2   Considerations of Varied Thermoregulatory

3   Expressions in Migration Theory

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13 **Abstract**

14

15 Optimal migration theory has been used for 3 decades to generate predictions of stopover

16 behavior and understand migration ecology. Yet, to date, there have been no attempts to

17 understand the impacts of thermoregulation on migration theory predictions of stopover

18 behavior. Though most migrants are homeothermic, a diverse group of migrants from bats to

19 hummingbirds and warblers make use of some degree of heterothermy. We consider how

20 thermoregulation influences stopover fuel deposition rates, and thus alters optimal migration

21 theory predictions of stopover behavior using a hypothetical migratory bat as a model organism.

22 We update the analytical models of optimal migration theory by considering scenarios of fixed

23 metabolic rate (the current assumption of optimal migration theory) and 3 different mass-specific

24 metabolic rates including homeothermy, shallow torpor heterothermy, and deep torpor

25 heterothermy. Our results predict that heterotherms will make shorter stopovers, have a

26 decreased departure fuel load, and reduce the overall time and energy costs associated with

27 stopovers relative to homeotherms, highlighting that thermoregulation can drastically influence

28 stopover behavior and ultimately play a critical role in population level patterns of migration.

29

30 **Keywords**: optimal migration theory, thermoregulation, migration ecology, torpor-assisted

31 migration, stopover ecology.

32 Seasonal abundance and paucity of resources, combined with physiological limitations to cope

33 with variable environmental conditions, has led to multiple independent evolutions of migration

34 in a variety of taxa (Winger et al. 2018). Highly mobile animals can travel great distances

35 between disjunct ranges taking advantage of disparate resource pools. The fitness benefits of

36 migration are clear, but migration is energetically demanding, time consuming, and exposes

37 migrants to a variety of uncertain and suboptimal habitats *en route*. Thus, migratory decisions

38 must balance these costs with the benefits of migration (Dingle and Drake 2007).

39   Optimal migration theory is an optimization modeling approach used to theoretically

40 frame the adaptive value associated with varied migratory strategies (Alerstam and Lindstrom

41 1990a). The goal of optimization modeling in biology is to generate predictions about the

42 behavioral traits that maximize fitness (Parker and Maynard Smith 1990). Migration theory

43 assumes that adaptations drive organisms to either maximize their benefits, reduce their costs, or

44 find some solution that best balances the trade-off between the two (Alexander 1996). Fitness is

45 difficult to quantify during migration, so migration theory seeks to generate predictions about the

46 stopover and flight behaviors that optimize a given alternative currency of time, energy, or

47 predation risk as fitness surrogates (Alerstam and Lindstrom 1990, Hedenström and Alerstam

48 1995, Hedenström and Alerstam 1997, Alerstam 2000, Lank et al. 2003, Schmaljohann and

49 Dierschke 2005, Jonker et al. 2010). The currency to be optimized under a given migration

50 theory model is determined by the assumed functional motivation (i. e., the current fitness utility

51 of a behavior) of the migrant. For example, it may be adaptive for a migrant to complete

52 migration as quickly as possible (i.e., time minimizer) and thus seek to maximize the speed of

53 migration (distance per unit time). Conversely, some migrants may achieve the highest fitness

54 value by completing migration for the lowest energy investment (i.e., energy minimizer). Each

55   optimization currency leads to predictions of distinct migratory behaviors. Migration theory is a

56   powerful framework because it generates testable predictions about migration behaviors in a

57   manner that requires assumptions to be made explicitly, sets study systems in the larger context

58   of ecological theory, and serves to improve our understanding of evolutionary adaptive forces

59   (Alexander 1996).

60   A migration theory framework has been broadly used in nearly all aspects of migration

61   ecology leading to important advances in the field (reviewed by; Alerstam 2011). The approach

62   has served as a natural launching point in studying flight speeds with respect to the power curve

63   for flapping flight (Pennycuick 1968, 2008), comparisons of stopover departure rules (Houston

64   1998, Erni et al. 2002, Bayly 2006), and trade-offs between flight routes (Alerstam 2000, Erni et

65   al. 2003), to name a few. Many of the predictions that have been put forth by migration theory

66   models have since been empirically supported (Lindstrom and Alerstam 1992, Wikelski et al.

67   2003, Hedenström 2008), and in cases where theoretical predictions have been unsupported,

68   models have served as working hypotheses to build from and refine (Alerstam 2011).

69   Perhaps the most productive application of migration theory has been in understanding

70   migratory stopovers. The ability to generate predictions about stopover behavior is an important

71   advance in migration ecology because of the critical importance of stopovers to overall migration

72   success (Weber et al. 1999, Bayly 2006, Delingat et al. 2006, Bayly et al. 2012, Chernetsov

73   2012). Stopovers represent discrete sites along the migration route where migrants can

74   temporarily interrupt their journey to rest and/or refuel. In an example of the application of

75   migration theory to stopover ecology, Hedenström and Alerstam (1997) used a migration theory

76   approach to predict that birds spend approximately 7 times longer and twice as much energy at

77   stopover sites compared to migratory flights, highlighting the importance of stopovers to overall

78   migration success. Subsequent empirical work by Wikelski et al. (2003) confirmed the two to

79   one energy use prediction as stopovers accounted for 71% of total energy expenditure during

80   migration in two North American thrush species (Swainson's Thrush *Catharus ustulatus* and

81   Hermit Thrush *Catharus guttatus*). This has been considered one of the greatest successes of

82   migration theory, as it opened up multiple lines of inquiry for future investigation.

83   The primary reason for increased energetic cost at stopovers relative to flight is the

84   necessity for homeothermic migrants to increase metabolic rate to maintain normal body

85   temperature (T_b) as ambient temperature (T_a) decreases below the thermoneutral zone

86   (Wikelski et al. 2003). Wikelski et al. (2003) found that for every degree Celsius decrease in

87   daily mean T_a, daily energy expenditure increased by approximately 1.5 kJ. For homeotherms,

88   such as thrushes and the majority of other volant migrants, stopover thermoregulatory costs have

89   the potential to be one of the greatest energetic expenditures during all of migration.

90   Despite thermoregulation being a major contributor to the overall stopover energy

91   budget, migration theory does not explicitly consider the influence of T_a on thermoregulation

92   during migration. While the majority of migrants are homeotherms, a growing body of literature

93   indicates that many migratory species employ some degree of heterothermy - whereby

94   individuals achieve hypometabolic states as T_a drops below the lower critical temperature

95   (McKechnie and Lovegrove 2002, Carere et al. 2010, Geiser and Brigham 2012, Ruf and Geiser

96   2014). Hypometabolic states range from deep torpor heterothermy where T_b is maintained just

97   slightly above T_a, to shallow torpor heterothermysometimes referred to as nocturnal

98   hypothermia), where T_b is reduced a few degrees below euthermic T_b (Boyles et al. 2013).

99

100   Energy savings from hypometabolic states relative to what would have been expended

101   otherwise maintaining euthermia during the stopover resting periods vary in magnitude

102   depending on T_b, torpor duration, minimum torpid T_b and species-specific torpid metabolic rates

103   (Hiebert 1990, Speakman and Thomas 2003, Shankar et al. 2020). Groups such as hummingbirds

104   and bats, that are considered deep torpor heterotherms, are capable of saving greater than 90% of

105   the energy that would otherwise be expended to remain euthermic during the inactive period

106   (McGuire et al. 2014, Shankar et al. 2020). The term 'torpor-assisted migration' describes the

107   energetic benefits and associated behavioral strategies resulting from the use of torpor during

108   migration to minimize non-flight energy costs (McGuire et al. 2014).

109   To date over 40 species representing 8 avian families and virtually all temperate bat

110   species have been documented expressing daily torpor (Ruf and Geiser 2014). Many more

111   species of birds are likely to use shallow torpor to some degree (e.g., (Wojciechowski and

112   Pinshow 2009, Carere et al. 2010, Benedetti et al. 2014). Increasing recognition that many

113   migrants have the capacity for heterothermy coupled with an interest in the influence of

114   thermoregulation on migration ecology, offers an opportunity to revisit some of the foundational

115   migration theory models to generate qualitative predictions about stopover behavior.

116   Here, we consider three related analyses that investigate the influence of varied

117   thermoregulatory modes on optimal migration theory predictions of stopover behavior using a

118   migratory bat as a hypothetical model organism. We first generate four models of metabolic rate

119   (fixed metabolic rate, homeothermy, deep torpor heterothermy, and shallow torpor heterothermy)

120   as a function of T_a and investigate how differences in thermoregulation alter fuel deposition

121   rates and the flight range equation (Alerstam and Lindström 1990). Second, we illustrate the

122   impact of thermoregulatory mode and migration strategy on predictions of stopover behavior by

6

123   considering a hypothetical homeotherm and a deep torpor heterotherm migratory bat, migrating

124   under two distinct migration strategies to compare differences in predicted optimal fuel load, and

125   stopover duration. Finally, we briefly investigate how varied thermoregulatory modes can

126   influence the ratio of energy and time spent in migratory flight compared to stopover, across the

127   entirety of a migratory journey.

128

129   **The Influence of Thermoregulation on Fuel Deposition Rate and the Range Equation**

130   With respect to refueling, stopover quality can be defined by the constant daily fuel deposition

131   rate (k) (daily gain in fuel mass relative to lean mass) that a migrant can achieve during

132   stopover. Fuel deposition rate is dependent on the availability, acquisition, and assimilation of

133   prey items during foraging periods as well as thermoregulatory costs incurred during foraging

134   and non-foraging resting periods. As stopover resting period costs increase, daily fuel deposition

135   rate decreases. Daily fuel deposition rate (k) is expressed as a proportion of lean mass (m_0) and

136   is the difference between the energy accumulation rate (E) and the energy expended during

137   daily foraging (C) and resting (A)such that,

138    $k = \frac{E(t_{forage}) - [C(t_{forage}) + A(1 - t_{rest})]}{m_0}$ **Eq 1**

139   where t_{forage} is stopover time per day associated with foraging and t_{rest} is the daily time at

140   stopover associated with resting. From Equation 1, and knowing that homeotherms have

141   relatively high resting period costs, and assuming migrants are adapted to express behavioral

142   mechanisms to reduce resting period costs (e.g., huddling, seeking thermally buffered roost sites,

143   etc.) we find that all possible solutions for homeotherms to increase fuel deposition rate (k)

144   require increased energy accumulation rates (E) relative to energy expenditure rates (Schaub and

7

145 Jenni 2000) (**Figure 1**). Conversely, while heterotherms can similarly increase energy

146 accumulation, they can also increase fuel deposition rate by reducing resting period costs rather

147 than increasing daily foraging effort (**Figure 1**). In this way heterotherms can increase fuel

148 deposition rates independent of local foraging conditions and instead as a function of ambient

149 temperature.

150   Previously, migration theory has not accounted for the manner in which heterotherms are

151 able to manipulate resting period fuel depletion. However, the ability to manipulate fuel

152 depletion rates and thus net fuel deposition rates independent of local foraging conditions can

153 have profound effects on the relationship between flight distance and fuel load, the so-called

154 flight range equation, because fuel load (f) is the product of fuel deposition rate (k) and stopover

155 duration (t) (Alerstam and Lindström 1990). Predictions of stopover behavior hinge on flight

156 range curves which are modeled from the flight range equation:

157 $Y = c(1 - \frac{1}{\sqrt{(1+f)}})$ **Eq 2**

158 where flight range (Y) in kilometers, is a negatively accelerating function of fuel load (unitless

159 ratio of mass of fat to mass of lean tissue), and c is a species-specific proportionality constant (in

160 kilometers) based on size, morphology, and flight efficiency (Alerstam and Lindstrom 1990,

161 Weber and Houston 1997). With increasing fuel load the cost of lift increases and the effective

162 lift to drag ratio decreases (Pennycuick 1968). Therefore flight range follows a diminishing

163 returns relationship with fuel load because of a reduction in fuel economy (Hedenström and

164 Lindstrom 1998).

165   Incorporating differences in thermoregulation into calculations of fuel deposition rate

166 generates updated flight range curves leading to qualitative predictions of stopover duration and

167 fuel load for heterotherms relative to homeotherms. To accomplish this, we first incorporated

168   metabolic rate as a function of T_a into the range equation (**Eq 1**). Rather than considering the

169   resting period energy use as a static parameter we considered it to be dynamic, whereby migrants

170   experiencing T_a within the thermoneutral zone exhibit a mass-specific resting metabolic rate

171   (RMR) independent of T_a and below the thermoneutral zone experience a mass-specific

172   metabolic rate as a function of T_a given thermoregulatory expression. This dynamic resting

173   period energy use parameter can then calculate a more realistic net fuel deposition rate and the

174   resulting influence on the flight range curve can be calculated.

175   We considered four expressions of thermoregulation, each having the same metabolic

176   rate within the thermoneutral zone, the same lower critical temperature, but expressing four

177   distinct modes of metabolism below the lower critical temperature. The four metabolic

178   expressions are fixed metabolic rate (as currently assumed in optimal migration theory models),

179   homeothermy, shallow torpor heterothermy, and deep torpor heterothermy (details below). We

180   parameterized our models with a hypothetical insectivorous bat with a body mass (M_b) of 9 g,

181   but the analysis here can be generalized to other volant taxa. Temperate insectivorous bats are

182   good models because they use torpor regularly at stopovers (Speakman and Thomas 2003,

183   McGuire et al. 2014) and their circadian rhythm constrains them to nocturnal flight activities

184   making the daylight hours a known resting period. We used Equation 1 to calculate fuel

185   deposition rates (k) assuming a fixed fuel accumulation rate (E) (Lindstrom and Alerstam

186   1992) and a static foraging and resting period time of 9 h and 15 h respectively. We assumed that

187   the migrant arrived at stopover with 1 g of fat and 8 g of lean mass and began refueling

188   immediately following a search/settling period (see below). We assumed the 9 h foraging period

189   was a combination of short foraging bouts (an accumulated total of 2 h of flight) and periods of

190   night roosting for digestion resulting in a hypothetical energy accumulation rate (E) of 1 g fat

191 day^{-1} (estimated from Jonasson 2018) and a foraging period cost (C) estimated to be 0.36 g fat

192 day^{-1}; 0.25 g in flight costs and 0.11 g in night roost digestive costs (2 times RMR) (Speakman

193 and Thomas 2003). Transforming the resting period energy cost A, in Equation 1 from a static

194 parameter to a dynamic parameter results in

195 $A = \frac{MR(T_a)\cdot(1-t)}{a}$ **Eq 3**

196 where a is the energy density of fuel (39,000 J g $^{-1}$ fat; Weathers 1996, Jenni and Jenni-

197 Eiermann 1998) such that the term converts to g fat expended and MR is mass-specific metabolic

198 rate in J g^{-1} h^{-1} and is dependent on the thermoregulatory expression of a migrant (i.e., sensitive

199 to T_a). We calculated fixed metabolic rate (MR_{fixed}) as RMR within the thermoneutral zone as

200 J h^{-1} by combining an allometric prediction of mLO_2h^{-1} (Speakman and Thomas 2003) with an

201 oxyjoule equivalent of 20.09 (assuming a respiratory quotient of 0.80) (Lighton 2018) such that

202 $MR_{fixed}\left(J\cdot h^{-1}\right) = ln\left(1.0895 + 0.744log_e M_b(g)\right)\cdot 20.09(JmLO_2^{-1})$ **Eq 4**

203 For MR_{fixed} we assumed metabolic rate was independent of T_a (**Figure 2A**), as in current forms

204 of optimal migration theory. From Speakman and Thomas (2003), we defined a lower critical

205 temperature (T_{lc}) allometrically as $T_{lc} = 30.0°C$. For purposes of our analysis we did not

206 consider scenarios where T_a exceeded the upper critical temperature of the thermoneutral zone.

207 From Speakman and Thomas (2003), we assumed that below T_{lc}, homeotherms had a metabolic

208 rate of

209 $MR_{homeotherm}\left(J\cdot h^{-1}\right) = MR_{fixed}\cdot(T_{lc}-T_a(°C))\cdot ln\left(-0.1037 + 0.534log_e M_b(g)\right)\cdot$

210 $20.09(JmLO_2^{-1})$ **Eq 5**, **Figure 2B**

211 Such that,

212                                     $MR_{fixed} if T_a > T_{lc}$

213 $$MR_{homeotherm} \: if \: T_a < T_{lc}$$

214 Most shallow torpor heterotherms reduce their T_b $2 - 4°C$ below euthermia as

215 temperatures decrease below the T_{lc} (McKechnie and Lovegrove 2002, Ruf and Geiser 2014),

216 though as much as 10°C reductions in T_b have been recorded in the context of stopovers in long-

217 distance migrating Icterine Warblers (*Hippolais polyglotta*) (Carere et al. 2010). Further, in a

218 non-migratory setting, Mountain Chickadees (*Poecile gambeli*) and Juniper Titmice (*Baeolophus*

219 *ridgwayi*) have been shown to reduce nocturnal T_b as much as 11°C below daytime T_b,

220 resulting in energy savings of 7 - 50% of what would have been expended maintaining euthermia

221 (Cooper and Gessaman 2005). For the sake of example, we assumed shallow torpor

222 heterotherms $MR_{shallowTorpor}$ have a metabolic rate 85% that of a strict homeotherm (**Figure**

223 **2C**) such that,

224 $$MR_{fixed} \: if \: T_a > T_{lc}$$

225 $$MR_{shallowTorpor} \: if \: T_a < T_{lc}$$

226 Finally, from Speakman and Thomas (2003) we assume that in deep torpor heterothermy,

227 migrants have a torpid metabolic rate (TMR)

228 $MR_{deepTorpor}(J \cdot h^{-1}) = ln(-3.87 + 0.163 \cdot (T_a) + 0.988 \cdot log(M_b)) \cdot 20.09$ **Eq 6**, **Figure**

229 **2D**

230 such that,

231 $$MR_{fixed} \: if \: T_a > T_{lc}$$

232 $$MR_{deepTorpor} \: if \: T_a < T_{lc}$$

233 We then combine Equation 2 with Equation 3 to calculate updated fuel deposition rates. Fuel

234 load f equates to kt where k is net fuel deposition rate as before. Substituting f with kt in the

235 flight range equation (**Eq 2**) results in range curves that are metabolically informed (**Figure 2E**).

236 It is important to note, that we rely on allometric equations of metabolic rates, and thus flight

237 range curves will lack quantitative detail and are therefore qualitative.

238 Within the thermoneutral zone, all four thermoregulatory scenarios have equivalent fuel

239 deposition rates (**Figure 2**). But for example at $T_a = 15°C$ (grey vertical line in **Figure 2 A-D**) ,

240 net fuel deposition rates are varied resulting in similarly varied range curves (Figure 2 E). At

241 $T_a = 15°C$ a migrant with a fixed metabolic rate would achieve a fuel deposition rate of 0.065

242 and a homeotherm would have a much lower fuel deposition rate of 0.008.. Deep torpor

243 heterotherms achieve a fuel deposition rate that is nearly 10 times greater than that of a

244 homeotherm. As mean T_a decreases the differences become magnified. For example, if we

245 assume a mean T_a of 5°C, deep torpor heterotherms would be predicted to achieve a fuel

246 deposition rate of 0.07 and hometherms would have a negative fuel deposition rate meaning that

247 under our assumed intake rate of 1 gram of fuel per day, homeotherms would be in negative

248 energy balance.. Though deep torpor heterothermy allows migrants to achieve greater fuel

249 deposition rates as metabolic rate continues to decrease with T_a (**Figure 2, D**), at some point

250 animals will be forced to increase their metabolic rate to maintain T_b above freezing or risk

251 cellular damage or death (Jonasson and Willis 2012, Wolf et al. 2020). Regardless, it is clear that

252 differences in stopover energy costs resulting from varied thermoregulatory expressions can

253 substantially influence fuel deposition rates and thus flight range curves which, as we

254 demonstrate below, can translate into dramatic differences in predicted stopover behavior.

255

256 **Migration Currencies**

257   We considered two migration currencies: minimizing time and minimizing the total

258 energy of migration (see Hedenström and Alerstam (1997) for detailed overview). Briefly, time

259   minimizers adopt strategies to complete migration as quickly as possible and achieve the greatest

260   speed of migration by maximizing the flight distance to time ratio expressed as

261    $R_{time} = \frac{Y(f) - Y(f_0)}{t + t_0}$ **Eq 7**

262   where Y is flight range, f is fuel load, t is the stopover duration in days, and f_0 and t_0 are fuel

263   and time costs, respectively, associated with search and settling at a new stopover site. Setting

264   the derivative of Equation 7 equal to zero yields the optimal stopover duration t^* (*i.e.*, the fuel

265   load that maximizes the instantaneous speed of migration). With the optimal stopover duration t^*

266   and $f = kt$ we can determine optimal fuel load f^*.

267   To minimize the total energy cost of migration, we assume migrants maximize the ratio

268   of flight distance to stopover energy investment

269    $R_{energy} = \frac{Y(e) - Y(e_0)}{e + e_1}$ **Eq 8**

270   where e is the stopover energy investment, e_0 is the energy associated with search and settling,

271   and e_1 is the existence metabolism associated with search and settling costs. The stopover

272   energy investment accounts for the fuel accumulated at stopover (i.e., the cost of migratory flight

273   from one stopover to the next) as well as energy expended at stopover and is expressed as

274    $e = (f \cdot m_0 \cdot a) + (t \cdot MR_{field})$ **Eq 9**

275   where f is fuel load, m_0 is lean mass, and a is the energy density of fuel as above. The first term

276   in Equation 9 accounts for the energy of the accumulated fuel load that is then expended to travel

277   distance Y. The second term of Equation 9 represents the existence metabolism at stopover

278   where t is stopover duration in days as above and MR_{field} is the field metabolic rate. The

279   optimal fuel load associated with the minimum total energy cost of migration can be determined

280 by calculating the minimum energetic investment to cover a migration distance Y, and then

281 converting the optimal stopover energetic investment e* to f* (Alerstam and Lindstrom 1990).

282

283 **Generating predictions of stopover behavior under varied currencies and**

284 **thermoregulatory expressions**

285 Considering both thermoregulatory expression and optimization currency, we generated new

286 qualitative predictions of optimal stopover duration and departure fuel load for the hypothetical

287 homeotherm (**Figure 2B**) and the deep torpor heterotherm (**Figure 2D**) across a range of

288 theoretical fuel deposition rates. We considered hypothetical migrants representing the extremes

289 of the heterothermic continuum by comparing migration theory predictions of time-minimizing

290 and energy-minimizing migration.

291   Thermoregulatory expression not only influences the net fuel deposition rate but in the

292 same way, resting period costs influence search and settling fuel costs f_0. These costs are a result

293 of the inability to localize suitable foraging grounds immediately upon arrival at a stopover site.

294 After a migrant arrives at a stopover site, search and settling costs may accumulate over multiple

295 days (Alerstam and Lindström 1990). Even under ideal circumstances there will likely be some

296 minimum search and settling costs accrued upon arrival at a stopover. Search and settling costs

297 are a combination of flight costs (initial search for suitable stopover habitat with access to a

298 combination of quality foraging sites, water, and roosting sites) and resting costs (waiting for

299 refueling conditions to become more favorable).

300   We considered a hypothetical scenario in which a bat arrives at stopover 1 h prior to

301 sunrise, and searches for 10 min for a suitable roosting site, after which the bat rests for 14.5 h

302 before emerging and finding suitable foraging grounds after a 10 min search flight. Under these

14

303   criteria search and settling time t_0= 0.62 d for both hypothetical migrants. We used an allometric

304   scaling equation (Speakman and Thomas 2003) to predict flight metabolic rate (MR_{flight}) from

305   body mass. For each hypothetical migrant we considered their optimal solutions across a range

306   of temperatures ranging from T_a = 4°C (T_a below which bats exhibit variable torpor use,

307   Jonasson and Willis 2012) to T_a = 26°C (temperature approaching T_{lc}). We further considered a

308   range of fuel deposition rates from k = 0.015 (1.5% gain in body mass per day) to k = 0.13 (13%

309   gain in body mass per day). We chose this range because fuel deposition rates that fell below

310   0.015 resulted in predictions of stopover duration that were unrealistically high and values

311   greater than 0.13 likely represent the highest end of what is achievable at stopover (Lindström

312   2003). Because of differences in search and settling resting period metabolic costs under our

313   hypothetical scenario, homeotherms have a search and settling fuel cost ranging between 0.92 g

314   (when T_a = 4°C) and 0.27 g (when T_a = 26°C) of fat expressed as fuel load, and deep torpor

315   heterotherms has a search and settling fuel cost ranging between 0.04 g (when T_a = 4°C) and 0.13

316   g (when T_a = 26°C) .

317   We first compared a time-minimizing homeotherm and deep torpor heterotherm. We

318   found that when considering the full treatment for all ambient temperatures and fuel deposition

319   rate combinations for time minimizing migrants the optimal departure fuel load (*f**) is predicted

320   to be greater for homeotherms than for deep torpor heterotherms (**Figure 3A, B)**. For example,

321   when stopover T_a = 15°C optimal departure fuel load ranges between 0.*f** = 0.43 (*k* = 0.015) to

322   0.*f** = 56 (*k* = 0.13) for homeotherms and between *f** = 0.16 to *f** = 0.36 for a deep torpor

323   heterotherm (**Figure 4 A**Further, the optimal stopover duration for time minimizing migrants is

324   predicted to be longer for homeotherms relative to deep torpor heterotherms ranging between

325   28.8 days (*k* = 0.015) and 4.3 days (*k* = 0.13) for hometherms, and between 10.5 days and 2.8

326   days for deep torpor heterotherms (**Figure 4 B**). Thus, time-minimizing homeotherms are

327   predicted to have greater search and settling fuel costs, increased departure fuel loads, and longer

328   stopover durations relative to time-minimizing deep torpor heterotherms.

329   We also investigated how thermoregulatory expression influences predicted stopover use

330   under an energy minimizing strategy. However, we must first consider how thermoregulatory

331   expression influences existence metabolism, MR_{field}. For the purposes of parameterizing the

332   model, we calculated daily existence metabolism for homeotherms to be the sum of 22 h of

333   resting metabolic rate and 2 h of flight metabolic rate. For deep torpor heterotherms we

334   calculated daily existence metabolism as the sum of 15 h of torpid metabolic rate, 7 h of

335   homeothermic resting metabolic rate, and 2 h of flight metabolic rate. Considering existence

336   metabolism and the same hypothetical parameters as above across all ambient temperature and

337   fuel deposition rate combinations demonstrates that energy-minimizing homeotherms are

338   predicted to have an increased optimal stopover departure fuel load relative to energy

339   minimizing heterotherms (**Figure 3 C, D**). Under the above criteria, and considering a stopover

340   ambient temperature of $T_a = 15°C$, energy minimizing homeotherms are predicted to have an

341   optimal departure fuel load ranging from $f^* = 0.43$ ($k = 0.015$) to $f^* = 0.49$ ($k = 0.13$) and a

342   stopover duration ranging from 28.6 days ($k = 0.015$) to 3.8 days ($k = 0.13$) – (**Figure 4**).

343   Conversely, an energy-minimizing deep torpor heterotherm is predicted to have an optimal

344   departure fuel load ranging from $f^* = 0.15$ to $f^* = 0.22$ and a stopover duration ranging from 9.8

345   – 1.7 days (**Figure 4**).

346   Independent of optimization criteria, heterotherms are predicted to have shorter stopover

347   durations and decreased fuel loads compared to homeotherms. Heterotherms achieve this by

348   being able to mitigate resting period fuel costs relative to homeotherms as T_a decreases,

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349   resulting in low search and settling cost, decreased existence metabolism cost at stopover, and

350   increased net fuel deposition rate compared with a homeotherm.

351

352   **The influence of thermoregulatory expression on the flight cost to stopover cost ratio**

353   Finally, we considered how thermoregulatory expression can influence the amount of

354   time and energy of the total migration that is spent on flight and stopover. Using the equations of

355   total energy cost of migration and total time of migration from Hedenström and Alerstam (1997)

356   we compared the proportion of the total energy and time costs of migration that a homeotherm

357   and a deep torpor heterotherm would theoretically incur across temperatures ranging from $T_a =$

358   4°C (to $T_a = 26$°C. Using the same estimated fuel deposition rates calculated above and applying

359   the stopover time and energy ratios across the range of T_a we find that homeotherms are

360   predicted to incur increasing time and energy costs as T_a drops below the thermoneutral zone,

361   whereby stopover accounts for greater than 90% of the total energy and time costs associated

362   with migration when T_a approaches 4°C (**Figure 4)** Stopover costs become so great for

363   homeotherms that under our scenario of a hypothetical energy accumulation rate of 1 g fat day^{-1}

364   migrants would be in negative energy balance at stopover if average temperatures reached $T_a = 6$

365   °C .Conversely, deep torpor heterotherms are able to reduce the cost of stopovers relative to

366   migratory flight. Energy costs incurred at stopover by deep torpor heterotherms increase slightly

367   as T_a drops from 22 °C to 4 °C as even heterotherms will have to spend some time euthermic

368   during the resting period, (e.g. digesting) and overall energy costs increase again between 22 °C

369   and 26 °C as the energy savings of torpor decrease when T_a approaches the thermoneutral zone

370   (**Figure 4 B).** Current predictions of the flight to stopover ratio of costs assume a fixed metabolic

371   rate resulting in underestimating stopover time and energy costs of homeothermic migrants

372 across a wide range of T_a. Conversely, generating predictions using fixed stopover costs will

373 overestimate both time and energy costs across the entire range of T_a for heterotherms.

Discussion

375 Thermoregulation is a component of the endotherm energy budget that can vary

376 drastically with environmental changes. Including varied thermoregulatory strategies into the

377 migration theory paradigm is essential to understand migratory strategies and overall migratory

378 success and leads to novel predictions that may be empirically tested or theoretically refined in

379 the future (**Table 1**).

380 Changes in thermoregulatory expression may lead to changes in landscape level stopover

381 use and therefore population level patterns of migration. Heterothermy allows migrants to

382 achieve positive energy balance at poor quality stopover sites that would lead to negative energy

383 balance in a homeotherm. When faced with high rest period costs or low-quality foraging,

384 homeotherms have no mechanism to compensate and fuel deposition rate is decreased.

385 Therefore, homeothermic migrants may be constrained to high quality migratory stopover

386 hotspots where they can maintain high fuel deposition rate. However, heterotherms can counter

387 these challenges by reducing rest period costs and therefore maintain positive energy balance

388 over a broader range of site qualities. Without the need to rely on high quality stopover sites, the

389 use of heterothermy may result in a more diffuse population level pattern of migration. Relative

390 to heterotherms, homeotherms may need to rely to a greater degree on migratory corridors that

391 provide a high probability of refueling hotspots. In contrast, heterotherms may be able follow a

392 broad front migration strategy.

393 Previous considerations of optimal migration theory incur a tradeoff between time and

394 energy. Migrants must choose between a time or energy minimizing strategy. However, as we

395 have shown here, the use of torpor simultaneously reduces both the total time and energy costs of

396 migration. Time and energy are generally considered to be the two most important currencies for

397 a migrant to consider, but by reducing these two costs, other currencies may become relatively

398 more important for heterothermic migrants. Currencies such as predation risk (Alerstam and

399 Lindstrom 1990) and reproductive considerations (particularly for certain bat species that mate

400 during migration; Cryan 2008, Cryan et al. 2012) may play more prominent roles in

401 heterothermic migrants than in homeotherms that are dominated by time and energy costs.

402 Similarly, it will be particularly informative in future studies to consider situations in which

403 heterothermic species forgo the use of torpor and remain euthermic. We have demonstrated the

404 clear time and energy benefits of using torpor, but there are also costs of using torpor. In addition

405 to potential physiological costs, torpid individuals make be less able to respond to predation

406 attacks or may face lost opportunity costs. Situations where animals forgo torpor despite the time

407 and energy benefits will provide insight into the relative importance of alternative currencies in

408 the overall success of migration and fitness of migrants.

409   As we have demonstrated here, torpor expression is an effective strategy for increasing

410 stopover fuel deposition rates. Jonasson (2017) found evidence of silver-haired bats achieving

411 energy accumulation rates of $k = 0.098$ and Carpenter et al. (1993) reasoned that heterothermic

412 hummingbirds have the potential to boast some of the highest recorded fuel deposition rates

413 among volant migrants, achieving net fuel deposition rates of $k = 0.10$. Hummingbirds also

414 exhibit biphasic fueling— switching their diet from being protein rich to rebuild muscle tissues

415 upon stopover arrival to a sugar diet to rebuild fat mass (Carpenter et al. 1993), exemplifying that

416 multiple alternative refueling strategies could contribute to increased energy accumulation at

417 stopover in lieu of, or in combination with, torpor expression. Hyperphagia, increased digestive

418 efficiency, and diet switching are all strategies used by volant migrants to reach optimal fuel

419 loads at stopover (Bairlein 2002, Lindström 2003). Incorporating different energy accumulation

420 strategies into models of stopover use will help disentangle how the relative contributions of

421 alternative refueling strategies alter stopover use and overall migratory success.

422   Our findings mark an improvement in our understanding of migration biology. Using

423 static metabolic rates to calculate net fuel deposition rate could lead to overestimates of 90%

424 under stopover conditions that are likely regularly encountered during migration. Such

425 differences in estimates drastically alter stopover behavior predictions of departure fuel load and

426 stopover duration. Furthermore, differences in the search and settling fuel costs and existence

427 metabolism can have major impacts on stopover behavior and is yet another reason for

428 accounting for the thermoregulatory expression of a migrant. Considering varied

429 thermoregulatory capacities in migration theory is an important addition that increases the

430 predictive power of stopover optimization models.

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536

537 **Table 1**. Revised models of optimal migration theory that account for varied thermoregulatory
538 strategies indicate that the energetics of migration are dramatically altered for heterothermic
539 species. As recommendations for future research, we pose several general predictions for
540 heterothermic migrants arising from the models we have developed.

	Predictions
General predictions for heterothermic migrants	1. Fuel deposition rate is a function of both habitat quality and thermoregulatory expression
	2. Heterothermic migrants will be able to take advantage of relatively poor-quality habitat compared to homeothermic migrants. This may reduce reliance on high-quality stopover sites and result in more broad front migration patterns
	3. Heterothermic migrants will have shorter stopover durations compared to homeothermic migrants
	4. Heterothermic migrants will have decreased fuel loads relative to homeothermic migrants
	5. Heterothermy reduces both time and energy costs, and therefore the relative importance of alternative currencies (e.g., predation risk) may be increased in heterothermic migrants
Prediction for heterothermic time minimizer	6. Heterothermic migrants will have greater fuel deposition rates compared to homeothermic migrants when ambient temperatures drop below the lower critical temperature
Prediction for heterothermic energy minimizers	7. Heterothermic energy minimizers may achieve greater speed of migration than homeothermic time minimizers

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