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Review

Energetic modelling: A comparison of the different approaches used in seabirds ☆

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ABSTRACT

Studying energetics of marine top predators is essential to understand their role within food-webs and mechanisms associated with their survival and population dynamics. Several methods exist to estimate energy expenditure in captive and free-ranging animals. However, most of them are difficult to implement, restrained to specific periods, and are consequently inappropriate for seabirds. Supplementary and complementary approaches are therefore needed, and the use of modelling appears as an excellent option allowing energetic studies when field data collection is challenging. Currently three main energetics models are used, with various degrees of complexity and accuracy: allometric equations, time–energy-budget analyses and thermodynamic models. However, a comparison of their practicability and accuracy was still lacking. Here, we present an overview of these 3 model types, their characteristics, advantages and disadvantages, and areas of application in seabirds. We then investigate their accuracy by using them in parallel for the same dataset, and by comparing outputs with direct measurements (doubly-labelled water technique). We show that, when detailed data are available, time–energy–budget analysis is the best model to accurately predict seabird energy expenditures. Conversely, thermodynamic modelling allows reasonably accurate calculations when field data are scarce, and is therefore ideal to study energetics during the inter-breeding season.

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1. Introduction

Bird energetics are studied to gain a better understanding of how they maintain their energy balance, survive and reproduce. More specifically, there are three good reasons to investigate avian energetics and those of other animals. (1) From an ecophysiological perspective, energy expenditure and energy balance allow a rating of

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current morphological, physiological, and behavioural features, and how animals employ these features to optimise their energy budgets (Le Maho, 2002). (2) From an evolutionary perspective, energetics can be used to rate the impact of phenotypic plasticity and microevolution on morphological, physiological, and behavioural traits, whereby natural selection tends to optimise energy balance to improve Darwinian fitness (Rezende et al., 2004). (3) Finally, from an ecological perspective, energetics allow calculation of food requirements, and an assessment of the role of birds within food webs (Brown et al., 2004). This is essential as birds often operate at the apex of trophic networks, where they exert top–down control onto lower trophic levels and/or react to bottom–up forcing. They therefore potentially function as ecological indicators, and detailed knowledge of their energetics enables a functional approach to avian ecology, testing for relationships between environment constraints (e.g. climate change), food web characteristics (e.g. resilience), and bird responses affecting their energy balance (Einoder, 2009).

Studies of animal energetics are highly attractive in ecology because they employ one single currency (energy, expressed in Joules; J) to investigate and evaluate an infinity of processes, thereby providing a unifying approach and a powerful tool for comparative work and ecological synthesis (MacNab, 2002). This tool is equally valid to investigate the ecology of individuals, populations, species and communities at any spatio-temporal scale.

While interest in animal energetics dates as far back as Da Vinci and Lavoisier, it is the advent of thermodynamics in the 19th century (e.g. the work of James Joule) and technological developments of gas sensors, stable isotopes dosages, and electronics following the second world war that led the way to systematic investigations of energy expenditure in animals. Measurements were initially conducted under controlled conditions in the laboratory, but from the 1950s pioneers such as Knut Schmidt-Nielsen took physiology 'into the field' (Schmidt-Nielsen, 1998). Miniaturisation of laboratory tools has been ongoing ever since, allowing measurement of an increasing number of parameters on an increasing number of (smaller) free-ranging species (Ropert-Coudert and Wilson, 2005).

Technically, there are seven main approaches to assessing energy requirements in birds. We briefly mention these possibilities, most of them being subject to in-depth reviews in other contributions to this special issue. (1) Automatic weighing of individuals at the nest before and after feeding allows quantifying food intake (e.g. Grémillet et al., 1996, 2000). Subsequently, knowledge of the calorific value of the food and of the assimilation efficiency of the animal studied enables calculation of the energy equivalent (J) of the ingested food mass. (2) Isotopic methods based on stable isotope injections and dosages to measure CO_2 production and thus energy expenditure. It includes the doubly-labelled water (DLW) technique (see Speakman, 1997; Harding et al., 2009, Shaffer, 2011) and the ^{13}C labelled bicarbonate technique (see Hambly et al., 2002, 2004, Hambly and Voigt, 2011). (3) Heart rate recordings of free-ranging animals can be used as an index of energy expenditure (see Green, 2011). Calibration curves of relationships between heart rate and oxygen consumption during different types of activities are then required to calculate the overall energy consumption of the animal during a given time period (Bevan et al., 1994). (4) Similarly to the heart-rate method, overall dynamic body acceleration (OBDA, sensu Wilson et al., 2006) can be used as a proxy for energy consumption in free-ranging animals (see Halsey et al., 2011). Converting OBDA to Joules also requires calibrating this variable vs. an indirect measurement of energy expenditure such as oxygen consumption. (5) Time–energy budgets can be programmed to estimate energy requirements. They are typically compiled using measurements of the energetic costs of specific activities per unit time (for instance through indirect calorimetric studies of oxygen consumption), and of a detailed time budget stipulating the duration of each activity (Kendeigh et al., 1977; Kooijman, 2000). (6) Allometric equations serve the same purpose, while being based upon previous measurements of energy requirements in a large number of bird species relative to their body mass (Nagy, 2005, White, this issue). (7) Finally, thermodynamic modelling uses the first principles of thermodynamics to perform theoretical calculations upon the energy requirements of birds of given shape, mass, and insulation within a specific abiotic environment (Fort et al., 2009).

All techniques mentioned here have been applied to seabirds (except the ^{13}C labelled bicarbonate method; see Hambly and Voigt, 2011), but the majority were species-specific; only few considered processes occurring at the population and community level (e.g. Wiens and Scott, 1975; Furness, 1978; Grandgeorge et al., 2008). Obviously these different techniques all have strengths and weaknesses. Direct measurements using automatic weighing, the DLW method, or respirometry are accurate, but they can only be performed under well-defined conditions (Grémillet et al., 2000). For instance automatic weighing only works when birds are breeding, or at least affiliated to a specific perch. DLW investigations require catching and retrapping birds within a limited time period of a few hours to a few days, and costly analyses potentially limit sample sizes. In the case of respirometry, measurements can rarely be performed in free-living individuals (but see Brown and Adams, 1984), and birds have to be investigated in captivity, which may introduce additional biases due to increased stress levels and lower flight muscle mass (McKechnie et al., 2006). Therefore, whereas these measurements are routinely employed to determine the energy requirements of birds during specific activities and for specific time periods, general assessments of seabird energetics over the annual cycle, at the population and community level are rather conducted using the heart rate method (Green et al., 2009) and/or energetics modelling. Modelling exercises so far applied to seabirds were based upon time–energy-budgets and/or the use of allometric equations. These calculations had varied levels of complexity/accuracy. The highest refinement was reached when a complete time budget was available, and when the costs of virtually all activities had been determined via direct measurements as mentioned above (e.g. Grémillet et al., 2003). However, such an approach is extremely time- and cost intensive, and a balance has to be found between model complexity and the accuracy of the final output (Burnham and Andersonn, 2002).

Moreover, many seabirds spend a large proportion (up to >90% of their time) offshore, where they are difficult, or even impossible to study directly. Hence the type of modelling approach might also be strongly conditioned by the amount of information available for a given species and time period. This is very much the case for pelagic seabirds during the winter phase. Indeed, their distribution zones, movements, and behavioural patterns are often totally unknown, and/or are currently being investigated using miniaturised electronic tags, stable isotopic and genetic analyses (e.g. Ramos et al., 2009). This is unfortunate since winter energetics can largely condition adult survival rates in some seabird species (Fort et al., 2009), adult winter survival being the most important parameter shaping population dynamics (Lebreton et al., 1992).

In this context thermodynamic modelling has been specifically designed to study the energetics of birds when very limited/no information is available beyond their morphological properties (Fort et al., 2009). This method has so far been employed to predict the energy requirements of little auks (*Alle alle*) and Brünnich's guillemots (*Uria lomvia*) wintering in the northwest Atlantic (Fort et al., 2009). However, a comparative approach with some of the other approaches mentioned above was still lacking.

The objective of the paper is consequently to use thermodynamics modelling, conventional time–energy–budget analysis, allometric equations, and a direct measurement of energy expenditure (using the DLW method) to determine energy requirements of a wintering seabird, the great cormorant *Phalacrocorax carbo*, and to compare the practicability and the accuracy of these different methods.