

Ectothermic omnivores increase herbivory in response to rising temperature

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Keywords: climate change, diet shift, food selection, poikilotherm, pond snail,
temperature rise, trophic interaction

Abstract

Higher temperatures as a consequence of global climate change may considerably alter trophic interactions. Ectothermic herbivores and carnivores generally ingest more food with rising temperature as their metabolic rates increase with rising temperature. However, omnivorous ectotherms may respond in two ways: quantitatively by consuming more food and qualitatively by altering their degree of herbivory or carnivory through a diet shift. We hypothesize that rising temperature will increase herbivory of ectothermic omnivores as herbivory increases towards the equator. We tested the hypothesis in a freshwater model system in which ectothermic omnivores are prevalent, by applying two approaches, a temperature manipulation experiment and a literature study. We performed feeding trials with a juvenile aquatic ectothermic omnivore (pond snail *Lymnaea stagnalis*) at different temperatures ranging from 12 to 27°C, supplying them with both animal food and plant material, and directly quantified their consumption rates over time. The results showed that snails cultured at high temperatures (> 21°C) increased the proportion of plant material in their diets after 17 days, which supports our hypothesis. In the literature survey, we found that rising temperature increased herbivory in multiple aquatic animal taxa, including zooplankton, amphibians, crayfish, fish and snails. This suggests that aquatic ectothermic omnivores might commonly increase herbivory with rising temperature. The mechanisms underlying this temperature-induced diet shift are not sufficiently explained by current theories related to the physiology, metabolism and stoichiometry of omnivores. We propose to incorporate the animals' ontogenetic development in the *Temperature Metabolic Stoichiometry Hypothesis* as a complementary explanation for the diet shift, namely that the diet shift could be due to faster development of the ectotherms and an earlier ontogenetic diet shift at higher

temperatures. We conclude that future global warming will most likely alter food webs by increasing the top-down control of aquatic herbivores and omnivores on primary producers.

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Author contribution

PZ and ESB formed the idea of the research. PZ, CHAL, DB, MP and ESB designed the experiment. PZ, DB and MP performed the experiment. PZ, CHAL and JX did the data analysis. PZ, CHAL, DB, MP, JX and ESB wrote and revised the paper.

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6 trophic interactions. Ectothermic herbivores and carnivores generally ingest more food with
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15 temperatures ranging from 12 to 27°C, supplying them with both animal food and plant
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21 omnivores might commonly increase herbivory with rising temperature. The mechanisms
22 underlying this temperature-induced diet shift are not sufficiently explained by current
23 theories related to the physiology, metabolism and stoichiometry of omnivores. We propose
24 to incorporate the animals' ontogenetic development in the *Temperature Metabolic*

25 *Stoichiometry Hypothesis* as a complementary explanation for the diet shift, namely that the
26 diet shift could be due to faster development of the ectotherms and an earlier ontogenetic diet
27 shift at higher temperatures. We conclude that future global warming will most likely alter
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29 primary producers.

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34

35 **Introduction**

36 Due to anthropogenic activities, our planet is undergoing rapid climate change, which
37 includes both a temperature rise and an increase in the occurrence of climate extremes (IPCC
38 2014). Temperature, as the fundamental abiotic factor underlying climate change, can directly
39 influence the metabolism of organisms (Gillooly et al. 2001, Brown et al. 2004), thereby
40 influencing trophic interactions, food web structures and the functioning of ecosystems (Traill
41 et al. 2010, Hansson et al. 2013, Cross et al. 2015, Schaum et al. 2018, Zhang et al. 2018a).
42 For ectotherms, their metabolic rates increase sharply with rising temperature (Brown et al.
43 2004), resulting in increased food consumption. In the case of herbivores and carnivores, this
44 implies enhanced feeding pressure on lower trophic levels at higher temperatures. However,
45 the response of omnivorous ectotherms to rising temperatures is less straightforward, as they
46 may respond in two ways: (1) quantitatively by consuming more food and (2) qualitatively by
47 altering their degree of herbivory or carnivory through a diet shift.

48 Across latitudinal gradients, there is a prevalence of herbivory towards the equator in
49 fish communities (Floeter et al. 2005, Jeppesen et al. 2010, Moss 2010, Behrens and Lafferty
50 2012, González-Bergonzoni et al. 2012). Many explanations for this latitudinal trend have
51 been proposed, including evolutionary constraints, food availability and food quality, but this
52 also includes the hypothesis that temperature is the key factor underlying this latitudinal trend
53 (Floeter et al. 2005, González-Bergonzoni et al. 2012). If herbivory increases towards lower
54 latitudes due to higher temperatures at the equator, this suggests that omnivorous animals may
55 also shift towards a more plant-based diet at higher temperatures. Hence, future global
56 warming could have more impacts on ecosystems than anticipated, by altering the trophic
57 level of animals and thereby changing the abundance or composition of primary producers.
58 This implies that there is an urgent need to test whether an increase in temperature would
59 change the diet selection of omnivores.

60

61 *Possible mechanisms causing temperature induced diet shifts*

62 There are several possible mechanisms that may underlie temperature-induced diet
63 shifts in omnivores (Fig. 1). First, the *Temperature Physiological Constraint Hypothesis*
64 (TPCH), which was initially developed for fish, poses that omnivores cannot meet their
65 energetic demands by only consuming plant materials at low temperatures (Gaines and
66 Lubchenco 1982, Floeter et al. 2005). Although both metabolic rates and feeding rates
67 generally decrease with decreasing temperatures, feeding rates decrease faster than metabolic
68 rates as temperature decreases (Floeter et al. 2005). Furthermore, digesting cellulose in plant
69 material requires the activity of microorganisms in the digestive system, which grow best
70 above certain temperatures (Vejříková et al. 2016). Compared to plant material, animal food
71 items are easier to digest at low temperatures and higher in nutrient content, hence
72 ectothermic omnivores ingest more animal food at low temperatures (Behrens and Lafferty
73 2007). However, there are also large herbivorous fish in cold regions which can digest plant
74 material, as they have long digestive tracts to increase the food retention time needed for
75 digestion (Targett and Arnold 1998, Clements et al. 2009). Additionally, the abundance of
76 herbivorous fish populations was found to be higher at high latitudes than at low latitudes in
77 the southern hemisphere, which does not support the TPCH (Trip et al. 2014). Therefore, the
78 TPCH alone might not be sufficient to explain why the omnivores increase the degree of
79 herbivory with increasing temperature.

80 An alternative explanation might be achieved under the framework of ecological
81 stoichiometry theory (Sterner and Elser 2002) and metabolic ecology (Brown et al. 2004). The
82 *Temperature Metabolic Stoichiometry Hypothesis* (TMSH), predicts that ectotherms need to
83 consume food with a higher carbohydrate:protein (or carbon (C):nitrogen (N)) ratio at higher
84 temperatures (Croll and Watts 2004, Acheampong et al. 2014, Lee et al. 2015, Malzahn et al.

85 2016). As temperature increases, ectotherm animals need to obtain more energy to sustain
86 their increased metabolism, resulting in an increased ingestion rate. However, the respiration
87 rate (catabolic) of animals increases faster than their growth rate (anabolic) as temperature
88 increases (Karl and Fischer 2008, Forster et al. 2011). Therefore, ectothermic animals need to
89 consume relatively more carbohydrates to sustain their increased metabolism. As plants
90 generally have a higher C:N ratio than animals (Zhang et al. 2018b), this could explain why
91 omnivorous ectotherms include more plant material in their diet at higher temperatures, if part
92 of the C is available as carbohydrates. Plant material can be rich in digestible carbohydrates
93 (e.g. sugars and starches), as found in aquatic plants (Chou et al. 2019) and algae (John et al.
94 2011). However, rising temperatures can also increase the preference for protein (N rich) such
95 as shown in grasshoppers (Schmitz et al. 2016), and the preference for carbohydrates and
96 protein was inconsistent with rising temperatures in mealworm beetles (Rho and Lee 2017).
97 Furthermore, model simulation showed that the requirement of zooplankton of a certain food
98 C:N ratio would not change with increasing temperature if the increased amount of food
99 intake is taken into consideration (Anderson et al. 2017). Together, these observations suggest
100 that more work is needed before we can judge the generality of the TMSH hypothesis.

101 To date, no study has tested a potential diet shift in ectotherm omnivores at different
102 temperatures over time, and when the shifts happen is also not clear. Here, we applied two
103 approaches to test whether ectothermic omnivores would increase the proportion of plant
104 material in their diet with rising temperatures. (1) We performed an experiment with juveniles
105 of a widespread ectotherm, the pond snail *Lymnaea stagnalis* L., to test its diet selection over
106 time at different temperatures. *L. stagnalis* is a generalist omnivore, which can feed on a wide
107 variety of food, including periphytic algae and macrophytes, as well as carrion, e.g. dead
108 crayfish, insects, frog tadpoles, fish and even snails (Bovbjerg 1968, Brönmark 1989, Elger
109 and Barrat-Segretain 2004, Zhang et al. 2019). Generally, the snail reaches adulthood when its

110 shell length is above 2.4 cm, and the snails can reach 3.0 cm in eight weeks from hatching
111 under favourable conditions (Van der Schalie and Berry 1973, Elger and Barrat-Segretain
112 2002, Koene et al. 2006). The snails can survive for a few years in nature, and live in a range
113 of temperatures from 6 to 30 °C, with an optimum for growth and reproduction between 20
114 and 25 °C (Van der Schalie and Berry 1973, Zhang et al. 2018b). (2) We provided an
115 overview of previously published effects of temperature on the diets of omnivores, integrating
116 our own data. We tested the hypothesis in a freshwater model system as most aquatic animals
117 are ectotherms (Isaak and Rieman 2013), and omnivorous feeding modes are prevalent in
118 aquatic ecosystems, where many animals can consume both plant material and animal food
119 (Wootton 2017).

120

121 **Materials and Methods**

122 *Agar-based food preparation*

123 To test the effects of temperature on diet selection, we first created agar-based foods
124 using two common food sources, plant food *Elodea nuttallii* (Planch.) St. John and animal
125 food Chironomidae larvae. The two types of food are very common in the habitat where the
126 pond snails live. The advantage of agar-based food is that we could remove the structural
127 differences and focus on the nutritional differences of the food types. This method has been
128 applied in many other experiments to test the feeding behaviour of aquatic animals
129 (Kampfraath et al. 2012, Crenier et al. 2017). The reason to choose *E. nuttallii* as the plant
130 food source in the experiment was that it is a cosmopolitan aquatic plant and also a palatable
131 plant for aquatic animals, including the pond snail *L. stagnalis* (Elger and Barrat-Segretain
132 2004, Grutters et al. 2017), fish (Dorenbosch and Bakker 2011) and waterfowl (Bakker and
133 Nolet 2014). *E. nuttallii* was collected in a pond on the terrain of NIOO-KNAW,

134 Wageningen, The Netherlands (51°59'12.7"N, 5°40'15.4"E). Plants were thoroughly cleaned
135 and freeze-dried. Chironomidae larvae were selected as the animal food source, as it is a
136 common animal food type eaten by many aquatic animals (Armitage 1995). Freeze-dried
137 Chironomidae larvae were commercially obtained (Dierenzaakonline, 's Hertogenbosch, The
138 Netherlands). To facilitate stoichiometric interpretations of diet choice by the animals, the C
139 and N content were measured in samples from dried plant material and animal food (Table 1)
140 using an auto elemental analyzer (FLASH 2000, Thermo Scientific, Waltham, MA, USA).

141 Before food was offered to individual animals in choice experiments, we standardized
142 the texture and concentration of the food by grinding the food to powder through a 0.5 mm
143 sieve and subsequently mixing the powder into agar solutions (P1001, Duchefa biochemie).
144 Ratios of food:agar were determined by pre-trials (Table 1). The water content in agar-based
145 food was comparable to the actual food, as the water content all around 90% (Armitage 1995,
146 Zhang et al. 2019). The agar-based food would partly dissolve in the water, and the animal
147 material dissolved more in the water than the plant material as appeared from our tests (Table
148 S1). In order to offer similar concentrations of plant and animal material of agar-based food to
149 the snail after dissolving, we mixed more animal material into the agar as calculated from pre-
150 trials (Table 1). The agar food was made according to the following procedure (Crenier et al.
151 2017): cooking the agar in demineralized water in a microwave until it completely dissolved;
152 stirring the solution until it cooled down to 55°C; adding a predetermined amount of ground
153 plant or animal material and stirring until well-mixed and pouring the mixture into a
154 polyethylene mould with 100 holes with a diameter of 7 mm and height of 5 mm. The mould
155 was constructed of two polyethylene boards and four clamps, holes were drilled on the top
156 one and the bottom one was a flat substrate, the agar-filled mould was left at 4°C for 2 h. The
157 agar pellets were collected from the mould and stored at 4°C until use (maximum preservation

158 of 3 days). The plant and animal agar food could be visually distinguished, because the plant
159 food was dark green and animal food was brown (Fig. S1).

160

161 *Experimental trials*

162 Adult pond snails were originally obtained from another pond at the terrain of NIOO-
163 KNAW (51°59'17.5"N, 5°40'28.5"E) and kept in the lab, where they reproduced. Egg clusters
164 were hatched, and reared in plastic buckets at 20°C, which is a suitable temperature for the
165 snails to grow (Van der Schalie and Berry 1973). The buckets were filled with tap water and
166 constantly aerated, and exposed to a day:night cycle of 16:8 hours. Hatched snails were fed *ad*
167 *libitum* with commercially obtained lettuce and fish food (Velda, Gold Sticks Basic Food, The
168 Netherlands), following established successful rearing methods (Elger and Barrat-Segretain
169 2002, Grutters et al. 2017, Zhang et al. 2019). After culturing for one month, 48 (6
170 temperatures × 8 replicates) juvenile snails with a shell length of 1.21 ± 0.07 cm (mean ± SD)
171 were selected for the experiment. Each snail was put in a plastic beaker (top diameter 12.5
172 cm, bottom diameter 11 cm and height 11 cm), filled with 500 ml temperature-acclimated tap
173 water and covered with mesh to prevent the snails from escaping. Four beakers were set in
174 one styrofoam platform, and placed in one aquarium (90×50×50 cm, l×w×h) in a 30 cm layer
175 of water. The aquaria functioned as a water bath set at six temperatures: 12, 15, 18, 21, 24 and
176 27°C. We varied the temperature between 12 and 27°C, where at the minimum temperature
177 the snail would still be feeding enough to yield a measurable consumption rate and at the
178 maximum temperature would still survive (Van der Schalie and Berry 1973). Every two
179 aquaria were controlled at the same temperature, and the temperatures were randomly
180 assigned to 12 aquaria in one room. The light intensity on the water surface was 10.35 ± 0.28
181 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (mean ± SD, n = 5), with a day:night cycle of 12:12h. These low light levels were
182 within the normal range of where the snails live.

183 During the experimental trials, snails were offered both plant-based and animal-based
184 agar pellet food *ad libitum*. Leftover food was checked every day for each snail to make sure
185 they had enough of both types of food for the next day; if not, new agar food pellets were
186 added. Every three days, water was replaced and the bucket was cleaned for each snail,
187 meanwhile, leftover food was retrieved, put in a pre-weighed aluminium cup, dried in the
188 oven at 60°C for 48h and weighed to quantify final food dry weight. New food pellets of both
189 types of plant and animal food were supplied to each snail, and quantities were increased if
190 necessary, to provide *ad libitum* food of both food types. The number of pellets offered to the
191 snails varied from one pellet of each type at the start of the experiment to maximum of 7 plant
192 pellets and 10 animal pellets in the highest temperature treatment at the end of the experiment.
193 The plant to animal food ratios offered to the snails varied between 1:1 to 1:4. However, these
194 relative differences in the amount of food for each food type offered to the snails did not
195 affect their feeding preferences, as the snails at the higher temperatures started to select more
196 plant food over time, despite the fact that relatively more animal food was offered. *L.*
197 *stagnalis* has a strong sense for food by perception of volatile organic compounds released by
198 the food (Moelzner and Fink 2014) and therefore would not have problems to distinguish
199 between the food types or to find the preferred food. The snails are known to go strongly for
200 the food they prefer, even though they encounter more of the unpreferred food (Zhang et al.
201 2018b, Zhang et al. 2018c). Agar food can lose some weight over time as part of it may
202 dissolve in the water. Therefore, we performed dissolving trials at different temperatures and
203 initial dry weight of an agar food pellet in the snail feeding trial was estimated based on these
204 dissolving trials (Table S1). The food consumption rate was expressed as how much food was
205 consumed by each snail per day: (Food initial dry weight – Food final dry weight) / days. The
206 experiment lasted for 24 days from October 20th to November 12th 2017 and snail wet weight

207 and shell length were measured at the start and end of the experiment. Snail relative growth
208 rate was expressed as: $[\ln(\text{Final snail weight}) - \ln(\text{Initial snail weight})] / \text{days}$.

209

210 *Data analysis*

211 General Linear Mixed-Effects models were employed to analyse the effects of
212 temperature on plant food consumption rates, animal food consumption rates and the
213 plant:animal food consumption ratio of the omnivore over time. Both temperature (ranging
214 from 12 to 27 °C) and time (in days) were included in the models as continuous explanatory
215 variables. Aquarium and species identification number were included as random factors to
216 account for the dependency structure in our experimental design and for the repeated
217 measurements, respectively. Normality and homoscedasticity of the dependent variables were
218 assessed visually by plotting model residuals versus fitted values and in quantile-quantile
219 plots of the model residuals. All the dependent variables were log-transformed to improve
220 their normality before performing the analysis.

221 To measure food consumption in dry mass, we converted wet weights into dry
222 weights, which introduced slight measurement errors, resulting in a few negative values ($n = 6$
223 for plant consumption rates and $n = 10$ for animal consumption rates, these mainly happened
224 in the first few days of the experiment). We replaced those negative values by a small positive
225 value of 0.1 mg, as negative consumption rates are ecologically meaningless, whereas
226 replacing them by 0 mg would not allow us to calculate the ratio of plant:animal food
227 consumed when the denominator was zero. To test whether this affected the results, we also
228 tried to standardize those negative values to 0 mg, or removed them or retained them all, none
229 of these methods changed the qualitative outcome of the data analysis and the statistical
230 significance. We chose to standardize all negative consumption rate values to 0.1 mg, as

231 herewith we retained all data and all data are ecologically meaningful, following previous
232 analyses of these types of feeding trials (Grutters et al. 2017). Diet selection was indicated by
233 the ratio of plant food consumption rate to animal food consumption rate. All statistics were
234 performed in R 3.4.3 (R Development Core Team 2017) and for the mixed-effect models we
235 used package *nlme* (Pinheiro et al. 2017).

236

237 *Literature study*

238 In addition to our experiment we also surveyed the available experimental evidence
239 for effects of temperature on the diets of omnivorous ectothermic animals in the literature. We
240 therefore used the following search terms in ISI: Web of Science: “temperature” OR “warm*”
241 OR “heat” in the title, “omnivor*” and “diet” OR “food” in the topic, and checked for cross-
242 references in the obtained literature. This resulted in 64 publications, of which 10 publications
243 presented suitable experimental data on how the diet of omnivorous ectotherms responded to
244 changing temperatures. This resulted in a database with 14 cases, covering 5 taxa and 10
245 species of aquatic animals which included our own experiment.

246

247 **Results**

248 *Snail experiment*

249 The animal food had a higher N content and a lower C:N ratio than the plant food used
250 in the experiment (Table 1). Pond snails increased their plant food consumption rates in
251 response to rising temperature, and when temperatures were $\geq 15^{\circ}\text{C}$, pond snails increased
252 plant consumption rates over time (Fig. 2a and Table 2). Animal food consumption rates by
253 pond snails increased with temperature rise and increased over time at all temperatures (Fig.

254 2b and Table 2). Temperature effects on the plant:animal consumption ratios emerged after 17
255 days; snails significantly increased plant:animal consumption ratios afterwards when
256 temperatures were above 21°C (Fig. 2c and Table 2). The average plant:animal food
257 consumption ratio over the entire experiment was 0.15 ± 0.14 (mean \pm SD, $n = 327$). Both
258 snail final shell length and relative growth rate significantly increased with temperature and
259 levelled off from 24 °C (Fig. 3). At the end of the experiment, snails had 1.6 times longer
260 shells and 2.2 times faster relative growth rates at 24 °C than at 12 °C. No indication was
261 found that the snails were suffering of dietary limitations in the experiment.

262

263 *Literature survey*

264 No study using a terrestrial model system to test effects of temperature on omnivorous
265 diet selection was found. Rising temperature increased the degree of herbivory by aquatic
266 omnivores in 12 of the 14 cases in our acquired dataset, which includes taxa in zooplankton,
267 amphibians, crayfish, fish and aquatic snails (Table 3). The two approaches to study potential
268 effects of temperature on omnivore diets were temperature manipulation experiments (11
269 cases) and seasonal comparison (3 cases). Differences between the lowest and highest
270 temperature tested in each case ranged from 4 to 20°C. Among the 11 cases that manipulated
271 temperature, the duration of the experiment ranged from 24 h to 2 months. Six cases focused
272 on fish, and all found temperature effects on diet selection, such that rising temperatures
273 increased the proportion of plant material in the fish diets.

274

275 **Discussion**

276 The pond snails increased their consumption rates and degree of herbivory with rising
277 temperature in our study, which confirms that the omnivore quantitatively increased its food

278 consumption rates and qualitatively shifted to more herbivory with rising temperature.
279 Furthermore, through the combination with a literature study, we found that several aquatic
280 omnivores increased their degree of herbivory when water temperatures increased, and only
281 two experimental cases out of 14 did not find a diet shift with rising temperatures. In the
282 following sections, we will discuss possible reasons for the absence of a diet-shift in these
283 studies, and discuss the implications of qualitative changes in omnivore diets for aquatic food
284 webs, as well as provide perspectives for future studies on this timely topic.

285

286 *Increased consumption and herbivory with rising temperature*

287 With rising temperature, the consumption rate of snails in our experiment increased,
288 which is consistent with previous studies (González-Bergonzoni et al. 2016, Zhang et al.
289 2018b). For ectotherms, the metabolic and consumption rates of organisms increase as
290 temperature increases (Gillooly et al. 2001, Brown et al. 2004), until an optimum temperature
291 is reached, after which then biological rates sharply decline (Sinclair et al. 2016, Rohr et al.
292 2018). The pond snail used in our experiment has an optimum temperature for growth and
293 reproduction between 20°C and 25°C (Van der Schalie and Berry 1973, Zhang et al. 2018b),
294 the maximum temperature in our experiment. Similar to other studies, we observed an
295 increase of consumption rate of snails with rising temperatures, and a stronger plant-consumer
296 interaction with rising temperature.

297 Through the combination of a controlled experiment and a literature study, we found
298 that studies supporting the hypothesis that rising temperature increases herbivory of aquatic
299 omnivores covered five aquatic taxa, including zooplankton (Boersma et al. 2016), tadpoles
300 (Carreira et al. 2016), crayfish (Carreira et al. 2017), aquatic snails (this study) and fish (Prejs
301 1984, Behrens and Lafferty 2007, Guinan Jr et al. 2015, Emde et al. 2016, González-

302 Bergonzoni et al. 2016, Vejříková et al. 2016). It is important to note that even though the
303 authors observed diet shifts in the three seasonal comparison studies, there still could be other
304 reasons accounting for the diet shift, such as changes in food abundance and food quality
305 among seasons (Guinan Jr et al. 2015, Boersma et al. 2016, González-Bergonzoni et al. 2016).
306 In addition, there may be an unknown bias against publishing non-significant results. Whereas
307 most studies confirmed our hypothesis, there were still two cases that did not find temperature
308 effects on aquatic omnivorous diet selection (Table 3).

309 The first case was that adult crayfish did not increase the proportion of plant material
310 in their diet with rising temperatures (Carreira et al. 2017). However, the parallel study using
311 juvenile crayfish found a trend of increasing herbivory with rising temperatures. Crayfish
312 have been shown to increase herbivory with increasing age (Momot 1995), which indicates
313 that rising temperature might enhance the growth of crayfish and increase herbivory. The
314 second case was that the adult pond snail did not increase herbivory with rising temperatures
315 in a 24 hours' diet selection experiment (Zhang et al. 2018b). However, in a longer term, the
316 juvenile pond snail in our study increased herbivory at higher temperatures after 17 days.
317 These two cases do not reject our hypothesis, but rather suggest that this hypothesis might
318 depend on the life stage and experimental duration, at least for some species.

319 Our snail experiment is the first to quantify the diet selection of juvenile ectotherm
320 omnivores over time. The snails at higher temperatures reached 2.4 cm shell length and the
321 growth levelled off from 24 °C at the end of the experiment (Fig. 3), indicating that the snails
322 reached adulthood (Van der Schalie and Berry 1973, Elger and Barrat-Segretain 2002, Koene
323 et al. 2006). This means that the diet shift of the snails after 17 days at higher temperatures
324 could be due to the ontogenetic development of the snails, namely the snails may have shifted
325 their diet when they become adults. This extrapolation is also supported by the study which
326 tested the diet selection of adult pond snails in a 24 h's feeding trial, but did not find

327 differential diet selection at higher temperatures (Zhang et al. 2018b). Animals often have
328 different nutrient demands at different life stages (Stockhoff 1993, Urabe and Sterner 2001,
329 Claes and Maarten 2003, Bullejos et al. 2014, Richard et al. 2018). Animal food has a higher
330 nutrient content compared to plant material (Elser et al. 2000, Zhang et al. 2018c), as also
331 shown in our study. Juveniles might need food with a lower C:nutrient ratio than their
332 conspecific adults, as they need more nitrogen and phosphorous for their growth, leading to
333 an ontogenetic shift in stoichiometric demand (Nakazawa 2011, Bullejos et al. 2014, Boros et
334 al. 2015). Many aquatic omnivores increase the proportion of plant material in their diet
335 during their ontogenetic development (Werner and Gilliam 1984, German and Horn 2006,
336 Burgett et al. 2018). At high temperatures, animals grow faster and mature earlier, resulting in
337 a smaller final body size (Kingsolver and Huey 2008, Daufresne et al. 2009), and accrue
338 relatively less nutrients in their bodies (Woods et al. 2003). Thus, they might shift their diet
339 earlier from food with a lower C:nutrient ratio to food with a higher C:nutrient ratio with
340 increasing temperature, which can be achieved by increasing herbivory at higher
341 temperatures.

342 Life stages and variation in ontogenetic stoichiometry demand during different life
343 stages of animals have so far been completely neglected in the previous hypotheses. We here
344 propose to include the ontogenetic development in the TMSH hypothesis to explain the
345 possible diet shift of omnivores with rising temperature (Fig. 1). However, for the ectotherms
346 with metamorphose or multiple life stages, their nutrient demands vary discretely at different
347 life stages (Werner and Gilliam 1984, Stockhoff 1993, Boros et al. 2015). Hence, the diet shift
348 of omnivores might occur multiple times during their lifetime, changing with their growth,
349 reproduction and senescence. We did not test these in our experiment, and this would be
350 something interesting to explore in the future. Therefore, there is not a universal simple rule

351 which can be applied to all cases; instead more studies are needed that test diet selection of
352 omnivores at different life stages over similar time scales to verify the hypotheses.

353

354 *Implications of increased herbivory under climate change*

355 As global temperatures increase, this might change the ratio of available food items. In
356 nature, omnivorous diet selection also depends on food availability (Guinan Jr et al. 2015,
357 Vejříková et al. 2016), as animal food is not always as abundant as plant material. If there is
358 no animal food available, omnivorous animals might become herbivores, and they might need
359 to consume more plant material to compensate for their nutrient demand due to the lower
360 nutrient content of plant material (Cruz-Rivera and Hay 2000, Fink and Von Elert 2006). This
361 will lead to enhanced top-down pressure on primary producers by herbivory with warming
362 (Fig. 4a,b), as ectothermic animals increase their metabolic rates with rising temperature
363 resulting in higher consumption rates. When there is animal food available, the omnivores
364 might increase the proportion of plant material in their diet with warming (Fig. 4c,d).
365 Together these changes in consumption rates and food availability suggest that future climate
366 change might lead to stronger grazing pressure on primary producers, by both herbivores and
367 omnivores.

368 In addition, with rising temperature, the omnivores might grow faster and shift earlier
369 to increase plant consumption and establish larger population sizes leading to more
370 consumption of primary producers (Meerhoff et al. 2007, Jeppesen et al. 2010, González-
371 Bergonzoni et al. 2012, O’Gorman et al. 2017). Furthermore, the consumption rate of animals
372 might increase faster than the biomass accumulation rate of primary producers with rising
373 temperature (O’Connor 2009, Gilbert et al. 2014, West and Post 2016, Schaum et al. 2018).
374 These findings indicate that the top-down control on primary producers by herbivory of

375 ectothermic omnivores might be even stronger in nature under future warming and heatwaves.
376 However, where the tipping point for the diet shift is, and when this will happen, has
377 implications for the impacts of future climate change. The increased degree of herbivory with
378 rising temperature will strengthen the omnivorous interaction between primary producers and
379 consumers, which might lead to an unstable food web (Wootton 2017). Therefore, a shift in
380 diet selection by omnivores due to climate change might first alter the relative and absolute
381 abundance of primary producers and animal prey, then followed by a collapse of the
382 community of omnivores and the food web.

383

384 *Future studies*

385 Clearly, more studies are needed to enable better predictions on the effects of global
386 warming on plant consumption in aquatic systems. We here list four key directions.

387 (1) Although aquatic ectothermic omnivores seem to generally increase herbivory with
388 rising temperature, the underlying mechanisms are still unclear. Explanations from the
389 aspects of temperature effects on animal physiology, metabolism, and stoichiometric
390 demands could not fully clarify why ectothermic omnivores increase herbivory with
391 rising temperature. We here propose to additionally take the animal ontogenetic diet
392 shift into consideration when interpreting diets shift by omnivores. More experiments
393 are needed to verify the various hypotheses.

394 (2) Compared to several other studies, our study was performed in a more direct way. We
395 measured the omnivore consumption rates on both types of food over time, whereas
396 other studies employed stable isotope methods (Guinan Jr et al. 2015, Boersma et al.
397 2016, Carreira et al. 2016, Carreira et al. 2017). The stable isotope method has been
398 used to indicate the food assimilation, which is not equal to consumption (Boecklen et

399 al. 2011). Both methods have their own strengths. Whereas isotope studies can better
400 indicate which type of food could be utilized best by omnivores, our study can better
401 indicate better the amount of plant consumption, which is important to assess direct
402 top-down grazing pressure of omnivores on primary producers. Future studies should
403 test more ectothermic omnivores in long-term diet-selection experiments at multiple
404 life-stages at different temperatures. Furthermore, multiple plant material should be
405 tested to generalize the conclusions, and also agar food composed with manipulated
406 nutrients is a very relevant approach. Agar-based food eliminates the physical
407 structure of natural food material, which allows to focus on the nutrient composition
408 of the food.

409 (3) Even though multiple studies have found that warming might increase herbivory by
410 aquatic omnivores, there is still no study that explored the consequences of this diet
411 shift for the impact of omnivores on the abundance or diversity of primary producers
412 at either the community or ecosystem level. Similarly, studies on the impact of
413 warming through increased herbivory by omnivores are lacking in terrestrial
414 ecosystems. Therefore, more studies are needed to test the effects of warming on
415 primary producers via increased herbivory, taking into account more complete and
416 thus more realistic food webs.

417

418 **Conflict of interests**

419 The authors declare no conflict of interest.

420

421 **Data availability Statement**

422 Data will be made available in the Dryad repository.

423

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604

605 **Table 1 Original nutrient concentration and stoichiometry of the food and the agar food**
 606 **composition used in the experiment.** All data are means \pm SD, n = 3. Weights are dry weight.
 607 Significant differences between the plant and animal food (independent t-tests) are indicated by
 608 different letters for each component.

Food type	Original food nutrients			Agar food composition		
	C (mg g ⁻¹)	N (mg g ⁻¹)	C:N (g g ⁻¹)	Agar	Demineralized water	Food materials
Plant	334.9 \pm 2.1 ^a	32.5 \pm 1.4 ^a	10.3 \pm 0.45 ^a	1g	50ml	2.5g
Animal	355.6 \pm 6.7 ^b	76.3 \pm 1.3 ^b	4.66 \pm 0.03 ^b	1g	50ml	4g

609

610 **Table 2 Time and temperature effects on pond snail food consumption.** Bold numbers indicate $p <$
 611 0.05.

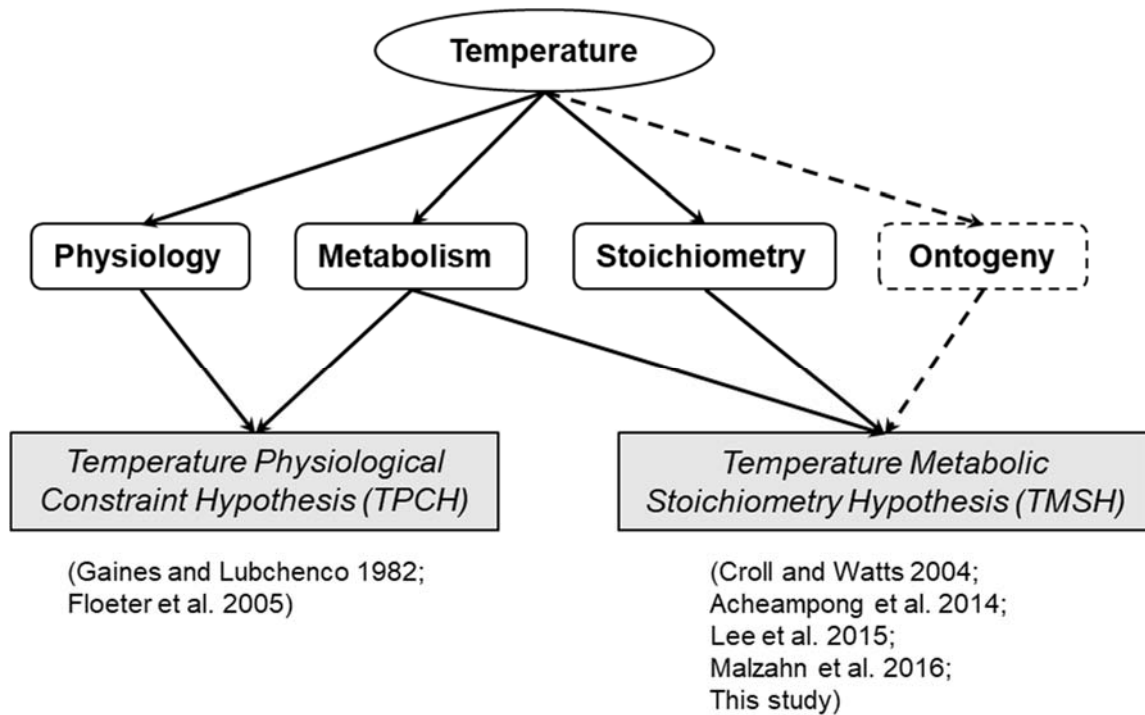
Parameters	Factors	numDF	denDF	<i>F</i>	<i>p</i>
Plant food consumption rate	Time	1	334	73.7	< 0.001
	Temperature	1	10	5.5	0.041
	Time × Temperature	1	334	257.7	< 0.001
Animal food consumption rate	Time	1	334	27.1	< 0.001
	Temperature	1	10	101.3	< 0.001
	Time × Temperature	1	334	4.9	0.028
Plant:animal consumption ratio	Time	1	334	35.5	< 0.001
	Temperature	1	10	13.0	0.005
	Time × Temperature	1	334	27.5	< 0.001

612

613 **Table 3 Results of studies which investigated rising temperature effects on diet selection of aquatic omnivores.**

Taxon	Omnivore	Plant food	Animal food	Experiment approach	Quantified methods	Time	Temperature range	Results	Reference
Zooplankton	Copepod (<i>Temora longicornis</i>)	Cryptophyte (<i>Rhodomonas salina</i>)	Dinoflagellate (<i>Oxyrrhis marina</i>)	Seasonal comparison	Stable isotope method	-	3 - 23 °C	Decreased trophic position with rising temperature	Boersma et al. 2016
				Temperature manipulation	Quantify grazing rate	24 h	8 - 26 °C	Preferred plant food at high temperature	Boersma et al. 2016
Amphibian	Tadpole (<i>Discoglossus galganoi</i>)	Macrophyte (<i>Juncus heterophyllus</i>)	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17 - 25 °C	Increased herbivory with rising temperature	Carreira et al. 2016
	Tadpole (<i>Hyla arborea</i>)	Macrophyte (<i>Ranunculus peltatus</i>)	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17 - 25 °C	Increased herbivory with rising temperature	Carreira et al. 2016
	Tadpole (<i>Hyla meridionalis</i>)	Macrophyte (<i>Ranunculus peltatus</i>)	Ephemeroptera (mayfly) larvae	Temperature manipulation	Stable isotope method	2 months	17 - 25 °C	Increased herbivory with rising temperature	Carreira et al. 2016
Crayfish	<i>Procambarus clarkii</i> -Juvenile	Macrophyte (<i>Juncus heterophyllus</i>)	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17 - 25 °C	Tendency of increasing herbivory with warming	Carreira et al. 2017
	<i>Procambarus clarkii</i> -Adult	Macrophyte (<i>Juncus heterophyllus</i>)	Chironomid larvae	Temperature manipulation	Stable isotope method	2 months	17 - 25 °C	No temperature effects on preference	Carreira et al. 2017
Fish	Rudd (<i>Scardinius erythrophthalmus</i>)	Macrophytes	-	-	Gut content analysis	-	15 - 23 °C	Increased plant consumption as temperature increased	Prejs 1984

Taxon	Omnivore	Plant food	Animal food	Experiment approach	Quantified methods	Time	Temperature range	Results	Reference
	Opaleye (<i>Girella nigricans</i>)	Algae (<i>Ulva</i> spp.)	Squid pieces	Temperature manipulation	Quantify performance	28 days	12 - 27 °C	Increased performance at low temperature feeding on animal food	Behrens & Lafferty 2007
	<i>Bryconamericus iheringii</i>	Filamentous algae	Tubificid worms	Seasonal comparison	Gut content analysis	4 days	10 - 22 °C	Increased herbivory in summer	González-Bergonzoni et al. 2016
	Rudd (<i>Scardinius erythrophthalmus</i>)	-	-	Seasonal comparison	Stable isotope method	-	9 - 25 °C	Increased herbivory in summer	Guinan Jr et al. 2015
	Rudd (<i>Scardinius erythrophthalmus</i>)	Macrophyte (<i>Potamogeton pectiatus</i>)	<i>Chironomus</i> larvae	Temperature manipulation	Gut content analysis	24 and 168 h	13 - 24 °C	Increased herbivory with rising temperature	Vejříková et al. 2016
	Cichlids (<i>Amatitlania nigrofasciata</i>)	Plants	Molluscs, insects, crustaceans	Field comparison	Gut content analysis	-	27 - 31°C	Increased herbivory at higher temperature	Emde et al. 2016
Snail	Pond snail (<i>Lymnaea stagnalis</i> , Adult)	Macrophyte (<i>Potamogeton lucens</i>)	Amphipod (<i>Gammarus pulex</i>)	Temperature manipulation	Quantify feeding rate	24 h	15 - 25 °C	No temperature effects on preference	Zhang et al. 2018b
	Pond snail (<i>L. stagnalis</i> , Juvenile)	Macrophyte (<i>Elodea nuttallii</i>)	<i>Chironomus</i> larvae	Temperature manipulation	Quantify feeding rate	23 days	12 - 27 °C	Increased herbivory at higher temperature after 17 days	This study



615

616 **Figure 1 Schematic graph of possible mechanisms for increased herbivory by aquatic omnivores**

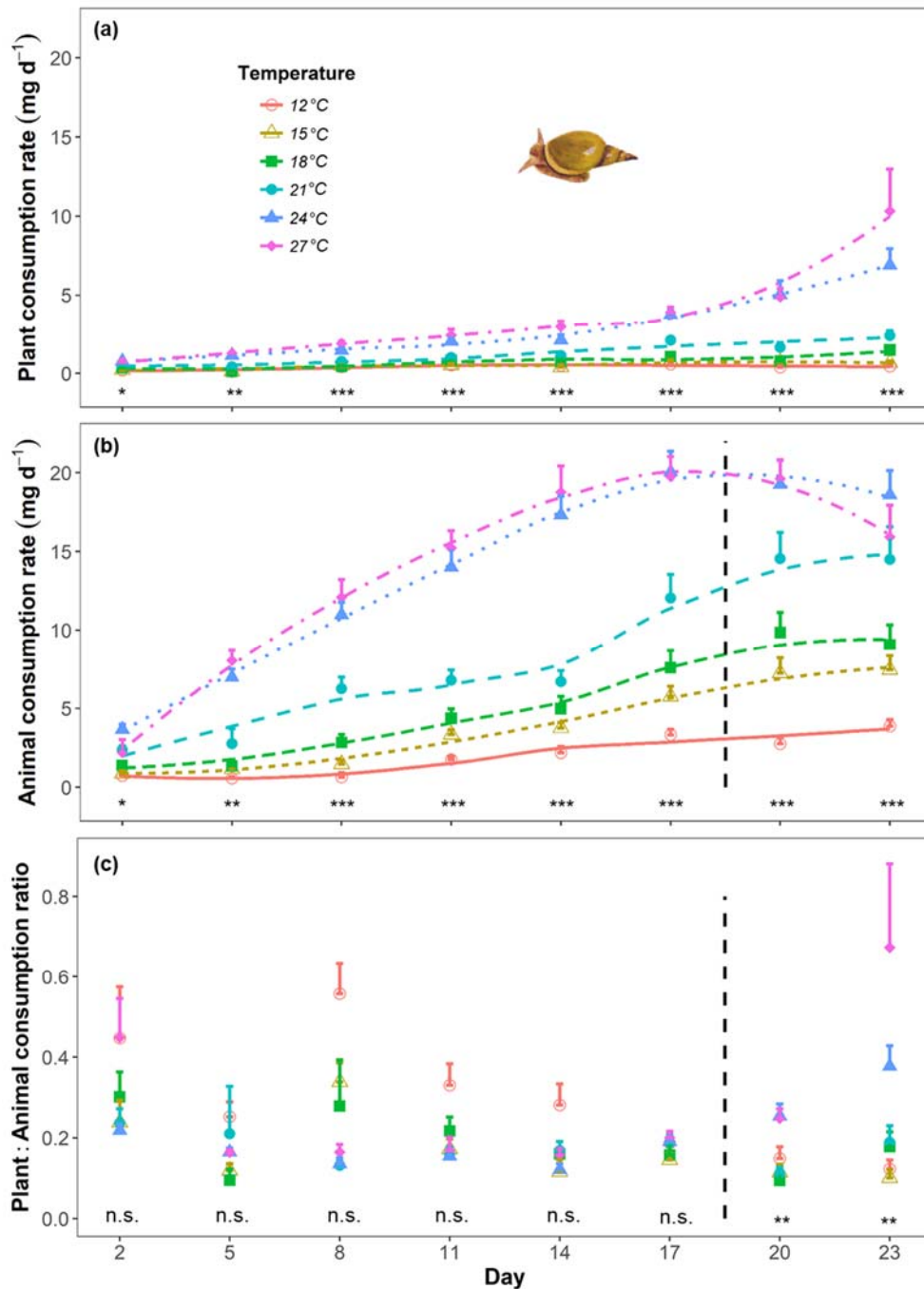
617 **with rising temperature.** Temperature influences different aspects of the omnivores and the

618 hypotheses are based on these effects. The dashed lines indicate the possible mechanism of ontogeny

619 that we propose to include as an explanatory mechanism based on the results from our study (see

620 Discussion section).

621



622

623 **Figure 2 Temperature effects on pond snail food consumption rates and diet selection during the**

624 **choice experiment. (a) Plant food consumption rates by snails; (b) Animal food consumption rates by**

625 **snails; (c) Plant:animal food consumption ratios during the experiment. Dashed vertical lines indicate**

626 **the diet shift time point. Standard errors are indicated by vertical bars (n = 8). Each data point**

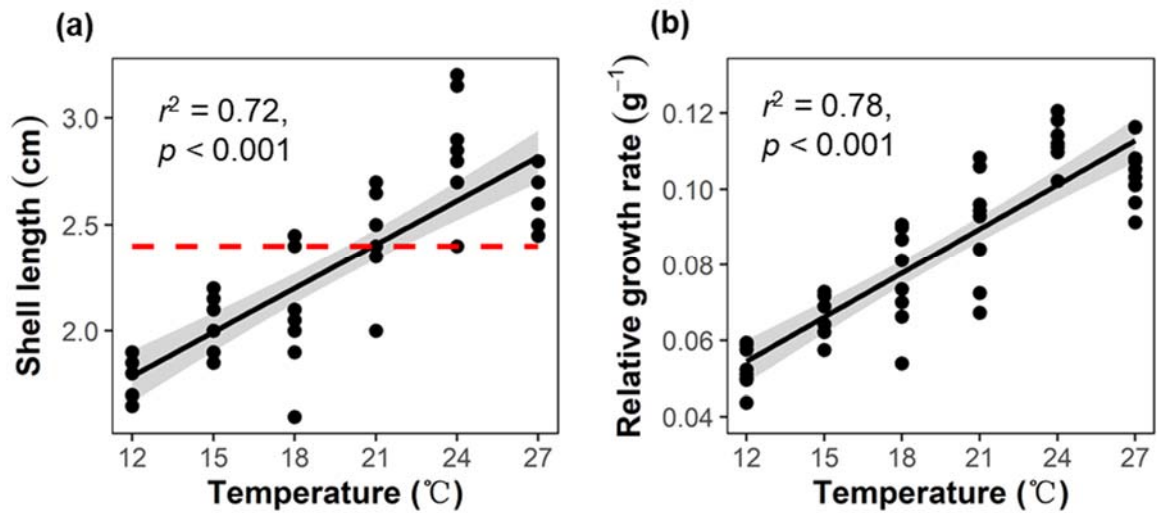
627 **represents the mean value over the three days of measurement and is displayed at the middle day.**

628 **Statistical results are shown in the figures. “n.s.” represents no significant effects at $p > 0.05$; ***

629 **indicates $p < 0.05$; ** indicates $p < 0.01$; and *** indicates $p < 0.001$.**

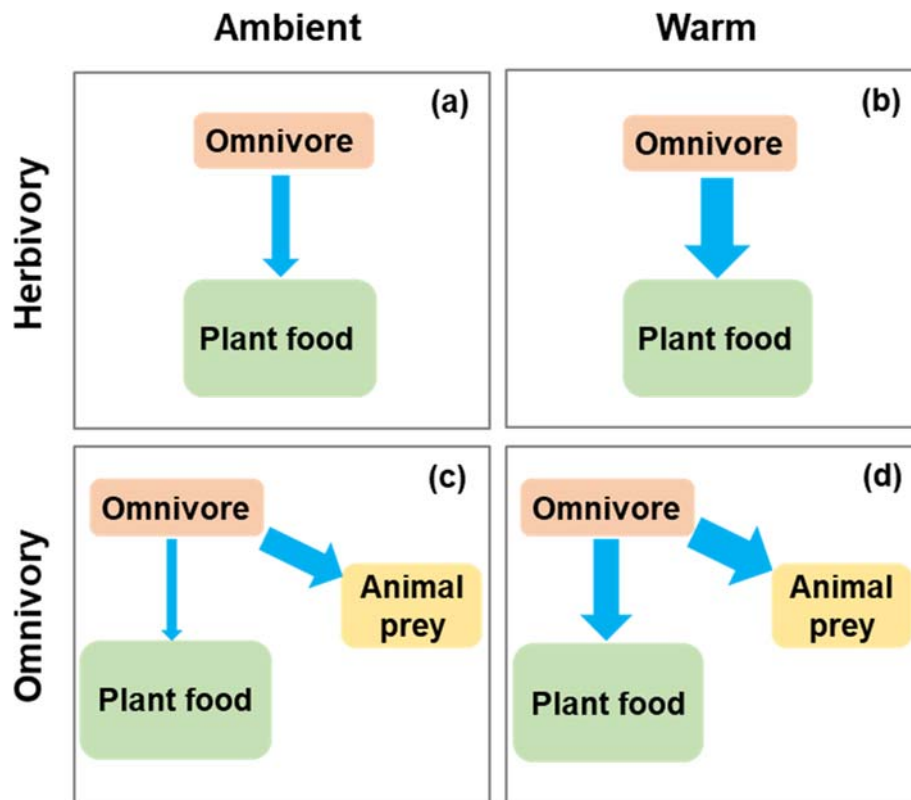
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631



632

633 **Figure 3** Temperature effects on snail growth parameters in the experiment. (a) Final shell length and
634 (b) Relative growth rate. Temperature effects on the growth parameters were tested by Linear-Mixed
635 Effects models, and results are indicated in the plot. Dashed horizontal red line (shell length = 2.4 cm)
636 indicates the threshold above which snails are generally sexually mature (Van der Schalie and Berry
637 1973; Elger and Barrat-Segretain 2002; Koene et al. 2006).



638

639 **Figure 4 Proposed implications of warming effects for plant consumption by ectotherm**
 640 **omnivores in the absence and presence of animal prey.** The omnivore is an animal that
 641 could consume both plant material and animal food. When there is no animal prey, the
 642 omnivore behaves as an herbivore and has a stronger top-down effect on the plant food in
 643 warm (b) compared to ambient (a) scenarios by increasing its consumption rate. When there is
 644 animal prey, the consumer behaves as an omnivore and when changing from an ambient (c) to
 645 a warm (d) scenario, the omnivore increases its consumption rate, thereby consuming
 646 more animal prey, but also increases its preference for plant food, thereby increasing the top-
 647 down effect on plant food. Arrows indicate the top-down effect. Width of the arrows indicates
 648 their magnitude.

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Supplementary materials

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652 **Below is the information for the supplementary materials:**

653 **Supplementary materials 1**

654 **Table S1** Dissolving test to calibrate the weight loss of the agar food pellet for snails

655 during the feeding period at different temperatures, in the absence of snails.

656 **Figure S1** Plant and animal food agar pellets.

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