PRIMARY RESEARCH PAPER

Heat waves trigger swift changes in the diet and life-history of a freshwater snail

Bruno M. Carreira · Pedro Segurado · Anssi Laurila · Rui Rebelo

Abstract Extreme climatic events, such as heat waves, may induce changes in nutrient acquisition by omnivorous ectotherms. Likely modulated by the intensity, frequency and duration of these events, dietary shifts during heat waves may threaten the stability of freshwaters. We investigated the effects of heat wave duration on diet assimilation and life-history traits of the freshwater gastropod *Radix balthica*. We compared the magnitude of the effects of a short (1 week) and a long heat wave (7 weeks) on the assimilation of animal- and plant-based diets, measuring performance in terms of growth rate and reproduction. We hypothesized that heat waves should increase the proportion of plant material assimilated on the mixed diet and change the performance of snails on the animal and plant-based diets. Both heat waves increased the assimilation of plant material on the mixed diet and growth rate, with minor negative effects on reproduction. However, responses were disproportional to heat wave duration, as the short heat wave elicited swift and relatively stronger responses. Our findings showcase the role of phenotypic plasticity in aiding ectotherms to cope with increased thermal stress and acclimate. Temporarily changing the strength of trophic interactions, heat waves may alter community dynamics in freshwater habitats.

Keywords Climate change · Diet selection · Extreme climatic event · *Radix balthica* · Stable isotopes

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Introduction

The climatic changes projected under the most recent scenarios demand a better understanding of the ecological responses to global warming and extreme climatic events, especially in organisms such as ectotherms (Stoks et al., 2017). Temperature governs

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many physiological and ecological processes (Gillooly et al., 2001; Angilletta, 2009), and there is a growing interest for its effects on nutrient acquisition. Changes in nutrient acquisition mediated by temperature may affect consumer interactions with both resources and other consumers, which may threaten the stability of ecosystems (Boukal et al., 2019). Freshwater communities are disproportionally at risk (Parmesan, 2006; Woodward et al., 2010), as they are mainly composed of ectotherms with a temperature-dependent metabolism (Parmesan & Yohe, 2003; Clusella-Trullas et al., 2011; Paaijmans et al., 2013). Studying temperature and nutrient interactions across organization levels will be a critical step to develop realistic predictions of the ecological responses to global changes (Cross et al., 2015; Kutz et al., 2019).

Two hypotheses link temperature, food quality (i.e. C:N:P nutrient ratios) and diet selection. The Growth Rate Hypothesis (Elser et al., 1996) predicts that higher temperatures increase phosphorous and nitrogen demand, needed to sustain increased growth (Persson et al., 2011) and protein turnover rates (Lemoine et al., 2013). In contrast, the Respiration Hypothesis predicts that higher temperatures increase the relative demand for carbon over nitrogen or phosphorus (Cross et al., 2015), as the stronger effect of temperature on catabolism than on anabolism promotes a greater increase in respiration than in growth (Karl & Fischer, 2008; Forster et al., 2011). Consequently, under higher temperatures ectotherms require extra carbon in their diet (Acheampong et al., 2014) and may select for increasingly carbon-rich foods (Anderson et al., 2017), which should better compensate for the energetic deficit induced by warming (Kingsolver & Woods, 1997; Lemoine & Burkepile, 2012). Additionally, temperature may influence nutrient acquisition through different scaling effects on other metabolic processes. For instance, higher temperatures promote a greater increase in feeding and gut passage rates than in assimilation rates (Seifert et al., 2014), and this imbalance may increase the assimilation efficiency of carbohydrates (Croll & Watts, 2004).

Phenotypic plasticity is a ubiquitous response to different environmental conditions (Ghalambor et al., 2007), and dietary shifts may constitute an important aspect of the plastic responses to different temperatures. Supporting increased herbivory at higher temperatures, dietary shifts have been documented

experimentally in several arthropod taxa—copepods (Boersma et al., 2016; Malzahn et al., 2016), decapods (Carreira et al., 2017) and insects (Lee & Roh, 2010; Lee et al., 2015; Rho & Lee, 2017), in anuran larvae (Carreira et al., 2016) and in fish (Emde et al., 2016; Vejříková et al., 2016). These findings agree with the higher prevalence of herbivory in fish communities of warmer waters (Floeter et al., 2005; Jeppesen et al., 2010; González-Bergonzoni et al., 2012) and with the seasonal increases in fish herbivory during summer (Guinan et al., 2015; González-Bergonzoni et al., 2016). However, other studies have reported opposite effects showing a greater protein intake at higher temperatures (Lemoine et al., 2013; Schmitz et al., 2016), context-dependent temperature effects on nutritional requirements (Anderson et al., 2017), and no temperature effects on feeding preferences (Miller et al., 2009; Zhang et al., 2018a). As such, the potential for temperature to change nutritional requirements and for warming to increase herbivory is still under debate (Anderson et al., 2017; Carreira, 2017). More studies are required to understand how temperature mediates changes in nutrient acquisition in ectotherms, and the extent to which this link may impact ecological communities (Rosenblatt & Schmitz, 2016; Rho & Lee, 2017).

Heat waves constitute large, infrequent and stochastic perturbations that can act as a major selective force, shaping population dynamics and species interactions (Parmesan, 2006; Walther, 2010; Palmer et al., 2017). These extreme climatic events are considered to occur when the daily maximum temperature exceeds the average maximum temperature by 5 °C, for more than five consecutive days, the reference period being 1961–1990 (Frich et al., 2002). The severity of heat waves has increased globally since 1950 (Perkins et al., 2012) and climatic models project an increase in their frequency (up to 31%) and average duration (up to 35%), as well as greater positive anomalies (over 3 °C)—especially in the areas currently most susceptible, like the Mediterranean basin (Easterling, 2000; Meehl & Tebaldi, 2004). Furthermore, there is a dramatic increase in the likelihood of statistically unlikely extreme events (Dasari et al., 2014), such as the one that afflicted Europe in 2003 (Christidis et al., 2015). Studies investigating heat wave effects have focused on changes in their frequency, but especially in their intensity (Sentis et al., 2013, 2017; Ma et al., 2015),

showing strong effects on the survival (Garrabou et al., 2009) and internal resource budgets of ectotherms. More frequent and intense heat waves often affect fitness and life-history traits, generally weakening immune defences, but with less clear effects on morphology, growth, development, body size and fecundity (Roth et al., 2010; Vinagre et al., 2012; Sentis et al., 2013, 2017; Chiu et al., 2014; Dittmar et al., 2014; Fischer et al., 2014; Dinh et al., 2016; Arambourou et al., 2017; Leicht et al., 2017; Salo et al., 2017, 2018).

Although the impact of changes in heat wave duration is far less well known, a study suggested that long heat waves may expose cryptic or antagonistic effects on ectotherms, as they fail to maintain performance over prolonged periods (Leicht et al., 2013). Recent work showed omnivorous ectotherms to increase the assimilation of plant diets during heat waves (Carreira et al., 2016, 2017), suggesting that these organisms optimized energy intake at higher temperatures by avoiding protein-rich diets. In natural systems, dietary shifts in response to heat waves may prove disruptive, temporarily changing the strength of trophic interactions and even the predominant impacts of invasive alien species (Carreira et al., 2017). The severity of heat wave effects on organisms and communities depends on their intensity, frequency and duration (Mironidis & Savopoulou-Soultani, 2010; Dowd et al., 2015). Likewise, these properties may also dictate the magnitude of the dietary shifts observed during heat waves and, in turn, the magnitude of their impacts on species functional roles and interactions. Among the macroinvertebrates with the highest biomass, gastropod pulmonates can reach high abundances and often play a key role in benthic communities (Fink & von Elert, 2006). Typically considered as herbivores feeding on bulk periphyton, these organisms may also feed on detritus and microbes (Barnese et al., 1990), and dietary shifts during heat waves may seriously impact gastropod-mediated transfer of energy to higher trophic levels in freshwater food webs.

Here, we studied the magnitude of heat wave effects on dietary choices and fitness-related traits of *Radix balthica* (Linnaeus, 1758), which regularly experiences heat waves in the Iberian Peninsula. We aimed to investigate both the effects of currently commonly occurring short heat waves, as well as the effects of uncommonly long heat waves, expected to become more frequent in the future (Meehl & Tebaldi, 2004; Diffenbaugh & Field, 2013). For this, snails were fed animal, plant or mixed diets and exposed to simulated heat waves for a short duration (1 week) or a long duration (7 weeks). Performance was measured in terms of growth rate and reproduction, and the proportion of animal and plant material assimilated by snails on the mixed diet was estimated using stable isotope mixing models. We predicted that heat wave effects should (1) increase the assimilation of plant material by snails on the mixed diet; (2) change the relative performance of snails on the animal diets (decrease) and plant diets (increase); and (3) be proportional to heat wave duration.

Methods

Heat wave characterization in the study area

Following global trends, the Iberian Peninsula (Western Europe) experienced an increase in mean temperature during the latter half of twentieth century, especially marked in early summer (Dasari et al., 2014). During the twenty-first century, the mean annual temperature in this climate change hotspot is expected to increase up to 6 °C (Giorgi, 2006; Jerez et al., 2013). In the southwest of Portugal, heat waves occur frequently during spring, when the larval and adult stages of many ectotherm species complete their life cycle in Mediterranean temporary ponds, before pond drying in the summer. Using a 10-year data set of air temperatures recorded during the period of 2002–2012, we characterized the most common spring heat waves occurring in southwestern Portugal. Typically, this region is afflicted by a heat wave in the end of April which lasts on average 7.8 ± 1.3 days and is often followed by another heat wave in mid-May lasting on average 7.5 ± 1.3 days (B. M. Carreira, unpubl. data 2002–2012). A 5-year survey carried out in 42 temporary ponds located in southwestern Portugal during April and May revealed that at this time water temperatures ranged from 17 to 25 °C, with an average temperature of 20 °C (R. Rebelo, unpubl. data 2010–2014).

Study species

The common pond snail, *R. balthica,* is a pulmonate species widespread across freshwaters in Europe and Asia (Seddon et al., 2014) and common in the Iberian Peninsula. With no particular demands regarding substrate or water quality, this species is commonly found in a variety of lentic habitats, such as the littoral zone of lowland lakes and ponds, oxbows, irrigation channels and fountains, but also in slow flowing rivers and streams (Pfenninger et al., 2011). Adults have a light to dark brown egg-shaped shell, typically with a length of 11–22 mm and 4–5 whorls that quickly increase in size (Pfenninger et al., 2011). Like many other pulmonate species, *R. balthica* is thought to have a mixed mating system (Pollak, 1987), which includes hermaphroditism, sperm storage (< 6 months) and multiple paternity. Nevertheless, while all pulmonates are capable of selfing, they prefer to mate as a male with another snail (Dillon, 2004). Gastropods of the *Radix* genus are typically considered herbivores, feeding on the bulk periphyton community. However, this species may feed on detritus, periphyton, diatoms and filamentous algae (Gordon et al., 2018) and is likely capable of foraging selectively for high-quality food particles (Fink & von Elert, 2006). The preferred thermal range for northern European populations of *R. balthica* is 16–20 °C, and they fail to reproduce at 24 °C (Johansson et al., 2016; Johansson & Laurila, 2017).

Experimental setup and procedures

Young adult individuals of *R. balthica* (10.5 ± 1.4 mm; N = 200) were collected in an artificial pond in the southwestern Portugal (38°47′30.6″N, 9°25′9.0″W) on 18 April 2014. The snails were brought to the facilities at the University of Lisbon and kept in an experimental room at 20 °C in 15L aquaria (ca. 25 snails per aquarium) under 12L:12D photoperiod. To ensure standardized isotopic signatures, snails were maintained in these conditions for a month, while being fed ad libitum commercial fish food (Pond Sticks, ©Tetra), every 2 days along with water change.

At the start of the experiment, snails were blotted dry in paper towel, weighed to nearest 0.1 mg, and photographed for determination of initial body size (using ImageJ software). Snails were then transferred

individually to 80 mL mesh-covered cups and placed in water baths. We followed a fully factorial experimental design with diet (three levels) and temperature (three levels) as factors and assigned 18 randomly selected snails to each treatment combination. While subject to the experimental treatments, snails produced egg clutches that were removed along with feeding and water renewal every 2 days. The position of the snails in the water baths within a given treatment was randomized after each water change and feeding, and the number of eggs per clutch was recorded. These eggs may have resulted from cross-fertilization in nature or in the lab during the acclimation period, or from selfing. Water bath temperatures were checked daily and adjusted when necessary. The experiment ended after 49 days, when snails were blotted dry in paper towel, weighed, photographed and euthanized by rapid freezing at − 18 °C.

The snails were fed one of three experimental diets offered ad libitum: animal diet (A)—defrosted Chironomidae larvae; plant diet (P)—defrosted spinach leaves; mixed diet (M)—both food items in diets A and P offered ad libitum in similar proportions of fresh weight. These food items were obtained commercially and selected based on previous experimental studies on *R. balthica* (Johansson et al., 2016). The food items complied with the basic assumptions that the animal diet was protein-rich and the plant diet protein-poor, and that both food items had distinct isotopic signatures and C:N ratios (Table 1).

Snails experienced one of three temperature treatments (Fig. 1): no heat wave (NHW)—constant temperature of 20 °C for 7 weeks; short heat wave (SHW)—constant temperature of 20 °C for 6 weeks, followed by 1 week at 25 °C; long heat wave (LHW)—constant temperature of 25 °C for 7 weeks. In all treatments, snails entered the experimental baths at 20 °C, which were gradually raised to 25 °C in the heat wave treatments, approximately at the rate of 1 °C per hour. The range of temperatures experienced

Table 1 Isotopic signature and elemental ratio of the experimental diets (average ± standard deviation)

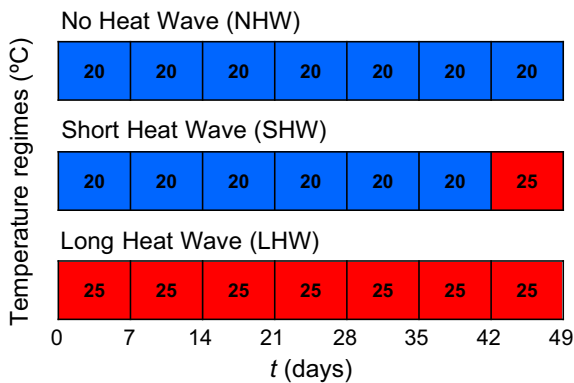|	Animal diet	Plant diet
δ^{13}C	− 24.61 ± 0.13	− 27.79 ± 0.12
δ^{15}N	5.09 ± 0.92	0.42 ± 1.01
C:N	3.79 ± 0.05	6.55 ± 0.71

Fig. 1 Temperature variation over time in the experimental treatments

by the snails in the experimental treatments was selected to match the water temperatures recorded in temporary ponds during spring. The duration of the short heat wave aimed to simulate current spring heat waves in the southwest of Portugal (ca. 1 week). Like in Roth et al. (2010), the duration of the long heat wave aimed to simulate unusually long heat waves, such as the one that afflicted Europe in 2003 for nearly 50 days (Schär et al., 2004), which are expected to become more frequent in the future (Meehl & Tebaldi, 2004; Diffenbaugh & Field, 2013).

Stable isotope analysis

A subsample of 9 snails per treatment was randomly selected for stable isotope analysis. After shell removal, the muscle tissue of each snail was dried at 60 °C for 24 h and ground to a fine powder with mortar and pestle. The samples were cleansed of storage lipids with chloroform–methanol (2:1; Dobush et al., 1985), and then re-dried at 60 °C for 24 h. Stable isotope ratios ($^{13}C/^{12}C$; $^{15}N/^{14}N$) and elemental analyses (C:N) were determined by continuous flow isotope mass spectrometry (CF-IRMS) (Preston & Owens, 1983), on a Hydra 20-22 (Sercon, UK) stable isotope ratio mass spectrometer, coupled to a EuroEA (EuroVector, Italy) elemental analyser for online sample preparation by Dumas combustion. The standards used were IAEA-CH6 and IAEA-CH7 for carbon isotope ratio, and IAEA-N1 and USGS-35 for nitrogen isotope ratio; $\delta^{13}C$ results were referred to PeeDee Belemnite (PDB) and $\delta^{15}N$ to Air. Precision of the isotope ratio analysis was ≤ 0.2‰ (6 to 9 replicates of laboratory standards in every batch).

Statistical analyses

Time-integrated estimates of the dietary choices of the snails maintained on the mixed diet were obtained with stable isotope mixing models. Using the Stable Isotope Analysis in R package (SIAR; Parnell et al., 2013), we fit a Bayesian model to the proportions of animal and plant material contributing to the isotopic signature of the snails on the mixed diet. The resulting probability distribution functions (10.000 iterations) for the proportions of the two sources assimilated by these consumers incorporated variability in the sources, trophic enrichment factors and elemental composition (Parnell et al., 2010). Following standard procedures, we specified the isotopic signatures and C:N ratios of the food items, building a model for each temperature treatment. We accounted for the variability in the trophic enrichment factors across sources by using the isotopic signatures of the snails fed on the single diets (animal or plant) at each temperature. The food items differed considerably in their C:N ratio and more than 2‰ in the isotopic signature of both isotopes (Table 1). Based on the data obtained by Thomas & Crowther (2015), we estimated the half-life for ^{13}C and ^{15}N turnover rates of the snails on the mixed diet (body weight: 167.6 ± 48.9 mg) as ca. 13 days.

Treatment effects on snail growth rate, calculated as ln of daily weight increase (mg), were tested with a general linear model in the software STATISTICA 12.6.255.0 (StatSoft 2012). Treatment effects on the total number of oviposited eggs were tested with a generalized linear model, specifying a negative binomial distribution with a log link function in the software SPSS 24 (IBM). Initial shell length (10.5 ± 1.4 mm; defined as the distance between the apex and the edge of the outer shell lip) was included as a covariate in both models. Post hoc pairwise comparisons were corrected for multiple comparisons with Bonferroni test.

Results

Regardless of the temperature treatment, plant material contributed two times more to the isotopic signature of *R. balthica* than animal material—the overall median proportion of plant material assimilated by snails on the mixed diet averaged 0.69. The

median proportion of plant material assimilated increased from 0.59 in NHW (Bayesian credible interval (BCI) = 0.34–0.81) to 0.70 in SHW (BCI = 0.52–0.85) and to 0.78 in LHW (BCI = 0.63–0.89) (Fig. 2a). Relative to NHW, the median proportion of plant material assimilated by snails on the mixed diet increased by 0.11 at the end of SHW and by 0.19 at the end of LHW. These effects were non-linear and, relative to heat wave duration, the snails' response in SHW was four times greater than in LHW. In other terms, the increment in the proportion of plant material assimilated by snails at the end of SHW corresponded to 58% of that of snails at the end of LHW.

The growth rates of snails on the plant and mixed diets were similar, and two times greater than on the animal diet (Table 2; Fig. 2b). The growth rate in LHW was two times greater than in NHW ($P < 0.001$) and 24% greater than in SHW ($P < 0.001$), while the growth rates in NHW and SHW were not significantly different (Table 2; Fig. 2b). Effects on the growth rate of *R. balthica* were non-linear and, relative to heat wave duration, the response to SHW was four times greater than to LHW. Overall, the increase in snail growth rate triggered by the one-week heat wave (SHW) corresponded to 59% of that triggered by the seven-week heat wave (LHW). This strong disproportion in the snails' response to heat wave effects in SHW and LHW was also verified in the snails on the mixed diet and its magnitude was comparable (61%). We found no significant effects of diet × temperature

interactions on snail growth rate (Table 2; Fig. 2b), but initial shell length had a significant effect on snail growth rate ($P < 0.001$; Table 2), which was higher in the smaller snails.

We found a positive relationship between reproduction (total number of eggs produced) and shell length at the end of the experiment ($r = 0.387$; $P < 0.01$). Reproduction on the plant diet was over two times greater than on the animal diet, but not significantly greater than on the mixed diet (Table 2; Fig. 2c). Temperature had no significant main factor effect on reproduction (Table 2; Fig. 2c), even though the mean number of eggs laid per individual decreased from 59 in NHW to 47 in SHW and to 30 eggs in LHW. Relative to heat wave duration, the reduction in reproduction observed in SHW was three times greater than in LHW, corresponding to 41% of the reduction observed in LHW. We found diet × temperature interactions indicating that (i) on the plant diet, reproduction in NHW and LHW was greater than in SHW ($P < 0.001$), unlike on the animal diet ($P = 0.531$) and on the mixed diet ($P = 0.633$); (ii) in SHW, there was no diet effect on reproduction ($P = 0.113$), unlike in NHW ($P < 0.05$) and LHW ($P < 0.01$) (Table 2; Fig. 2c). These interactions were caused by a lower proportion of ovipositing snails on the plant diet in the SHW treatment ($\chi X^2 = 9.186$; $P < 0.01$). While egg production on plant diet by the animals that oviposited was similar in all temperature treatments, the proportion of snails that oviposited in
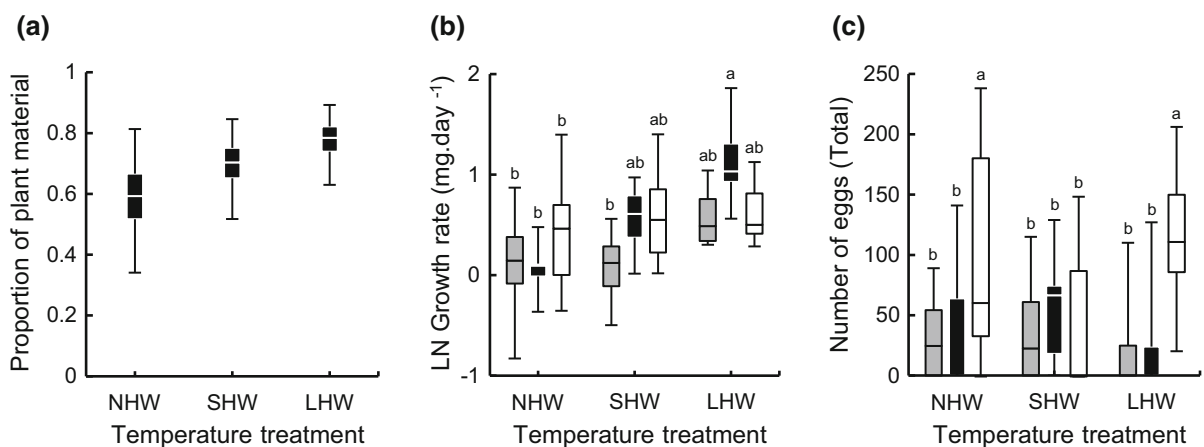

Fig. 2 Proportion of plant material assimilated (**a**), LN of growth rate in mg day^{-1} (**b**) and total number of oviposited eggs (**c**) on animal (grey), plant (white) and mixed diets (black). Boxes show the median and the 25th–75th percentiles and whiskers indicate the 2.5th–97.5th percentiles (**a**) or the minimum and maximum (**b**, **c**). Significant contrasts are depicted with different letters

Table 2 General linear model for growth rate and generalized linear model for reproduction (negative binomial distribution)

Factors	Growth			Reproduction		
	df	F	P	df	χ^2	P
Diet	2, 68	5.29	< 0.01*	2, 68	11.71	< 0.01*
Temperature	2, 68	3.94	< 0.05*	2, 68	3.23	0.199
Diet × temperature	4, 68	1.49	0.216	4, 68	10.97	< 0.05*
Shell length	1, 68	14.19	< 0.001*	1, 68	4.12	< 0.05*

*P values < 0.05

SHW (46%) was half of the proportion of the snails that oviposited in NHW (91%) and LHW (100%). Initial shell length had a significant effect on reproduction ($P < 0.05$; Table 2), with smaller snails producing fewer eggs.

Discussion

Previous studies reported heat wave effects on the survival (Garrabou et al., 2009) and internal resource budgets of organisms, leading to changes in life-history traits (Jiguet et al., 2007; Chiu et al., 2014; Fischer et al., 2014; Dinh et al., 2016; Arambourou et al., 2017). We investigated the expression of phenotypic plasticity as a function of heat wave duration, comparing the magnitude of the effects of short- and long-lasting heat waves on the diet and life-history traits of a freshwater gastropod. Although both types of heat wave increased the assimilation of plant material and the growth rate of *R. balthica*, with minor costs in reproductive output, the magnitude of these responses was disproportional to heat wave duration. Our results revealed a steep thermal reaction norm and suggest that organisms may be unable to sustain the magnitude of short-term responses over long periods. The strong responses deployed by *R. balthica* under the relatively short exposure to high temperatures showcase the major role of phenotypic plasticity as an important mechanism aiding ectotherms to cope with heat waves. Furthermore, presenting the first evidence for temperature-induced dietary shifts in gastropods, our findings add to those obtained in other taxa, supporting a general temperature effect on nutrient acquisition in omnivorous ectotherms and warming to increase herbivory.

Assimilation shifts

Snails on the mixed diet increased the assimilation of plant material under the heat waves, in agreement with the findings of other studies in omnivorous ectotherms (Boersma et al., 2016; Carreira et al., 2016, 2017). Supporting the Respiration Hypothesis (Cross et al., 2015), *R. balthica* used trophic plasticity to increase the relative assimilation of carbon at higher temperatures. The assimilation shifts in SHW (11%) and LHW (19%) are similar to those reported in tadpoles (Carreira et al., 2016) and crayfish (Carreira et al., 2017) under short heat waves (5–11%) and long heat waves (22%). However, the magnitude of the responses displayed may be partially driven by the difference in the C:N ratios of the food items available, as suggested by the findings of Zhang et al. (2018b) showing a relationship between relative consumption rates and the C:N and C:P ratios of animal and plant food items offered to amphipods and gastropods. If the C:N ratios of the food items offered are relatively close, individuals may need to perform larger dietary shifts to efficiently achieve nutritional balance. While the magnitude of the assimilation shifts was similar, the net increase in the C:N ratio of the snails' diet (SHW: 6%; LHW: 9%) was not as high as in the previous studies (10–90%). The C:N ratios of the diets offered to the snails differed only by a factor of two (Table 1), whereas in the two other studies there was a three- to sevenfold difference in the C:N ratio of the food items composing the animal and plant diets. The weaker response by *R. balthica* may indicate a higher tolerance to heat waves than in tadpoles or crayfish, supporting that these extreme events impact species differently and may change freshwater communities.

The increased assimilation of plant material at higher temperatures in our study is typically interpreted as increased herbivory (Lee et al., 2015;

Boersma et al., 2016; Vejříková et al., 2016). However, the single study examining temperature-induced changes in the feeding choices of a freshwater snail (*Lymnaea stagnalis,* Linnaeus 1758) found no evidence for dietary shifts (Zhang et al., 2018a). The seemingly contradictory findings in the two studies suggest that temperature effects on ectotherm feeding preferences could be species-specific or may simply reflect differences in the thermal sensitivity of the two model species. Additionally, the difference in the methodologies used may have also contributed to this contradiction. Owing to the impracticality of obtaining reliable consumption rates in a small-sized species, we used stable isotopes analysis to estimate assimilation rates. Mismatches between consumption and assimilation are known to occur (Schmidt et al., 2017) and could be amplified or partially modulated by temperature, as the greater feeding and gut passage rates at higher temperatures may increase the relative assimilation efficiency of plant diets (Myrick & Cech, 2000; Seifert et al., 2014).

Performance on animal and plant diets

The higher performance on the plant diet, in terms of growth and reproduction, supports the diet assimilation results. Despite the substantial contribution of animal material, *R. balthica* snails on the mixed diet were closer to the herbivory end of the omnivory gradient, with plant material contributing to ca. 70% of their isotopic signature. Previous studies found diet × temperature interactions supporting higher temperatures to decrease performance on animal diets (protein-rich) and to increase performance on plant diets (carbohydrate-rich) (Boersma et al., 2016; Carreira et al., 2016, 2017; Malzahn et al., 2016; Rendon et al., 2019). However, we found no evidence for the performance of the snails on the single diets to change across the temperature regimes. Our experimental setup aimed to compare the effects of short and uncommonly long heat waves, replicating spring conditions. Thus, the thermal contrast provided (5 °C) may have been insufficient to detect changes in the relative performance of the diets, especially for temperatures close to the species' preferred thermal range—16–20 °C in Icelandic populations (Johansson et al., 2016; Johansson & Laurila, 2017). The reduction in oviposition observed in the snails on the plant diet in SHW could be interpreted as a cost of the

acclimation to the short heat wave. However, it resulted from fewer snails reproducing throughout the experiment, rather than from fewer oviposited eggs after snails experienced the short heat wave. Thus, we cannot link the short heat wave to any direct effect on the reproduction of snails on the plant diet. We used data from the snails alive at the end of the experiment and it is possible that random variation in the number of reproducing snails, together with a small sample size ($N = 11$), may be responsible for the interaction found in SHW.

Heat wave effects on dietary shifts and life-history traits

Generally, the two heat waves had similar effects, with the long heat wave prompting stronger responses in *R. balthica*. The increases in the assimilation of plant material on the mixed diet and in the overall snail growth rate were substantially larger in LHW than in SHW. Heat waves also caused an apparent reduction in the number of eggs produced (non-significant), in agreement with results obtained in northern European populations of *R. balthica*, indicating failure of reproduction at 24 °C (Johansson et al., 2016). The increased growth rate in the heat waves, together with the apparent reduction in fecundity, could suggest a trade-off between these traits, not observed in other freshwater snails (Leicht et al., 2013). The positive relationship between size and fecundity supports that allocating resources to growth, by temporarily reducing reproduction under heat waves, could potentially increase snail fecundity in the adult stage. Thus, close to the minimum reproductive size, *R. balthica* snails may have maximized fitness by postponing reproduction to a larger size during optimal growth conditions. However, such a trade-off could prove non-adaptive over prolonged periods.

Heat wave effects on fitness-related traits of freshwater snails have been reported in *L. stagnalis* (Leicht et al., 2013, 2017). This species increased growth and reproduction under heat wave conditions, while their immune defences were reduced (Leicht et al., 2013, 2017). Phenotypic plasticity was also evident in *R. balthica*, with the relatively stronger effects of the short heat wave on plant material assimilation and growth rate suggesting a steep thermal reaction norm. Within a week under heat wave conditions, the snails deployed the equivalent to

60% of the plastic responses observed in the snails under heat wave conditions for 7 weeks. Heat waves have been proposed to affect survival, behaviour and life-history traits in non-linear ways (Chiu et al., 2014), but the responses to the short heat wave were particularly strong. Although snails in LHW should be close to isotopic equilibrium at the end of the experiment, snails in SHW are unlikely to have reached the half-life values for ^{13}C and ^{15}N turnover rates (13 days), even when accounting for weight gain during the short heat wave (9%). Likely underestimating the assimilation of plant material in SHW, our results suggest a larger assimilation shift in SHW than in LHW. As negative effects on performance get pronounced under prolonged heat waves (Leicht et al., 2013), snails may have been unable to sustain the strong assimilation shift implicit in SHW for a long period, reducing the assimilation of plant material as they acclimated to heat wave conditions in LHW.

Methodological issues

Logistic constraints prevented the implementation of cyclical dial variation in our experimental setup, which could have buffered the effects of high daytime temperatures and helped snails to recover from the thermal stress (Davis et al., 2006; Putnam et al., 2010). While our results may overestimate the strength of *R. balthica*'s responses in nature, this may be only partially true. We tested the effects of spring heat waves, characterized by relatively mild temperatures (25 °C) and this species occurs more frequently in semi-permanent and permanent habitats, experiencing higher temperatures and more intense heat waves during summer. Although the narrow temperature range tested here may prevent generalizations, it showed strong responses to small changes in temperature that otherwise may have been masked or replaced by responses to extreme temperatures. For instance, acute heat stress may increase the demand for nitrogen used in the synthesis of heat shock proteins (Podrabsky & Somero, 2004; Lemoine et al., 2013).

Although we cannot disentangle the contribution of the two pathways (consumption and assimilation), our results support temperature to modulate nutrient intake in *R. balthica*. However, without consumption estimates, we cannot be sure on what hinges the greater dependence on plant material at higher temperatures, which may arise from the avoidance of animal material, increased consumption of plant material or a combination of both. Future studies should assess both feeding preferences and assimilation to determine their role in mediating temperature-induced changes in ectotherm nutrient intake.

Conclusions

Short-term climatic stress arising from extreme events, such as heat waves, poses organisms with a greater challenge than changes in mean climatic conditions (Easterling, 2000; Chapman et al., 2014; Vasseur et al., 2014). As climate change progresses and the severity of heat waves increases, phenotypic plasticity may prove determinant for immediate and effective responses. Although diet regulation and changes in life-history traits may help omnivore ectotherms to cope with short-term thermal stress from heat waves, drastic changes may be unsustainable over long periods. Generally, higher temperatures increase the strength of predator–prey interactions in ectotherms, either through faster locomotion rates, more frequent encounters between individuals or faster prey capture (Boukal et al., 2019). However, both sedentary (e.g. snails) and active omnivore ectotherms (e.g. tadpoles and crayfish) increase the proportion of plant material in their diet at higher temperatures—even in lab experiments where the energetic costs of predation are removed (Carreira et al., 2016, 2017). Thus, increased herbivory by active omnivorous ectotherms may be even more beneficial in natural settings than suggested by our experimental findings. Nevertheless, the adaptive value of increasing herbivory may depend on the degree of specialization of the species along the trophic gradient, which may reveal maladaptive in species closer to strict carnivory (Carreira et al., 2016). The greater dependence on plants diets at higher temperatures underscores the potential for warming and heat waves to alter trophic interactions, threatening the stability of ectotherm-dominated ecosystems like freshwaters. While individuals may experience heat waves only briefly in the lifecycle, their responses are likely to have cascading effects, as feeding behaviour is key in shaping the structure and functioning of communities and food webs (Kortsch et al., 2015). Understanding how the multiple temperature effects on metabolism,

growth and intake impact nutritional requirements under normal and extreme physiological conditions will be critical to assess the ecological effects of climate change on ectotherms.

Data availability   The data that support the findings of this study are available from the corresponding author upon reasonable request.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

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