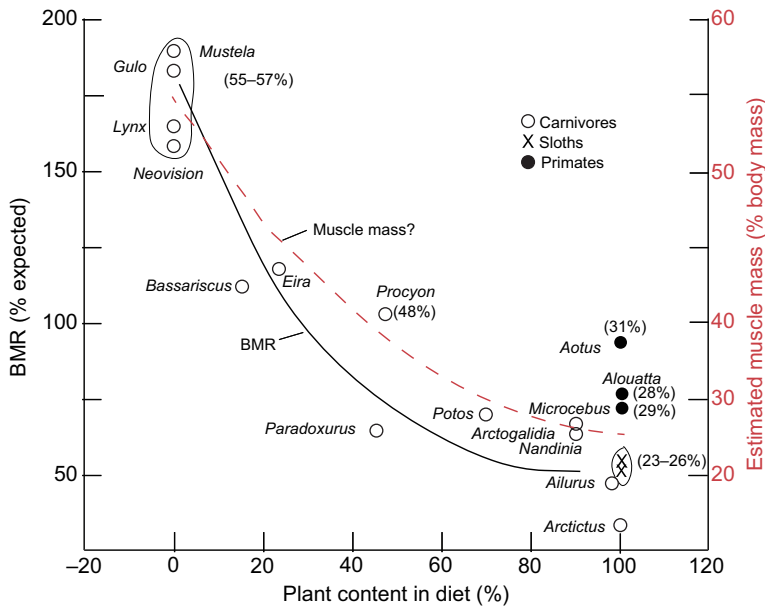


Fig. 5. BMR (% expected from mass from a mammalian scaling curve) as a function of the proportion of plants in the diet. Data are from McNab (1995), McDonald et al. (2000) and Larivière and Jennings (2009). Basal rates of two sloths and primates (*Alouatta pallida* and *Aotus trivirgatus*) are indicated. The proportion of mass that is muscle is indicated in parentheses. A curve (red dashed line) that tentatively describes the relationship between muscle mass (% of body mass) and the proportion of plants in the diet is shown.

Migrating ducks and shorebirds have large pectoral muscles, large hearts, and may have an increased blood flow and mitochondrial density in their pectoral muscles beyond that of other birds. Of interest is the energy status of the wrybill (*Anarhynchus frontalis*), a sedentary plover limited to South Island, New Zealand. Is its energetics similar to that of sedentary ducks?

Like ducks, rails have BMRs with great variation, independent of pectoral muscle masses from 9 to 15% of body mass (Fig. 7). Their BMRs vary between 80 and 100% of the value expected from mass. But unlike ducks, no rail has high BMR by an avian standard. The corncrake (*Crex crex*) is the only long-distance migrating rail in this

study. Its pectoral muscle mass is 15% of body mass and its BMR is 100%. The common coot (*Fulica atra*) is an intermediate-distance migrator; its pectoral muscle mass is 10% of body mass and BMR is 103% (Fig. 7). Why do herbivorous rails have such higher BMRs than omnivorous species at the same pectoral muscle masses (Fig. 7)?

A flightless condition is found in kiwis, ducks and rails when pectoral muscle masses are <9% of body mass. One duck, *Anas aucklandica*, has a BMR that decreases with pectoral muscle mass, at 2% and 8% in its two island populations that are flightless. Its volant population, *A. a. chlorotis*, a sedentary resident on mainland

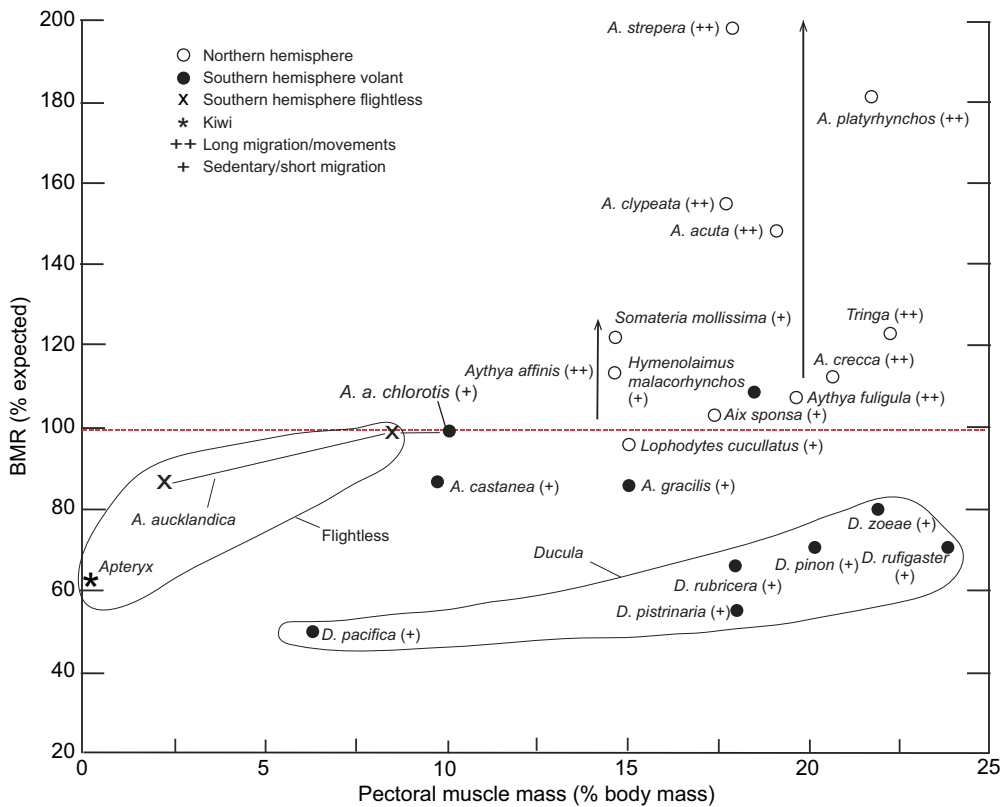


Fig. 6. BMR (% expected from an avian scaling curve) as a function of pectoral muscle mass (% body mass) in ducks, pigeons, a kiwi and a shorebird (*Tringa*). Pectoral muscle masses derived from Hartman (1961), McNab (1994) and Wright et al. (2016). Avian BMRs and the avian scaling curve obtained from McNab (2009). Ducks of the genus *Anas* are abbreviated to *A.* and *Ducula* to *D.* Red dotted line is the standard rate of metabolism (100%) against which the metabolic rates of species are compared. The two arrows indicate the increase in the basal rate of species with respect to their geographical distributions.

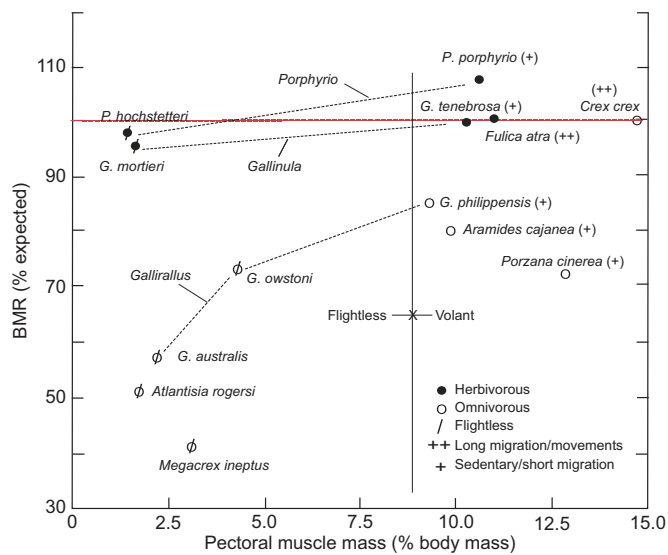


Fig. 7. Basal rate of metabolism (% expected from an avian scaling curve) as a function of heart mass (% of body mass) of rails. Pectoral muscle masses derived from Hartman (1961). Avian BMRs and scaling curve obtained from McNab (2009). Solid vertical line separates flightless and volant species. Dashed black lines indicate members of the same genus. Red dotted line is the standard rate of metabolism (100%) against which the metabolic rates of species are compared.

New Zealand, has a pectoral muscle mass equal to 10% (Fig. 6) (McNab, 2003a) (sometimes these ducks are considered to be separate species, but if so, they are closely related).

A kiwi (*Apteryx australis*) has almost no pectoral muscle mass (0.12% of body mass) and a BMR that is 61% of the value expected in birds (McNab, 1994) (Fig. 6). A flightless parrot, the kakapo (*Strigops habroptilus*), has a pectoral muscle mass equal to 1.4% of body mass (McNab, 1994), whereas volant parrots have pectoral muscle masses from 19 to 24% of body mass (Hartman, 1961). They have BMRs between 92 and 156% of the values expected from mass (McNab, 2009). Unfortunately, no data are available on the kakapo's BMR.

The response of birds to residence on islands is more complicated than the occasional evolution of a flightless condition. Wright et al. (2016) demonstrated in island endemics a widespread reduction in pectoral muscle mass and the evolution of long legs as commitments to a terrestrial existence. It occurs principally in birds endemic to small islands, where a small species diversity is present coupled with few avian predators. Furthermore, '...the profound shape change exhibited during the transition to flightlessness is the extreme manifestation of a predictable pattern of avian evolution in response to ecological release from predators' (Wright et al., 2016, p. 4769).

Volant fruit pigeons of the genus *Ducula* have BMRs (McNab, 2000a) similar to those found in flightless ducks and rails (Fig. 6). This is most striking in the small (350 g) pacific pigeon, *Ducula pacifica*, a small-island specialist. It has a pectoral muscle mass that is only 6% of body mass and a BMR lower than that in the kiwi, but is volant. Other *Ducula* species are also characterized by low BMRs, two of which are as low as that in the kiwi, although with larger pectoral muscle masses compared with the pacific pigeon. Three extinct flightless island pigeons, the dodo (*Raphus cucullatus*) from Mauritius, the solitaire (*Pezophaps solitaria*) from Rodriguez and the Fiji giant pigeon (*Natunaornis gigoura*) (Worthy, 2001), were very large for a pigeon at ~10–28 kg. These

masses, combined with small pectoral masses and a frugivorous diet (Livezey, 1993), required these pigeons to be flightless.

The pacific pigeon has a very wide geographic distribution limited to small islands in Melanesia and Polynesia. It is a 'supertramp' in that it readily moves from one island to another (Diamond, 1974, 1982; Steadman et al., 1990; Steadman, 1997, 2006). It has expanded its range since the arrival of humans, responding to habitat modification (Steadman, 2006). Another small (340–400 g) supertramp, *Ducula oceanica*, is similar in that it is widely distributed on small islands in Micronesia, and likely has physiological characteristics similar to those of *D. pacifica*, a low BMR and small pectoral muscle mass. These species are closely related (Cibois et al., 2017). How can they expand their range with such low BMRs and small pectoral muscle masses? Pigeons are usually characterized by strong, swift flight. The flight of *D. pacifica*, however, is not as forced and rapid, which may facilitate its widespread dispersal (David Steadman, Florida Museum of Natural History, University of Florida, personal communication). Its cost of flight per unit distance would be reduced (Dietz et al., 2007).

DISCUSSION

Basal rates reflect the limitations and opportunities present in their ecological niches and geographical distributions. Behavior and the environment do not directly determine BMR, they reflect adjustments made of muscle mass and activity. A quality food can be profitably exploited through an increased BMR attained in terrestrial mammals by an increased muscle mass and in birds and bats by an increased blood flow and mitochondrial density in their pectoral muscles, and in some cases, by an increase in pectoral muscle mass. The exploitation of an unreliable food resource requires a reduction of energy expenditure, which is facilitated by a reversal of these adjustments. This was seen in the response of birds to island endemism, i.e. a reduction in the size and activity of their muscle masses. With reference to a polar distribution in birds, an increase in their pectoral muscle mass, blood flow and mitochondrial density facilitate long-distance migration, as in ducks and is likely in shorebirds.

High-quality resources support high levels of energy expenditure in endotherms. They are not exploited by ectotherms, except in the absence of ecologically equivalent endotherms (through an increase of mass in lizards, snakes, crocodiles and tortoises endemic to islands). Ultimately, the evolution of endothermy from ectothermy was a means of exploiting resources that sustain high levels of energy expenditure and their consequences, as noted by Swanson et al. (2017). This opportunism may have evolved in ectotherms through an increase in the activity and size of their muscle masses. Unfortunately, there appear to be no data available on the body composition of lizards to test this suggestion.

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Competing interests

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