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SYMPOSIUM

Heterothermic Migration Strategies in Flying Vertebrates

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Synopsis Migration is a widespread and highly variable trait among animals. Population-level patterns arise from individual-level decisions, including physiological and energetic constraints. Many aspects of migration are influenced by behaviors and strategies employed during periods of stopover, where migrants may encounter variable or unpredictable conditions. Thermoregulation can be a major cost for homeotherms which largely encounter ambient temperatures below the lower critical temperature during migration, especially during the rest phase of the daily cycle. In this review we describe the empirical evidence, theoretical models, and potential implications of bats and birds that use heterothermy to reduce thermoregulatory costs during migration. Torpor-assisted migration is a strategy described for migrating temperate insectivorous bats, whereby torpor can be used during periods of inactivity to drastically reduce thermoregulatory costs and increase net refueling rate, leading to shorter stopover duration, reduced fuel load requirement, and potential consequences for broad-scale movement patterns and survival. Hummingbirds can adopt a similar strategy, but most birds are not capable of torpor. However, there is an increasing recognition of the use of more shallow heterothermic strategies by diverse bird species during migration, with similarly important implications for migration energetics. A growing body of published literature and preliminary data from ongoing research indicate that heterothermic migration strategies in birds may be more common than traditionally appreciated. We further take a broad evolutionary perspective to consider heterothermy as an alternative to migration in some species, or as a conceptual link to consider alternatives to seasonal resource limitations. There is a growing body of evidence related to heterothermic migration strategies in bats and birds, but many important questions related to the broader implications of this strategy remain.

Introduction

Migration has evolved repeatedly among vertebrates (Alerstam et al. 2003; Bisson et al. 2009) and can be simply conceptualized as the outcome of fitness trade-offs. If the fitness benefits associated with migration outweigh the costs, then the evolution of migration will be favoured. Yet, migration is a highly variable trait (Dingle 2014), ranging from obligate to-and-fro migration of complete populations to facultative migration or variable migration patterns among subsets of populations (e.g., partial and differential migration). Migration patterns result in population- and ecosystem-level consequences (Bauer and Hoye 2014), but migration is fundamentally a behavior that is undertaken by individual animals. To gain a holistic understanding of how discrete behavioral choices made by individuals translate to population-level patterns of migration, we must understand the physiological constraints associated with migration. Research focusing on the underlying physiology and energetics of migration has therefore been a major focus of the field (Bowlin et al. 2010; Guglielmo 2010; 2018; Gwinner 1990; Lennox et al. 2016; McGuire and Guglielmo 2009; McWilliams et al. 2004).

Highly mobile animals that inhabit seasonally variable environments, especially volant (flying) species, can travel long distances in relatively short periods of time (but note that not all migration movements need be long distance; Boyle 2017; McGuire and Boyle 2013). Flying migrants are therefore able to seasonally take advantage of resource abundances and escape periods of

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resource limitation. But migration incurs extreme energetic demand, is time consuming, and exposes migrants to habitats and landscapes that may be unfamiliar and risky. Migration is among the most energetically demanding periods of the annual cycle and can be associated with high annual mortality in some systems (Sillett and Holmes 2002).

As birds and bats migrate long distances between seasonal home ranges, periods of migratory flight are interspersed by periods of stopover, where they take up temporary residence in an area while they rest and refuel for the subsequent migratory flight (Alerstam and Bäckman 2018; Schmaljohann et al. 2022). While migratory flight is a physiological challenge, theoretical and empirical evidence from bird migration systems indicates that periods of stopover may take seven times longer and cost twice as much energy compared to periods of migratory flight (Hedenström and Alerstam 1997; Wikelski et al. 2003). The energetic cost of stopovers is driven in large part by thermoregulatory costs (Wikelski et al. 2003). Vertebrates generally inhabit environments where the ambient temperature remains below the lower limit of the thermoneutral zone (i.e., the lower critical temperature, which defines the lower limit of the thermoneutral zone, is typically greater than ambient temperature) and during migration seasons animals may encounter particularly harsh conditions (e.g., storms, unseasonable cold; Newton 2007; Whitmore et al. 1977). As endotherms, migrating birds and bats are able to increase endogenous heat production with stored energy to maintain stable body temperature despite variable environmental conditions (i.e., homeothermy). In a study of Swainson's thrushes (*Catharus ustulatus*) and hermit thrushes (*Catharus guttatus*), Wikelski et al. (2003) used doubly labelled water to demonstrate that daily energy expenditure at stopover was closely related to ambient temperature. As ambient temperature drops farther below the lower critical temperature, endotherms must spend more energy (shivering or nonshivering thermogenesis) to maintain euthermic body temperature. In the case of migrating thrushes, the increased thermoregulatory cost was equivalent to several hours of migratory flight (Wikelski et al. 2003).

Thermoregulatory costs are a major component of the energetic costs incurred during stopover, which may account for two-thirds of total migration energy cost. However, not all migrants seek to maintain a stable, euthermic body temperature during inactive periods at stopover sites. The use of heterothermy could save substantial amounts of energy during migration (Fig. 1). The earliest such observation was of an immature male rufous hummingbird (*Selasphorus rufus*) observed using night-time torpor during fall migration (Carpenter and Hixon 1988). At the time of this observation, the use of torpor was generally considered to be an emergency response to depleted energy stores (see Geiser and Brigham 2012), but based on calculations of the energy consequences of using torpor compared to remaining euthermic, Carpenter and Hixon (1988) suggested torpor functioned as a mechanism to conserve energy for subsequent periods of migratory flight. Consistent with this hypothesis, the use of torpor has regularly been observed in migrating temperate bats (e.g., Barclay et al. 1988; Cryan and Wolf 2003). In migrating silver-haired bats (*Lasionycteris noctivagans*), the use of torpor during the inactive period saved up to 90% of the energy the bats would have spent had they remained strictly homeothermic (McGuire et al. 2014).

The term "Torpor-assisted Migration" has been used to describe the strategy of using torpor during inactive periods to save energy for subsequent periods of migratory flight (McGuire et al. 2014). It is likely that torpor-assisted migration is widespread among temperate migratory bats and hummingbirds, but torpor is generally a rare phenomenon among birds (McKechnie and Lovegrove 2002). There are families of birds that include species known to use torpor, such as hummingbirds or nightjars (McKechnie and Lovegrove 2002), but likely more common are scenarios where migrants may experience a shallow decrease in body temperature and metabolic rate (Fig. 1). Body temperature reduction of just a few degrees can result in substantial energy savings. In much the same way that Carpenter and Hixon (1988) demonstrated the use of torpor for saving fuel stores in a hummingbird, Wojciechowski and Pinshow (2009) suggested that shallow heterothermy (body temperature reduced ~5°C) would allow migrating Eurasian blackcaps (*Sylvia atricapilla*) to more rapidly deposit fuel for subsequent periods of migratory flight.

The use of heterothermy during inactive periods at stopover, whether deep torpor or shallow heterothermy (Fig. 1), has the potential to yield substantial energy savings. As a major cost of migration, such energetic savings could have far-reaching influences on the strategies that migrants employ and the behavioral expressions used to achieve them. However, while daily torpor is common in temperate migratory bats, tropical bats are thought to be more strictly homeothermic. Deep torpor is uncommon in birds, but it is not clear how widespread the use of shallow heterothermy might be during migration. In this review, we consider the role of heterothermic strategies in migrating bats and birds. We begin by summarizing research that has focused on integrating empirical studies of migrating bats and theoretical models of optimal migration that have been formulated to account for varied thermoregulatory strate-

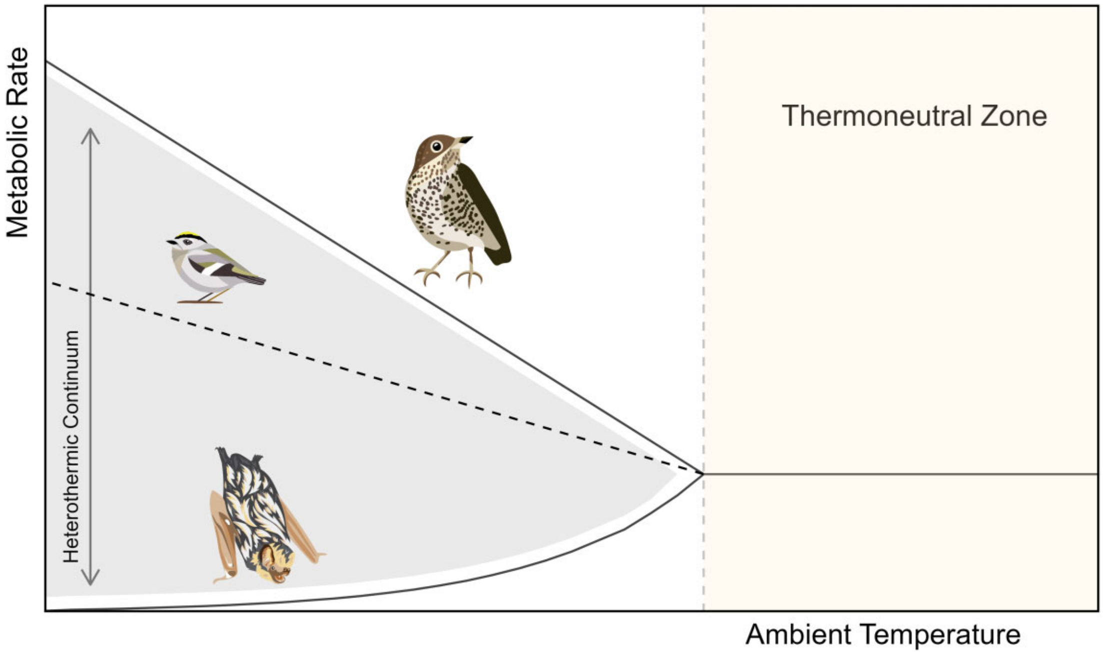

Fig. 1 The metabolic cost of thermoregulation varies with ambient temperature below the lower critical temperature (vertical dashed line). During the rest phase at stopover sites, homeothermic migrants must increase metabolic rate to generate heat to maintain normal body temperature, exemplified here by Swainson's thrushes (*C. ustulatus*; straight solid line below the lower critical temperature). Alternatively, species that use deep torpor, exemplified here by the hoary bat (*Lasiurus cinereus*; curved solid line below the lower critical temperature), reduce body temperature to near ambient with a metabolic rate that is a small fraction of euthermic metabolic rate. In between these extremes there is a continuum of potential heterothermic responses. Shallow heterothermy is a strategy, exemplified here by the golden-crowned kinglet (*Regulus satrapa;* straight dashed line below the lower critical temperature), where body temperature is reduced at an intermediate level, not in deep torpor, but achieving reduced metabolic rate and associated energy savings compared to homeothermy.

gies. Next, we expand our scope to consider the growing body of evidence that indicates the use of some degree of heterothermy in a variety of migrating birds. Finally, we consider the role of heterothermy as an alternative to migration. We conclude with a brief overview of the long list of exciting and important questions that remain to be addressed. There have been relatively few explicit studies of heterothermy in migration but given the wide-ranging potential consequences of this energy-saving strategy, it is important that thermoregulation is included in a holistic understanding of migration.

Empirical and theoretical integration

Despite the fact that the first observations of heterothermy during migration came from a hummingbird (Carpenter and Hixon 1988), heterothermic migration strategies in birds have received limited attention (see "*Beyond bats: heterothermy in migrating birds*" below). Much of the empirical research of heterothermic migration strategies has come from studies of migrating bats and has formed the basis for a re-developed version of optimal migration theory which allows for varied thermoregulatory expression (Clerc and McGuire 2021).

Daily torpor is important for many species of temperate bats (Stawski et al. 2014), and thus it is not surprising that bats use torpor during migration. In a study of silver-haired bats (*L. noctivagans*) during spring migration, the surface temperature of roosting bats was within 1–2°C of ambient temperature, and all were sluggish and cool to the touch (Barclay et al. 1988). When faced with periods of extended inclement weather and low prey availability, silver-haired bats used multi-day torpor bouts (Barclay et al. 1988). A study of spring migrating hoary bats (*L. cinereus*) similarly documented regular torpor use (including discussion of implications for water balance), but in a sex-biased manner (Cryan and Wolf 2003). Under laboratory conditions, male hoary bats regularly used torpor across a range of test temperatures, but females rarely used torpor and instead defended normal body temperature, even as test temperature was decreased to 0°C. Female hoary bats are pregnant with twins during spring migration (McGuire et al. 2013; Shump and Shump 1982), and torpor use would delay the development of the fetuses (Racey 1973).

The use of torpor during inactive periods could have dramatic effects on many aspects of migration. In one example, the energy savings of torpor was suggested as the likely explanation for the discrepancy be-

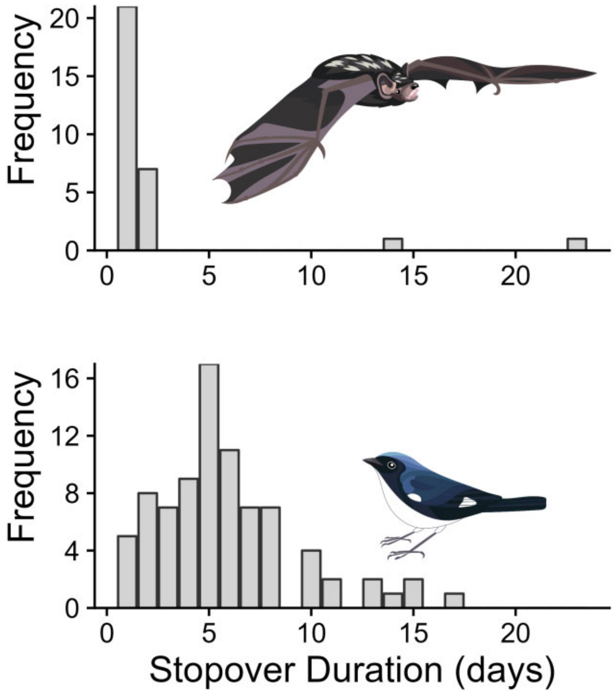

Fig. 2 Stopover durations of (A) silver-haired bats (*L. noctivagans*) using a torpor-assisted migration strategy, compared with (B) black-throated blue warblers (*S. caerulescens*), a presumed homeothermic migrant. Both studies were conducted at the same study site over the same time period. It is hypothesized that the energy savings of torpor allow silver-haired bats to make shorter stopovers than black-throated blue warblers. Fig. adapted from data presented in McGuire et al. (2012) and Taylor et al. (2011).

tween apparent stopover durations of silver-haired bats (McGuire et al. 2012) and black-throated blue warblers (*Setophaga caerulescens*) (Taylor et al. 2011). Both studies were conducted at the same site at the same time and using the same radiotracking methods for these similar-sized migrants. Silver-haired bat stopover durations were very short, with most bats departing either the same day they arrived or the next, whereas the presumed homeothermic black-throated blue warblers stayed much longer, with most individuals staying many days (Fig. 2). Although no direct observations of torpor use were made in the McGuire et al. (2012) study, a follow-up study observed daily torpor use in every free-living bat included the study (McGuire et al. 2014). The study included primarily silver-haired bats, but also opportunistic observations of a smaller number of hoary bats and eastern red bats (*Lasiurus borealis*). Notably, the study was conducted during fall migration when there would be no conflict between torpor use and reproductive consequences for pregnant females. With measurements of metabolic rate under controlled temperature conditions, it was possible to model energy expenditure during the daytime inactive period under observed patterns of torpor use and the assumption of strict homeothermy. On colder days when there is a greater difference between torpid and euthermic metabolic rates (Fig. 1) bats spent more time in torpor (Fig. 3), saving of up to 90% of the energetic cost of remaining homeothermic (McGuire et al. 2014).

Subsequent studies have continued to investigate aspects of torpor-assisted migration in silver-haired bats, including more detailed energetic calculations, the influence of body composition, trade-offs between foraging and torpor, sex differences in phenology, and seasonal comparisons of spring and fall migration (Baloun and Guglielmo 2019; Baloun et al. 2020; Jonasson and Guglielmo 2016; 2019). Torpor-assisted migration has also been used to provide context for temporal foraging patterns in migrating Nathusius' pipistrelles (*Pipistrellus nathusii*) in Europe (Voigt et al. 2012). The ability to reduce energetic demand by using torpor may reduce the need for extensive refuelling during migration, as evidenced by reduced size of digestive tract during migration (McGuire et al. 2013), yet there is ample evidence of bats foraging during migration periods (Baloun et al. 2020; Jonasson and Guglielmo 2019; Reimer et al. 2010; Valdez and Cryan 2009; Voigt et al. 2012). Despite increasing evidence for regular torpor use in long-distance migratory bats, there has been little investigation of torpor-assisted migration in regional migrants (but see Roby 2019). Given that the ability to use torpor is ubiquitous among temperate bats (Stawski et al. 2014), it is likely that torpor plays a role, even in relatively short-distance regional migrations.

To better understand the behavioral consequences of varied thermoregulatory expressions during migration Clerc and McGuire (2021) considered the effects of different thermoregulatory expressions on migration ecology within an optimal migration theory framework. Optimal migration theory is an optimization modeling approach used to theoretically frame the adaptive value associated with varied migratory strategies (Alerstam and Lindström 1990). The goal of optimization modeling in biology is to generate predictions about behavioral traits that maximize fitness (Parker and Smith 1990). Migration theory assumes that adaptations drive organisms to either maximize benefits, reduce costs, or find some solution that best balances the trade-off between the two (Alexander 1996). Though flight behaviors, such as orientation and flight altitude in response to wind speed and direction (Liechti 2006) are important to how migrants trade-off energy and time, migrants are constrained in their metabolic expressions during migratory flights and thus the role of heterothermy during migration is focused on periods of stopover.

Heterothermy allows migrants to achieve positive energy balance at low-quality stopover sites that would

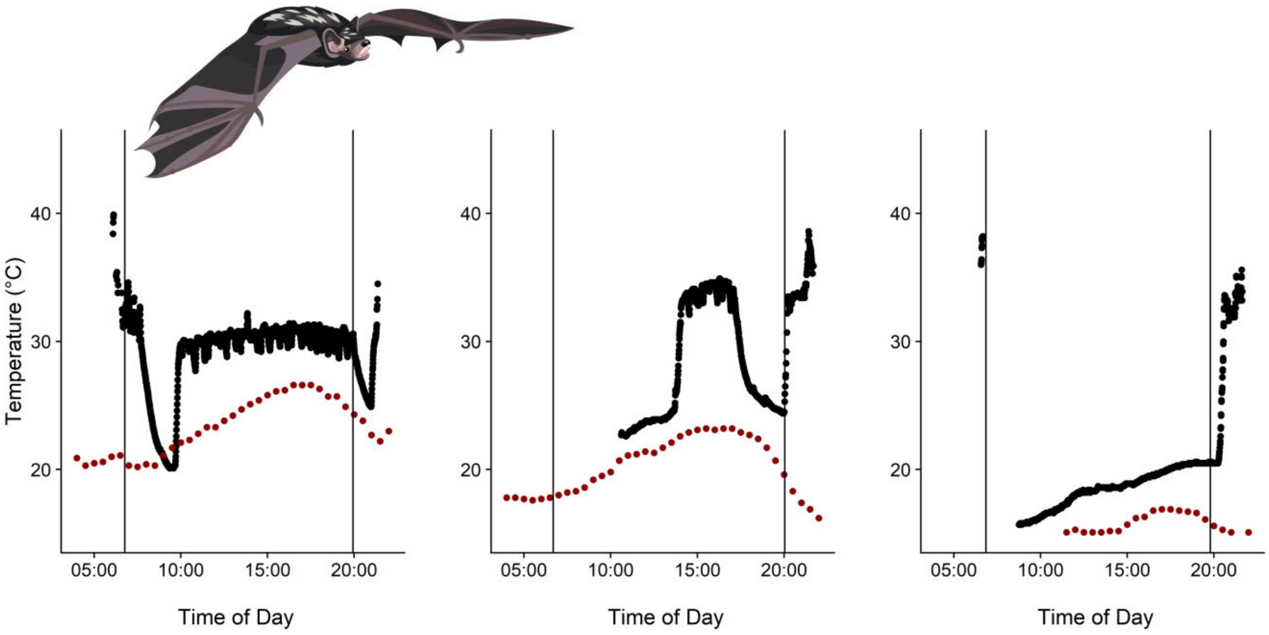

Fig. 3 Torpor used by silver-haired bats (*L. noctivagans*) during stopover. Solid black dots represent skin temperature from temperature-sensitive radiotelemetry, red dots represent ambient temperature, and vertical lines indicate sunrise and sunset. (A) Under warmer ambient temperatures, bats used relatively short torpor bouts during the cooler morning and evening. (B) At cooler ambient temperatures, bats maintained normal body temperature for only a relatively short period of the afternoon when ambient temperature approached the lower critical temperature. (C) On the coolest days bats used torpor for the entire daytime period of inactivity, warming up to normal body temperature at, or shortly after, sunset. Fig. adapted from data included in McGuire et al. (2014).

lead to negative energy balance in homeotherms. When faced with high rest period costs or low-quality foraging, homeotherms have no mechanism to compensate and net fuel deposition rate is decreased (Fig. 4). However, heterotherms can counter these challenges by reducing rest period costs and therefore maintain positive energy balance over a range of site qualities (Fig. 4). One implication is that while homeotherms face a trade-off between time and energy minimization, heterotherms that reduce the energetic cost of thermoregulation can also refuel faster and are therefore able to simultaneously minimize time and energy cost. Furthermore, the facultative use of heterothermy also allows heterothermic migrants to manage energy budgets independent of weather conditions experienced at stopover, increasing or decreasing the use of torpor in response to current conditions (e.g., Fig. 3; McGuire et al. 2014). Therefore, differences in thermoregulatory expression may affect landscape-level stopover use and thus, population-level patterns of migration. Homeothermic migrants may be constrained to high-quality migratory stopover sites where they can maintain a high fuel deposition rate. Without the need to rely on high-quality stopover sites, the use of heterothermy may result in a more diffuse population-level pattern of migration. Heterotherms may be able to follow a “broad front” migration strategy, dispersed broadly across the landscape during migration.

Given the same environmental quality (habitat quality, foraging opportunities, and weather conditions) heterotherms can achieve equal or greater net refueling rates relative to homeotherms by reducing rest period costs (Fig. 4). Consequently, optimal migration theory models allowing for heterothermy predict that heterotherms make shorter stopovers, have decreased departure fuel load burdens, and therefore reduce the overall time and energy costs associated with stopovers relative to homeotherms (Clerc and McGuire 2021). Combined, these model predictions highlight that thermoregulation can drastically influence stopover behavior and ultimately plays a critical role in population-level patterns of migration.

Several predictions arising from optimal migration theory models remain untested and exciting opportunities for future research (see Clerc and McGuire 2021 and "*Future directions*" below) but there are some predictions for which there is empirical support. For example, heterothermic migrants are predicted to have shorter stopover durations compared to homeothermic migrants. Short-duration stopovers have been observed in both migrating ruby-throated hummingbirds (*Archilochus colubris*; Zenzal Jr et al. 2018) and silver-

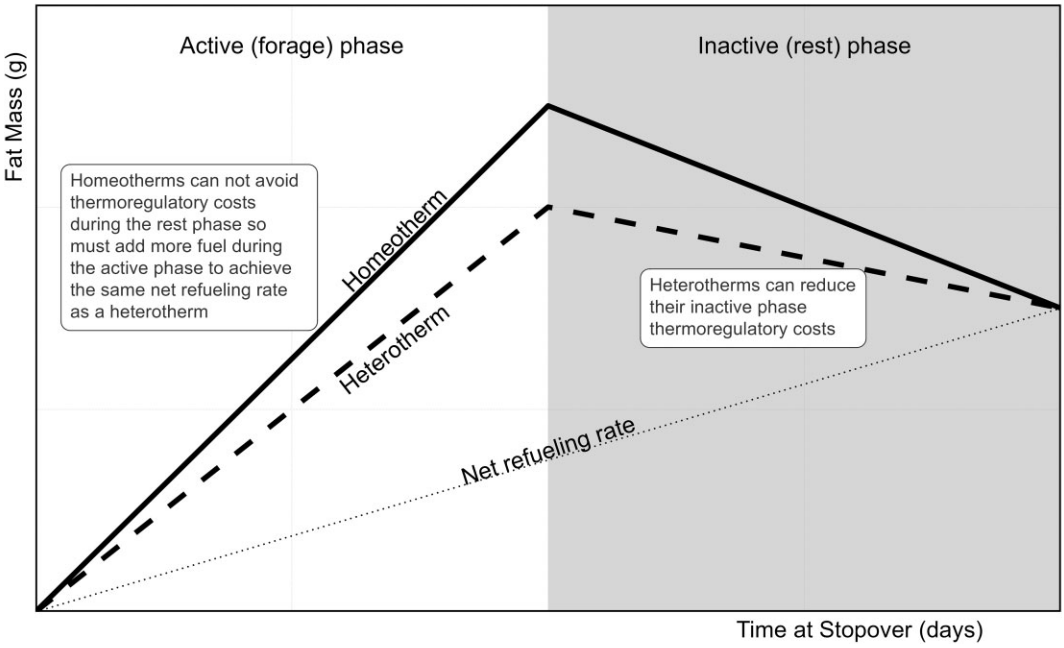

Fig. 4 Graphic illustration of net refueling rate for homeothermic (solid line) and heterothermic migrants (dashed line). Under a baseline set of conditions, a homeothermic migrant can deposit fuel (fat) during the active phase (white panel), but then uses some of that fat for thermoregulation during the inactive (rest) phase (grey panel). The thermoregulatory cost for a homeothermic migrant during the rest phase will cause fuel deposits to deplete more rapidly than heterotherms and therefore must achieve greater energy intake rates during the active phase to achieve the same net refueling rate (fine dotted line) as heterotherms. A heterothermic migrant could achieve this same increased net refueling rate instead by using heterothermy to reduce thermoregulatory cost. Thus, for the same rate of energy intake during the active phase, a heterothermic migrant can achieve a greater net refueling rate. Similarly, a heterothermic migrant can achieve a comparable net refueling rate even at a site where energy intake rate is lower. Fig. adapted from data presented in Clerc and McGuire (2021).

haired bats (Fig. 2; McGuire et al. 2012). Ruby-throated hummingbirds had a mean stopover duration of ∼1.5 days, with 59% of individuals departing on the same day that they were captured (Zenzal Jr et al. 2018). Similarly, 70% of silver-haired bats captured during fall migration departed on the same day that they were captured, and 93% of migrants departed by the second evening following capture (McGuire et al. 2012). Stopover duration was similarly brief in spring migration (median stopover duration 0.8 days) but there was a clear effect of weather conditions, with longer stopovers occurring when northbound bats encountered ambient temperatures below 15°C (Jonasson and Guglielmo 2019).

Another model prediction is that heterothermic migrants will have decreased fuel loads relative to homeothermic migrants. Spring-migrating bats present an opportunity to test this prediction at the intraspecific level, avoiding potential confounding interspecific factors. The coincidence of pregnancy and spring migration drives differences in thermoregulatory expression of male and female bats. Female hoary bats are pregnant with twins during spring migration and therefore remain homeothermic while males regularly use torpor (Cryan and Wolf 2003). Consistent with model predictions, heterothermic males had smaller fuel loads than homeothermic females which reduces flight cost and allows greater maneuverability (Clerc et al. 2021). Homeothermic females had greater fuel loads than heterothermic males (Clerc et al. 2021), but counterintuitively foraged less. One possible explanation is that females may rely on ephemeral pulses of extreme prey abundance. For example, in New Mexico (USA) geometrid and noctuid moths emerge synchronously and in great numbers, making up the majority of hoary bat diets (male and female) during spring migration (Valdez and Cryan 2009). If moth emergence is spatially predictable, it would fit with the high-quality stopover site prediction for homeothermic female hoary bats. Waves of migratory moths may serve as another important food pulse for migrating bats (Krauel et al. 2018; Krauel et al. 2015). Homeothermic female migrants may only reach positive energy balance under foraging conditions where they encounter abundant prey. Reliance on ephemeral prey pulses as the primary means of building large fuel loads is an inherently risky tactic and would require gut functional capacity to be preemptively maintained at a high-performance level to take advantage of pulses of high-density prey when encountered. However, there may be a trade-off in maintaining excess digestive tract that precludes maintaining high digestive efficiency throughout migration (Piersma 1998). Two lines of evidence suggest this may be the case. Female hoary bats do not maintain larger digestive organs during migration compared to the summer nonmigratory period (McGuire et al. 2013) and do not maintain greater digestive capacity than heterothermic males during migration (Clerc et al. 2021). Alternatively, migrating female hoary bats may maintain larger fuel stores by carrying over fat deposited prior to migration. This idea raises many intriguing questions about the importance of carry-over effects, differential premigration hyperphagia between males and females, and overwinter behaviors and habitat quality. It may be that heterothermic male migrants act as income migrants, compared to a capital migration strategy in homeothermic females (Evans and Bearhop 2022).

With an established modelling framework, it has been possible to conduct initial tests of model predictions, which have generally supported the framework, with a few exceptions. Going forward, building a larger pool of empirical observations will allow for an iterative approach, alternating between empirical tests of model predictions and revisions of the theoretical model. A major limitation at this point is the relatively limited taxonomic scope of empirical field tests, primarily migrating bats that use deep torpor during migration, and from only a few species. Future studies of migrating bats will be important, but studies of migrants with intermediate heterothermic strategies (e.g., shallow heterothermy in bird migrants) will be especially valuable.

Beyond bats: heterothermy in migrating birds

The migration literature is dominated by studies of birds, but thermoregulatory patterns remain an understudied topic. Approximately 19% of global bird species are migratory (Kirby et al. 2008), increasing to as much as 30–45% of species from Nearctic and Palearctic regions (Cox 1985). Thus, there are thousands of migratory bird species, representing great diversity in many ecological, behavioral, and physiological traits. Many migratory birds have traits that are predicted to increase the value and likelihood of heterothermy. Heterothermy is predicted to be more common in species with small body size (high surface-area to volume ratio, greater heat loss to the environment, greater mass-specific metabolic rate), variable body condition (more easily assessed in birds than bats due to transparent skin in birds), variable prey availability (e.g., insects which are relatively unavailable in cold weather), and harsh conditions encountered during migration (species that migrate early in spring or late in autumn).

There has been an increasing recognition of the benefits of heterothermy in both migratory and nonmigratory bird species (Nowack et al. 2017). In the first comprehensive review of heterothermy in birds, McKechnie and Lovegrove (2002) documented heterothermic responses in birds from 29 different families (see also more recent reviews; Brigham et al. 2012; McKechnie and Mzilikazi 2011; Ruf and Geiser 2015). Recent studies provide evidence of heterothermy in a growing list of bird species, including, for example, superb fairywrens (*Malurus cyaneus*; Romano et al. 2019) and eastern yellow robins (*Eopsaltria australis*; Aharon-Rotman et al. 2021), and more as described below. There is also variation in the expression of heterothermy in birds, both within and among taxonomic groups. Deep torpor is only known from a few taxonomic groups, perhaps most famously the hummingbirds (Shankar et al. 2022; Shankar et al. submitted for publication; Wolf et al. 2020), variation with body size and phylogeny (Spence and Tingley 2021; Wolf et al. 2020), seasonal variation (Eberts et al. 2021), and use of both shallow heterothermy and deep torpor (Shankar et al. 2022). Thus, thermoregulatory patterns in hummingbirds are best described as a heterothermic spectrum (Shankar et al. 2022). However, most heterothermic birds (e.g., most heterothermic passerines) may only reduce their body temperature a few degrees below normothermic levels. Even shallow changes in body temperature, and the associated reduction of metabolic rate, can lead to important energy savings (e.g., Maddocks and Geiser 1997; Schaeffer et al. 2015).

The majority of studies on heterothermy in birds have focussed on nonmigratory species, but there is increasing evidence that nocturnal heterothermy is used by migratory species (Benedetti et al. 2014; Carere et al. 2010; McKechnie and Lovegrove 2002; Wojciechowski and Pinshow 2009). We now know that hummingbirds adjust the expression of torpor seasonally, with definitive evidence of torpor used to facilitate migratory fattening (Eberts et al. 2021, see also Rossi and Welch 2023). The partially migratory silvereye (*Zosterops lateralis*) reduces body temperature by up to 5.5°C at night, providing a net energy savings of up to 24% during an ∼11-hour period during the winter (Maddocks and Geiser 1997). During migration, such energy savings can increase net refueling rate as suggested for Eurasian blackcaps (*S. atricapilla*; Wojciechowski and Pinshow 2009). Eurasian blackcaps reduced body temperature to 33–40°C at night from normothermic body temperature of 42.5°C, with up to 30% decrease in metabolic rate compared to homeothermic individuals (Wojciechowski and Pinshow 2009). However, the facultative use of nocturnal heterothermy during stopover may be based on several factors, including body condition upon arrival at a stopover site. Migrating garden warblers (*Sylvia borin*) in poor body condition were more likely to use nocturnal heterothermy when they arrived at a stopover site than individuals in good body condition (Benedetti et al. 2014). The benefits of using nocturnal heterothermy (i.e., energy savings) must outweigh the potential costs. Individuals in good condition may not use heterothermy to avoid costs such as decreased immunocompetence (Butler et al. 2013), increased predation risk (Carr and Lima 2013), and increased oxidative stress (Buzadžić et al. 1997). Though energy savings are the main proximate focus of nocturnal heterothermy during migration, there are potential indirect fitness benefits including increased survival or earlier arrival on breeding and overwinter ranges, although these remain to be studied.

As further illustration of the prevalence and energetic consequence of nocturnal heterothermy in migratory birds, we present preliminary results from ongoing research (Leys and McGuire, unpublished data) using subcutaneously implanted temperature-sensitive PIT tags (Biomark, Merck Animal Health, Boise, Idaho USA) to monitor temperature of birds either under natural weather conditions (overnight in an outdoor aviary) or under controlled laboratory conditions (overnight in a temperature-controlled cabinet). Our research includes an opportunistic observational study of nocturnal heterothermy in a variety of migrating birds (outdoor aviary), and more rigorous study of four focal species (outdoor aviary or temperature-controlled cabinet) selected based on traits that we expected to be associated with heterothermy (small body size, early spring/late fall migration dates, insect diet). Our focal species include brown creeper (*Certhia americana*), golden-crowned kinglet (*R. satrapa*), ruby-crowned kinglet (*Corthylio calendula*), and yellow-rumped warbler (*Setophaga coronata coronata*). All fieldwork and data collection were conducted at the Long Point Bird Observatory on the north shore of Lake Erie in southern Ontario, Canada (42.583°N 80.398°W).

One challenge in identifying shallow heterothermy is differentiating heterothermic reductions in body temperature from the daily fluctuations in body temperature that would be expected in a homeotherm. Homeothermic body temperature is not perfectly stable, and body temperature is typically lower during the rest phase (Refinetti and Menaker 1992). Diurnal variation in homeothermic body temperature scales with body size (Aschoff 1981) and therefore we use allometrically predicted values (separately for passerines and non-passerines) to identify cases where body temperature is reduced beyond the expected homeothermic variation. Our preliminary analysis ($n = 1$–14 individuals per species) indicates that as many as one third of the 36 species opportunistically tested thus far may use some degree of nocturnal heterothermy during migration. For our focal species we have more robust sample sizes ($n = 44$–95 individuals per species). Each of our four focal species used nocturnal heterothermy and the most extreme example was a golden-crowned kinglet with the lowest recorded body temperature of 28.8°C (Fig. 5). However, we observed both inter- and intraspecific variation in the use of heterothermy with minimum nocturnal body temperature ranging from 34.6–38.4°C in brown creepers, 28.8–38.6°C in golden-crowned kinglets (Fig. 5), 33.8–38.9°C in ruby-crowned kinglets, and 33.4–39.2°C in yellow-rumped warblers. For birds measured under controlled temperature conditions, we also used open-flow respirometry to measure metabolic rate. Analysis of these data are ongoing, but preliminary results suggest that metabolic rate varies by as much as 36% among individuals measured under the same temperature conditions. As we continue our analysis of these data, we are considering a variety of intrinsic and extrinsic factors that may influence the expression of nocturnal heterothermy, including body condition, weather, and date.

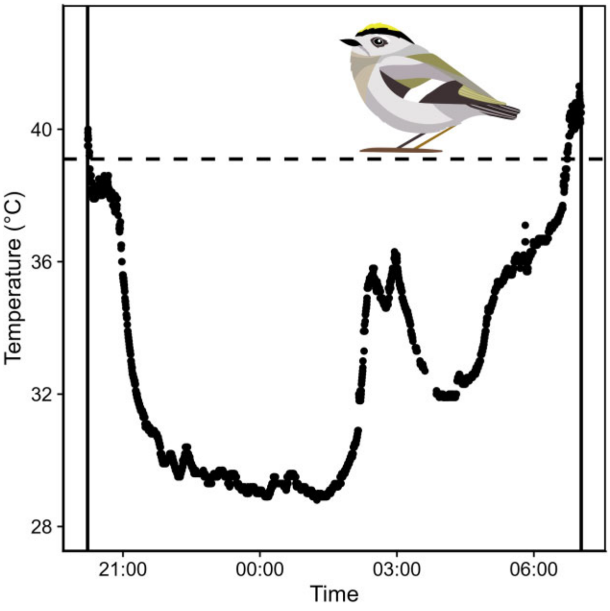

Fig. 5 Nocturnal heterothermy in a golden-crowned kinglet (*R. satrapa*). Body temperature (black circles, recorded with subcutaneously implanted temperature-sensitive PIT-tag) decreased overnight to a low value of 28.8°C. The horizontal dashed line indicates the allometrically-predicted variation in body temperature expected for a homeotherm. Vertical lines indicate sunset and sunrise.

Our preliminary results indicate that heterothermic migration strategies may be more prevalent among birds than has been traditionally assumed, with important implications for stopover energetics. Notably, unlike migratory bats where migration and pregnancy are coincident in the spring, migratory birds do not initiate reproduction until they have arrived on the breeding grounds. Heterothermic migration strategies may allow for earlier northward migration in spring and later southward migration in autumn. Early arrival to breeding sites is associated with increased fitness (Aebischer et al. 1996; Kokko et al. 2006) and heterothermic migrants would also benefit from a longer breeding season which could increase survival of hatch-year birds or even increase fecundity by allowing for a greater number of broods, which is particularly important in short-lived species (Aebischer et al. 1996).

Integrating the evolution of heterothermy and migration

The time and energy costs of migration are important evolutionary drivers (Alerstam et al. 2003) and while homeothermic migrants face a trade-off between time and energy minimization (Alerstam and Lindström 1990) the use of heterothermy allows migrants to reduce both time and energy costs simultaneously (Clerc and McGuire 2021). However, for species capable of deep and prolonged torpor, heterothermy may represent a “logical” (sensu Ruf and Geiser 2015) alternative to migration. Hibernation provides an alternative strategy to avoid seasonal resource limitation, but few studies have considered the evolutionary implications of heterothermy and migration as nonmutually exclusive. The common poorwill (*Phalaenoptilus nuttallii*) is the only bird known to hibernate (Woods et al. 2019), but among mammals there are diverse migrating and hibernating species.

Most mammalian migrants are large-bodied with limited capacity for heterothermy (Avgar et al. 2014; Fryxell and Sinclair 1988; Webber and McGuire 2022). Conversely, most heterothermic mammals are small-bodied with limited capacity for long-distance movement (Geiser 1998; 2004; Webber and McGuire 2022). Given these constraints, we tested the hypothesis that heterothermy is an alternative to migration, or potentially a complementary strategy, to avoid seasonal resource scarcity. We compiled a dataset of 722 mammal species and, as expected, found that large-bodied mammals (e.g., ungulates) are homeotherms that tend to migrate, whereas small-bodied terrestrial mammals (e.g., rodents) are non-migratory species with potential for heterothermy (Webber and McGuire 2022). Bats are therefore a taxonomic group for which body size is not a constraint for heterothermy (as in for ungulates) or for migration (as in for rodents). Among bats, thermoregulatory scope (thermoregulatory scope = mean body temperature—minimum body temperature, larger values imply animals that reduce body temperature to lower values; Boyles et al. 2013) provides a metric, which may allow comparative analysis of heterothermy and migration. For example, plotting thermoregulatory scope against phylogeny, diet, and migratory tendency highlights opportunities to target species for empirical study, conduct fine-scale phylogenetic analyses of multiple closely related species, or assess genomic correlates of heterothermic migration strategies (Fig. 6).

The pronounced expression of heterothermy (i.e., hibernation) provides an alternative strategy to allow endotherms to occupy regions of seasonal resource limitations. Rather than considering migration and hibernation as alternative strategies, heterothermic thermoregulation patterns may provide a conceptual link for comparing strategies across taxa. In the case of birds, this thinking provides a hypothesis for why such a large proportion of bird species are migratory (Cox 1985; Kirby et al. 2008). Deep torpor is rare among birds, and especially so among songbirds (McKechnie et al. 2023). Therefore, while migration allows highly mobile birds to seasonally occupy habitats that provide necessary resources, migration may in some ways be considered an obligate response in the absence of the ability to hibernate seasonally as many mammals do (for those species that cannot remain active throughout the winter months). Conversely, heterothermic migration strategies may present an intermediate or integrated evolutionary strategy driving differences in broader patterns of migration when compared to birds. Relatively few species of bats make long-distance latitudinal migration movements and many more species make regional migrations travelling to and from winter hibernacula (Fleming and Eby 2003; Hutterer et al. 2005). Even among long-distance migrating bats, the distances travelled (perhaps 1,000–2,000 km; Bisson et al. 2009) would only be considered short-distance migration for birds. Although long-distance migration may take some migratory bats to regions where they could continue to be active throughout the winter months (e.g., Mexican free-tailed bats *Tadarida brasiliensis*; Fleming and Eby 2003; Villa and Cockrum 1962) many long-distance temperate migrants hibernate to some extent during the winter months. Winter hibernation has now been documented in several species of long-distance migratory bats, including hoary bats (Marín et al. 2021; Weller et al. 2016), silver-haired bats (Kurta et al. 2017), and eastern red bats (Dunbar and Tomasi 2006) in North America, or common noctules (*Nyctalus noctula*; Dechmann et al. 2014) and Nathusius’ pipistrelles (*P. nathusii*; Petersons 2004) in Europe (among others). Therefore, variation in the use of torpor or shallow heterothermy has important implications for the energetics of migration (and related consequences), but may also

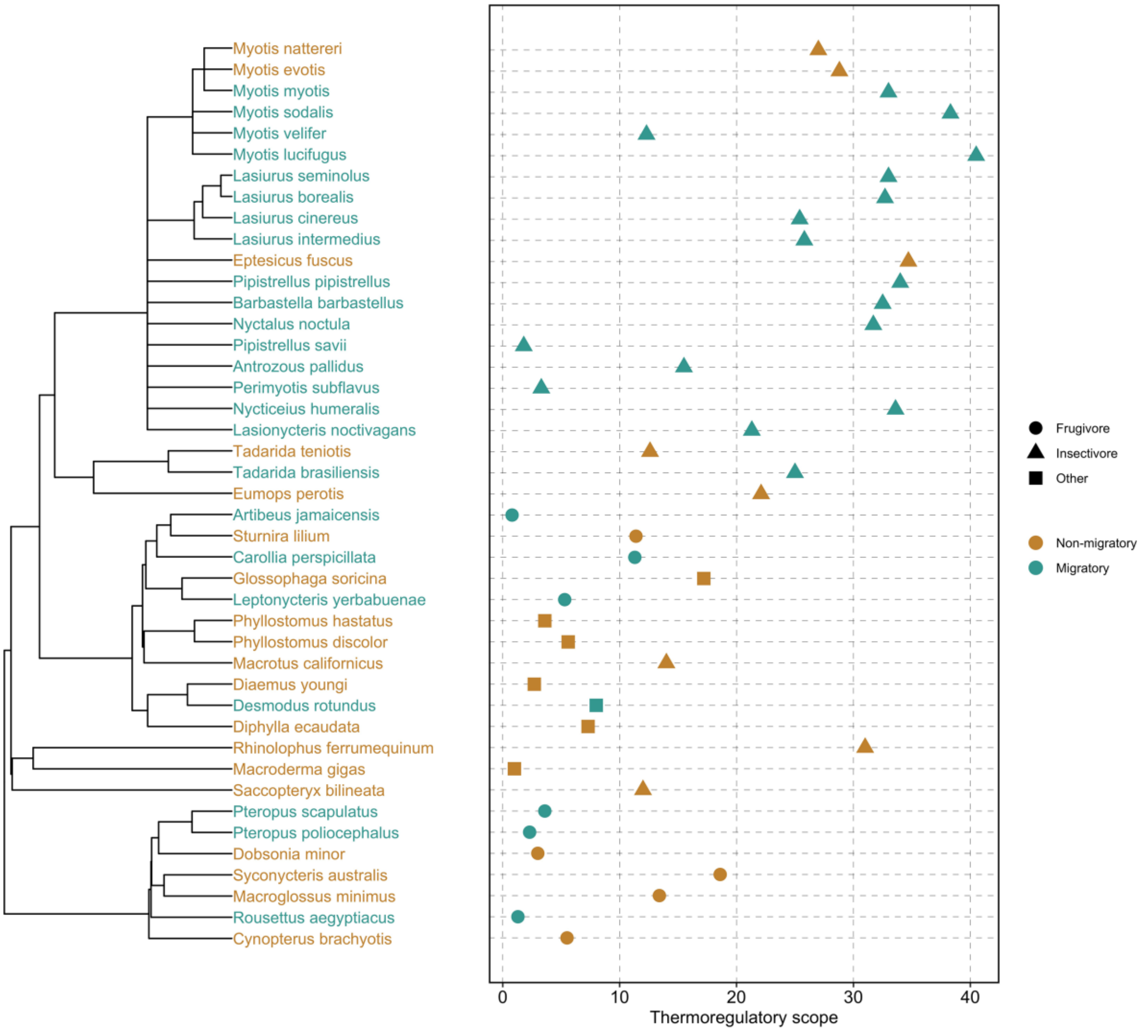

Fig. 6 Comparison between bat phylogeny (left) and thermoregulatory scope (right, a metric of the degree to which body temperature is reduced during torpor) for a variety of bats. Notably, many insectivores have high thermoregulatory scope (i.e., more heterothermic) and a high probability of migration, whereas frugivores or other dietary strategies are associated with lower thermoregulatory scope (i.e., less heterothermic) and fewer migratory species. This distinction is driven in large part by temperate and tropical distributions (not illustrated here). Such presentations can be used to identify priority species for study, or identifying groups that might be the focus of studies of closely related species that differ in diet, thermoregulation, or migratory tendency. Fig. adapted from data presented in Webber and McGuire (2022).

contribute to evolutionary explanations for variation in migratory propensity among taxa, or the ecology, energetics, and physiology of migratory individuals during the winter months.

Future directions

Initial studies of heterothermic migration strategies focussed on identifying the use of torpor but we have now begun to appreciate the diversity of heterothermic expressions in migration. With a broadening base of empirical evidence and a robust theoretical framework, we can now ask broader evolutionary questions (e.g., fitness consequences of heterothermic migration strategies, sex-specific trade-offs, heterothermy as complementary or alternative to migration). With this strong basis, there are many opportunities for future investigations and many important next steps.

Studies of intraspecific and interindividual variation in the use of heterothermy can contribute to understanding trade-offs in the costs and benefits of heterothermy. For example, how does individual condition affect the expression of heterothermy? Is there variation among populations? Or perhaps, is there variation among individuals that migrate earlier or later in the migration season? There may be an interesting parallel between the migration and hibernation literature, with an initial inclination to think of heterothermy as a strategy to minimize energy expenditure, while more recent and nuanced conversations have considered the cost-benefit balance of heterothermy (Boyles et al. 2020).

Given the clear connection between environmental conditions and the energetics of migration and heterothermy, there are many important questions about the impact of climate change on heterothermic migrants, including general temperature increases and the increasing frequency of extreme weather events (Seebacher and Post 2015). Related, there are important questions about how heterothermic migration strategies may be related to survival. Heterothermic migrants can reduce both time and energy costs, likely leading to increased survival, and can also use heterothermy to avoid brief periods of inclement weather. Consistent with this hypothesis, migration represented approximately 85% of annual mortality in a presumed homeothermic migrant, the black-throated blue warbler (Sillett and Holmes 2002), compared to low migration mortality in a presumed torpor-assisted migrant, Leisler's noctule (*Nyctalus leisleri*; Giavi et al. 2014). Clearly there are many differences beyond just thermoregulatory strategy in these systems, but there is an intriguing opportunity for future research. Studies should investigate the relative survival rates of homeothermic and heterothermic migrants under current conditions, and also consider how changing climate might affect survival rates.

Another area for future research is investigating the influence of heterothermic migration strategies on reproductive success. The coincidence of pregnancy and spring migration may preclude the use of torpor-assisted migration strategies for spring migrating female bats of some species (Clerc et al. 2021; Cryan and Wolf 2003), but reproductive phenology varies among species (Jonasson and Guglielmo 2016). Among birds, migration and reproduction are temporally separated, but heterothermic migration strategies may allow for earlier spring migration and later fall migration, extending the breeding season. There may be great fitness benefits for heterothermic migrants that are able to increase the number of broods or increase survival of offspring that have a longer growing season to prepare for their first migration.

There are many exciting questions related to the variable expression of heterothermy during migration. The degree and duration of heterothermy varies temporally, even within individuals during a single rest period (McGuire et al. 2014; Shankar et al. 2022). Variable expression of heterothermy in response to variation in environmental conditions may underly the independence of the energy cost of stopover and environmental conditions (Baloun and Guglielmo 2019; McGuire et al. 2014). Heterothermic migration strategies may allow migrants to arrive at their destination faster and cheaper, but may also allow for a greater degree of behavioral flexibility (including capital and income migration strategies where animals fatten up prior to or throughout migration; Evans and Bearhop 2022). For example, mating season coincides with fall migration for some temperate North American migratory bats (but see also Clerc et al. 2022; Cryan et al. 2012). The use of torpor during inactive periods reduces the energy cost of migration and reduces the potential for negative consequences of inclement weather, which may provide more time and energy which may be allocated to social behaviors associated with mating. Seasonal carryover effects then become interesting when trying to understand how heterothermic migration strategies may be related to overwintering strategies. For example, pregnant female hoary bats during spring migration avoid using torpor, but carry larger fuel stores in the absence of apparent increased foraging effort or digestive efficiency, suggesting that fuel stores for migration may have been deposited on the wintering grounds (Clerc et al. 2021). This and other questions related to carryover effects will be important to understand the evolution and implications of migration strategies in the context of the full annual cycle.

There are also many possible aspects of thermoregulatory expression that have only received limited attention in studies of heterothermic migration strategies to date. For example, most current research has focussed on temperate migration systems where heterothermy is likely more pronounced. Torpor and shallow heterothermy may also be used in tropical or subtropical systems (e.g., Merola-Zwartjes and Ligon 2000; Stawski and Geiser 2010). There may also be a much greater diversity of thermoregulatory expressions than currently appreciated (see Nowack et al. 2023; Levesque et al. submitted for publication). Even more intriguing is recent evidence of metabolic depression in the absence of body temperature reduction, suggesting mechanisms for energetic savings that would not be detected with methods commonly used in current research (see Keicher et al. 2022 and Keicher et al. 2023).

Finally, it is clear that there is far more taxonomic breadth and diversity in the use of heterothermic migration strategies than just a small number of migratory bats using torpor-assisted migration. There are many opportunities for investigating variation in thermoregulatory strategies in migrating bats, but even more possibilities for considering heterothermy in migrating birds. McKechnie and Lovegrove (2002) compiled a list of birds that use varying degrees of heterothermy, and that list continues to grow (see McKechnie et al. 2023). Our preliminary research indicates that heterothermic strategies may be common in bird migration, but with great potential variation in thermoregulatory expression among species. Broader investigations of thermoregulatory patterns in migrating birds have great potential for providing more nuanced and generalized understanding of the expression and implications of heterothermic migration strategies.

Conclusions

Many studies to date have largely overlooked the consequences of thermoregulatory costs in migration. Indeed, the original implementation of optimal migration theory assumed that thermoregulation was static and did not explicitly account for variation in metabolic rate associated with ambient temperature. Now, with a theoretical framework that explicitly includes variation in thermoregulatory patterns (Clerc and McGuire 2021) and a growing body of empirical evidence, it is clear that heterothermic migration strategies are diverse, and have important implications for the time and energy costs of migration. However, many of the ideas that we have expressed in this review are speculative or theoretical possibilities and remain to be critically evaluated, providing many exciting opportunities for future studies.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

Data sources are cited in the text. Unpublished data are available from the corresponding author by reasonable request.

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