

# Long-term exposure to higher temperature increases the thermal sensitivity of grazer metabolism and movement

**Running head:** Long-term warming on snail metabolism and behavior

## Authors

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CSC, AID, TH, RLK, and EJO all conceived the experiment, which was performed by CSC, TH, and RLK and was supervised by AID and EJO. CSC, TH, and RLK analysed data, and CSC wrote the manuscript. All author contributed to later versions of the manuscript.

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**Abstract**

1. Ecological studies of global warming impacts have many constraints. Organisms are often exposed to higher temperatures for short periods of time, probably underestimating their ability to acclimate or adapt relative to slower but real rates of warming. Many studies also focus on a limited number of traits and miss the multifaceted effects that warming may have on organisms, from physiology to behavior. Organisms exhibit different movement traits, some of which are primarily driven by metabolic processes and others by decision-making, which should influence the extent to which temperature affects them.
2. We collected snails from streams that have been differentially heated by geothermal activity for decades to determine how multi-generational exposure to different temperatures affected their metabolism and movement (long-term exposure). Additionally, we collected snails from a cold stream (5° C) and measured their metabolism and movement at higher temperatures (short-term exposure). We used respirometry to measure metabolic rates and automated *in situ* image-based tracking to quantify several movement traits in streams from 5 - 21° C.
3. Long-term exposure to higher temperatures resulted in a greater thermal sensitivity of metabolic rate compared to snails exposed for short durations, highlighting the need for caution when conducting acute temperature exposures in global warming research. Average speed, which is largely driven by metabolism, also increased more with temperature for long-term exposure compared to short-term exposure. Movement traits we interpret as more decision-based, such as time spent moving and trajectory shape, were less affected by temperature. Step length increased and step angle decreased at

higher temperatures for both long- and short-term exposure, resulting in overall straighter trajectories. The power-law exponent of the step length distributions and fractal dimension of trajectories were independent of temperature, however, suggesting that snails retained the same movement strategy.

4. The observed changes in snail movement at higher temperatures should lead to higher encounter rates and more efficient searching, providing a behavioral mechanism for stronger plant-herbivore interactions in warmer environments. Our research is among the first to show that temperature has contrasting effects on different movement traits, which may be determined by the metabolic contribution to those behaviors.

**Keywords:** acclimation, adaptation, locomotor performance, respiration, *Radix balthica*, climate change, oxygen consumption

## Introduction

How organisms cope with warming will play an important role in how ecological systems respond to climate change (Eliason *et al.* 2011; Hoffmann & Sgrò 2011; Bush *et al.* 2016). To avoid extinction, organisms that cannot track changing climates by shifting their distribution or phenology must adjust their thermal sensitivity to cope with higher temperatures (Hoffmann & Sgrò 2011; Bush *et al.* 2016). Species can alter their thermal sensitivity within the lifetime of an individual organism (thermal acclimation; Lagerspetz 2006) or across generations (genetic adaptation; Eliason *et al.* 2011; Donelson *et al.* 2012; Bush *et al.* 2016). The relative contributions of these short- and long-term responses to warming will depend on multiple factors, including the plasticity of an organism's thermal response, the ability of its population to evolve, and the rate of environmental warming (Visser 2008; Somero 2010; Rohr *et al.* 2018). However, experiments used to infer how organisms and species will respond to climate change are often undertaken over relatively short timescales compared to the generation time of the focal organism(s), and therefore often only represent within-generational responses (Somero 2010; Schulte, Healy & Fanguie 2011; Seebacher, White & Franklin 2015). These studies should underestimate the ability of populations to cope with global warming because they do not account for adaptation (Hoffmann & Sgrò 2011) and are often too short to capture the full scope of acclimation (Rohr *et al.* 2018).

Another major issue with studies of how organisms will respond to warming is that most existing work focuses on the thermal response of a single or small number of functional traits of organisms. Yet temperature is known to influence a large number of traits in different ways and across multiple levels of biological organization (Dell, Pawar & Savage 2011). For example, metabolic rate is predictably altered by temperature because it is primarily driven by

physiological processes that are subject to the laws of thermodynamics (Gillooly *et al.* 2001; Brown *et al.* 2004). Other traits, such as movement and feeding, involve processes that are less driven by physiology, such as decision-making, and so are likely to be less strongly influenced by temperature. Thus, understanding the extent to which a particular trait is driven by physiology could help us to predict the effects of warming on it.

The speed of an organism is partly determined by how fast muscle contractions occur (Wardle *et al.* 1989; Jayne & Lauder 1995), and the rates of the neurophysiological processes underpinning this should comprise a proportion of an organism's metabolic rate (Savage *et al.* 2007). Thus, temperature may strongly affect certain types of organismal movement *via* their links to metabolic rate (Bennett 1990; Blank *et al.* 2007; Angilletta *et al.* 2008; Marshall *et al.* 2011). Greater movement at higher temperatures leads to higher encounter rates with resources (food, mates, or shelter) and predators (Shipley *et al.* 1996; Bowman, Jaeger & Fahrig 2002; Visser & Kjørboe 2006). These traits in turn drive species interactions and population, community, and ecosystem organization. Thus, while evidence to date suggests the effects of warming on individual organisms are multifaceted, our understanding of the relationships between multiple traits is not well developed.

Not all behavioral traits are underpinned by metabolic processes to the same extent as speed, however, and so may not share the same temperature dependence. Movement traits such as time spent moving and trajectory shape are more likely to be driven by decision-making (Nolet & Mooij 2002; Forester *et al.* 2007; Nathan *et al.* 2008), which should be less thermally sensitive than physiological processes like metabolism. Nevertheless, temperature effects on these decision-based traits have been shown, albeit rarely. In the one study we know of, Angilletta *et al.* (2008) showed that ants have less tortuous (i.e. straighter) trajectories at higher

temperatures, thought to be due to the difficulty and physiological cost of turning at higher speeds (Clemente & Wilson 2015; Wynn *et al.* 2015). The tortuosity of an organism's trajectory through the landscape is also strongly determined by factors that are independent of temperature, such as resource distribution and habitat complexity (Viswanathan *et al.* 1996; Sims *et al.* 2008; Humphries *et al.* 2012). Given the importance of these movements for optimal foraging, with implications for consumer-resource interactions, fitness, and population persistence (Viswanathan *et al.* 1996; Sims *et al.* 2008; Humphries *et al.* 2012), more work is needed to determine if and how they are likely to change under future climates.

Here, we utilize a series of naturally heated streams to determine how temperature affects metabolic rate and movement in freshwater snail populations. These populations have been naturally exposed to different environmental temperatures over many generations and thus should illuminate the long-term effects of temperature on metabolic rate and movement. We measured the metabolic rate of snails at the same water temperature as their natal streams (long-term exposure) and of snails from a cold stream at water temperatures corresponding to warmer streams in the valley (short-term exposure). We also performed *in situ* behavioral experiments on snails within their natal streams and snails transplanted from a cold stream to warmer streams. We predicted that: (1) metabolic rates will increase with temperature at a faster rate after long-term compared to short-term exposure to each temperature; (2) average speed would increase with temperature because the neurophysiological processes determining it are strongly associated with metabolism and this increase would be greater in snails exposed to each temperature for long time periods; (3) decision-based movement traits such as time spent moving and trajectory shape would be less influenced by temperature, as they are less directly associated with thermally dependent metabolic processes.

## Materials and Methods

### *Study system*

Our study was performed in the Hengill Valley, a small catchment (2 km<sup>2</sup>) in southwest Iceland that comprises a series of spring-fed streams flowing into the river Hengladalsá (Figure S1). The streams span a temperature gradient of 5-25°C due to indirect geothermal heating of groundwater through bedrock or soils (Saemundsson 1995; O’Gorman *et al.* 2017). Chemical and physical properties vary slightly among streams but do not co-vary with temperature (Woodward *et al.* 2010). This system has been relatively stable over the past few centuries (Saemundsson 1995), with the streams isolated from one another and exhibiting their characteristic temperatures for at least the past 16 years of research in the area (Friberg *et al.* 2009; Woodward *et al.* 2010; O’Gorman *et al.* 2012; 2017). Thus, it provides an ideal natural experiment – using space-for-time-substitution – to explore how species respond to temperature change over multiple generations (Saemundsson 1995; O’Gorman *et al.* 2014).

*Radix balthica* is a freshwater snail commonly found throughout European ponds and streams (Pfenninger *et al.* 2011) that can exert strong top-down control on primary production (Wullschleger & Ward 1998; O’Gorman *et al.* 2012). Thus, temperature-dependent changes in the metabolism and movement of *R. balthica* are likely to alter the structure and function of stream ecosystems (Woodward *et al.* 2010; Nelson *et al.* 2017a). Furthermore, little genetic mixing of *R. balthica* populations occurs among Hengill streams (Johansson, Quintela & Laurila 2016) and so populations from each stream are probably exposed to these thermal habitats over many generations. Any changes in metabolic rates and movement should thus be

the result of long-term exposure to different environmental temperatures, mimicking the multi-generational effects of climate change on populations.

### *Metabolic measurements*

We carried out two sets of experiments to assess the effects of short-term (acute) and long-term (multi-generational) exposure to different temperatures on aerobic metabolism in *R. balthica*. The short-term exposure experiments consisted of snails collected from a single cold stream (5°C) and acutely exposed to temperatures of 5, 10, 15, and 20°C in the lab. The long-term exposure experiments consisted of snails collected from six streams and exposed, in the lab, to the mean temperatures of their natal streams in the valley:  $4.9 \pm 1.9$ ,  $9.3 \pm 2.2$ ,  $12.8 \pm 1.9$ ,  $13.9 \pm 1.9$ ,  $14.1 \pm 1.6$ , and  $19.4 \pm 1.0$  °C, representing the annual mean ( $\pm$  standard deviation, SD) stream temperatures in the year leading up to the experiments, measured every four hours (O’Gorman *et al.* 2017). For both experiments, adult snails measuring  $11.6 \pm 10.1$  mg dry weight (mean  $\pm$  SD) were hand-collected and immediately transported to the University of Iceland and placed in environmental chambers that were set to the same temperature as the stream from where each snail was collected. Each environmental chamber contained a 1.5 L aquarium filled with continually aerated water from the river Hengladalsá. Snails from each stream were kept together in the same aquarium for 24 hours prior to respiration experiments to clear their guts, since metabolic rates vary depending on the stage of digestion.

We measured the metabolic rate of 5-10 snails for each experimental temperature in both the short- and long-term exposure experiments. For each experimental trial, eight glass vials were filled with air-saturated water from the river Hengladalsá, which was filtered using a 0.45  $\mu$ m membrane, and maintained at the desired experimental temperature using a water bath. A



magnetic stir-bar maintained mixing of the water column in each glass vial. For the short-term exposure experiment, snails were transitioned from the temperature of the environmental chamber to that of the experimental trial over a period of 15 minutes. In the long-term exposure experiment, snails had a similar adjustment period, but the temperature of the environmental chamber and the experimental vials was consistent. After this adjustment period, snails from both experiments were placed individually in seven of the glass vials. The eighth vial comprised filtered river water only and thus served as a control to account for sensor drift and the respiration and/or photosynthesis of micro-organisms in the stream water. All eight vials were then sealed with an air-tight lid and fully immersed in the water bath. Oxygen consumption was measured during three periods of 1-2 minutes each (logging every second) using an oxygen microelectrode (MicroResp, Unisense, Denmark) fitted through a capillary in the lid of each vial. Oxygen concentrations were not allowed to drop below 70% of the starting value to avoid stressing the snails, measuring anaerobic metabolism, or quantifying non-linear respiration rates. Oxygen consumption rate of each snail was calculated as the slope of the linear regression through all of the data points and was corrected for vial volume and minimal background rates in the control vial. The body lengths of all snails were measured and converted to dry mass using published length-weight relationships from the Hengill streams (Hannesdóttir *et al.* 2013).

### *Behavioral experiments*

We developed portable tracking stations (Figure 1A) to record video sequences of trials and thus quantify the movement of individual snails, constrained within arenas, in seven streams using automated image-based tracking (Dell *et al.* 2014). Tracking stations were

constructed using an infrared (850 nm) light-emitting diode panel (Smart Vision Lights, Muskegon, MI, USA) that backlit the experimental arenas and produced an even and diffuse illuminated area of  $45.7 \times 45.7$  cm (Figure 1A). Backlighting created a high-contrast silhouette of each snail that allowed processing with automated tracking software (see below). A stainless-steel frame supported a GoPro Hero4+ Silver (GoPro, San Mateo, CA, U.S.A.) positioned 61 cm above the surface of the arena and faced straight down on to the light panel (Figure 1A). We replaced the factory-installed GoPro lens with a 4.2 mm wide angle flat lens fitted with an 850 nm pass filter (Rage Cams, Sparta, MI, USA). Experiments were undertaken from June 22<sup>nd</sup> to July 8<sup>th</sup>, 2016. The mean ( $\pm$  SD) of the stream temperatures during this time was  $5.5 \pm 0.1$ ,  $6.4 \pm 0.1$ ,  $11.7 \pm 0.2$ ,  $13.6 \pm 0.4$ ,  $14.3 \pm 0.2$ ,  $15.4 \pm 0.5$ , and  $20.5^\circ\text{C} \pm 0.1$ , which we measured every five minutes with Onset HOBO data loggers (Bourne, MA, USA) placed adjacent to each tracking station.

Adult snails measuring  $9.9 \pm 11.2$  mg dry weight (mean  $\pm$  SD) were used in the video-tracking experiments. For each trial in the short-term exposure experiment, 16 snails were collected from the coldest stream and transplanted to a tracking station in one of the other experimental streams within 15 minutes. For each trial in the long-term exposure experiment, 16 snails were collected from the stream within 30 m of where the tracking station was embedded. In both experiments, one snail was placed into each of 16 arenas (9 cm diameter plastic petri dishes), which were pre-glued to a transparent acrylic sheet as a base, and subsequently covered with a similar sheet to ensure snails stayed within their arenas (Figure 1A). This enabled us to simultaneously collect data from 16 snails, and we tracked up to 32 snails per stream (i.e., two tracking stations per stream) for both the short- and long-term exposure experiments. Tracking stations were submerged in the streams, so that the tops of the

petri dishes were 1-2 cm below the water surface. Installing stations directly into each stream ensured that snails experienced the same temperature and water chemistry of their home stream. Thus, while we did not include physical cues in the experiment, such as habitat or resources, the snails should have experienced the typical chemical cues present in the environment. This design allowed us to isolate the effects of temperature on movement without other potentially confounding factors. Two layers of light-colored canvas were tented over each station (Figure 1B), to minimize fluctuations in levels of ambient infrared light that would have impeded automated tracking. Video recording commenced after all snails were placed into the tracking stations and the canvas cover was positioned. Videos were recorded at a resolution of  $1,280 \times 1,080$  pixels and 0.5 frames per second (fps) onto microSD cards. Each trial ran for 2 hours, and all trials were undertaken during daylight hours between 09:00 and 18:00.

Videos of snails were analyzed using the open-source automated tracking software *Ctrax* (Branson *et al.* 2009; Caltech, Pasadena CA), which provided estimates of the *x-y* coordinates of the 16 snails in every frame of the videos (Figure 1C). Due to slight movements of the camera caused by wind, trajectories were smoothed with a moving average algorithm using the '*filter*' function in the '*stats*' package of R 3.3.2 (Team & Worldwide 2002), with the average calculated over the previous five frames. We compared these smoothed trajectories to the original videos to confirm that they accurately estimated the real trajectories taken by each snail.

### *Behavioral analysis*

Arena walls affect animal movements within bounded spaces, so we divided the arena into peripheral and central zones (Jeanson *et al.* 2003; Mancinelli 2010). All tracks within  $\sim 1$  body length (1 cm) of the wall were considered to be in the peripheral zone and all other tracks in the central zone (Figure 1C). We performed analysis on movements in the peripheral and central zones separately, as well as for all data combined.

Tracking results comprising  $x$ - $y$  coordinates of each snail were used to calculate seven properties describing different aspects of snail movement, including two locomotor behaviors (average speed and time spent moving) and four metrics that quantified trajectory shape (average step length, average step angle, power-law exponent of the frequency distribution of step lengths, and fractal dimension). For the locomotor behaviors, we considered snails to have moved if the distance values between frames was  $> 0.5$  mm, as smaller values may have been caused by camera movement. We calculated average speed as:

$$\frac{\sum [F(d)_{i+1} - d_i]}{N} \quad (1),$$

where  $d_i$  and  $d_{i+1}$  refer to the coordinates of the snail in the arena at times  $i$  and  $i + 1$ ,  $F$  is the frame rate (0.5 fps), and  $N$  is the total number of frames in which the snail was moving. We calculated the time spent moving as  $N \times F$ .

Trajectory traits included step lengths (i.e. the straight segments of a trajectory) and step angles (i.e. the angles between adjacent step lengths), which were calculated using the ‘*prepData*’ function in the ‘*moveHMM*’ package of R (Michelot, Langrock & Patterson 2016). Other trajectory traits included the power-law exponent of the frequency distribution of step lengths and the fractal dimension, which measure the tortuosity of a trajectory. Power-law exponents describe the pattern of motion exhibited by an organism; exponents  $> 3.0$  indicate trajectories that follow Brownian motion; exponents of  $1 - 3.0$  indicate Lévy motion;

exponents approaching 1 indicate ballistic motion (Viswanathan *et al.* 1996; James, Plank & Brown 2008; Zhao *et al.* 2015). Purely ballistic motion is empirically unattainable because  $\mu = 1$  is not a probability function, and so power-law exponents  $< 1.7$  indicate movement that is characteristic of ballistic motion (James, Plank & Brown 2008; Zhao *et al.* 2015). Fractal dimensions ( $D$ ) can vary between 1 – 2, with values of  $D$  from 1 – 1.2 associated with straight trajectories (ballistic motion), values from 1.2 – 1.6 associated with trajectories of intermediate tortuosity, and values  $> 1.6$  with highly tortuous trajectories (Brownian motion; Tremblay, Roberts & Costa 2007). We used maximum likelihood estimators to determine the power-law exponent ( $\mu$ ) of the frequency distribution of step lengths using the ‘*estimate\_pars*’ function in the ‘*poweRlaw*’ package of R (Gillespie 2016). We used the boxcount method to calculate the fractal dimension ( $D$ ) of each trajectory using the ‘*fd.estim.boxcount*’ function in the ‘*fractaldim*’ package of R (Sevcikova *et al.* 2014).

### *Statistical analyses*

We determined the body mass dependence of each response variable,  $R$  (metabolic rate, average speed, time spent moving, etc.), using the ‘*lm*’ function in the ‘*stats*’ package of R, according to the following model:

$$\ln R = \ln a_R + b_R \ln M + E_R \frac{T - T_0}{kTT_0} \quad (2),$$

where  $a_R$  is the intercept,  $b_R$  is the allometric exponent,  $M$  is the body mass of each snail (in mg),  $E_R$  is the activation energy (the amount of energy required to initiate the biochemical reactions in eV),  $T$  is environmental temperature (in Kelvin, K),  $T_0$  sets the intercept of the relationship at the median stream temperature (287.45 K), and  $k$  is the Boltzmann constant ( $8.618 \times 10^{-5}$  eV K<sup>-1</sup>) (Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981).

Each response variable was mass-corrected by dividing the trait value by  $M^{b_R}$  (Brown *et al.* 2004), to account for the measured effect of body mass on metabolism and movement (Table S1; Figures S2 & S3). The temperature dependence of each mass-normalized response variable ( $R_M$ ) was then determined using:

$$\ln R_M = \ln a_{R_M} + E_{R_M} \frac{T - T_0}{kTT_0} \quad (3).$$

To ensure that these responses were tested at temperatures in the rise part of the thermal performance curve (i.e., most thermal response curves are unimodal; Dell, Pawar & Savage 2011), we plotted the residuals *versus* the fitted values for each trait of the long-term exposure experiment. Concave down curvature in these plots would indicate that snails from the warmest streams were above their thermal optimum and thus not in the rise part of the curve, but no curvature was found (Figure S4 & S5).

## Results

Snail metabolic rate increased with stream temperature in the short-term exposure experiment ( $F_{1,39} = 102.8$ ,  $p < 0.001$ ,  $R^2 = 0.72$ ) with a slope of 0.737 eV and in the long-term exposure experiment ( $F_{1,19} = 67.34$ ,  $p < 0.001$ ,  $R^2 = 0.77$ ) with a slope of 1.186 eV (Table 1; Figure 2). The 95% confidence intervals (CI) of the slopes from these two experiments do not overlap (Figure 2), indicating that there was a significantly stronger temperature dependence of metabolic rate after long-term compared to short-term exposure to each temperature.

Movement was similarly affected by temperature in the central and peripheral zones for snails in the long-term exposure experiment, e.g., speed increased with temperature but time spent moving did not (Tables S2 & S3; Figure S6). The outer wall influenced trajectory shape (see supplementary discussion), however, so we focus only on movements in the central

zone below. The average speed of snails increased significantly with temperature in the short-term exposure experiment ( $F_{1, 106} = 22.08, p < 0.001, R^2 = 0.16$ ) with a slope of 0.463 eV and in the long-term exposure experiment ( $F_{1, 154} = 65.90, p < 0.001, R^2 = 0.30$ ) with a slope of 0.720 eV (Table 1; Figure 3A).

The average time that snails spent moving increased with temperature in short-term exposure experiment ( $F_{1, 107} = 10.54, p = 0.002, R^2 = 0.08$ ) with a slope of 0.403 eV, but was not affected by temperature in the long-term exposure experiment ( $F_{1, 154} = 0.56, p = 0.46$ ; Table 1; Figure 3B). Snail trajectories were straighter in warmer streams in both experiments. Specifically, average step length increased with stream temperature for the short-term exposure experiment ( $F_{1, 113} = 49.75, p < 0.001, R^2 = 0.30$ ) with a slope of 0.839 eV and for the long-term exposure experiment ( $F_{1, 154} = 91.77, p < 0.001, R^2 = 0.37$ ) with a slope of 0.694 eV (Table 1; Figure 3C). Average step angle decreased with temperature in the short-term exposure experiment ( $F_{1, 113} = 15.71, p < 0.001, R^2 = 0.11$ ) with a slope of -0.277 eV and in the long-term exposure experiment ( $F_{1, 154} = 14.5, p < 0.001, R^2 = 0.08$ ; Table 1; Figure 3D) with a slope of -0.231 eV (Table 1; Figure 3D). Nevertheless, the pattern of motion that the snails exhibited did not change with temperature, as trajectory shapes were ballistic in character across streams, with low power-law exponents in both the short-term ( $F_{1, 113} = 0.00, p = 0.994$ ) and long-term ( $F_{1, 154} = 0.76, p = 0.385$ ; Table 1; Figure 3E) experiments, and low fractal dimensions for the short-term ( $F_{1, 113} = 2.209, p = 0.14$ ) and long-term ( $F_{1, 154} = 2.618, p = 0.108$ ; Table 1; Figure 3F) experiments.

## Discussion

Our study shows that long-term exposure to warmer environments can lead to elevated metabolic rates, with consequences for how snails move around the landscape. The activation energies of metabolic rate and average speed, which is largely powered by physiological processes, were higher in the long-term than in the short-term exposure experiments, indicating that the snails have become adapted to these warmer environments. Time spent moving, a trait probably driven more by decision-making (Lima & Dill 1990), increased with temperature in the short-term exposure experiment, but was unaffected by temperature in the long-term exposure experiment. This difference in time spent moving between the short- and long-term exposure experiments may have been caused by snails being stressed from the sudden transplant from their cold natal stream to much warmer streams, leading to more time spent moving in search of an escape back to their natal stream temperature. Some traits associated with decision-making, such as step lengths and angles (Nolet & Mooij 2002; Forester *et al.* 2007), also changed with temperature in both experiments, giving snails straighter trajectories in warmer streams. However, increased step length and decreased step angle in warmer streams did not translate into altered power-law exponents or fractal dimensions, which determine the type of motion, i.e., ballistic, Lévy, or Brownian. These changes in behavior, or lack thereof, have important consequences when predicting ecological responses to global warming.

The thermal sensitivity of metabolic rate of snails in the long-term exposure experiment was very strong (1.19 eV; 95% CI: 0.95 – 1.42 eV) compared to predictive frameworks such as Metabolic Theory of Ecology (0.6 – 0.7 eV) (Gillooly *et al.* 2001). Indeed, this thermal sensitivity of metabolic rate is at the upper end of within-species estimates (0.2 – 1.2 eV) (Gillooly *et al.* 2001; Dell, Pawar & Savage 2011). Note that these differences would have been masked if we had simply studied metabolic rates after short-term exposure of cold-stream



snails to experimental temperatures (0.74 eV; 95% CI: 0.56 – 0.91 eV), as in most climate change research. Deviations from metabolic theory have been reported for intertidal snails that experience large temperature fluctuations (Marshall & McQuaid 2011), although the mechanism here is likely to be very different to the temperature insensitive metabolism found in such variable environments. The high activation energy for metabolic rate was likely due to a combination of acclimation and evolution, as snails were exposed to the temperatures we used in our experiments for at least their lifetime or, most likely, for many generations before them (Johansson, Quintela & Laurila 2016). Acclimation can shift the thermal optimum for metabolic rate closer to the acclimation temperature (Schulte, Healy & Fangué 2011; Schaum *et al.* 2017), while adaptation to stream temperature across generations is likely to magnify acclimation effects, as natural selection shapes populations to maximize performance (Hoffmann & Sgrò 2011; Bush *et al.* 2016; Schaum *et al.* 2017). This is likely to be problematic for studies that extrapolate the effects of acute temperature change on the metabolism of organisms to the chronic exposures that will occur due to climate change (Dillon, Wang & Huey 2010; Bush *et al.* 2016). This practice is still commonplace despite commentaries and evidence emphasizing the importance of considering time scales of temperature exposure (Hoffmann & Sgrò 2011; Schulte, Healy & Fangué 2011; Bush *et al.* 2016; Schaum *et al.* 2017).

Average speed, a behavior deeply rooted in metabolism, increased with temperature. The thermal sensitivity of speed for snails in our long-term exposure experiment (0.72 eV; 95% CI: 0.55 – 0.89 eV) was much greater than snails from the short-term exposure experiment (0.46 eV; 95% CI: 0.27 – 0.66 eV) and reported elsewhere (0.46 eV [95% CI: 0.43 - 0.49 eV]; Dell, Pawar & Savage 2014), and was likely driven by the increase in metabolic rate from long-

term exposure to stream temperatures. However, individuals must increase their energy intake to maintain these higher metabolic rates (Rall *et al.* 2010; Vucic-Pestic *et al.* 2011). Snail population densities are highest in the warmer streams in our study system (Nelson *et al.* 2017b; O’Gorman *et al.* 2017), indicating they are capable of meeting their elevated energetic demands at higher temperatures, despite a lower standing stock of algal resources (O’Gorman *et al.* 2017). This may occur if snails select more energetically profitable resources, such as more readily accessible diatom patches (Gordon *et al.* 2018), or if they move faster and farther to find and consume resources (Shipley *et al.* 1996; Visser & Kiørboe 2006). Faster snails that cover more ground in the warmer streams are likely to increase their encounters with, and thus consumption of, resource patches. Such behavioral changes may help to explain the stronger plant-herbivore interactions at higher temperatures shown for *R. balthica* in Iceland (O’Gorman *et al.* 2012; Schaum *et al.* 2017) as well as aquatic grazers in other systems (O’Connor 2009). Speed and consumption rates increase with temperature in many ectotherms (Grigaltchik, Ward & Seebacher 2012; Öhlund *et al.* 2015; Quenta Herrera *et al.* 2018), suggesting that as metabolic rate increases so does movement, resulting in higher foraging rates. If resource supply increases with temperature, as primary production does in Hengill (O’Gorman *et al.* 2012; Nelson *et al.* 2017b) and in many other systems (Sturm, Racine & Tape 2001; Nemani *et al.* 2003; Albon *et al.* 2017), the increased foraging rate arising from temperature-dependent movement can meet the increased energy demand that arises with higher temperatures.

Very little work has shown how trajectory shape changes with temperature (but see Angilletta *et al.* 2008). We showed that average step length increased and average step angle decreased with increasing temperature in both short- and long-term exposure experiments, resulting in straighter trajectories in warmer streams. Straighter trajectories in warmer

environments may be a trade-off between speed and maneuverability, as has been found in ants (Angilletta *et al.* 2008). Snails only have one locomotor appendage (i.e., their foot) and move *via* a series of contractile waves along it (Jones 1973). They can change their forward direction either by spinning, which they do by stopping, pivoting their body, and then continuing in the new direction, or by turning, which they do by reorienting their forward direction between contractile waves (Jones 1973; Tanaka *et al.* 2012). The snails in these experiments rarely spun in the center region of the arena, preferring instead to turn in wide arcs, and these arcs become wider at higher speeds. If snails are subject to the same trade-off between speed and maneuverability (Clemente & Wilson 2015; Wynn *et al.* 2015), which has been argued to favor faster speeds at higher temperatures in ants (Angilletta *et al.* 2008), then the thermal sensitivity of metabolic rate can indirectly affect trajectory shape by increasing speed and decreasing maneuverability.

Longer step lengths and lower step angles should in turn have led to a reduction in power-law exponents and fractal dimension values at higher temperatures, but there was no significant effect of temperature on these trajectory traits. Our results oppose those of Angilletta *et al.* (2008), who found decreasing fractal dimensions of ant trajectories with increasing temperature. This disparity may be due to the difference in the relative speed of ants and snails, with the former moving at maximum speeds that were more likely to hinder maneuverability and accentuate the reduction in tortuosity at higher temperatures (Angilletta *et al.* 2008). The snails in our experiment were moving at average speeds that may not have been relatively fast enough to alter tortuosity of their trajectories. Furthermore, the snails approximated ballistic motion at all temperatures, with most power-law exponents  $< 1.7$  and most fractal dimension values  $< 1.1$  (James, Plank & Brown 2008; Zhao *et al.* 2015). Ballistic

motion has been associated with low-resource environments where organisms may be searching, while more tortuous trajectories typical of Brownian or Lévy motion are indicative of foraging within resource patches (De Knecht *et al.* 2007; Humphries *et al.* 2012). Since we did not include habitat or resources in our experiment, it is likely that the snails were searching for an escape from the arenas. Thus, it makes sense that their motion was ballistic and that their trajectory shape was less constrained by temperature than traits like average speed. Future experiments should incorporate habitat and resource complexity to determine whether they interact with temperature to alter the movement of snails.

Our results demonstrate the necessity for an improved understanding of the hierarchy underpinning the relative contribution of physiology and cognition to patterns of animal movement. We suggest that speed is a more physiological-based trait, while time spent moving and trajectory shape are more decision-based traits. This is emphasized by the thermal sensitivity of metabolic rate and average speed and the ability of both traits to become elevated after long-term exposure to warmer environments, suggesting a strong physiological underpinning to both. Nevertheless, all movement likely incorporates elements of both physiology and decision-making. For example, many organisms increase their speed when threatened or chased by a predator or when moving through hostile habitats (Lindstrom 1990; Watkins 1996). Likewise, movement traits that require more decision-making can be affected by physiological constraints. For example, organisms spend more time moving and obtaining resources when nutritionally stressed (Weimerskirch *et al.* 1993; Werner & Anholt 1993). Some traits may even form links across this hierarchy, such as distance moved, which is the product of speed and time spent moving. Discerning this hierarchy of behavioral traits in

relation to physiology and cognition is a promising future avenue for understanding the mechanisms underpinning temperature effects on organismal movement.

As global warming intensifies, there is increasing urgency to understand and predict how species and their ecological interactions will respond. Here, we show that long-term exposure to different temperatures affected metabolic rate and movement of snails in ways that are likely to help them sustain larger populations at higher temperatures (Nelson *et al.* 2017b; O’Gorman *et al.* 2017). The thermal dependence of snail metabolic rates was steeper than expected from theory (Gillooly *et al.* 2001; Brown *et al.* 2004), increasing the capacity for speed and thus for foraging, mate-finding, migration, and dispersal. Additionally, while snails moved in straighter, longer paths in warmer streams, the overall shape of their trajectories did not change with temperature, as they always approximated ballistic motion in our experiment. Trajectory traits of snails responded in the same manner between long- and short-term exposure, suggesting these traits are not affected by the duration of exposure to higher temperatures, and supporting our idea that decision-based movement traits are less constrained by temperature. Our results are not only relevant to changes in temperature associated with global warming, but also to how temperature affects metabolic rate and movement across broad-scale latitudinal and altitudinal gradients.

Our study provides a link between the thermal dependence of metabolic rate and individual movement, but future experiments need to link additional levels of biological organization, from physiological processes and individual behaviors to species interactions and population persistence. Furthermore, testing how trajectory traits interact with both temperature and resource availability is required to determine whether organisms can maintain

optimal movement patterns with warming given changes in resource abundance and distribution.

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**Table 1. Linear regression results for the temperature dependence of metabolism and movement from the short- and long-term exposure experiments.** Response variables included metabolic rate, locomotor behaviors, and trajectory traits. The slope value is the activation energy ( $E_{R_u}$  in Equation 2) for each response variable.

Trait	Exposure	Value	Intercept			Value	Slope			
			95% CI	<i>t</i> value	<i>p</i> value		95% CI	<i>t</i> value	<i>p</i> value	
Metabolic rate	Short	-4.639	0.163	-56.182	< 0.001	0.737	0.176	8.206	< 0.001	
Metabolic rate	Long	-4.252	0.169	-49.230	< 0.001	1.186	0.229	10.140	< 0.001	
Average speed	Short	-0.152	0.127	-2.343	0.021	0.463	0.194	4.699	< 0.001	
Average speed	Long	-0.403	0.115	-6.814	< 0.001	0.720	0.174	8.118	< 0.001	
Time spent moving	Short	2.990	0.163	36.191	< 0.001	0.403	0.243	3.246	0.002	
Time spent moving	Long	2.225	0.155	28.020	< 0.001	-0.089	0.233	-0.750	0.455	
Average step length	Short	0.408	0.153	5.210	< 0.001	0.839	0.233	7.053	< 0.001	
Average step length	Long	0.191	0.094	4.003	< 0.001	0.694	0.139	9.682	< 0.001	
Average step angle	Short	-2.051	0.090	-44.540	< 0.001	-0.277	0.137	-3.963	< 0.001	
Average step angle	Long	-2.000	0.078	-50.285	< 0.001	-0.231	0.118	-3.869	< 0.001	
Power-law exponent	Short	0.490	0.043	22.439	< 0.001	-0.000	0.065	-0.007	0.994	
Power-law exponent	Long	0.519	0.122	8.331	< 0.001	-0.004	0.010	-0.870	0.385	
Fractal dimension	Short	0.090	0.006	25.885	< 0.001	0.008	0.010	1.486	0.140	
Fractal dimension	Long	0.103	0.008	27.899	< 0.001	0.009	0.012	1.599	0.112	

### Figure Legends

**Figure 1: Overview of tracking stations and example of a snail trajectory.** (A) Photo of a tracking station submerged 1-2 cm into a stream with an array of 16 arenas attached, each containing one snail. (B) Tracking stations deployed in a stream, with canvas covers to block direct sunlight. (C) Example of a snail's trajectory with the black segments corresponding to the central zone of the arena and grey segments corresponding to the peripheral zone.

**Figure 2: The temperature dependence of mass-corrected respiration rate.** The significant lines of best fit for both short- and long-term exposure to experimental temperatures are described in Table 1. The values for the mass correction (exponent  $b$  in the units) are the slopes described in Table S1.

**Figure 3: The effects of temperature on mass-corrected movement traits.** (A) average speed, (B) time spent moving, (C) average step length, (D) average step angle, (E) power-law exponent of the step length distribution, and (F) fractal dimension. Average speed and average step length increased with temperature, while average step angle decreased with temperature for both the short- and long-term exposure experiments. Time spent moving only increased with temperature for the short-term exposure experiment. The power-law exponent, and fractal dimension were unaffected by temperature. The significant lines of best fit are described in Table 1. The values for the mass correction (exponent  $b$  in the units) are the slopes described in Table S1.

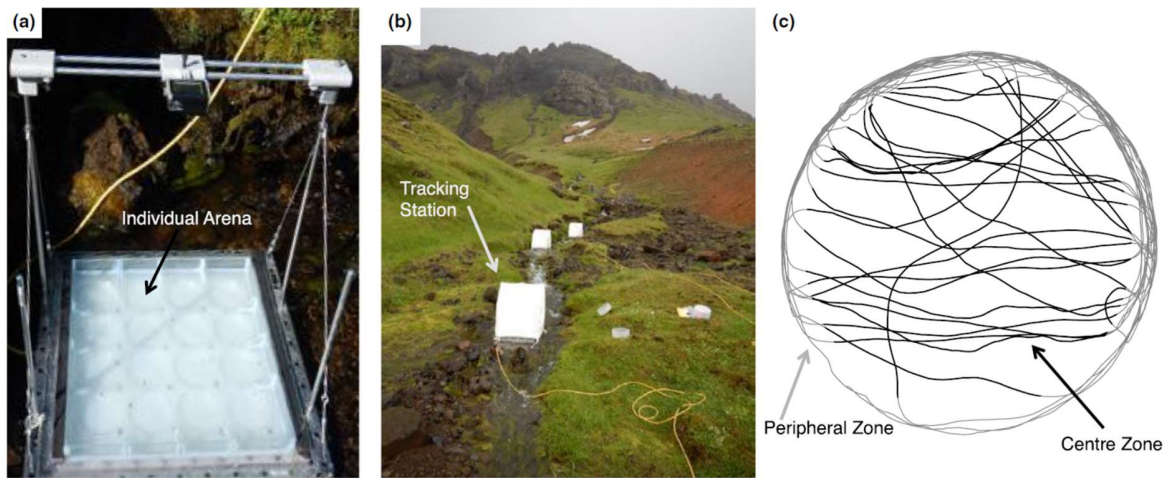
**Figure 1**

Figure 2

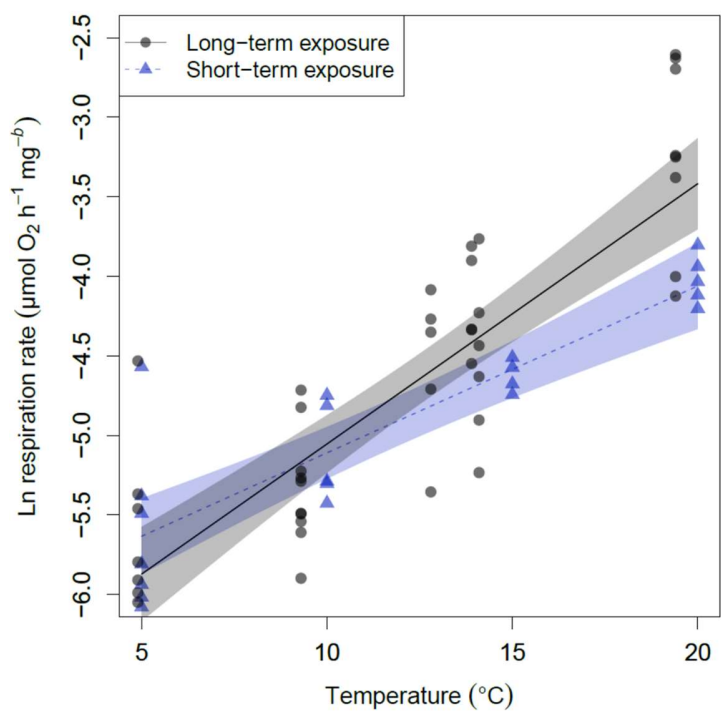


Figure 3

