1   Predicted asymmetrical effects of warming on nocturnal and diurnal ectotherms.

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24 **<u>Abstract</u>**

25 Many ectotherms restrict activity to times and places with favorable temperatures. This

26 widespread pattern of habitat use in fluctuating environments may alter predictions of

27 how climate change will affect ectotherms. By considering time elapsed within a range of

28 suitable temperatures as a resource, I demonstrate that warming is expected to affect

29 thermally restricted nocturnal and diurnal activity windows asymmetrically. Under

30 warming scenarios, thermally restricted nocturnal activity windows lengthen while

31 diurnal activity windows contract. This divergent prediction results from the shape of the

32 function relating time to temperature within a day, which is typically concave during the

33 day and convex during the night. This characteristic shape is nearly universal across

34 terrestrial environments due to the changing angle of the sun throughout each day and

35 exponential decay of overnight temperatures. These predicted asymmetries are

36 exacerbated by expectations of diurnally asymmetric warming (more warming during the

37 night compared to the day). Using example data from a montane ant community, I

38 demonstrate that, as predicted, moderate simulated warming expands activity time

39 available to cool active species and reduces activity time available to warm active

40 species. Together these results suggest that the time of day during which an ectotherms

41 optimal temperature occurs can be an important factor in determining response to

42 warming.

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44 Keywords: climate change, ectotherms, behavioral thermoregulation, thermal refuge,

45 diurnally asymmetric warming

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47 **Introduction**

48   A commonly observed response to climate change within plants, animals, and

49 fungi is to move across either space or time such that favorable abiotic conditions,

50 including moisture and temperature, are maintained (Parmesan and Yohe 2003; Kelly and

51 Goulden 2008; Diez et al. 2013). Historical shifts in calendar date and movement across

52 landscapes suggest that species vary in these responses, and that particular life-history

53 traits may increase the likelihood of experiencing negative consequences of warming

54 (Deutsch et al. 2008). Particularly susceptible species may be long-lived and sessile, have

55 demographic parameters sensitive to the environment (Clark et al. 2011), live in a

56 location where climate is expected to change more quickly, have narrow thermal

57 tolerances (Gilchrist 1995), or be engaged in tightly co-evolved mutualisms (Bennett and

58 Moran 2015). A topic that has received comparatively less attention in evaluating

59 capacity to adapt to temperature is activity time. Here, I aim to address how susceptibility

60 to warming varies between organisms active at different times of the day.

61   Ectotherms face a daunting task safely regulating their internal body temperatures

62 (Kearney et al. 2009). They must move through a dynamic thermal landscape in an

63 attempt to maximize fitness through expression of a diversity of behaviors. Ectotherms

64 often seek shelter from extreme conditions in thermal refuges, defined here as thermally

65 buffered microhabitats, such as leaf litter, space beneath rocks, or in bodies of water.

66 Time can only be spent in one place, and while time in a refuge may be put toward useful

67 processes such as digestion, growth, predator avoidance (Karban et al. 2015), or colony

68 maintenance (Gordon 1983), it comes at an opportunity cost in terms of foraging, seeking

69 mates, defending territory, or any other engagement with the community lying outside the

70   refuge (Amo et al. 2007). Due to movement between microhabitats, mobile ectotherm

71   body temperature regularly deviates from local air temperature, which is often used in

72   predictions of the fitness consequences of climate change (Gaitán-Espitia et al. 2014).

73   The ability to decouple internal and environmental temperatures through movement and

74   behavior confounds efforts to predict the impact of climate change on mobile ectotherms,

75   as any one location used to characterize environmental temperature is insufficient to

76   predict fitness outcomes.

77   Despite this challenge, thermal fitness curves associated with ectotherms are

78   commonly used predict consequences of global climate change (Sinclair et al. 2016). A

79   recent framework provides guidance as to how diurnal fluctuations in body temperature

80   affect the ability of organisms to acclimate, and the importance of considering the effects

81   of brief periods of exposure (Kingsolver and Woods 2016). However, many ectotherms,

82   in particular soil-dwelling arthropods, can fully escape extreme temperature exposure,

83   and may limit activity to times that are suitable (Sinclair et al. 2016). By using high

84   quality thermal refuges, arthropods violate assumptions implicit in any predictions that

85   depend on single microhabitat measures of environmental temperature. Through the use

86   of high-quality thermal refuges, many ectotherms escape the severe consequences

87   associated with exceeding optimal temperature (T_{opt}) (Huey and Pianka 1977).

88   Due to the commonality of temperature based behavioral plasticity and the

89   ubiquity of diurnal temperature variability, the duration of daily thermal activity windows

90   could play an important role in mitigating the response of ecological communities to

91   climate change (Kearney et al. 2009). Time elapsed within suitable temperature ranges is

92   an important but rarely characterized resource of ectotherms. There are currently no

93   predictions for how durations of suitable temperature may be altered for species active at

94   different times of the day.

95   Daily temperature variation in terrestrial ecosystems is affected by many local

96   factors including geography, elevation, humidity, and season (Dai et al. 1999). Despite

97   local differences, there are several characteristics of daily temperatures that are nearly

98   universal in terrestrial ecosystems. The sun's local zenith results in a peak of incoming

99   radiation at solar noon. Air temperature lags behind this peak solar radiation, as infrared

100   radiation from the ground also contributes to warming of the air (Karl et al. 1991). Due to

101   the continuously changing angle of the sun, a function relating time (x) to temperature

102   (f(x)) is concave during the day. Further, temperatures surrounding solar midnight are on

103   average, convex, as nighttime cooling results from a decelerating loss of heat that was

104   accumulated during the day.

105   Global climate change is leading to uneven surface temperature warming across

106   the globe. Poleward regions and high elevation sites are warming faster than low-lying

107   and tropical regions. In addition to a geographic mosaic of warming, temperatures are

108   changing unevenly in time (Davy et al. 2016). Across broad geographic regions,

109   nighttime low temperatures are increasing faster than daytime highs. This diurnal

110   asymmetry, represented by proportionally more warming occurring during the night,

111   reduces the daily range of temperatures at any given site. Diurnal asymmetry of

112   temperature may result in differential outcomes of warming for organisms depending on

113   when during the day optimal temperatures occur.

114   Here, I describe and test a model predicting how diurnal temperature variation can

115   interact with ectotherm behavioral thermoregulation based on a simple assumption that

116   ectotherm activity is limited by local temperature and that the time elapsed within a

117   favorable temperature range is itself a resource. I estimate the extent to which species-

118   specific and local factors such as activity temperatures, diurnal asymmetry of warming,

119   thermal activity breadth, daily temperature range, and day-to-day variation in temperature

120   alter expectations of changes in available activity time under warming. Finally, I apply

121   this approach to an observational dataset of fine-scale ant activity and temperature

122   measurements to estimate the magnitude of these impacts on activity duration across a

123   community of montane ants.

124   **Methods**

125   I used a simulation-based approach to explore how durations of daily thermal windows

126   are affected under a variety of warming and cooling scenarios. Simulations quantified

127   thermal window duration across potential species thermal ranges and local environmental

128   conditions. Each simulation resulted in a calculation of the change in the amount of time

129   elapsed each day within a range of temperatures following warming. analyses were

130   conducted in R version 3.5.1 (R Core Team 2017) and all figures were created using the

131   package *ggplot2* (Wickham 2009).

132   Summary of simulation methods

133   Activity windows were calculated as the duration of each day spent between the

134   species minimum and maximum temperature tolerance. The key biological assumption in

135   discussing results of these simulations as relevant to organismal fitness is that time

136   elapsed within suitable temperature ranges itself is a limited resource for many

137   ectotherms. This approach assumes uniformly distributed activity across suitable

138   temperatures, but general conclusions drawn from simulations are robust to changes in

139   activity distribution shape. I employed two common approximations of daily temperature

140   variation, each using 10,000 observations of temperature within a day: 1) a sine wave

141   model, oscillating between minimum and maximum daily temperatures with a period of

142   24 hours and 2) a truncated sine wave for daytime temperatures linked to a negative

143   exponential function for nighttime cooling (Parton-Logan function – Eq 1 modified from

144   (Parton and Logan 1981; Lambrechts et al. 2011).

145   Equation 1 – daytime temperature

146
$$T_i = (T_X - T_N) * \sin(\frac{\pi m}{12 + 2a}) + T_N$$

147   Equation 2 – nighttime temperature

148
$$T_i = T_N + (T_S - T_N)^{-(bn/12)}$$

149   Where T_X and T_N are maximum and minimum daily temperatures respectively, T_S is

150   temperature at sunset (results from Eq 1 evaluated at m = 12), m is the number of hours

151   past sunrise, n is the number of hours past sunset, a is a lag coefficient for maximum

152   temperature, and b is a nighttime cooling coefficient. The parameters a and b were fit in

153   R using the nls function for data corresponding to ant activity measurements (see field

154   methods below) and were found to provide a best fit at a = 1.15, and b = 3.37. This curve

155   shape was then normalized such that minimum temperature = 0, and maximum

156   temperature = 1, and scaled to the desired amplitude for each simulation.

157   Both functions yielded qualitatively similar results with one important exception:

158   nighttime cooling via a negative exponential produces a long, flat tail as nighttime

159   temperatures stabilize, exaggerating the change in activity duration for nighttime species

160   in response to temperature shifts (Figure 1). This characteristic is realistic however, as

161   nighttime cooling in most habitats is effectively modeled through exponential decline

162 toward an equilibrium temperature (Parton and Logan 1981), and a Parton-Logan

163 function was used for all simulations beyond initial comparison to a sine wave.

164 All simulations were repeated with species thermal optimums (the average of

165 thermal minimum and maximum temperatures) ranging from 10°C below the daily

166 minimum temperature to 10°C above the daily maximum temperature (Table 1). A

167 central set of parameters were chosen approximately in line with those observed in an

168 empirical dataset (see field methods below) to limit exploration of parameter space to one

169 factor at a time for clarity and understanding. These parameters were: a 10°C activity

170 breadth for each species, a 2°C diurnally symmetric increase in temperature, a pre-

171 warming (initial) daily temperature range from 10 °C to 40 °C, and a 12-hour day and 12-

172 hour night. These choices are not central to conclusions drawn from the models, but

173 alignment with the empirical dataset enhances comparisons between the two.

174 Table 1 – Summary of simulations performed

Property investigated	Temperature changes simulated	Parameter range 1	Parameter range 2	Figure
Sine wave vs. Parton-Logan	$\Delta T = 0°C$ to $\Delta T = +4°C$	$T_{opt} = 5°C$ $T_{opt} = 45°C$	NA	Figure 2
Diurnal asymmetry of warming	$\Delta T_{day} = +2°C$	$T_{opt} = 5°C$ $T_{opt} = 45°C$	$\Delta T_{night} = +2°C$ $\Delta T_{night} = +6°C$	Figure 3
Variance between days	$\Delta T = +2°C$	$T_{opt} = 5°C$ $T_{opt} = 45°C$	$SD_T = 0°C$ $SD_T = 12°C$	Figure 4
Activity breadth	$\Delta T = +2°C$	$T_{opt} = -5°C$ $T_{opt} = 60°C$	$\sigma_S = 0°C$ $\sigma_S = 25°C$	Figure 5
Daily temperature range	$\Delta T = +2°C$	$T_{opt} = 5°C$ $T_{opt} = 45°C$	$T_X-T_N = 0$ $T_X-T_N = 30$	Figure 6

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176   Table 1: A summary of all simulations reported. Each row in the table represents a set of

177   simulations across 2 changing parameters, species activity temperature and another

178   parameter of interest. This 2-dimensional parameter space was explored using a 400x400

179   matrix of equally spaced values across the ranges listed above. Symbols used in the table:

180   ΔT = the change in temperature from initial in °C, σ_S = breadth of species activity

181   temperature (unless otherwise specified, σ_S=10°C in all simulations), T_{opt} = the center of

182   a species activity range or optimal temperature, T_X-T_N = daily environmental temperature

183   range (where T_X is maximum daily temperature and T_N is minimum daily temperature),

184   SD_T = standard deviation of temperature at a given time resulting from day-to-day

185   temperature variation.

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187   The first set of parameters varied explored the effect of using either a sine

188   function or a Parton-Logan function. The next scenario explored differing degrees of

189   diurnal asymmetry of warming, ranging from even warming (+2°C day, +2°C night), to

190   highly skewed warming (+2°C day, +6°C night). Increased nighttime warming not only

191   modifies the minimum temperature reached, but also all temperatures between sunset and

192   the new nighttime minimum, such that the effect of diurnal asymmetry was dampened in

193   proportion with proximity to the temperature at sunset (Eq. 3).

194   Equation 3: dampening of diurnally asymmetric warming

195   For temperatures below T_S:

196
$$\Delta T_i \ = \ \Delta T_{night} \left(\frac{T_S - T_i}{T_S - T_N} \right)$$

197   Third, the impact of day-to-day variation in temperatures was explored, by adding

198   normally distributed noise to each daily temperature profile. This noise was added using

199   the function *rnorm* with a mean of 0 and a standard deviation reported as a proportion of

200   the daily temperature range (0-0.4). Next, I investigated whether species with broad

201   thermal ranges will better tolerate environmental changes. This was accomplished by

202   varying the breadth of temperatures available to species from 0°C to 25°C (near the

203   extent of the daily temperature range).

204   Finally, I investigated the importance of daily temperature range while holding

205   forager breadth fixed at 10°C. I simulated temperature curves ranging from 0 °C daily

206   temperature range (unchanging temperature) to 30°C daily temperature range.

207   Empirical dataset

208   *Study site*

209   I conducted field collections of ants in a small area (4.2 hectares) of mixed sagebrush

210   shrubs and coniferous forest in the Sierra Nevada mountain range (2000m, 39.435583°N,

211   120.264017° W). Ants within this habitat are ground and litter dwelling, and forage on

212   the ground, in the leaf litter, and amongst the local vegetation. The temperature on the

213   surface of the ground, where ants frequently forage, frequently exceeds species critical

214   thermal maximum temperatures, while nighttime temperatures are near species critical

215   thermal minimum temperatures (McMunn, personal observations). Dominant plants

216   include mountain sagebrush (*Artemisia tridentata ssp. vaseyana*), wyethia (*Wyethia*

217   *mollis*), Jeffrey pine (*Pinus Jefferyi*), and white fir (*Abies concolor*).

218   *Field Collections*

219   I collected ground-active ants and ground surface temperature measurements

220   using automated time-sorting pitfall traps (McMunn 2017). The traps captured ants active

221   on the surface of the ground and within the surrounding leaf litter. Each trap contains 24

222   collection vials, filled with 70% ethanol, that rotate on a circular rack, with each vial

223   being positioned under the funnel for 1 hour. I observed ants slipping quickly into the

224   funnel and dying within seconds of submergence in the ethanol.

225   From a grid of 600 potential sites across the habitat, I randomly selected 127 sites

226   for ant collection. I made collections between June 19 and October 14 2015, concentrated

227   in one or two week sampling bouts each month. Over the season, this resulted in 3048

228   hour-long samples of ant abundance (24 hrs x 127 sites = 3048 hourly samples). The

229   traps recorded temperature measurements every 5 minutes during collections using a K-

230   type thermocouple datalogger at a height of 1-3 mm above the surface of the leaf litter or

231   above the surface of the soil if no litter was present (McMunn 2017).

232   To install traps, I carefully removed leaf litter and dug a small hole approximately

233   20cm wide, 30cm long, and 20cm deep. I then buried the trap; replacing soil and then the

234   leaf litter, taking care to minimize the disturbance to the surrounding litter and soil. After

235   installation, the traps remained closed to ants for 24 hours to avoid a "digging-in" effect,

236   when ants are initially attracted the soil disturbance following pitfall trap installation

237   (Greenslade 1973). I separated ants from all other collected arthropods, identified each

238   individual to species, and after confirmation of species ID's by Phil Ward, deposited

239   vouchers at the Bohart Museum of Entomology (UC Davis).

240   *Empirical Activity Distributions*

241   I estimated the degree of overlap between observed activity temperatures for each

242   species and two scenarios 1) the set of all observed soil surface temperatures (from all

243   sites, over 41,000 measurements) and 2) a simulated warming scenario (+2° C for every

244   measure,e). Ant species thermal activity distributions were calculated using hourly

245   temperature averages that occurred during each collection; weighted for species

246   abundance in each sample. Empirical distribution overlap between ant species thermal

247   activity distributions and environmental temperatures were calculated as a proportion

248   using the R package *overlapping* version 1.5.0 (Pastore 2017). To determine the extent to

249   which simulated warming would affect ant species active at different temperatures, I

250   calculated empirical overlap of ant activity temperatures with 2 environmental

251   temperature distributions: 1) all observed surface temperatures (over 41,000

252   measurements) and 2) even heating (+2°C for each surface temperature observation). I

253   calculated total available activity time for each species in the 2 scenarios, observed and

254   warming, as the proportion overlap between each species with environmental

255   temperatures multiplied by number of minutes within a day. I then calculated the

256   difference between these foraging windows and performed a linear regression to describe

257   the relationship between median species activity temperature and the change in available

258   activity time per day in response to each warming scenario (effect of warming = overlap

259   warming – overlap observed).

260   **Results**

261   I found that species activity temperatures, and when in the day those temperatures occur,

262   are both important in determining the sign and magnitude of change in time available for

263   activity with warming and cooling. This effect is due to the relative concavity of daily

264   temperature curves (supplemental proof 1), which consistently have concave regions

265   around daily maxima, and convex regions around daily minima (Figure 1).

266   Warming expands activity time for cold active species

267   Species with activity temperatures that occur during the evening and morning, and

268   nocturnal species, are predicted to broaden their daily temporal range due to warming

269   (Figure 2, points 2). This broadened temporal range for species active during cooler times

270   following warming is at first counter-intuitive, but results from a shift in timing of these

271   colder temperatures toward relatively stable nocturnal temperature windows. This activity

272   expansion is reversed for (likely rare) nocturnal species with activity temperatures lower

273   than the observed daily minimum (Figure 2 – points 1). Species with optimal

274   temperatures that lie within the concave portion of the daily temperature profile (early

275   and late afternoon) are expected to have contracted daily activity windows following

276   warming (Figure 2 – points 3). Again, species with optimal activity temperatures already

277   beyond the observed daily maximum temperature will be able to take advantage of an

278   expanded daily activity window (Figure 2 – points 4). It is reasonable to assume that

279   activity ranges should more frequently lie within local daily temperature ranges during an

280   organisms season of activity.

281   <u>Gradual nighttime cooling creates asymmetry in magnitude</u>

282   Sine approximations of daily temperature are symmetric in their shape across their

283   midline and spend equally as little time at the daily minimum temperature as the daily

284   maximum temperature. This symmetry does not reflect the large amount of time spent

285   near nighttime lows in most terrestrial habitats as radiant cooling occurs. Exponential

286   nighttime temperature decay exacerbates differences in the expected effect for diurnal

287   and nocturnal species (figure 2 – comparing points 3 and 4 across A and B).

288   <u>Diurnally asymmetric warming</u>

289   Diurnal asymmetry of warming (more nighttime warming than daytime) increases the

290   relative magnitude of expansions and contractions in activity time available to species

291   active below the daily temperature midpoint. Due to this, asymmetry of warming further

292   exacerbates the divergence of results between diurnal species and nocturnal species with

293   warming (Figure 3 – darker colors on bottom right of right panel).

294   <u>Variable habitats</u>

295   Day-to-day temperature variation diminishes the magnitude of change in the time spent

296   within particular thermal windows with warming (Figure 4 - increasingly weak color

297   gradient on right side). As day-to-day variation in temperature increases, the frequency of

298   previously rare temperatures, those occurring during fast-changing times of day,

299   increases. Temperatures that occur during slow changing portions of the day, such as near

300   the nighttime minimum, become relatively rarer as day-to-day variation increases.

301   <u>Species with broad activity temperatures</u>

302   As species activity ranges become broader, the transition temperatures between activity

303   expansion and contraction following warming move toward the daily midpoint

304   temperature (25 °C) (Figure 5 - comparing points 3 and 4). If local species have very

305   narrow thermal activity ranges, then most cold tolerant species would experience very

306   weak expansion of activity windows and most heat tolerant species would experience

307   very weak contraction of activity windows with warming (Figure 5 – right panel, left

308   side). Conversely, if species activity ranges are very broad relative to the daily

309   temperature range, then only species near the daily midpoint temperature experience

310   changes in available activity time (Figure 5 – right panel, left side).

311   <u>Habitats with little diurnal change in temperature</u>

312   As local daily temperature range is reduced (Figure 6 – right panel, left side) and activity

313   breadth is held fixed, a smaller range of activity temperatures experience expansion and

314   contraction due to concavity of the daily temperature profile. These effects, due to

315   changes in concavity between different portions of the temperature profile, disappear

316   entirely if daily temperature range is less than species thermal breadth (Figure 6 – 10°C

317   thermal range).

318   <u>Application to observations of animal activity – ground foraging ants</u>

319   In a community of montane, ground-nesting ants, species active at cooler temperatures

320   experienced greater overlap with observed temperature following simulated

321   environmental warming, while species active at warmer temperatures experienced

322   activity time contraction. A linear model confirmed the negative relationship between

323   median activity temperature and change in overlap with environmental temperature

324   following warming ($p<0.003$, adjusted $R^2=0.41$, $t=-3.51$, 15 d.f.). Changes in the duration

325   of available activity time for each species ranged from approximately a 10-minute daily

326   expansion to a 20-minute daily contraction of temporal range. Over 4 months (the

327   duration of sampling in this community) 10 minutes per day accumulates to a 20-hour

328   gain in available time.

329   **Discussion**

330   The effect of warming on the availability of activity times within days is predicted to be

331   stronger in magnitude and positive for ectotherms that are active during the temperatures

332   that occur during the evenings, mornings, and much of the night (Figure 1 and 2). This

333   relatively larger magnitude shift for species active below the local median temperature is

334   enhanced due to the relative stability of nighttime temperatures during the cooling phase

335   (negative exponential cooling - Figure 2) and diurnally asymmetric warming (relatively

336   more warming occurring during the night - Figure 3). Conversely, animals with activity

337   windows that lie within the range of observed afternoon temperatures will find their daily

338   activity windows contracting with warming, as their preferred temperatures will occur

339   during faster changing times of the day. These results are both reversed if median activity

340   ranges lie outside observed local temperatures, a result may apply to local extremophiles

341   or for times of the year when environmental temperature is currently unfavorable for

342   local species.

343   Several aspects of local environment alter the magnitude of change in activity

344   window size, as well as the temperatures at which sign changes in this effect occur. For

345   an equal amount of warming, greater changes in activity time occur in more stable

346   environments (lower daily temperature range) (Figure 6). This could lead to greater

347   changes in available activity times in environments where high humidity or low angle

348   sunlight limit daily temperature range, such as coastal environments, polar regions, or the

349   tropics. Variation between days has the potential to weaken the magnitude of change in

350   available activity times (Figure 4).

351   Investigating a 2°C warming scenario using ant observational data, the effect of

352   morning activity expansion and afternoon activity contraction persisted, but at a lower

353   magnitude than in simulations (Figure 7). This incorporates 4 months of temperature

354   data, from mid-June to mid-October, and suggests that one very likely compensatory

355   mechanism could be seasonal shifts in phenology. Future research characterizing

356   seasonal phenological shifts among animals could investigate whether diurnal species

357   demonstrate larger shifts in calendar date than species active in morning, evening, or

358   night.

359   Quality of thermal refuge in this study was assumed to be perfect, and negative

360   consequences of temperature outside of the preferred range were not estimated. While

361   this assumption is perhaps reasonable for ground-nesting ants, many animals are

362   incapable of limiting exposure to such an extreme temperature. These negative effects of

363   exceeding critical thermal maximum temperature are thought to be of particular

364   importance, due to the steep decline in fitness once enzyme denaturation begins (Martin

365   and Huey 2008). Even slight exposure to increased daily maximum temperatures could

366   override the broadened activity time in the morning or evening for species with imperfect

367   thermal refuges. Small ectotherms, and insects in particular, are notoriously hard to find

368   if they do not return to a nest, and thus the quality of many ectotherms' thermal refuges

369   are not known. However, future research could compare the effect of warming on species

370   of nesting animals with varying degrees of insulation, such as ground-nesting, tree-

371   nesting, and litter-dwelling ants. Refuge quality could play an important role in

372   determining whether a morning-active species benefits from an expanded available time

373   or is harmed by exposure to now lethal afternoon temperature.

374   Earth's thermal habitats are highly structured by latitude. Day length, angle of the

375   sun, and the rate of seasonal change all shape expectations of available activity time for

376   animals. In temperate regions, summer active animals experience a relatively short night,

377   potentially diminishing the larger magnitude change in available activity time for

378   morning, evening, and night-active species. Future work investigating time available

379   within ranges of temperature could incorporate this interaction between latitude, season,

380   and day-length.

381   A framework that incorporates additional factors that shape how species interact

382   with temperature, beyond discrete availability of activity time, is necessary to accurately

383   predict fitness outcomes of climate change for individual species of ectotherms.

384   Ectotherm microhabitat choice, and time devoted toward thermoregulatory behaviors,

385   such as basking, can extend activity times at a cost of decreased efficiency in foraging,

386   hunting, mating, or any other behavior contributing to fitness. Additionally, fitness

387   outcomes of increased temperatures depend on interactions among local species. Diel

388   phenological mismatch could result in either enemy release or decreased resource

389   availability depending on thermal refuge qualities among participant species.

390   The effect of warming on ectotherms depends on when activity times of

391   ectotherms occur. This result is generalizable to many species that utilize high quality

392   thermal refuges to persist in variable environments. The framework suggested here,

393   estimating time elapsed within a range of temperature as a resource, should be included

394   when estimating fitness impacts of climate change on species that utilize thermal refuges.

395   **Acknowledgements**

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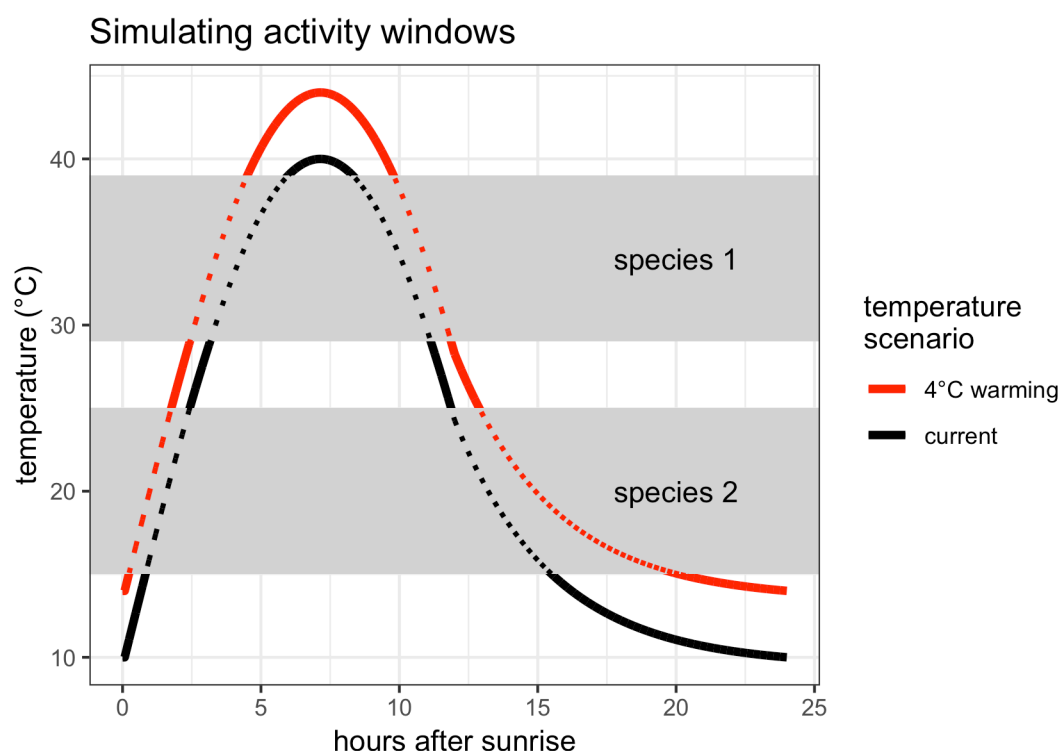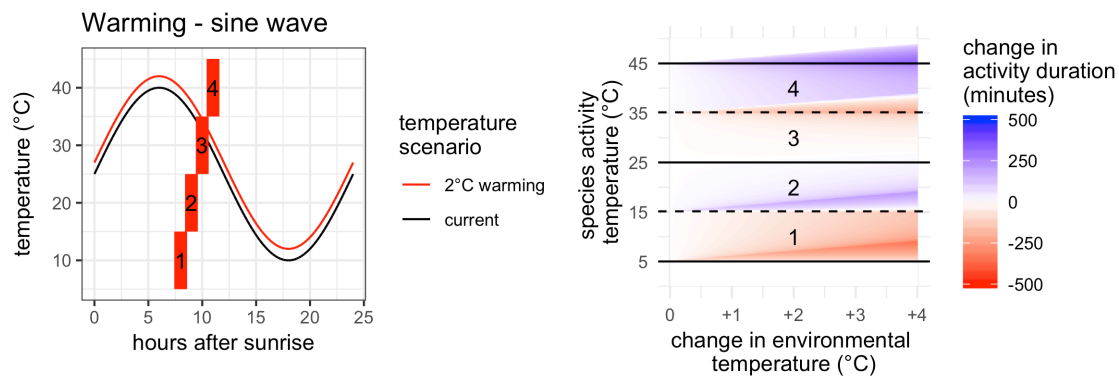
492 Figure 1

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494 Figure 1: A graphical depiction of the source of divergent outcomes between a cold

495 tolerant, morning and evening active, species and a heat tolerant afternoon active species

496 under a warming scenario. Simulated temperature over the course of one day (black),

497 with time measured in hours after sunrise (x-axis) and habitat temperature in °C (y-axis).

498 The daily temperature ranges from 10°C to 40°C and follows a Parton-Logan function. A

499 4°C even warming scenario (increase in 4°C at all times) is also shown (red). Two

500 potential species activity temperature windows are shown (grey), with species 1 active at

501 warm temperatures (29°C-39°C) and species 2 active at cooler temperatures (15°C-

502 25°C). During periods of time when the daily temperature in either scenario lies within

503 the range of temperatures accessible to a species, the lines appear dotted, with dots evenly

504 spaced along the x-axis. Here, species 1 (the warm active species) experiences a

505 contraction in daily activity time available, as its preferred temperatures lie on a steeper

506 portion of the temperature curve following warming. Conversely, following warming,

507 species 2 (the cold active species) experiences a dramatic expansion of daily activity time

508 available, as its activity temperature now lies on the long flat exponential decline of

509 nighttime cooling (hours after sunrise 12-24).

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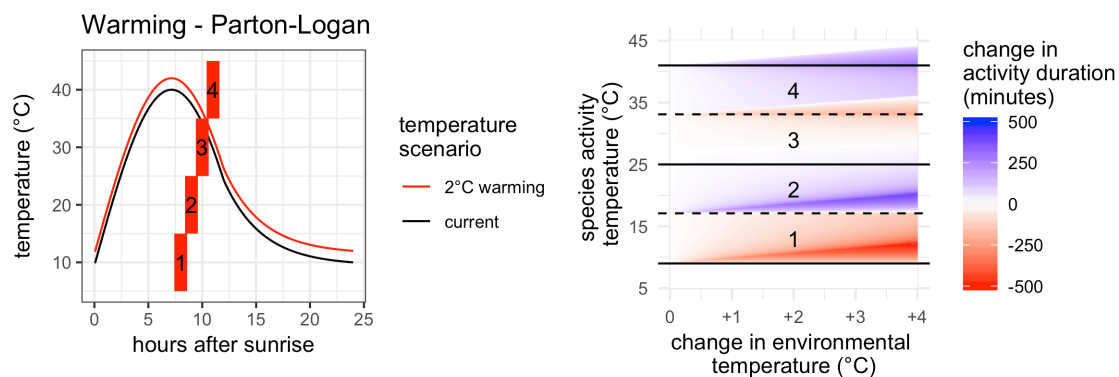524

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527 <u>Figure 2</u>

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530 B)

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532 Figure 2: Simulations of change in available activity time with warming A) a sine wave

533 daily temperature function and B) a Parton-Logan daily temperature function. Both

534 panels on the left illustrate two realizations from the simulations on the right and are

535 linked by numbers printed in each panel. On the left, colored bars represent hypothetical

536   species thermal activity ranges (each with a breadth of 10°C). The panels on the right

537   shows the change in available activity time (minutes/day) for a simulated species with

538   different activity temperatures (y-axis) under scenarios of temperature change ranging

539   from 0°C to 4°C warming. The results of 160,000 simulations are plotted with white

540   representing no change in activity duration, red as a decrease in time available, and blue

541   as an increase in time available between the initial daily temperature profile and the new

542   temperature profile. The magnitude of the change in activity time under any scenario is

543   larger for cooler activity temperatures when the Parton-Logan function is used. This

544   discrepancy is caused by the long, convex portion of the graph during the negative

545   exponential cooling phase (hours 12-24). The regions of the plot are qualitatively

546   describes

547   **Species 1:** Extremely cold tolerant species have median activity temperatures below

548   observed daily minimum temperatures and lose available activity time under warming.

549   **Species 2:** Cold tolerant species have median activity temperatures that lie between the

550   observed daily minimum temperature, and the daily midpoint (25°C), and thus occupy a

551   largely convex portion of the day. These species expand their activity time under

552   warming scenarios, as their thermal ranges move onto a flatter part of the temperature

553   curve (point 2).

554   **Species 3:** Heat tolerant species have median activity temperatures that lie between the

555   daily midpoint (25°C) observed daily maximum temperature, and thus cover a concave

556   portion of the graph. Under warming scenarios these species are moved onto a steeper

557   portion of the temperature curve, reducing time available for activity.

558   **Species 4:** Extremely heat tolerant species have median activity temperatures above

559   observed daily maximum temperatures, and benefit from warming (point 4).

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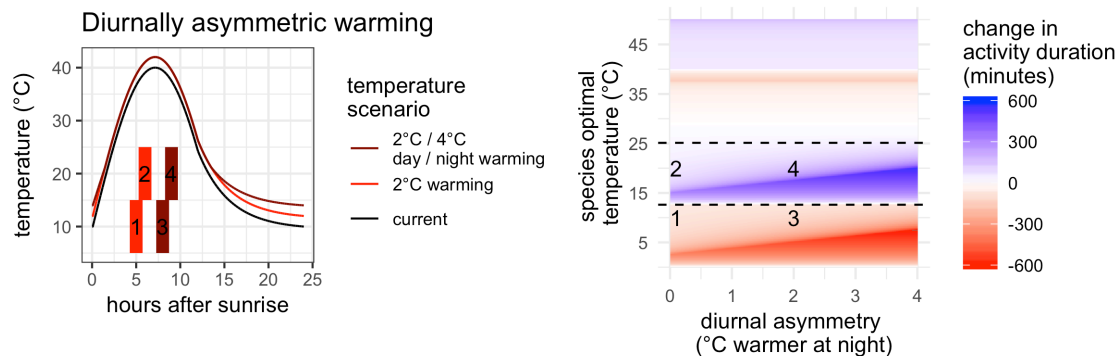
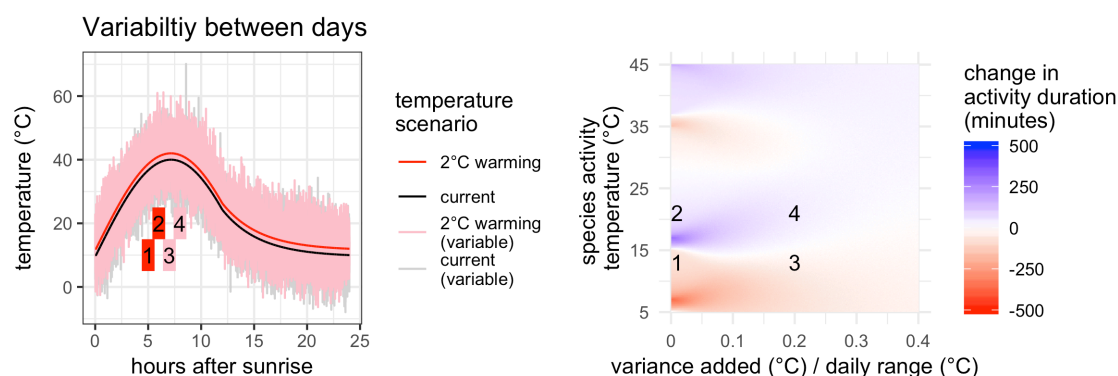578

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582   Figure 3

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584   Figure 3: Simulations of change in available activity time for scenarios ranging from

585   diurnally symmetric warming to highly asymmetric warming. The panel on the left

586   illustrates four realizations from the simulations on the right, linked with numbers printed

587   in the right panel. On the left, colored bars represent hypothetical species thermal activity

588   ranges (each with a breadth of 10°C). The color of the bar indicates which scenario is

589   being considered (red = diurnally symmetric warming, dark red = diurnally asymmetric

590   warming), matching the color of the two realized temperature scenarios (red = +2°C, dark

591   red = +2°C day/+4°C night). The panel on the right shows the change in available

592   activity time (minutes/day) for simulated species with different activity temperatures (y-

593   axis) under scenarios of temperature change ranging from no diurnal asymmetry to a 4°C

594   difference in warming between night and day (+2°C day and +6°C night). The results of

595   160,000 simulations are plotted with white representing no change in activity duration,

596   red as a decrease in time available, and blue as an increase in time available between the

597   initial daily temperature profile and the new temperature profile. Diurnal asymmetry of

598   warming increases the magnitude of changes in activity time for cold tolerant species

599   (darker colors left and bottom). Diurnal asymmetry also leads to a wider range of cold

600   tolerant species experiencing expanded activity windows (transition from blue to red at

601   higher activity temperature).

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621   <u>Figure 4</u>

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623   Figure 4: Simulations of change in available activity time for scenarios ranging from no

624   day-to-day variation in temperature, to day-to-day variation of 40% of the daily

625   temperature range (normally distributed with standard deviation = 12°C). The panel on

626   the left illustrates four realizations from the simulations on the right, and is linked by

627   numbers printed in the right panel. On the left, colored bars represent hypothetical

628   species thermal activity ranges (each with a breadth of 10°C). The color of the bar

629   indicates which scenario is being considered (red = warming, pink = warming with noise)

630   matching the color of the realized temperature scenarios (black = initial, red = 2°C

631   warming, pink = 2°C warming with random normal noise added, mean = 0, SD = 6°C).

632   The panel on the right shows the change in available activity time (minutes/day) for

633   simulated species with different activity temperatures (y-axis) under scenarios of

634   temperature change ranging from no variation to large variation. The results of 160,000

635   simulations are plotted with white representing no change in activity duration, red as a

636   decrease in time available, and blue as an increase in time available between the initial

637 daily temperature profile and the new temperature profile. Day-to-day variation

638 diminishes both the effect of activity expansion in morning/evening active species and

639 the effect of activity contraction in afternoon active species. As variation is added around

640 each point in time in the temperature curve, regions that are flat (e.g. nighttime) are

641 transformed into a distribution of temperatures, rather than a narrow line. Along the

642 length of the temperature curve, this has the effect of making rare temperatures more

643 common, and common temperatures rarer.

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660   Figure 5
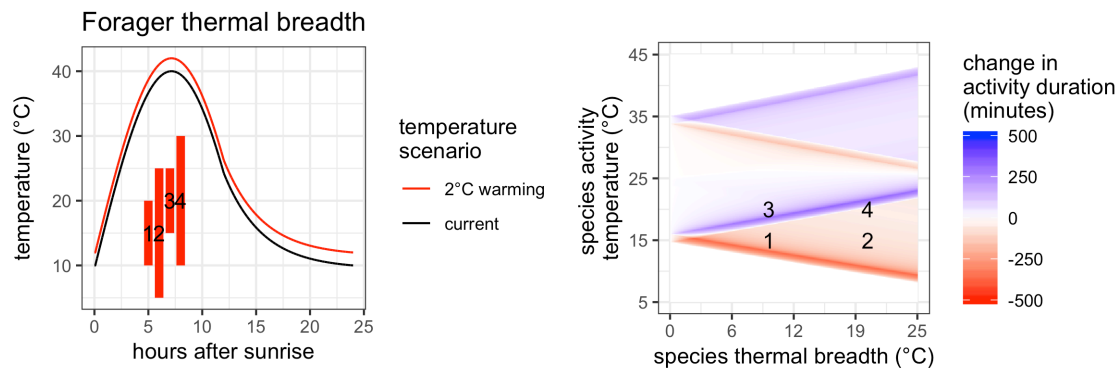
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662   Figure 5: Simulations of change in available activity time for scenarios ranging from

663   species with narrow thermal activity windows (0°C) to species with broad activity

664   windows (25°C). The panel on the left illustrates four realizations from the simulations

665   on the right, and is linked by numbers printed in the right panel. On the left, colored bars

666   represent hypothetical species thermal activity ranges (two with a breadth of 10°C, and

667   two with a breadth of 20°C). The panel on the right shows the change in available

668   activity time (minutes/day) for simulated species with different activity temperatures (y-

669   axis) under 2°C warming ranging from infinitely narrow ranges, to 25°C, nearly the

670   entire daily temperature range. The results of 160,000 simulations are plotted with white

671   representing no change in activity duration, red as a decrease in time available, and blue

672   as an increase in time available between the initial daily temperature profile and the new

673   temperature profile. If local species have broad thermal ranges relative to the
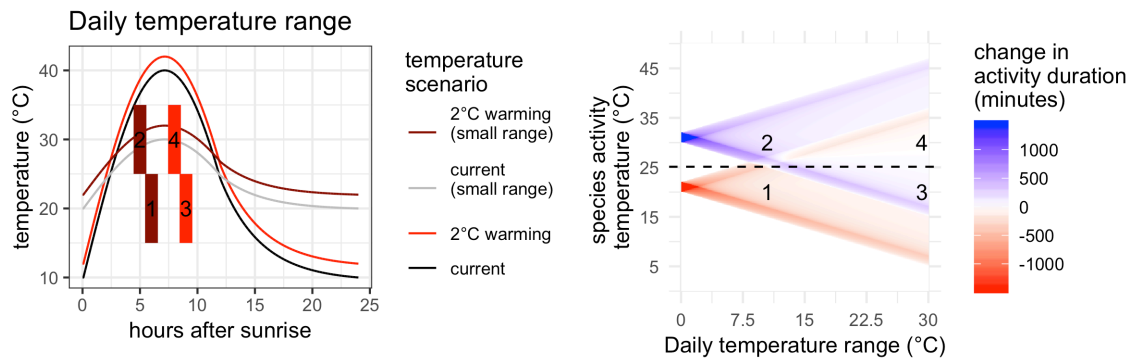
674   environmental temperature range, only a small subset, with their activity windows

675   centered at the daily temperature midpoint, experience expansion from warming due to

676   the long cold nights (comparing points 3 and 4).

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699   Figure 6

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701   Figure 6: Simulations of change in available activity time for scenarios ranging from

702   narrow daily environmental temperature range (unchanging temperature) to a daily

703   temperature range of 30°C. The panel on the left illustrates four realizations from the

704   simulations on the right, and is linked by numbers printed in the right panel. On the left,

705   colored bars represent hypothetical species thermal activity ranges (all with a breadth of

706   10°C). The color of the bar indicates which scenario is being considered (red = warming

707   in an environment with a 30°C temperature range, dark red = warming in an environment

708   that has 10°C daily temperature range) matching the color of the realized temperature

709   scenarios (black = initial, red = 2°C warming, dark red = 2°C warming, grey = initial low

710   amplitude temperature). The panel on the right shows the change in available activity

711   time (minutes/day) for simulated species with different activity temperatures (y-axis)
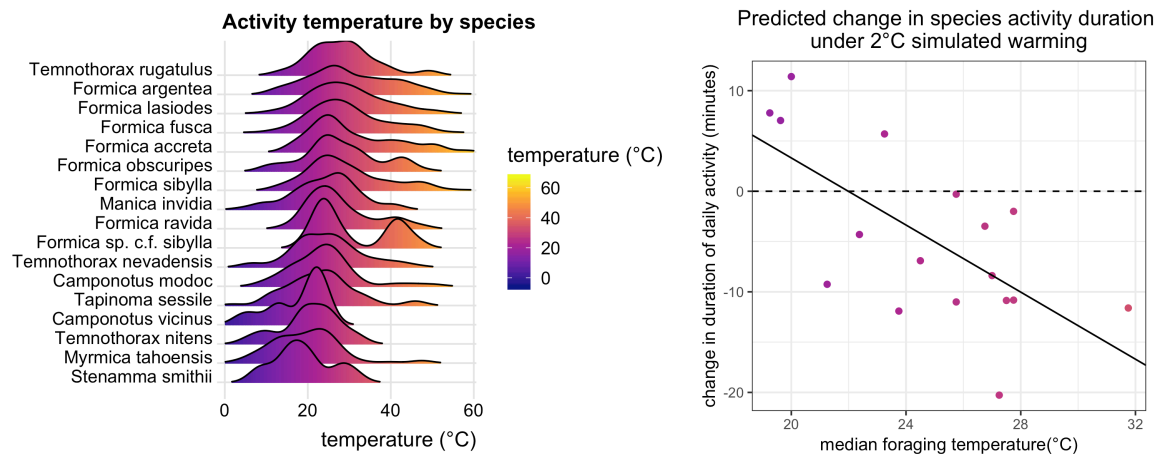
712   under 2°C warming ranging from infinitely narrow environmental temperatures, to 30°C

713   daily temperature range. The results of 160,000 simulations are plotted with white

714   representing no change in activity duration, red as a decrease in time available, and blue

715   as an increase in time available between the initial daily temperature profile and the new

716   temperature profile. The effect of concavity of local temperature profiles only occurs if

717   the daily temperature range exceeds local species activity breadth (everything right of

718   points 1 and 2). In increasingly broad daily temperature ranges, species farther from the

719   daily temperature midpoint (25 °C) experience enhancement of activity from increased

720   exposure to long cool nights (point 3).

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738   Figure 7

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740   Figure 7: Observed median ant activity temperatures and change in estimated activity

741   time per day with 2°C warming. Temperature measurements used in calculating

742   empirical overlap were taken every 5 minutes, and include both day-to-day variation and

743   site-to-site variation. Each dot is an ant species within the same community, collected at

744   least 10 times across a period of 4 months. Available activity time for each species was

745   calculated using an empirical estimation of overlap between environmental and species

746   level temperature observations. A linear regression (change in activity ~ median activity

747   temperature) is overlaid. Species with higher median activity temperatures experience a

748   contraction in the observed environmental temperatures that overlap with their activity

749   distributions. 4 species, all low activity temperatures, experience an increase in overlap of

750   their activity temperatures and their environment. The sign change for change in activity

751   time is modeled to occur at 22°C , approximately the temperature at which the daily

752   temperature begins a long decline toward a nighttime low (figure 1 – black line represents

753   Parton-Logan function fitted to these temperature observations). There are no species in

754   this community whose activity ranges are very cold or very hot.