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Review

Measurement of flying and diving metabolic rate in wild animals: Review and recommendations☆

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A R T I C L E   I N F O

A B S T R A C T

Animals' abilities to fly long distances and dive to profound depths fascinate earthbound researchers. Due to the difficulty of making direct measurements during flying and diving, many researchers resort to modeling so as to estimate metabolic rate during each of those activities in the wild, but those models can be inaccurate. Fortunately, the miniaturization, customization and commercialization of biologgers has allowed researchers to increasingly follow animals on their journeys, unravel some of their mysteries and test the accuracy of biomechanical models. I provide a review of the measurement of flying and diving metabolic rate in the wild, paying particular attention to mass loss, doubly-labelled water, heart rate and accelerometry. Biologgers can impact animal behavior and influence the very measurements they are designed to make, and I provide seven guidelines for the ethical use of biologgers. If biologgers are properly applied, quantification of metabolic rate across a range of species could produce robust allometric relationships that could then be generally applied. As measuring flying and diving metabolic rate in captivity is difficult, and often not directly translatable to field conditions, I suggest that applying multiple techniques in the field to reinforce one another may be a viable alternative. The coupling of multi-sensor biologgers with biomechanical modeling promises to improve precision in the measurement of flying and diving metabolic rate in wild animals.

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Contents

☆ This contribution is part of a Special Issue entitled "Ecophysiology methods: refining the old, validating the new and developing for the future", a set of ten articles reviewing methodological developments to facilitate physiological studies in field situations or in non-invasive scenarios.

"Nothing is more difficult to study than what you cannot see." (Tremblay et al., 2009, citing Monod 1991).

1. Introduction

Animals fly over the Himalayas, dive thousands of meters beneath the sea and fly tens of thousands of kilometers around the globe. Given that scientists cannot directly follow animals on these journeys or replicate such extreme conditions in the laboratory, it is challenging to understand how they accomplish those feats. Although questions about such extraordinary accomplishments have perplexed ecophysiologists for decades, recent work has revealed some of the solutions to these mysteries.

This review summarizes existing techniques for measuring flying and diving metabolic rate under field conditions. Field physiology plays an important role because laboratory studies are not always transferable to the wild (Costa and Sinervo, 2004). Diving physiology provides a good example of the importance of field physiology as early lab studies using forcibly-constrained animals confounded the stress response and the dive response; the deep bradycardia of forcibly-submerged individuals is not representative of the shallow bradycardia typical of most dives.

Metabolic rate is, of course, a key physiological parameter during flying and diving. For instance, oxygen stores and oxygen consumption rate are two key parameters that constrain dive duration (Butler and Jones, 1997; Kooyman and Ponganis, 1998; Halsey et al., 2006). The goal of measuring oxygen consumption during diving has led to the development of novel techniques for measuring metabolic rate in the field (Nagy et al., 1984; Ponganis et al., 2009). Likewise, oxygen consumption limits the ability to fly at extremely high altitudes, and measuring flying metabolic rate helped unravel the mystery of high altitude flight (Bishop et al., 2015). Many studies have examined metabolic rate in captive insects, small mammals, ducks and marine mammals. I include only those studies that measured metabolic rate in the wild.

Research has focused on extreme physiology: those animals that dive the deepest, fly the highest or have the shortest wings. Understanding such extreme athletes not only satisfies an inherent human curiosity for 'record-holders', but also provides scenarios for the extreme constraints operating on flying and diving physiology. By measuring the extreme values, we can then interpolate the flying and diving physiology of all species. Many studies recorded incredible feats, such as common swifts (*Apus apus*) flying continuously for 200 days (Liechti et al., 2013), bar-tailed godwits (*Limosa lapponica*) flying 11,000 km nonstop (Gill et al., 2005), and Cuvier's beaked whales (*Ziphius cavirostris*) diving to almost 3000 m for over two hours (Schorr et al., 2014). Extreme behavioural feats are often accompanied by extreme changes in physiology, including dramatic remodeling of organ size. Birds sacrificed at either end of long migrations have shown large changes in organ size (Jehl, 1997; Biebach, 1998; Piersma and Gill, 1998). For instance, bar-tailed godwits (*Limosa lapponica*) leaving Alaska to fly non-stop to New Zealand have atrophied digestive organs, presumably an adaptation to reduce load (lean mass) and flying metabolic rate (Piersma and Gill, 1998). This review focuses on studies that have measured the underlying processes allowing extreme feats rather than those that merely document 'extreme' behavior.

A few decades ago, as noted in the opening quote referring to science completed aboard the first bathyscape, the physiology of animals at depth could only be guessed at based on experiments in shallow laboratory tanks or observations from large underwater vehicles. Recently, the miniaturization of electronic recorders has allowed researchers to follow animals on their adventures and 'see' what is happening in even the most extreme environments. Classic experiments at dive holes in Antarctica, where penguins and seals could dive naturally and yet be recaptured and electronic recorders easily retrieved, revealed dramatically altered physiology during deep diving compared with shallow diving (Kooyman et al., 1971). Similar measurements on elephant seals showed they were able to sustain exceptionally deep dives aerobically by lowering metabolic rate, at times reducing heart rate as low as three beats per minute (Andrews et al., 1997). Likewise, recent experiments with bar-headed geese (*Anser indicus*) migrating over the Himalayas (Bishop et al., 2015), thick-billed murres (*Uria lomvia*) flying long distances with wings optimized for underwater propulsion (Elliott et al., 2013a) and northern bald ibises (*Geronticus eremita*) migrating in flock formation (Portugal et al., 2014) have revealed the physiological capabilities of flying birds. A unifying principle behind these measurements is the Krogh principle that there will be some animal of choice on which a biological problem can be most conveniently studied. For the study of the physiology of flying and diving, the animals that satisfy the Krogh principle are large-bodied species able to carry large recorders that can be easily retrieved because the individuals cannot escape from researchers (penguins, Weddell seals at isolated holes), are trained to follow an ultralight (ibises), are displaced so that they return to a known haulout (elephant seals) or can be easily recaptured (geese and murres).
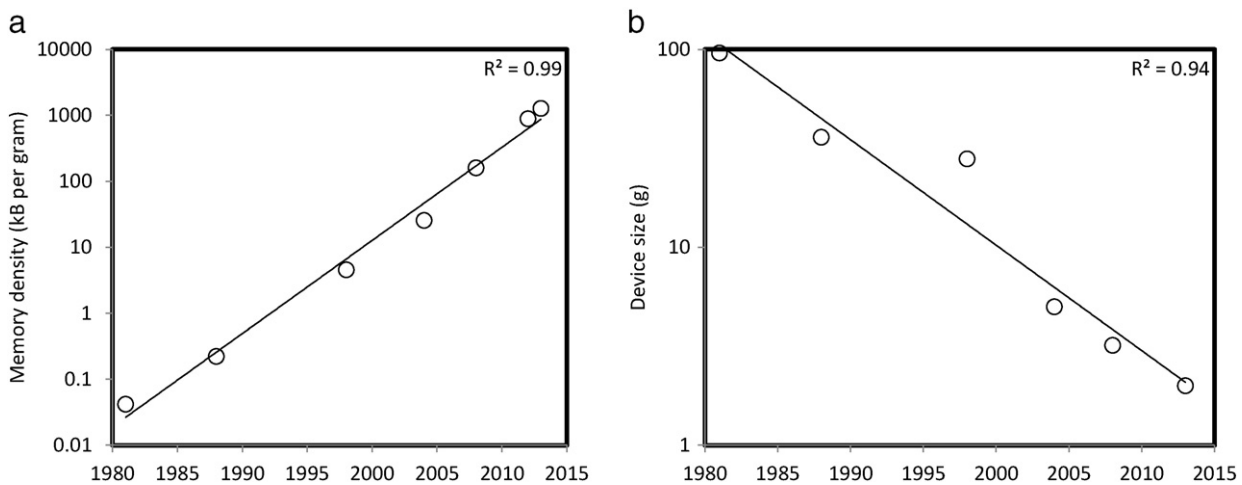

Fig. 1. 'Murre's law' (a) The memory density of an instrument attached to a diving bird doubles every 2.1 years. With the exception of the 1981 datapoint presented for comparative purposes and which refers to a penguin, all points are for instruments attached to murres (Uria spp.) that are small diving seabirds and consequently strongly impacted by tag size. It is assumed that scientists studying murres are therefore placing strong demand on minimizing tag size. (b) The size of time-depth recorders attached to a diving bird halves every 5.5 years. The data are the same as for (b) except they include data only from time-depth recorders.

1.1. Biologging

Biologging plays an important role in the measurement of the physiology of flying and diving (Ropert-Coudert and Wilson, 2005; Burger and Shaffer, 2008; Wilson et al., 2015). The development of biologgers is driven by increasing memory density in commercial electronics. The number of transistors on an integrated circuit of a particular size doubles every two years ('Moore's law', Moore, 1965). Likewise, the memory per unit gram of a time-depth recorder attached to a small seabird—and therefore under continual demand for ever smaller recorders—has doubled every two years ('Murre's law', Fig. 1). The parallel slopes between Moore's law (doubling time of two years) and Murre's law (doubling time of 2.1 years, Fig. 1a) illustrate that the miniaturization of animal-borne recorders has been a consequence of the demand for smaller and faster portable electronic equipment. Indeed, the time between the application of an instrument to a marine mammal and its application to a flying, diving bird is typically ~13 years (e.g. 1975 vs. 1988 for a time-depth recorder lasting days (Kooyman, 2004; Croll et al., 1992), 1992 vs. 2005 for an animal-borne camera (Kooyman, 2004; Watanuki et al., 2008)). The time-depth recorder was first used over 50 years ago, but did not become widely available until the first commercial companies focused on wildlife biologists began in the 1980s. It is the customization and commercialization of biologgers, especially tiny sensors, which drives forward the field of flying and diving field physiology (Andrews, 1998; Kooyman, 2004; Grémillet, 2015).

The creation of ever smaller and more sophisticated biologgers provides the opportunity to make measurements on small animals that do not satisfy the Krogh principle. If we assume that Moore's law holds for another 50 years, then by 2065 we will have a 1 g electronic recorder with 18.5 GB of flash memory—enough to collect a 35 kB photo every minute for a year. By that point, according to Fig. 1b, a conventional time-depth recorder will weigh only 2 mg. There are indications that the speed of miniaturization of electronic equipment will slow down by 2020 (Waldrop, 2016)—but past predictions of the demise of Moore's law have been premature (Kish, 2002). The parallelism between Moore's law and trends in biologging equipment demonstrates that increased energy efficiency of electronics, not improved battery power, drives trends. Of course, many applications require active sensors, such as a GPS antennae, camera shutter or antennae for remote downloading, which increase power use and constrain miniaturization because battery power efficiency has not improved as rapidly as memory capacity. Furthermore, processor speed has not increased in the past decade due to thermal constraints (Waldrop, 2016), meaning that there is unlikely to be improvement in the ability

to process accelerometer and heart rate data on-board tags (which would have reduced space needs and facilitated remote transfer of processed data). Tag size has decreased more slowly over time than memory density (Fig. 1b) as scientists have chosen more data over tag miniaturization—both of which are options afforded by Moore's law—and because battery size has not diminished greatly over the past 40 years.

1.2. Tag effects: the observer effect in wildlife biology

A basic principle in wildlife biology is that it is impossible to observe a wild animal without altering the very parameter that you are aiming to observe. Direct observation may alter heart rate, movement patterns and time budgets of wild animals, and animals may be aware of observers even if the observers attempt to remain hidden. It is a goal of the biologist to minimize such effects, but they can be present even if there is no statistically significant difference between observed and unobserved animals because other sources of variation overwhelm any signal.

Biologging provides a method for obtaining observations without direct observation and potential associated disturbance (Ropert-Coudert and Wilson, 2005). However, biologgers can cause altered time budgets, increased comfort behaviors (e.g. preening), increased mortality, reduced reproductive success and other impacts (Wilson et al., 1986; Barron et al. 2010; White et al., 2013). In some cases, those behaviors may be a consequence of handling stress, which can lead to mortality, nest abandonment, avoidance of capture location or increased wariness. In other cases, the tag itself can disrupt thermoregulation or increase locomotory costs via increased weight and drag.

Both handling and tag effects can influence the measurement of energy expenditure during flying and diving (Barron et al. 2010). Indeed, all six studies on the effect of tags on flying or diving metabolic rate documented higher metabolic rates for tagged than untagged animals, and five of those studies showed statistically significant differences despite an average sample size of only eight tagged individuals (Fig. 2). In contrast, daily energy expenditure does not vary between tagged and untagged individuals (Fig. 2) because tagged individuals spend less time in energetically expensive activities as limitations to energy intake prevent animals from expending more total energy (Elliott et al., 2014a).

Seven points summarize best practices for considering tag effects:

(1) Acknowledge that all tags have some impact, even if that impact is hard to measure. Titles such as "Geolocators on golden-winged warblers do not affect migratory ecology" (Peterson et al., 2015) or "Radio-tags have no behavioral or physiological effects on a migratory songbird" (Gow et al., 2011) are misleading. Given the necessarily limited number of parameters examined and potential for Type II errors due to small sample sizes ($N = 39$ and 10 tagged individuals, respectively), it would be better to state that no effect was *measured*. Similarly, the absence of a tag effect on one parameter does not mean there is no overall effect; tags do not affect daily energy expenditure but strongly impact locomotory costs (Fig. 2). Some species pass costs onto their offspring or partners while others bear the costs themselves (Paredes et al. 2004; Fig. 2a in Elliott et al., 2014a), and measuring only one parameter will miss an important effect.

(2) Distinguish the effect of handling from the effect of the tag.

(3) Use stream-lined tags and place tags centred as far back as possible (Obrecht et al., 1988; Bannasch et al., 1994; Culik et al., 1994). Drag is more important than load, and placing the tag farther back reduces flow separation and turbulence. Although attaching tags to the leg or tail may reduce drag, such positioning can cause instability (Vandenabeele et al., 2014).

(4) Implant tags because lower drag reduces impacts (White et al., 2013). However, extended restraint and anesthesia needed for
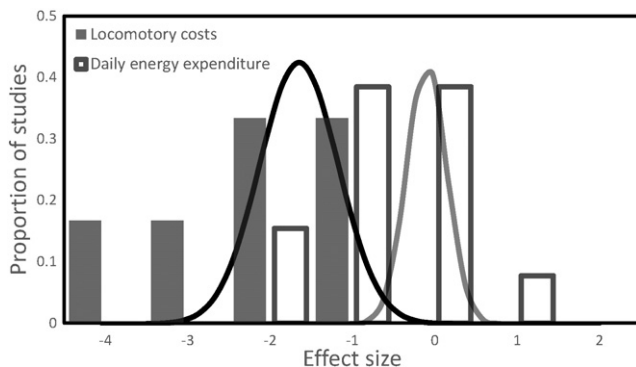

Fig. 2. Summary of all studies that have examined energy expenditure in tagged and untagged individuals. Proportion of studies with a particular effect size (untagged − tagged) / (pooled SD) is shown. Column plots are actual study results. Five out of six studies of locomotory costs were significant at the sequential Bonferroni-corrected alpha value of 0.017, but none of the 13 studies of daily energy expenditure were significant at the sequential Bonferroni-corrected alpha value of 0.004. Line plots show estimated distributions for all studies. All data are from Table 1 in Elliott et al. (2014a).

surgery can cause desertion or mortality (e.g. Meyers et al., 1998).

(5) Use smaller tags. There is no minimum tag size where there is no effect; effects have been clearly documented below purported tag size limits of 5% or 3% of body mass (Vandenabeele et al., 2012; Elliott et al., 2007, 2012). Indeed, every study that has examined multiple tag sizes within a single study has found a larger effect associated with a larger tag size (e.g. Wilson et al., 1986; Bannasch et al., 1994; Ropert-Coudert et al., 2007; Elliott et al., 2007; Chivers et al., 2015). Statements to the contrary from meta-analyses (Barron et al., 2010) are likely due to confounding noise from interspecific variation. Smaller tags have fewer effects, but there is no critical threshold size.

(6) Avoid young individuals. Older individuals, where current brood value is higher, mount a lower stress response to handling and are less likely to desert following tagging (Elliott et al., 2014a, 2014b).

(7) No X% rule will be universal as tag effects are more pronounced on species with high locomotory costs (Vandenabeele et al., 2012; Elliott et al., 2014a). Other aspects than locomotory costs, such as sex or life history strategy, show no consistent effect (Barron et al., 2010; Elliott et al., 2014a).

2. Measuring time budgets and applying activity-specific metabolic rates derived from captivity or modeling

Prior to the biologging revolution, it was usually impossible to directly measure energy budgets during flying or diving in the wild. The only exception was when animals spent all of their time diving or flying when not at an easily observable location, such as a nest, and flying or diving metabolic rate could be estimated based on difference in mass or isotopic signature over the period of flying or diving (e.g. Lyuleeva, 1970). Otherwise, rather than being able to directly quantify energy budgets, authors quantified time budgets and calculated energy budgets using activity-specific metabolic rates estimated from biomechanical modeling or measured on captive animals flying in wind tunnels or

swimming in dive tanks (e.g. Croll et al., 1991; Stanley, 2002). In contrast to running or swimming, allometry is not a particularly useful approach for flying and diving—there is much more variation from the body mass-energy cost regression in flyers or divers than runners or swimming fish (Schmidt-Nielsen, 1972). Diverse uses of biomechanical models included inferring if extinct animals could fly (Speakman, 1993), estimating the minimum distance between stop over sites for migrating birds (Hedenström, 2002), documenting the influence of altered wind patterns on migration (Liechti, 2006), quantifying the cost of removing fecal sacs from the nest (Guigueno and Sealy, 2012), supporting the idea that mass loss is adaptive not stress-related (Croll et al., 1991; Elliott et al., 2008), delineating marine protected areas for an endangered diving duck (Lovvorn et al., 2009), approximating how much energy it takes to construct a nest (Stanley, 2002), and demonstrating a limit to body size in whales (Goldbogen et al., 2012). I argue that such models are often inaccurate, meaning that much of the research based on the models is suspect.

For flying birds, the Pennycuick model (Pennycuick, 1975, 1989, 2008), a model for flying metabolic rate requiring only the input of body mass and wingspan, is by far the most widely used model by ecologists (e.g. cited well over 1000 times as of December 2015, including 90 times in 2015 alone). However, measured flying metabolic rate is typically two to three times higher than flying metabolic rate estimated from the Pennycuick model for small birds and varies by ±30% for large birds (Fig. 3a; see also McWilliams et al., 2004, Videler, 2006). After accounting for variation with body mass, the Pennycuick model explains less than 30% of residual variation in metabolic rate (Fig. 3b). Although there are issues with biomechanical modeling (e.g. estimating the drag coefficient and profile power for a live bird), the Pennycuick and related models usually provide relatively good approximations of biomechanical costs (Dial et al., 1997; Rayner, 1999; Tobalske et al., 2003). The main problem is the conversion of biomechanical work into oxygen consumption (Rayner, 1999; McWilliams et al., 2004). Given that only ~20% of chemical energy obtained by the animal is transferred into biomechanical work, what happens in the transfer is as or more important than the biomechanics. The constant value usually assumed by modeling ignores what is likely substantial variation in muscle efficiency with speed and body mass (Rayner, 1999; Pennycuick, 2008). The Pennycuick model
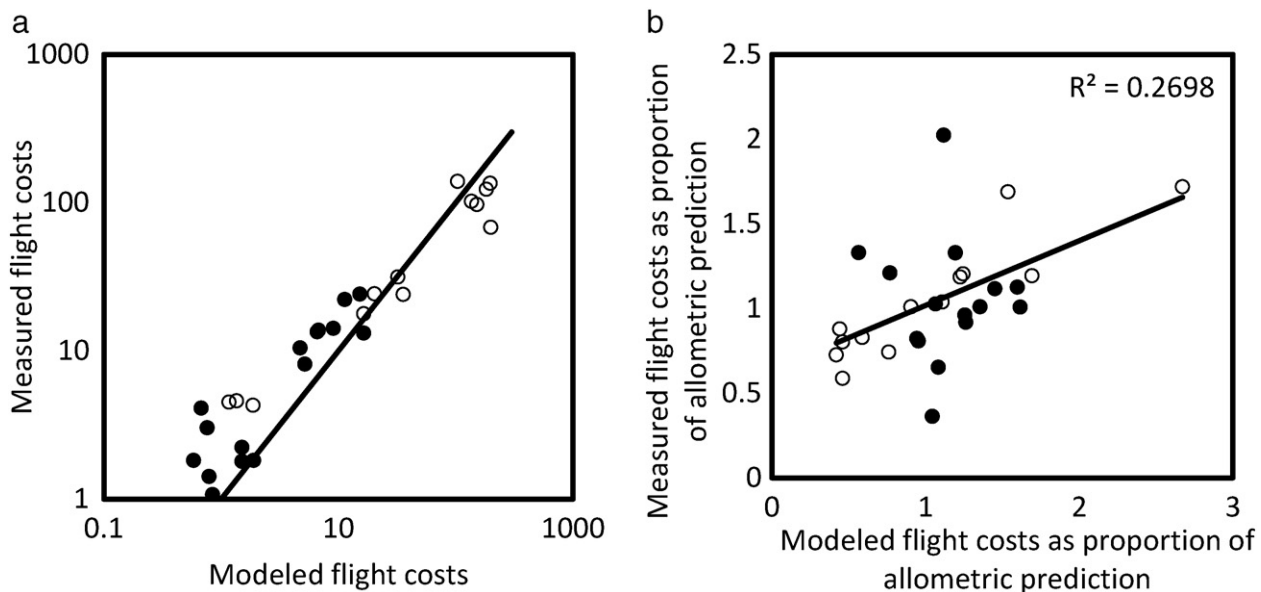

Fig. 3. (a) Measured flying metabolic rate (in a wind tunnel or in the field) relative to modeled flying metabolic rate, assuming flight at maximum range speed, as estimated from the Pennycuick model. The solid line represents the 1:1 relationship showing that the Pennycuick model underestimates flying metabolic rate for small birds and overestimates flying metabolic rate for large birds. (b) The same relationship after accounting for body mass by dividing each value by the predicted value based on the allometric (best fit power law) relationship, with a separate relationship calculated for both modeled and measured metabolic rates. Open symbols are from birds flying in the wild (primarily measured via doubly-labelled water or heart rate) and closed symbols are birds flying in captivity (primarily via respirometry or mass loss). All values are archived with Elliott et al. (2013b).

Table 1

Studies that have measured flying and diving metabolic rate in the wild. Although many studies of captive insects, reptiles, small mammals and ducks may be realistic of field conditions, I only included studies occurring in the wild. Similarly, I only included studies that directly measured metabolic rate and excluded those studies that measured behaviour or kinematics or that estimated metabolic rate via biomechanical modeling. I also only include heart rate data for homeotherms because of complications in measuring energy expenditure from heart rate in non- homeotherms (Green, 2011). R = Respirometry; ML = Mass loss; DLW = doubly-labelled water; BE = bicarbonate enrichment; ACC = accelerometry; PPO = partial pressure of oxygen recorder; DEE = daily energy expenditure.

Species	Method	Results	Source
Flyers			
Various songbird species	ML	Flying metabolic rate estimated based on mass loss of birds over known migrating routes. These studies used various assumptions (see Videler, 2006), such that all birds started at the same time. If birds arriving later started migrating later, then flying metabolic rate would be underestimated. Because such estimates are quite variable, and in some cases substantially underestimate flying metabolic rate for the same or similar species compared to wind tunnel studies, I consider these values unreliable for the purpose of this review.	e.g. Nisbet et al., 1963; Hussell, 1969; Hussell and Lambert, 1980
Northern house martin *Delichon urbanica*; Barn swallow *Hirundo rustica*; common swift *Apus apus*	ML	Flying metabolic rate estimated based on mass loss of birds, and assuming all time was spent in the air. Bills were sewn shut to prevent foraging.	Lyuleeva (1970)
Pine siskin *Carduelis pinus*; chaffinch *Fringilla coelebs*; brambling *Fringilla montifringilla*; bullfinch *Pyrrhula pyrrhula*	ML	Flying metabolic rate estimated based on mass loss of birds migrating for about one hour along a spit.	Dolnik and Gavrilov (1973)
Bar-tailed godwit *Limosa lapponica*	ML	Mass lost over a non-stop migration from Africa to Europe. Percent of mass loss due to loss of lipids estimated from dead birds.	Lindström and Piersma (1993)
Six species of bats	ML	Bats lived in an indoor greenhouse and the only available roost was attached to an electronic balance, allowing measurement of body mass before and after each flight. Feeder visits (volume of nectar consumed) was also measured to account for mass gain due to food.	Winter and Von Helversen (1998)
Rock pigeon *Columba livia*	DLW	Birds were displaced 300 miles and flew back to their loft, allowing estimation of flying metabolic rate from regression of energy expended on flight time.	LeFebvre (1964)
Purple martin *Progne subis*	DLW	Moved birds 100 km away and recaught them upon return to the colony. Assumed a constant value of 1.8 times standard metabolic rate after recapture and prior to final blood sample. Flying metabolic rates were 4.8 to 6.1 standard metabolic rate, lower than previous estimates for birds.	Utter and LeFebvre (1970)
Barn Swallow *Hirundo rustica*; Northern house martin *Delichon urbanica*	DLW	DEE measured while recording total time at nest (assumed no resting away from nest). By assuming that metabolic rate at nest is the same as resting metabolic rate, flying metabolic rate was estimated. Flying metabolic rate for hirudines was lower than other passerines.	Hails (1979)
Wandering albatross *Diomedea exulans*	DLW	Flying metabolic rate estimated as 2.35 times basal metabolic rate for albatrosses at Prince Edward Islands.	Adams et al. (1986)
Grey-headed albatross *Diomedea chrysostoma*	DLW	Flying metabolic rate estimated assuming a constant metabolic rate when on land or resting at sea. Bevan et al., 1995 critique this approach as resting on water is more costly that resting on land.	Costa and Prince (1987)
Wilson's storm-petrel *Oceanites oceanicus*	DLW	Flying metabolic rate estimated from regression of DEE on time spent away from colony, as storm-petrels almost always fly continuously away from the colony.	Obst et al. (1987)
Laysan albatross *Phoebastria immutabilis*	DLW	Flying metabolic rate was 2.6 times incubation metabolic rate, assuming that the metabolic rate of birds resting on the water was similar to flying metabolic rate.	Pettit et al. (1988)
Northern gannet *Morus bassanus*	DLW	Flying metabolic rate (97 W) estimated from regression of DEE on time spent flying. Because the intercept could "hide" some of the variance associated with the slope (flying metabolic rate), Wilson and Culik (1993) reanalyzed the data using a multivariate regression on three activities and determined flying metabolic rate of 88 W.	Birt-Friesen et al. (1989)
Southern giant-petrel	DLW	Flying metabolic rate estimated from regression of DEE on time spent at sea, and assuming that all time spent at sea was spent flying.	Obst and Nagy (1992)
Northern fulmar *Fulmarus glacialis*	DLW	Flying metabolic rate estimated at 4.5 times basal metabolic rate, assuming all time spent at sea was spent flying. DEE at sea and wingbeat frequency declined with wind speed.	Furness and Bryant (1996)
Sooty tern *Onychoprion fuscatus*	DLW	Flying metabolic rate (slope of the regression of DEE on percent time flying) was 4.8 times standard metabolic rate, which was low considering terns used primarily flapping flight.	Flint and Nagy (1984)
Red-footed booby *Sula sula*	DLW	DEE measured while recording time at nest, time on water and time flying. Flying metabolic rate estimated while assuming metabolic rate on water and on nest was equal to resting metabolic rate. Flying metabolic rate was lower than predicted by the Pennycuick model, possibly because energy required for lift was provided by high levels of wind at sea.	Ballance (1995)
Wandering albatross *Diomedea exulans*	DLW	Percent of time flying was not related to DEE for albatrosses at South Georgia, implying that flying metabolic rate was low.	Arnould et al. (1996)
Black-legged kittiwake *Rissa tridactyla*	DLW	Flying metabolic rate estimated at 6.2–7.3 times basal metabolic rate. Flying metabolic rate during plunge diving estimated at 47 times basal metabolic rate.	Jodice et al. (2003)
Swainson's thrush	DLW	Flying metabolic rate estimated from regression of DEE on time spent flying. Because much more time was spent foraging and resting during migration than flying, time spent at stop overs was more important to DEE than time spent flying.	Wikelski et al. (2003)
Black-browed albatross *Diomedea melanophrys*	DLW	Estimated flying metabolic rate assuming metabolic rates while resting on the water were those given by Bevan et al. (1997).	Shaffer et al. (2004)
Ring-billed gull *Larus delawarensis*	DLW	Mass-specific DEE was negatively associated with nest attendance but was not associated with time spent flying.	Marteinson et al. (2015)
Bonda and Sinaloan mastiff bats *Molossus*	BE	Flying metabolic rate of 3.0 W (*currentium*) and 3.3 W (*sinaloae*) for bats flying	Voigt and Holderied (2012)

Table 1 (continued)

Species	Method	Results	Source
currentium, Molossus sinaloae		in a confined space (120 m^2) under semi-captive conditions in the Costa Rican rainforest was ~20 times resting metabolism. High flying metabolic rate may be associated with maneuvering within a confined space.	
Black-browed albatross *Diomedea melanophrys*	HR	Used a calibration equation developed on captive, walking albatrosses to estimate DEE in the wild. Flying metabolic rate was half those estimated by earlier DLW studies because resting metabolism was higher than assumed in earlier studies.	Bevan et al. (1997)
Barnacle goose *Branta leucopsis*	HR	Heart rate declined during migration from 317 to 226 beats min^{-1}, which they estimated as equivalent to 300 W at the start of migration. Later studies would convert these values to anomalously low estimated metabolic rate based on captive calibrations, implying different heart rate-oxygen consumption calibrations in the wild vs. captivity.	Butler et al. (1998)
Swainson's thrush	HR	Flying metabolic rate was higher for individuals with rounded wings and higher wing loading, and during windy periods. Because no heart rate-oxygen consumption rate calibration was available, flying metabolic rate was not estimated quantitatively.	Bowlin and Wikelski (2008)
Spotted antbird *Hylophylax naevioides*	HR	Used a calibration equation developed on the same individuals in captivity to estimate metabolic rate in the wild. Low metabolic rate was associated with little time spent flying.	Steiger et al. (2009)
Velvety free-tailed bat *Molossus molossus*	HR	Used a calibration equation developed on most of the same individuals at rest to estimate flying metabolic rate from heart rate. A heart rate of 847 min^{-1} during flight was equivalent to 0.28 W although the authors do not report that value as calibration occurred on resting bats. Bats had low resting metabolic rate and spent little time flying, and so had low daily energy expenditure.	Dechmann et al. (2011)
Bar-headed goose *Anser indicus*	HR, ACC	Used a calibration equation developed on captive geese in a wind tunnel to estimate flying metabolic rate from heart rate. Simultaneously used accelerometers to estimate biomechanical costs. Flying metabolic rate increased with altitude due to low air density at high altitudes, and geese spent little time at high altitude even though that would have minimized the direct flight path.	Bishop et al. (2015)
Flying divers			
Great white pelican *Pelecanus onocrotalus*	HR	Lower heart rate during flight formation assumed to convert directly into 11.4–14% reduction in flying metabolic rate for pelicans flying in formation. However, because no calibration equation was created, actual metabolic rate or savings are unknown.	Weimerskirch et al. (2001)
Razorbill *Alca torda*	DLW	Flying metabolic rate estimated as 108 W/kg and diving metabolic rate (including surface intervals) as 72 W/kg based on a multiple regression with the intercept set to zero.	Hansen (2003)
Thick-billed murre *Uria lomvia*	DLW, ACC	DEE estimated from DBA correlated with metabolism estimated from DLW. Flying metabolic rate (~150 W) were high while diving metabolic rate (~30 W) were quite low, and suppressed during deep dives. Flying and diving metabolic rate were higher when a device was attached.	Elliott et al. (2013a, 2013b), Elliott et al., 2014a)
Pelagic cormorant *Phalacrocorax pelagicus*	DLW, ACC	DEE estimated from accelerometers correlated with that estimated from DLW. Flying metabolic rate (~160 W) were high while diving metabolic rate (~60 W) were expected from allometric predictions.	Elliott et al. (2013a), Stothart et al. (in press)
Great cormorant *Phalacrocorax carbo*	HR	Used a calibration equation developed in captivity to estimate DEE for an entire year from heart rate. Low DEE during Arctic winters was associated with little time spent diving.	Grémillet et al., 2005; White et al., 2011
Common eider *Somateria mollissima*	HR	Used a calibration equation developed in captivity to estimate non-flying metabolic rate, including diving metabolic rate. Used Fick's equation to estimate metabolic rate during flying. Used heart rate to develop time budgets, and estimated daily energy expenditure from heart rate over 7 months. Main conclusion was that despite high flying metabolic rate, DEE was low because time spent flying was low.	Pelletier et al. (2008)
Divers			
Weddell seal *Leptonychotes weddellii*	R	Oxygen consumption directly measured as seals surfaced in isolated dive holes. Diving metabolic rate was higher during short dives than long dives. Oxygen consumption correlated with number of flipper strokes per dive.	Kooyman et al., 1973; Castellini et al., 1992; Williams et al., 2004
Steller sea lion *Eumetopias jubatus*	R	Oxygen consumption directly measured on sea lions diving in the open ocean, but trained to surface into an oxygen chamber. High diving metabolic rate may be partially due to short dive durations, which did not allow for full metabolic suppression.	Fahlman et al., 2008; Gerlinsky et al., 2013
African penguin *Spheniscus demersus*	DLW	Diving metabolic rate estimated from regression of DEE on distance travelled. Because the value is double the allometric relationship for penguins, and because Shaffer (2011) found that the Nagy equation overestimated DEE relative to other methods, Elliott et al. (2013a) excluded this value from their analyses.	Nagy et al. (1984)
Antarctic fur seal *Arctocephalus gazella*	DLW	Diving metabolic rate estimated from regression of DEE on time spent at sea for lactating females.	Costa et al. (1989)
Australian sea lion *Neophoca cinerea*	DLW	Diving metabolic rate estimated from regression of DEE on time spent at sea for lactating females.	Costa and Gales (2003)
New Zealand sea lion *Phocarctos hookeri*	DLW	Diving metabolic rate estimated from regression of DEE on time spent at sea for lactating females. Individuals diving deeper had lower dive costs.	Costa and Gales (2000)
Eight penguin species	DLW	Diving metabolic rate estimated from regression of DEE on time spent at sea. Because much of the time at sea is likely not spent diving, and metabolism is suppressed during diving, these values may be unreliable.	Reviewed by Nagy et al. (2001)

Table 1 (*continued*)

Species	Method	Results	Source
Australian sea lion *Neophoca cinerea*	DLW	Diving metabolic rate estimated from regression of DEE on time spent at sea for females and juveniles.	Fowler et al. (2007)
Leatherback turtle *Dermochelys coriacea*	DLW	At-sea metabolic rate estimated as 0.20–0.74 W/kg. Jones et al. (2009) suggested that DLW may be inaccurate in turtles due to high water flux and low metabolic rate.	Wallace et al. (2005)
Olive ridley turtle *Lepidochelys olivacea*	DLW	At-sea metabolic rate for hatchlings estimated as seven times resting metabolic rate and higher than digging out of nest. Jones et al. (2009) suggested that DLW may be inaccurate in turtles due to high water flux and low metabolic rate.	Trullas et al. (2006)
Green turtle *Chelonia mydas*	DLW	At-sea metabolic rate for juveniles did not vary with season. Andrews et al. (2009) suggested that DLW may be inaccurate in turtles due to high water flux and low metabolic rate	Southwood et al. (2006)
Macaroni penguin *Eudyptes chrysolophus*	HR	Used a calibration equation for the same individuals to estimate DEE throughout the year. DEE was highest across the breeding season, not just during chick-rearing. Penguins suppressed metabolism during deep dives.	Green et al. (2001, 2005, 2009a)
Gentoo penguin *Pygoscelis papua*	HR	Used a calibration equation developed in flow chambers and treadmills to estimate daily energy expenditure across the breeding season. DEE was higher when penguins had large chicks than during incubation or guard stages primarily because penguins spent more time at sea. Metabolic rate during diving was lower than swimming in flow chambers.	Bevan et al. (2002)
King penguin *Aptenodytes patagonicus*	HR	Used a calibration equation developed on captive birds to estimate diving metabolic rate. Penguins suppressed metabolism during deep dives, especially if those dives had long bottom times. Prey pursuit did not influence metabolic rate. Dive costs increased throughout the breeding season, but DEE did not change.	Froget et al., 2004; Halsey et al., 2010
Emperor penguin *Aptenodytes fosteri*	PPO	Decline of blood oxygen concentrations during diving, including extremely low concentrations during long dives. Could be used to estimate diving metabolic rate.	Ponganis et al. (2009)
California sea lion *Zalophus californianus*	PPO	Decline of blood oxygen concentrations during diving, including extremely low concentrations during long dives. Could be used to estimate diving metabolic rate.	McDonald and Ponganis (2013)
Northern elephant seal *Mirounga angustirostris*	PPO	Decline of blood oxygen concentrations during diving, including extremely low concentrations during long dives, and was independent of activity during the dive.	Meir et al. (2013)
Green turtle *Chelonia mydas*	DBA	Diving metabolic rate estimated based on laboratory calibrations of DBA.	Okuyama et al. (2014)

(and other similar models) predicts that flying metabolic rate should be U-shaped, with lowest metabolic rate at intermediate flight speeds (Tobalske et al., 2003; Pennycuick, 2008). Only 8 species out of 19 tested have shown a U-shaped power curve (Rayner, 1999; Clark and Dudley, 2010; Engel et al. 2010). Thus, actual measurements often fail to support even qualitative predictions from theory, let alone robust, quantitative measurements (see debate between Hedenström, 2012 and Chernetsov, 2012, and citations therein).

Biomechanical modeling of diving faces all the same problems as modeling of flying—difficulty of modeling biomechanics in a fluid medium and uncertainty of how biomechanical work is converted into oxygen consumption—as well as the issue of hypometabolism. During deep dives, breath-hold divers alter their circulatory system, reduce heart rate and decrease body temperature to minimize oxygen consumption (Butler and Jones, 1997; Kooyman and Ponganis, 1998; Ponganis et al. 2009). Such drastic changes in whole animal metabolism obscure any effect of biomechanics in many deep-diving homeotherms (e.g. Halsey et al., 2011b; Meir et al., 2013; Elliott et al., 2013a). At the moment, it is not possible to predict oxygen consumption rates from biomechanical modeling for diving animals.

Applying values measured in the laboratory avoid some of those issues, and there are some good examples of such approaches in shallow-diving mammals (e.g. Nolet et al., 1993; Yeates et al., 2007). However, applying measurements of diving metabolic rate in shallow dive tanks is problematic for deep-diving animals as those measurements are often 3–4 times higher than actual deep dives due to hypometabolism and reduced buoyancy (Green, 2011; Ponganis et al. 2011; Elliott et al., 2013a). Studies that use freely diving, trained sea lions or seals and penguins at isolated dive holes overcome those issues, but are not applicable for many organisms, and measure only a single integrated signal from the entire dive (Kooyman, 2004; Fahlman et al., 2008; Ponganis et al. 2011). Unsteady wind effects, alterations of air flow

due the gas mask during respirometry and energy substitution mean that wild animals may also have altered flying metabolic rate compared to laboratory tests (Rayner, 1999; Bishop et al., 2002).

Biologging approaches provide opportunities for direct measurement of energy expenditure proxies (i.e. heart rate, acceleration, blood oxygen levels) in situ that overcome many of these drawbacks. They also provide the ability to directly test, and therefore refine, biomechanical models. An excellent example was employed by Portugal et al. (2014), who combined biomechanical modeling with GPS-accelerometry to show that ibises flying in V-formation were finely tuning their wingbeats to take advantage of the wake of the preceding bird—providing strong empirical confirmation for theory. The measurements would have been stronger were they coupled with measurements of oxygen consumption via heart rate, blood oxygen levels or doubly-labelled water.

3. Measuring diving and flying metabolic rate in the field

Respirometry is the gold standard for measuring metabolic rate, and is typically used to calibrate other techniques, although even whole-organism oxygen consumption is merely an approximation of true energy use at the cellular level (Salin et al., 2015). While respirometry has been used in semi-wild situations (Table 1), it is difficult to imagine how a truly wild animal could be induced to wear an oxygen mask while foraging in the wild. Thermal imagery can also be used to examine heat loss and refine estimates of flying metabolic rate from respirometry in a wind tunnel (Ward et al., 2004), but, again that technique has not been used in the wild because of the difficulty of getting accurate images in field conditions. A third technique, used for measuring diving metabolic rate, involves counting breaths following surfacing, either using a beak-opening sensors (Wilson et al., 2002, 2003), accelerometers or video recorders (Okuyama et al., 2014) or acoustic recorders (Le Boeuf et al., 2000; Genin et al., 2015). Although the number of

breaths correlates with diving behavior, because of variation in tidal volume and oxygen content during breaths, the technique has yet been used to estimate metabolic rate directly. Recently, Paul Ponganis and colleagues have used electrodes that measure partial pressure of oxygen to measure the oxygen content of blood at various points in the circulatory system (Ponganis et al., 2009). Originally applied to emperor penguins at isolated dive holes, the technique has now been used on wild elephant seals and sea lions (Ponganis et al., 2009; McDonald and Ponganis, 2013; Meir et al., 2013). By measuring oxygen depletion over the course of a dive, the technique directly measures oxygen consumption rate during diving. Indeed, by placing sensors at different locations within the cardiovascular system, the technique can, in principle, measure the oxygen consumption of a particular organ. As that technique has been reviewed in detail elsewhere in this issue, I only review in detail the four 'established' techniques for measuring diving and flying metabolic rate in the field: mass loss, isotopic enrichment (primarily doubly-labelled water), heart rate and accelerometry. I also summarize other techniques, such as metabolites and body temperature, which have provided insight into the physiology of flying and diving, and provide broad-scale information on flying and diving metabolic rate.

3.1. Mass loss

The mass loss technique uses loss of mass over a fixed period of time to measure energy expenditure, by assuming a fixed rate of evaporative water loss and lipid depletion. The technique has primarily been used in the field to measure resting metabolic rate for fasting birds, an approach which has been reviewed in detail (Portugal and Guillemette, 2011). The mass loss approach is effective for animals in phase II fasting if the substrate being consumed and its kinetics during mass loss is known (Portugal and Guillemette, 2011). No flying or diving animal is likely to satisfy those assumptions, yet the technique has been used to estimate flying metabolic rate assuming that flight is fueled exclusively by lipids. For example, wind tunnel studies, where accurate measurements of lean and lipid mass are possible before and after flights, have used this method (e.g. Gerson and Guglielmo 2011). In the field, mass loss was one of the first techniques used to measure flying metabolic rate in the wild (Table 1). Those pioneering studies used measurements of mean population mass before and after a migration of known or assumed duration. However, measurements were highly variable and sometimes an order of magnitude lower than estimates using other methods (Videler, 2006). In the field, apart from the possibility that individuals gain mass through foraging, variation in evaporative water loss and in use of lipids relative to proteins as fuel means that the technique is often unreliable. The mass loss technique holds promise if lipid depletion during flight is measured via sacrificing animals or magnetic resonance (Lindström and Piersma, 1993; Seewagen and Guglielmo, 2011). The technique was also used on bats living in a greenhouse (where feeding could be controlled for) to provide some of the first flying metabolic rate values for bats (Winter and Von Helversen, 1998).

3.2. Isotopic enrichment including doubly-labelled water

The doubly-labelled water method is by far the most widely used method for measuring daily energy expenditure in the field, including flying and diving metabolic rate (Speakman, 1997; Videler, 2006). The method involves injecting an animal with water labelled with both ^{2}H and ^{18}O and using the difference in the rate of disappearance of the two isotopes, and an estimate of the respiratory quotient, to estimate oxygen consumption. Several equations have been developed to estimate energy expenditure, varying in their estimates of one or two pools for body water, the fractionation of isotopes, how total body water is estimated and the respiratory quotient. Those different equations can lead to a 45% variation in estimates of daily energy
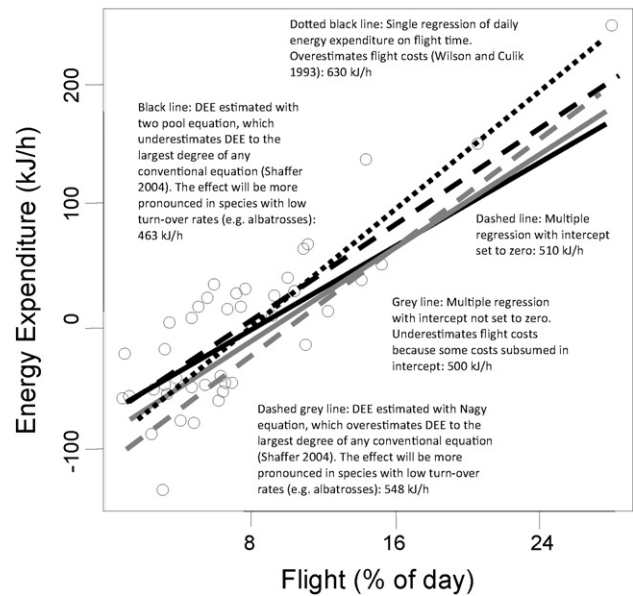

Fig. 4. Partial regression of energy expenditure on time spent flying in thick-billed murres (solid black line). The y-axis represents the residual after accounting for time spent diving, resting on the water and resting on land. Daily energy expenditure using doubly-labelled water typically has error of ± 20% for individuals. Effects of potential sources of error are shown. Flying metabolic rate (slope of energy expenditure relative to time spent flying) estimated by each technique is shown at the end of each annotation. Reproduced from Data Appendix to Elliott et al. (2013a).

expenditure (Shaffer 2011). Nonetheless, if properly applied—for instance, there is growing evidence that the single-pool model with the plateau method is appropriate in most birds—error in the estimation of daily energy expenditure of individual animals using doubly-labelled water is typically less than 20% (Butler et al., 2004). As that error is largely randomly distributed, error at the level of a group is then smaller, with mean error typically less than 5% (Speakman, 1997; Butler et al., 2004), with the exception of aquatic species with high water turnover, such as sea turtles (Jones et al., 2009). The doubly-labelled water method's application to wild animals has been reviewed previously (Speakman, 1997; Butler et al., 2004; Shaffer 2011; Speakman and Hambly, 2016), and I review only its application to measure flying and diving metabolic rate.

Doubly-labelled water provides average daily energy expenditure over a particular time period for individual animals. For the purposes of this review, and because caveats and challenges have been well reviewed elsewhere, I assume that the technique accurately estimates daily energy expenditure. If activity budgets are monitored simultaneously (T_a, proportion of time in activity a; T_b, proportion of time in activity b; etc. such that proportion of time in all activities adds to 100%), then a multiple regression can be used to determine activity-specific metabolic rates from average daily energy expenditure (DEE):

$$DEE = a\,T_a + b\,T_b + c\,T_c + d\,T_d\ldots \qquad (1)$$

In that case, each slope (a, b, c, etc.) is equal to the activity-specific metabolic rate, such as flying metabolic rate or diving metabolic rate. A model selection approach, such as Akaike's Information Criterion, can be used to provide a rationale for determining if particular activities are energetically different from one another or should be subsumed into a single term. Fig. 4 demonstrates an application of Eq. (1) where activity a (flying) is estimated after accounting for activity b (diving), activity c (resting on water) and d (resting on land). It is important that a multiple regression with the intercept forced to zero is used (dashed line in Fig. 4) rather than a simple regression (dotted line) because of likely covariation between different activities (Wilson and Culik, 1993)—although most studies continue to use the inaccurate

simple regression approach (e.g. Wikelski et al., 2003). Setting the intercept to zero, because all activities sum to zero so that if no time passes no energy is expended, avoids subsuming variation in energy expenditure within the intercept term (which would alter activity-specific metabolic rates). It is also important that average daily energy expenditure, and not total energy expenditure, is used as the response variable, to avoid spurious correlations because both axes depend on time (e.g. Pettit et al., 1988). A final caveat is that sample sizes need to be large so that there are sufficient degrees of freedom per estimated slope. In the case of Fig. 4, 43 individuals were sampled, meaning that sample size per activity was only 10–11.

An alternative approach is to assume a metabolic rate for one activity, typically resting, so that all of the residual variation can be assigned to the second activity, such as flight (Hails, 1979; Costa and Prince, 1987; Ballance, 1995). However, because metabolism during 'resting' in the wild is often elevated by digestion, activity or thermoregulation, such approaches can overestimate flying metabolic rate (Bevan et al., 1997).

Capture, injection and handling of an animal for an hour or longer to wait for the isotope to dilute can cause altered behavior and consequently biased estimates of typical daily energy expenditure. For instance, some animals to cease normal behaviors and 'sulk' following capture (Schultner et al., 2010; Harris and Wanless, 2011), leading to an underestimate of daily energy expenditure (Schultner et al., 2010). One benefit of Eq. (1) is that it is not biased by such altered behavior. If an animal flies less, then it will expend less energy flying, but the slope (activity-specific metabolic rate) will be unaltered. Those activity-specific metabolic rates can then be applied to activity budgets from animals that were not handled extensively to estimate unbiased daily energy expenditure.

A second isotopic enrichment technique, ^{13}C labelled bicarbonate (NaH^{13}CO$_3$), has also been used to measure flying metabolic rate using similar techniques to doubly-labelled water (Hambly et al., 2002). Because CO$_2$ rapidly disappears from the body, the technique can be used to measure flying metabolic rate over a timescale of minutes. Although most applications have been in captivity, one study used the technique to measure the flying metabolic rate of bats in a large enclosure in the Costa Rican jungle (Voigt and Holderied, 2012). In that case, CO$_2$ consumption was directly measured via respirometry at rest before and after flights so that flying metabolic rate could be estimated directly via subtraction.

The doubly-labelled water approach has been widely used to estimate flying (20 times, Table 1) and diving (19 times, Table 1) metabolic rate in the field, and those estimates are quite similar to those measured in wind tunnels and dive tanks (Videler, 2006). A study using doubly-labelled water led to the first direct measurements of the metabolic cost of migration (Wikelski et al., 2003). Migrating thrushes were radio-tagged and injected with doubly-labelled water, and then followed by car so that a second blood sample could be obtained, flight duration estimated and flying metabolic rate estimated. Surprisingly, most migration metabolic costs were associated with stop-overs rather than migratory flights because so much more time was spent at stop overs. The doubly-labelled water approach allowed only for a single estimate of flying metabolic rate. The same research group continued their studies using the heart rate method to examine inter-individual and intra-individual variation in flying metabolic rate. In particular, they showed that thrushes with pointed wings and low wing loadings flying on calm nights had low heart rates—and by extension low metabolism (Bowlin and Wikelski, 2008). That approach is the subject of the next section.

3.3. Heart rate

After the doubly-labelled water technique, heart rate is the most frequently used technique to assess flying and diving metabolic rate in wild animals (9 times for flying and 5 times for diving, Table 1). The underlying principle, evident to anyone who has spent time exercising, is that heart rate increases when an animal's metabolism increases, so as to deliver more oxygen to the organs. The heart rate method is described quantitatively by Fick's equation:

$$V_{O2} = f_H V_s (C_{aO2} - C_{vO2}) \qquad (2)$$

where V_{O2} is the rate of oxygen consumption, f_H is the heart rate, V_s is the stroke volume of the heart, C_{aO2} is the oxygen content of arterial blood and C_{vO2} is the oxygen content of venous blood (Fick, 1870). From Fick's equation, it is apparent that heart rate will tend to correlate with oxygen consumption, but that relationship will also be affected by stroke volume and blood oxygen content. The cardiovascular system of fish and invertebrates is substantially different than those of tetrapods, and the effect of temperature is a complicating factor in studies of heterotherms (Green, 2011). Consequently, the heart rate method is primarily used on birds and mammals (Green, 2011). The heart rate method's application to wild animals has been reviewed by others (Butler et al., 2004; Green, 2011), and here I only provide a short summary as it pertains to diving and flying.

To provide a quantitative estimate of oxygen consumption rate in the wild, it is necessary to first develop a heart rate-oxygen consumption rate calibration under conditions that mimic as much as possible those occurring in the wild (Butler et al., 2004; Green, 2011). Because of the difficulty of conducting such validations for flying and diving animals, there are more studies of qualitative changes in metabolic rate during flying and diving than studies that attempt to quantify those changes (Green, 2011). For instance, heart rate is often higher during flapping flight than gliding or soaring (e.g. Sapir et al., 2010; Duriez et al., 2014), but because heart rate is seldom calibrated, it is not possible to directly estimate the difference in metabolic rate between flapping and gliding. As the heart rate-oxygen consumption rate relationship is seldom 1:1, it is not possible from qualitative studies to conclude that, for instance, a four-fold increase in heart rate is equivalent to a four-fold increase in metabolic rate (Green, 2011). Even where validations are completed in captivity, transferring the calibration equation to the wild may be problematic because stress, social interactions or muscle disuse (reduced heart size) in captivity may lead to variation in heart rate independent of changes in metabolic rate (McPhee et al., 2003; Green, 2011). The cardiovascular system can also change in complex ways with body mass, and the calibration between heart rate and oxygen consumption rate can vary either as a power law or isometrically with body mass, structural size, or a combination of both (Green et al., 2001; Froget et al., 2001; Fahlman et al., 2004; Halsey et al., 2007; Green, 2011). Due to variation in body mass or stress physiology, there is high inter-individual variation in heart rate-oxygen consumption rate calibrations. Thus, as was noted for doubly-labelled water, estimates of metabolic rate derived from heart rate are more accurate for average group values (coefficient of variation <5%) than for individuals (coefficient of variation >12%; Butler et al., 2004; Green, 2011). Indeed, it is often simply not possibly to reliably estimate metabolic rate for an individual from heart rate (Green, 2011).

Bradycardia during diving and tachycardia during surfacing cause particular problems for the heart rate method that are not present for running or flying animals. Some diving animals have shunts that bypass capillary beds during deep dives while others add blood from the spleen to the circulatory system, both of which can alter the relationship between heart rate and oxygen consumption rate beyond validations in shallow lab tanks (Woakes and Butler, 1983; Butler et al., 2004). In some cases, tachycardia during surfacing offsets bradycardia during diving such that average heart rate across an entire dive cycle correlates with metabolic rate (Woakes and Butler, 1983; Fedak, 1986; Webb et al., 1998). However, such validations have not been tested for very deep dives where cardiovascular changes are particularly pronounced (but see Green et al., 2007). The recent deployment of units measuring oxygen partial pressure at different points in the body offer the

possibility of finer understanding of oxygen store management during deep dives, potentially improving the ability of heart rate to predict metabolic rate during diving (Ponganis et al., 2009).

A major benefit of the heart rate method over the doubly-labelled water method is that it can be used to estimate energy expenditure at both short and long temporal scales. Whereas the doubly-labelled water method is limited by the dilution half-life of the isotope in the body to typically hours to a few days, the heart rate method has been used to measure energy expenditure of activities lasting seconds and of organisms throughout the annual cycle. However, at short time scales, transitory cardiovascular adjustments, such as those during diving, can mean that heart rate is not very accurate. For instance, it is unclear how one would use heart rate to measure the metabolic cost of fine-scale activities during diving, such as lunge-feeding or buoyancy-controlled ascent. That such adjustments are not restricted to diving is evident from the observation that heart rate-oxygen consumption rate correlation coefficients are generally higher when values are averaged over longer time scales than short time scales (Yamamoto et al., 1979). At the same time, the cardiovascular system can be extensively remodeled throughout the annual cycle, as body size, heart size and blood oxygen content are known to vary throughout the year (Jehl, 1997; Piersma et al., 1999; Landys-Ciannelli et al., 2002; Elliott et al., 2008; Portugal et al., 2009). Thus, heart rate-oxygen consumption rate calibrations completed at one stage of the annual cycle may not apply to other stages.

Both qualitative and quantitative estimates of metabolic rate via heart rate have greatly enhanced understanding of animal flying and diving. Several studies have demonstrated the importance of inactivity as an energy saving technique. Spotted antbirds (*Hylophylax naevioides*), small songbirds with poor flight ability that have limited foraging opportunities when their main foraging source, army ants, are dormant, save considerable energy by spending most of the day inactive (Steiger et al., 2009). Their inactivity is coincident with a 'slow' life history strategy of few offspring, high survival, high immunity and low basal metabolic rate. The same research group also documented low daily energy expenditure for tropical bats due to low time spent flying (Dechmann et al., 2011). Similarly, although flying metabolic rate is very high for eider ducks, daily energy expenditure is low because they spend little time flying (Pelletier et al., 2008; Guillemette and Butler, 2012). Given that the relative proportion of time active often plays a strong role in determining metabolism, acceleration can potentially provide additional insight into metabolic costs, which is the topic of the next section.

3.4. Accelerometry

Energy expended is defined as equal to the mechanical work done, W. W is defined to be the integral of force, F, applied in the direction of travel, integrated over the distance travelled, x. For a body moving at a nearly-constant speed, v, such as a car, F is equal to the counteracting forces (i.e. drag, gravity, etc.). However, animals rapidly accelerate and decelerate during each gait cycle so there is a net force unequal to the counteracting forces (Gleiss et al., 2011; Halsey et al., 2011a). Accelerometry is based on the principle that most energy expenditure is associated with that net force. According to Newton's second law, net force, F_{net}, is proportional to the product of mass, m, and acceleration, a, such that:

$$W = \int F dx \approx \int F_{net} dx = mv \int a \, dt = mvDBA \qquad (3)$$

For a given constant mass and speed, mechanical work is then approximated by the integral of acceleration over time and is termed dynamic body acceleration, DBA (see also Eq. (7) in Gleiss et al., 2011). In practice, DBA is calculated after removing the static component (gravity) unassociated with work (Wilson et al., 2006), and DBA must be

calculated as the integral of acceleration over several muscle cycles (e.g. wing beats during flight, flipper beats during swimming or steps during running).

DBA correlates with energy expenditure in humans, captive or semi-captive animals and wild animals (Wilson et al., 2006; reviewed by Halsey et al., 2009, 2011a, 2011b; Stothart et al., in press), and has been used to quantify the fine-scale energy use of animals in the wild (Williams et al., 2014; Bishop et al., 2015). The technique assumes not only that an accurate measure of mechanical work can be derived from DBA, but also that energy expenditure in animals is primarily associated with mechanical power. However, as argued in Section 2, oxygen consumption rates can sometimes only correlate weakly with mechanical power because of variation in muscle efficiency, thermoregulation, digestion and other factors (Rayner, 1999; Pennycuick, 2008). Nonetheless, accelerometry has proven accurate in spite of this and indeed activity may be an important component of thermoregulation and "resting" metabolism (Green et al., 2009a, 2009b). The appropriate formulation of DBA—the L1 norm, termed overall DBA, or the L2 norm, termed vectorial DBA (Gleiss et al., 2011)—has been contested, although there is little practical difference as both measures are highly correlated (Qasem et al., 2012; Stothart et al., in press). Other metrics than DBA have been derived from biomechanical principles (e.g. Spivey and Bishop 2013), and more work is needed to validate those other metrics in the wild.

To measure flying and diving metabolic rate with accelerometry, DBA (or any other metric) must first be calibrated. Many of the same issues that cause inaccuracies with the heart rate method likely play a role in accelerometry. Although the stress response should not affect mechanical work in a similar way as heart rate, changes in body temperature or similar adjustments leading to hypermetabolism or hypometabolism should be more difficult to detect via accelerometry than heart rate. Specifically, (1) average metabolic rate estimated for a group using DBA is likely more accurate than metabolic rate estimated for an individual assuming individual calibrations are not obtained (it is difficult to envision calibrating every individual in a wind tunnel or dive tank before field work), (2) metabolic rate estimated from DBA averaged over long time scales is likely more accurate than metabolic rate estimated from DBA averaged over short time scales because anaerobic respiration can power short bursts altering oxygen consumption rate-DBA calibrations, and (3) DBA is a proxy for mass-specific energy expenditure, not total energy expenditure (see Eq. (3)).

One application of accelerometers has been to measure fine-scale metabolic costs, such as those associated with turning (Wilson et al., 2013; Amélineau et al., 2014), windscapes (Amélineau et al., 2014), diving (Meir et al., 2013) and burst sprints to capture prey (Williams et al., 2014). In addition, accelerometers provide robust time budgets that can be used to partition metabolic costs. Although heart rate can also provide time budgets, because heart rate during different activities often overlap (Pelletier et al., 2008), coupling heart rate-oxygen consumption calibrations with accelerometry to determine time budgets can be particularly powerful. One of the best examples of this approach followed bar-headed geese as they migrated over the Himalayas (Bishop et al., 2015). Heart rate correlated with biomechanical costs measured from the accelerometers, providing strong support that flying metabolic rate was being accurately estimated. Flying metabolic rate increased rapidly (exponent of 7) with altitude, and geese made longer trips to avoid high altitudes.

3.5. Diving and flying metabolic rate measurements in the field

Diving or flying metabolic rates have been measured in the field for over 50 species of animals (Fig. 5). Diving metabolic rate was generally lower than flying metabolic rate for a given body mass, although flying metabolic rate for aerial insectivores (swallows and swifts) and gliders (albatrosses, petrels and relatives) were nearly as low or even lower. Estimates for at-sea metabolic rate, all from doubly-labelled water, were
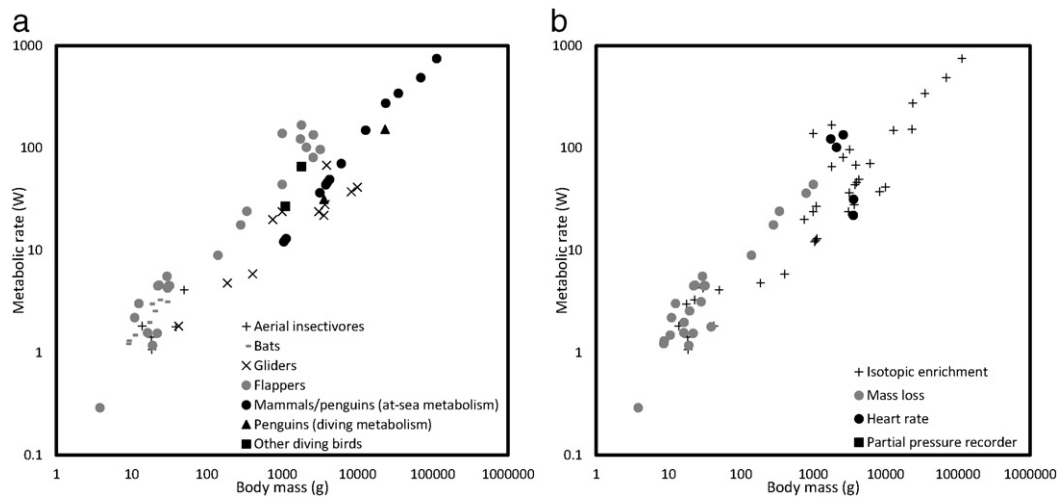
Fig. 5. (a) Diving (black symbols) and flying (gray symbols) metabolic rates for animals measured in the field. Data from studies in Table 1 and available in Data Appendix to Elliott et al. (2013a). Studies that measured at-sea metabolic rate (average energy expenditure while at sea), often considered the same as diving metabolic rate, are shown separately from studies that measured diving metabolic rate (average energy expenditure while diving at sea). Estimates for diving metabolic rate for sea turtles were excluded from analyses because of high water turnover (Jones et al., 2009). (b) The same data subdivided by technique used to measure metabolic rate.

somewhat higher than estimates for diving metabolic rate, implying that metabolism was suppressed during dives—and that future studies using doubly-labelled water should subpartition at-sea metabolic rate into surface and diving metabolic rate. Diving metabolic rate for non-penguins ("other diving birds") was higher than for penguins. Finally, estimates of flying metabolic rate from mass loss were variable and sometimes quite low, whereas estimates from doubly-labelled water and heart rate were comparable (and in line with estimates from wind tunnels, Videler, 2006).

4. Proxies for metabolism during flying and diving

Apart from metabolism, several other physiological parameters have been inferred from field measurements, including measurements of organ size, body temperature and plasma metabolites. Many of those parameters can be considered proxies for metabolism as they are altered depending on energy gain or expenditure. For instance, plasma triglyceride levels, associated with lipid deposition rate, were higher in migrants at a high quality stop-over site than in migrants at a low quality site, while β-OH-butyrate, associated with fasting, showed the opposite trends (Guglielmo et al., 2005). It can be assumed that those individuals with high triglycerides are typically expending more energy than those with high β-OH-butyrate.

Other plasma metabolites have also been used in the lab to understand flying and diving physiology. For instance, birds flying in low humidity have high levels of uric acid in the plasma, implying that they fuel flight partially with protein, which provides more water than lipids (Gerson and Guglielmo, 2011). In another study, plasma creatinine kinase, an indicator of muscle damage, was highest just after long distance flights, implying that long flights may cause muscle damage analogous to sports injuries (Guglielmo et al., 2001). Similar applications during diving demonstrated that plasma lactate in penguins and seals increases during long dives, providing evidence for anaerobic metabolism (Kooyman et al., 1980; Kooyman and Ponganis, 1998). Related to changes in metabolites, both diving and flying can be associated with changes in hematocrit, regulated by changes in plasma volume or the input of red blood cells from the spleen. In a similar vein, flying and diving can lead to increased oxidative stress. For instance, hypoxia coupled with repeated ischaemia-reperfusion at the surface should lead to increased oxidative stress during diving (Ramirez et al., 2007). Similarly, old homing pigeons (*Columba livia*) had higher oxidative stress after long flights (Costantini et al., 2008). Finally, variation in plasma hormone levels can play an important role in the physiology of flying and diving. The

invention of a miniaturized biosensor that measures uric acid levels *in vivo* heralds the potential for miniature sensors to revolutionize the field by measuring metabolite levels during flying and diving, although to prevent excessive bleeding, such tags are likely to measure interstitial metabolite levels (Gumus et al., 2014). Periodic measurements of uric acid, nitrogen tension, hemoglobin content, glucose, triglycerides, lactate, β-OH-butyrate, oxidative stress or hormone levels over the course of a dive or flight would provide detailed information on the processes ongoing within those behaviors.

Body temperature is another proxy for metabolism, with high body temperature often associated with high metabolic rate, such as birds ascending in air. Body temperature generally declines during diving (Hill et al., 1987; Bevan et al. 2002; Niizuma et al., 2007), which helps reduce diving metabolic rate and increase dive duration. In some, but not all species, even core body temperature has been reported to decrease (e.g. Handrich et al., 1997; Bevan et al., 1997 vs. Grémillet et al., 1998; Niizuma et al., 2007). In contrast, flight induces a 1–2 °C increase in body temperature, and body temperature sometimes increases with flight duration in birds and bats (Speakman, 1991; Grémillet et al., 1998; Adams et al., 1999; Voigt and Lewanzik, 2011). During bouts of high activity flight body temperature can increase by ~2 °C above stable flight (Bishop et al., 2015).

5. Future recommendations

Many more studies have developed calibrations for heart rate and accelerometers than have actually used those studies to measure metabolic rate in the wild (e.g. Green, 2011). Although more work is needed on developing such calibrations for diving and flying across a wide variety of body plans, I urge others to conduct more studies that actually use such calibrations to measure metabolism in the wild. To accurately measure metabolic rate during flying and diving in the wild, I provide the following recommendations:

(1) Calibrate biologger-derived estimates under conditions that are as similar as possible to those where the calibration will be applied. Due to the technical difficulties associated with calibrations in wind tunnels or during deep dives, and differences between captive and wild animals, the use of multiple techniques simultaneously in the wild can provide added insight and can be used to calibrate one another (e.g. Elliott et al., 2013b; Duriez et al., 2014; Bishop et al., 2015).

(2) Derive confidence intervals for the calibrations and apply those intervals to the estimates in the wild. Examine the repeatability of calibration equations across variation in stress, body mass and behaviours that are likely to occur in the wild so that robust confidence intervals can be created.

(3) Ideally, due to considerable inter-individual variation, calibrations would occur on the same individuals as those used to estimate metabolic rate.

(4) Incorporate body mass into calibrations, as variation in body mass can have a strong impact on acceleration, heart size and other relevant variables.

(5) Use the seven principles for minimizing tag effects listed previously so that the tag itself does not lead to inaccurate estimates of metabolic rate.

(6) Calibrations are more accurate over longer time scales (hours) than shorter scales (seconds; Yamamoto et al., 1979; Green, 2011).

(7) Create the simplest possible calibration equations that still have small confidence intervals by using information theoretic (AIC) or other approaches to maximize model parsimony.

(8) Calibration equations cannot always be extrapolated beyond the scale at which they were calibrated (Green, 2011), especially for metrics such as heart rate that do not change instantaneously as work changes.

Point 8 notwithstanding, the greatest asset of the biologging approach is the ability to measure energy expenditure at both short and long scales. At the fine scale, the combined use of heart rate, body temperature and acceleration logging, potentially in combination with sensors that measure oxygen or metabolite levels *in vivo*, provides the potential for assessing the metabolic costs of relatively short behaviors. Fine-scale behaviours include foraging during diving, flying near a surface (i.e. the ground effect), flying or diving during moult, energetics of short or intermittent flights and takeoff—all of which have been modelled biomechanically or measured in the laboratory but never estimated directly in the field. At very long time scales, the combined use of heart rate loggers and accelerometers, potentially alongside other loggers, could provide insight into diving and flying metabolism across the annual cycle. Ground-breaking work on penguins (Green et al., 2005, 2009a, 2009b), cormorants (Grémillet et al., 2005; White et al., 2011) and eiders (Guillemette and Butler, 2012) revealed relatively little variation in daily energy expenditure across the annual cycle. However, those measurements may have been confounded by variation in cardiovascular systems or body mass throughout the annual cycle with linear effects on heart rate and acceleration, respectively.

An exciting result from new approaches to understanding the energetics of flying and diving is the potential to test and refine biomechanical models. For instance, if natural variation in air speed could be measured from GPS and wind speed, then the U-shaped power curve could be directly estimated in the wild from heart rate or acceleration. Many behavioral models are built upon such basic biomechanical principles, and accurate biomechanical models would provide robust tests of those models, just as data from time-depth recorders in the 1980s allowed robust application of foraging theory to dive behavior (Kramer, 1988). Furthermore, measurement of flying and diving metabolic rate across a variety of body plans could result in the development of allometric models that would predict such metabolic rates for any animal. The use of multi-sensor biologging equipment promises to fully exploit the continual advancements afforded by Moore's law to unravel the mysteries of animal non-terrestrial locomotion.

Acknowledgments

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