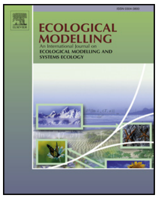
Ecological Modelling 378 (2018) 46–58

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Temperature-influenced energetics model for migrating waterfowl

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ARTICLE INFO

Keywords:
Climate change
Metabolic rate
Migration
Physiology
Waterfowl

ABSTRACT

Climate and weather affect avian migration by influencing when and where birds fly, the energy costs and risks of flight, and the ability to sense cues necessary for proper navigation. We review the literature of the physiology of avian migration and the influence of climate, specifically temperature, on avian migration dynamics. We use waterfowl as a model guild because of the ready availability of empirical physiological data and their enormous economic value, but our discussion and expectations are broadly generalizable to migratory birds in general. We detail potential consequences of an increasingly warm climate on avian migration, including the possibility of the cessation of migration by some populations and species. Our intent is to lay the groundwork for including temperature effects on energetic gains and losses of migratory birds with the expected consequences of increasing temperatures into a predictive modeling framework. To this end, we provide a simulation of migration progression exclusively focused on the influence of temperature on the physiological determinants of migration. This simulation produced comparable results to empirically derived and observed values for different migratory factors (e.g., body fat content, flight range, departure date). By merging knowledge from the arenas of avian physiology and migratory theory we have identified a clear need for research and have developed hypotheses for a path forward.

1. Introduction

Each year hundreds of millions of birds from hundreds of species complete migratory journeys across continents and oceans, punctuated by periods of breeding and over-wintering. The multi-species, spatio-temporal aspects of these global events provide a unique opportunity to assess the ecology of geographically disparate, behaviorally connected environments; that is, avian migration and its associated components (e.g., number of migrants, duration, survivorship) can serve as an integrative bio-indicator for changing conditions across a wide range of spatial and temporal scales (Gordo and Sanz, 2006; Culp et al., 2017; López-Hoffman et al., 2017). Many migratory species are experiencing declines in abundance and, in some cases, long-distance migrants are more likely to experience declines than short-distance migrants or residents (Zöckler et al., 2003; Vickery et al., 2014). The migration phenomenon itself is imperiled as a result of changing land cover and climate (Wilcove and Wikelski, 2008; Runge et al., 2015). Given an increasing body of evidence surrounding the occurrence and consequences of global climate change (e.g., Walther et al., 2002; Karl and Trenberth, 2003; Hansen and Sato, 2016), rigorous and robust techniques are required for elucidating effects of a changing climate on migratory bird species and the habitats on which they rely (Richardson, 1978; Both and Visser, 2005; Visser and Both, 2005; Robinson et al., 2009; Runge et al., 2014; Berchtold et al., 2017).

Climate change is threatening migratory birds in profound and myriad ways (e.g., Walther et al., 2002; Drent et al., 2003; Jenni and Kéry, 2003; Both et al., 2004, 2006, 2010; Wilcove and Wikelski, 2008; National Wildlife Federation, 2013; National Audubon Society, 2014; Berchtold et al., 2017). In terms of migration dynamics, a strong case can be made for temperature being the most influential of climate change-related environmental factors (Smith and Prince, 1973; Klaassen, 1996; Piersma, 2002; Gordo, 2007; Swanson, 2010). Metabolic rate is closely tied to temperature, dictating whether an organism can operate at its lowest metabolic rate in its thermal neutral zone, or if it must expend energy to either cool down (sweat, pant, increase blood flow to extremities) or heat up (shiver, burn fat, constrict blood flow). Food availability (and its subsequent utility as energy) will dictate the success of a migrant in reaching its goal; temperature influences energy availability through plant phenology (Gordo and Sanz, 2006; Knudsen et al., 2011; Teitelbaum et al., 2015). Precipitation and wind currents are also altered by temperature. Other potentially important factors, like photoperiod or genetics (which have strong influences on the

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https://doi.org/10.1016/j.ecolmodel.2018.04.001
Received 13 September 2017; Received in revised form 5 March 2018; Accepted 1 April 2018

0304-3800/ Published by Elsevier B.V.

timing of migration departure), are inert relative to climate change and therefore of little interest in terms of forecasting changes brought about by a changing climate. Thus, focusing on the role temperature plays in shaping avian migration patterns, and how those patterns might be expected to change as temperature generally increases is clearly a valuable endeavor. We note that each of these other considerations is worthy of its own dedicated investigation, but we exclude them from further consideration here.

In terms of the behavioral responses to changing temperatures, recent studies have shown an increased tendency for sedentary behavior given sufficient feeding throughout the winter as temperatures in breeding grounds remain sufficiently warm (Wilcove and Wikelski, 2008; Visser et al., 2009; Knudsen et al., 2011; Robinson et al., 2016; Berchtold et al., 2017). Indeed, the occurrence of partially migratory species and populations is well founded (Barta et al., 2008), and it is reasonable to believe that in a warmer climate it may be evolutionarily advantageous to stay in place rather than suffer the reduced survivorship of a migratory journey (Wilcove and Wikelski, 2008; Visser et al., 2009; Berchtold et al., 2017). Species that seem to have an immutable instinct to migrate regardless of the temperature at their breeding grounds are also highly susceptible to the repercussions of a changing climate (Walther et al., 2002; Sanz-Aguilar et al., 2012). While migration still takes place in these species, the routes they take and dynamics they display along the way are being modified as the atmosphere warms, and the timing of these migration events is changing as well, largely occurring earlier in the spring and later in the fall to match the shifting patterns of plant growth and production (Jonzén et al., 2006, 2007; Gordo, 2007; Si et al., 2015). However, there are reproductive obstacles that appear to represent fixed deadlines for when breeding can occur, so even though migration timing shifts to match the phenology of forage, when birds reach their breeding grounds they are still faced with the challenge of trying to produce offspring within a prescribed window of time (Both and Visser, 2001; Both et al., 2004, 2010; Arzel et al., 2006; Si et al., 2015). Additionally, for some species, a breeding season extended by warmer temperatures is prompting some individuals to produce extra clutches (Gordo, 2007; Knudsen et al., 2011), putting pressure on parents to fledge that final clutch faster so as to depart for the return trip before intolerable conditions set in.

In this paper, we review the literature related to the energetics of migration and the interaction of migration and temperature. We seek to explicate the effects of temperature on energetic gains and losses during migration with an eye toward accounting for warmer atmospheric temperatures. Our aim is to connect the extensive literature of physiological investigations into the dynamics of bird metabolism with the rich and rapidly expanding literature of avian migration. The litany of species participating in annual migratory cycles includes a wide range of associated habitat types and ecosystems; e.g., passerine forest birds and grassland birds, coastal shorebirds and pelagic seabirds, wetland waterfowl, and birds of prey. While all of these taxa and landscapes require conservation and management attention, we focus on waterfowl and the wetlands they use. We stress that while we parameterize the model we develop for waterfowl, it is readily generalizable for migratory birds in general, given the availability of requisite data.

Waterfowl are a heavily managed group (National Wildlife Federation, 2013; National Audubon Society, 2014), and have been equally heavily studied in terms of their physiology and flight dynamics (Pennycuick, 1975; Whyte and Bolen, 1988; Lindström and Kvist, 1995; van Wijk et al., 2012; Thorup et al., 2014). Thus, we use waterfowl as a model to form our specific expectations for the effects of temperature on energetic dynamics but these expectations are conceptually applicable to avian migration in general. We leverage the available literature to explore the selective forces acting on migrants via the suite of available migratory strategies. We introduce a simulation modeling framework to evaluate the effects of climate change (especially varying temperature) on the energetic gains and losses of migrants during their migratory journeys, giving particular attention to the connections between temperature, metabolism, and migration. Finally, we elaborate on the factors of selection acting on each strategy.

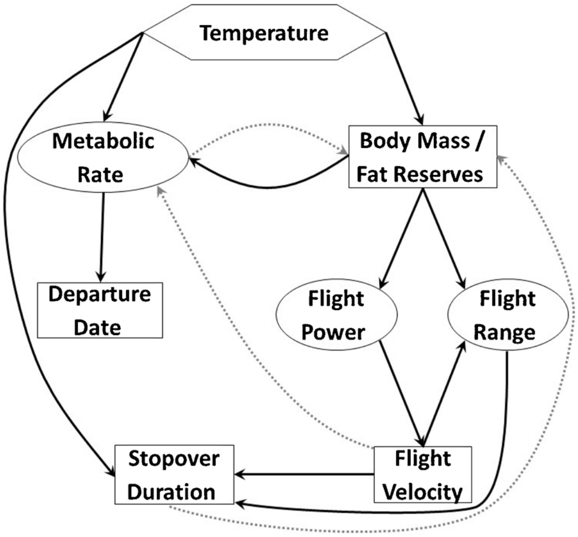

Fig. 1. Diagrammatic overview of the relationship between temperature and the variables of migration (rectangles). Objects in ovals represent fixed factors that directly affect migratory strategies but are not under immediate control of migrants (i.e., they are constrained physiologically). Solid lines indicate direct relationships between variables and factors, dotted lines indicate indirect or feedback effects.

2. Materials and methods

2.1. Thermal-energetics of migration

In a classic review, Alerstam and Lindström (1990) consider the consequences of what they call the ‘selective forces’ of avian migration; time, energy, and predation. A fourth selective force fitting neatly in this group is competition. Each of these forces is sensitive to changes in temperature, some more directly than others (see Fig. 1). For instance, temperature affects migration directly by modifying metabolic requirements (Smith and Prince, 1973; Klaassen, 1996; Piersma, 2002; Swanson, 2010) and body mass—in terms of fat load (Witter and Cuthill, 1993; and see citations therein establishing the connection between increasing fat reserves with decreasing temperatures). A successful (or optimal, as in Alerstam and Lindström, 1990) migratory strategy minimizes (or optimizes) the selective forces of migration as much as possible. The magnitude of influence of the selective forces of migration can be modified according to behaviorally influenced variables: departure date, flight velocity, stopover time, and fat reserves (the main energy source for flight, i.e., fuel level). Each of these variables can be thought of on a spectrum—early to late departure, slow to fast flight velocity, short to long stopover time, lean to ample fat reserves—along which individuals in the population are distributed (Pennycuick, 1975; Alerstam and Lindström, 1990; Hedenström, 1992; Bruderer and Boldt, 2001; Drent et al., 2003; Pennycuick and Battley, 2003; La Sorte et al., 2013; Pennycuick et al., 2013). Selection acts to craft migration strategies by occupying points on each of these spectra, and the overall strategies correspond to an optimization scheme of the selective forces. Which selective forces are minimized in a given strategy is a function of the intensity of selection on each variable. In general, time minimization is considered the strongest selective force over the course of migration (Alerstam and Lindström, 1990; Weber and Houston, 1997). Optimal migration, however, requires several smaller scale minimization/optimization strategies, operating at the level of flight “jumps” and stopovers rather than over the entire migration journey. Considering all of these small-scale strategies, it