

1 **Metabolic rate and foraging behaviour: A mechanistic link across body size and temperature**
2 **gradients**

3
4 *Milad Shokri*^{1,2*}, *Francesco Cozzoli*^{1,2,3}, *Alberto Basset*^{1,2,3}

5 ¹Laboratory of Ecology, Department of Biological and Environmental Sciences and Technologies,
6 University of Salento, 73100 Lecce, Italy.

7 ²National Biodiversity Future Center (NBFC), 90133 Palermo, Italy.

8 ³Research Institute on Terrestrial Ecosystems (IRET) - National Research Council of Italy (CNR) via
9 Salaria, Monterotondo Scalo (Rome), Italy.

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11 * Corresponding author: milad.shokri@unisalento.it

12

13 **Abstract**

14 The mechanistic link between metabolic rate and foraging behaviour is a crucial aspect of several energy-
15 based ecological theories. Despite its importance to ecology however, it remains unclear whether and how
16 energy requirements and behavioural patterns are mechanistically connected. Here we aimed to assess
17 how modes of behaviour, in terms of cumulative space use, patch selection and time spent in an
18 experimental resource patchy environment, are influenced by the foragers' metabolic rate (SMR) and its
19 main determinants i.e. body mass and temperature. We tested the individual behavioural patterns and
20 metabolic rates of a model organism, the amphipod *Gammarus insensibilis*, across a range of body
21 masses and temperatures. We demonstrated that body mass and temperature exert a major influence on
22 foraging decisions and space use behaviour via their effects on metabolic rates. Individual cumulative
23 space use was found to scale allometrically with body mass and exponentially with temperature, with
24 patch giving-up time falling as body mass and temperature increased. Moreover, SMR had greater
25 predictive power for behavioural patterns, explaining variation beyond that accounted for by body mass
26 and temperature combined. Our results showed that cumulative space use scaled positively with Mass-
27 and-Temperature-independent SMR (residual). Furthermore, the foraging decisions regarding patch
28 choice and partitioning were strongly related to M-T independent SMR; individuals with higher M-T

29 independent SMR initially preferred the most profitable patch and, as time progressed, abandoned the
30 patch earlier compared to others. Our findings regarding the mechanistic relationship between
31 behavioural patterns and metabolic rate across body mass and temperature shed light on higher-order
32 energy-based ecological processes, with implications in the face of climate change.

33

34 **Keywords:** Behavioral ecology, Body mass, Climate change, Metabolic rate, Optimal foraging,
35 Physiological ecology, Space use, Temperature

36

37 **Introduction**

38 Individuals differ considerably in their patterns of resource use in a heterogenous environment (Auer et al.
39 2020a), which has crucial evolutionary and ecological implications as it influences individual life history
40 and space use, as well as population dynamics and community structure (Basset 1995, Auer et al. 2020b,
41 Laskowski et al. 2022). Despite its importance to the higher-order ecological phenomena, the mechanisms
42 underpinning individual behavioural variability remain the subject of active research debate.

43 At the fundamental level, foraging behaviour aims to fulfil organisms' energy requirements (MacArthur
44 and Pianka 1966). It is thus intuitively reasonable that metabolic rate, i.e. the baseline energy
45 requirements of an organism (Brown et al. 2004), might be linked to foraging behaviour and resource
46 acquisition strategies. Metabolic rate increases allometrically with organism body mass (Brown et al.
47 2004), and motile foragers need to adjust their space and resource use to fulfil their mass-dependent needs
48 (Brose, 2010; Petchey et al., 2008). For example, larger foragers generally need larger home ranges and
49 exploit a resource patch only if and for as long as it allows high ingestion rates (Basset, 1995; Charnov,
50 1976; Holling, 1959; McNab, 1963). In addition to individual body mass, as temperature increases, the
51 higher kinetic energy of biochemical reactions speeds up the rate of metabolic processes (Gillooly et al.
52 2001), affecting the behavioural patterns of individual organisms (Abram et al. 2017). It follows that
53 animals might adjust their foraging strategies in accordance with their energy requirements in response to
54 body mass, ambient temperature or both (Dell et al., 2011; Petchey et al., 2008). Several studies have

55 investigated the link between individual energy requirements and foraging behaviour, often focusing on
56 one of the main determinants of metabolic rate, e.g. individual body mass (Brose, 2010; Cozzoli et al.,
57 2019, 2022; Petchey et al., 2008) or, more recently, temperature (Abram et al. 2017, Cloyed et al. 2019,
58 Jermacz et al. 2020). However, despite the key importance of body size and temperature *per se* in
59 predicting behavioural patterns (Brose 2010, Cozzoli et al. 2022), they are not sufficient to crystalize the
60 mechanism behind them (Brandl et al. 2022). The complexity of resource-consumer interactions often
61 hinders the predictive power of mass and temperature-based models (Dell et al. 2014b). For instance,
62 individuals may react to increased energy requirements by increasing foraging efforts and nutrient
63 intake/ingestion (Réveillon et al. 2022) or, conversely, by limiting their movements (Warne et al. 2019).
64 This is because animals are generally characterized by a set of biological rates that respond differently
65 depending on the conditions (Barrios-O'Neill et al., 2019; Glazier, 2015). Alternative energy management
66 hypotheses have been developed to explain the interdependence between metabolic rate and behavioural
67 patterns. The performance model predicts that metabolic rate and activity will correlate positively because
68 metabolic rate reflects activity (Biro and Stamps 2010). However, (Careau and Garland 2012) suggested
69 that there is not always a positive correlation between metabolic rate and behavioural patterns. The
70 allocation model assumes a negative relationship between metabolic rate and behavioural patterns, as a
71 higher metabolic rate results in less energy available to spend on active behaviours such as locomotion
72 and space exploration (Careau et al. 2008). The independent model sees individual behavioural activity
73 and metabolic rate as independent (Careau and Garland 2012).

74 No consensus has emerged because metabolic syndromes cannot be completely understood without
75 considering the effects of subsidiary environmental factors (Killen et al. 2013) and because behavioural
76 studies have applied sharply differing methods, hampering comparative analysis (Montiglio et al. 2018).
77 Additionally, investigating behavioural patterns in landscapes with homogenously distributed resources
78 (or no resources at all) may mask the individual behavioural decisions related to energy requirements
79 (Spiegel et al. 2017, Cloyed and Dell 2019). Here we aimed to investigate the interdependency across size
80 and temperature gradients between metabolic rates and modes of behaviour (in terms of cumulative space

81 use, patch choice and time spent) in a resource-patchy environment. Given the temperature-dependence of
82 ectotherm metabolic rates, the incorporation of temperature into behavioural patterns via a metabolic
83 framework can be expected to shed light on the responses to ongoing climate change of consumer-
84 resource and predator-prey interactions.

85 To reduce the influence of confounding environmental factors, we performed controlled microcosm
86 experiments using the aquatic amphipod *Gammarus insensibilis* as a model organism across a wide range
87 of body masses and temperature regimes. Individual behavioural patterns were remotely quantified by
88 using advanced automated image-based tracking (Dell et al. 2014a), and the standard metabolic rate of the
89 specimens was accurately measured with an open-flow respirometry system (Glazier & Sparks, 1997).
90 The factorial design allowed us to disentangle the link between standard metabolic rate (SMR) and the
91 descriptors of time and space use behaviour across body mass (M) and temperature (T) gradients. To our
92 knowledge, this is one of the first studies (see also (Réveillon et al. 2022) of multi-trait resource and space
93 use behaviour accounting for factorial interactions among M, T and SMR under highly controlled
94 microcosm conditions.

95 **Materials and methods**

96 - *Experimental design*

97 The experiment made use of a full factorial design to assess the co-variation of individual foraging
98 behaviour with SMR in an aquatic ectotherm model organism, i.e. *Gammarus insensibilis*, across a range
99 of body masses and temperatures. The temperatures were selected to match the seasonal range
100 experienced by *G. insensibilis* in its local environment. The water temperature of the collection site was
101 monitored weekly from 2015 to 2019, and the assessment temperatures were *i.* the average winter
102 temperature (13°C), *ii.* the average annual temperature (18°C) and *iii.* the average summer temperature
103 (25°C). At each temperature level, we tested model organism specimens in a range of body sizes
104 corresponding to the species' size range in nature. The individual behaviour of *G. insensibilis* was
105 assessed using automated video tracking while foraging alone in a heterogeneous environment under
106 controlled microcosm conditions. The experimental microcosm (maze) was made up of six interconnected

107 patches, two of which contained differing amounts of resources, i.e. a rich patch (1 g) and a poor patch
108 (0.5 g), and four were empty, thus creating a heterogenous environment. After assessing foraging
109 behaviour, individual SMR was measured using an open-flow respirometer system.

110 - *Model organism*

111 *Gammarus insensibilis* (Stock 1966) is a widespread Atlantic-Mediterranean amphipod species living in
112 coastal and transitional waters, reaching maturity at 0.4 cm and growing to a maximum length of ~2 cm
113 (Costello et al. 2001). *Gammarus* species are selective foragers, feeding preferentially on fungi with high
114 protein content colonizing decomposed leaf litter (Bärlocher and Kendrick 1973). While foraging they
115 scroll the surface of the leaves seeking valuable resources, and when high-quality resources are not
116 available, they consume resources with a lower value (Cozzoli et al. 2022). Daily consumption rates are
117 from 46% to 103% of their body mass, depending on the type of exploited resource (Berezina 2007).
118 Additionally, when resources are abundant, they have a gut throughput time of 45-59 minutes at 14°C
119 (Welton et al. 1983). For the purposes of this study, the amphipod *G. insensibilis* is an ideal model
120 organism due to the ease of manipulation in the laboratory and the recent development of experimental
121 protocols (Shokri et al. 2021).

122 - *Specimen collection and acclimation*

123 Specimens of *G. insensibilis* were collected from the Cesine nature reserve, a transitional water body in
124 Italy, at the southern end of the Adriatic Sea (40.3624 N, 18.3325 E). Authorization for specimen
125 collection was issued by the competent authority (WWF, World Wildlife Fund for Nature, Italy). After
126 collection, the specimens were transferred alive to the laboratory in thermo-insulated containers filled
127 with water from the sampling sites and aerated during transport. The specimens were maintained in the
128 laboratory aquaria at a salinity of 7 g l⁻¹, similar to that of the sampling site, and acclimated to each of the
129 assessment temperatures for two weeks in order to reduce the risk of temperature shock that might affect
130 individual metabolic rates (Semsar-kazerouni and Verberk 2018). Acclimation to the low and high
131 temperatures with respect to that of the sampling site at the moment of collection was achieved gradually
132 at a rate of ±1.5 °C day⁻¹ in aquaria under controlled climatic conditions (KW apparecchi scientifici, WR

133 UR). Prior to the experiment, specimens were sorted by sex under a Nikon stereoscope (SMZ1270). Only
134 adult males were selected for behavioural assessment, since oocyte production in females may induce
135 non-size-related variability in energy requirements and behaviour, and to reduce potential variation due to
136 different ontogenic stages (Glazier et al., 2011).

137 - *Trophic resource preparation*

138 Leaves of *Phragmites australis* (Cav.) Trin. ex Steud were collected at the specimen collection site, cut
139 into approximately 10 cm lengths, oven dried at 60 °C for 72 hrs, weighed into separate portions (1 g for
140 the Rich patch and 0.5 g for the Poor patch) and placed in 5 mm mesh plastic bags. The amount of
141 resource in each patch (1 g, 0.5 g and 0 g) was considered to be sufficiently different for animals to
142 distinguish between them (Cozzoli et al. 2022). The leaves were then leached and conditioned for two
143 weeks in running environmental water at 18°C. The nutritional quality of the leaves is known to increase
144 during conditioning because of microbial colonization and the assimilation of nutrients from the water
145 (Boling et al. 1975).

146 - *Foraging behaviour setup and measurements*

147 The experimental system consisted of a microcosm (maze) made of transparent Plexiglas installed in an
148 isolated and temperature-controlled room (KW apparecchi scientifici, WR UR). The microcosm was
149 composed of six circular patches [13 cm in diameter, 3 cm high], connected by a network of channels [2.5
150 cm wide, 3 cm high] (Fig. 1b). The microcosm (maze) was placed on top of a near infrared backlight
151 source in order to achieve high contrast, which facilitated specimen detection. Three infrared-sensitive
152 cameras (Basler, aca1300-60gm) were mounted above the microcosm to film individual movement and
153 patch use. The temperature treatments were evenly spaced throughout the experimental period to
154 minimize possible varying acclimation effects.

155 Prior to the behaviour assessment, each of the analysed specimens was kept unfed for 24 hrs in the
156 climate-controlled room at the assessment temperature. This served to standardize specimens' resource
157 requirements at the start of experimental trials. For each experimental trial, 1 g dry weight of conditioned
158 leaf fragments was placed in one patch and 0.5 g dry weight of conditioned leaf fragments was placed in

159 another patch, thereby simulating a heterogenous resource distribution with two resource patches, “Rich”
160 and “Poor”, while the other four patches were “Empty”. The distribution of the resource patches was
161 randomized for each experimental trial to prevent any effect of microcosm geometry. The resource
162 patches were placed in the microcosm 30 min before starting the experiment. Each experimental trial was
163 performed on a single specimen foraging alone in the microcosm. The experimental trials were always
164 conducted at the same time of day (09:00 to 15:00) to prevent any effect of the model organism’s
165 circadian rhythms. Recordings were initiated 10 min after the specimen was released into the microcosm
166 and lasted for 6 hrs. The video files were then processed by Ethovision XT 14 in batch acquisition mode,
167 with the specimens identified by the software as moving elements with respect to the static background. A
168 patch was considered to have been “visited” once the specimen had travelled the full length of a channel,
169 entered a neighbouring patch and stayed there for at least 30 seconds.

170 - *SMR and body mass measurements*

171 After the behavioural measurement, the specimens’ Standard Metabolic Rate (SMR, J day⁻¹) was
172 measured. Although the sequential arrangement of metabolic measurements following behavioural
173 observations might hold the potential to introduce a degree of uncertainty, specimens were kept unfed
174 individually for 24 hrs before the SMR measurements. This step was taken to standardize the conditions,
175 minimize residual effects from the behaviour experiment, and also ensure the specimens were in post
176 absorptive state, as 24 hrs is sufficient to complete digestion in *Gammarus* sp. (Welton et al. 1983).
177 Following (Glazier & Sparks, 1997), individual Standard Metabolic Rate (SMR, J day⁻¹) was determined
178 by measuring the oxygen consumption. Animals were placed individually in Strathkelvin open-flow
179 system respirometers where the oxygen concentration was continuously measured by Clark-type
180 microelectrodes connected to an oximeter and recorded using the Strathkelvin software (SI, 929). A 0.3
181 mm nylon mesh with a nominal outer diameter of 12.07 mm was placed in each respirometer chamber in
182 order to minimize the individual’s spontaneous movement. After metabolic measurement, the animals
183 were dried individually in an oven at 60 °C for 72 hrs and then weighed on a micro balance (Sartorius
184 MC5) to the nearest ± 0.001 mg.

185 - *Data analysis*

186 The scaling of individual standard metabolic rate (SMR, j day^{-1}) with individual body mass (M, mg) and
187 temperature (T) was assessed via multiple linear regression. The response variable individual SMR and
188 the explanatory variable M were log-transformed in order to fit the size-scaling relationship as a power
189 law (Brown et al. 2004), and the temperature was inverse transformed to linearize its effect (Brown et al.,
190 2004; Gillooly et al., 2001):

191 $\log(\text{SMR}) \sim \log(M) \times (-T_A)$ (Eq. 1)

192 $T_A = \left(\frac{1}{k_B T_e} - \frac{1}{k_B T_0} \right)$ (Eq. 2)

193 T_A is a standardised inverse temperature, k_B is the Boltzman constant ($8.618 \times 10^{-5} \text{ eV/k}$), T_e is the
194 assessment temperature, and T_0 sets the intercept of the relationship at 286.15 K, corresponding to the
195 lowest temperature level (i.e., 13 °C in this study). Standardising the inverse temperature at T_0 , simplified
196 the interpretation of the main effect coefficients in the presence of interactions. The multiple linear
197 regression was fitted with full interaction between explanatory variables.

198 We analysed the specimens' behavioural patterns in the experimental microcosm with reference to three
199 descriptors of space and time use behaviour. (1) cumulative space used, approximated as the total number
200 of patches visited or revisited during the experiment. For the temporal trends in patch use throughout the
201 experimental time (i.e. 360 min), we quantified (2) the proportion of specimen's time spent in patches
202 with resources (rich and poor) within each 5-min time interval, and (3) the proportion of time spent in the
203 Rich patch relative to the time spent in patches with resources within each 5-min time interval. Descriptor
204 (2) describes the temporal trends of the specimens' time spent in resource patches compared to empty
205 patches, and descriptor (3) reflects how the specimens allocated their time between resource-rich and
206 resource-poor patches. A higher value indicates more time spent in the Rich patch, whereas a lower value
207 shows more time spent in the Poor patch by the specimens.

208 Individual variation in the behavioural descriptors was analysed across individual body mass (M),
209 temperature (T), and M and T independent SMR (residual SMR) gradients. We estimated the SMR
210 residuals, the components of a metabolic phenotype that is independent of mass and temperature, using
211 Eq. 1. This is hereafter referred to as M-T independent SMRs. We used this approach to examine whether
212 SMR affects behavioural patterns beyond the combined effects of size and temperature.

213 The variation in descriptor (1) (i.e. the cumulative number of patches visited during the experiment (N))
214 was investigated by linear regression along the M, T, and the M-and T-independent SMR gradient. Both
215 the response variable N and the explanatory variable M were log-transformed. As with the previous
216 analysis (Eq. 1), the explanatory variable temperature was inverse transformed. The multiple linear
217 regression was fitted with full interaction between explanatory variables.

218 For both descriptors of the temporal trend in patch use (2 and 3) we conducted binomial Generalized
219 Linear Mixed Models (GLMMs) with a logit link. For descriptor (3) the model accounted for trial
220 binomial data, wherein each observation represents the number of successes out of a given number of
221 trials (Douma & Weedon, 2019). This was chosen to handle the varying denominators associated with the
222 proportions of time spent in the Rich patch relative to patches with resources. For both of temporal trends
223 in patch use descriptors, the models were defined as a function of the continuous explanatory variables M,
224 T, and M-T independent SMR along with the experimental time. The explanatory variable forager body
225 mass was log-transformed in order to model size dependency as a power law and the temperature was
226 inverse transformed. In our models assessing temporal trends in patch use, to account for the non-
227 independence of observations repeated over time on the same individual, we initially fit the models with
228 both random intercepts and slopes at the individual level. However, the variance attributed to the random
229 slope for time was negligible (τ_{11} in all models was <0.0001). Given the minimal contribution of the
230 random slope and to avoid potential model overcomplication, we allowed random variation in the
231 intercepts at the individual level.

232 The relative importance of mass, temperature, and M- and T-independent SMR in explaining the variance
233 of the response variable was assessed by the LMG metric (R^2 partitioned by averaging over orders
234 (Lindeman et al. 1980)). The uncertainty of model estimates was reported as the 95% Confidence Interval
235 [lower-upper]. All analyses were performed within the ‘R’ free software environment (R Core Team
236 2019) using the lme4 (Bates et al. 2015), relaimpo (Groemping 2006), partR2 (Stoffel et al. 2021) and
237 sjPlot (Lüdecke 2018) packages.

238 **Results**

239 - *Specimen characterization*

240 The 75 male specimens of *G. insensibilis* used in this experiment ranged from 4.73 to 19.86 mm in body
241 length (on average 11.55 mm [\pm 4.04 SD]) and from 0.98 to 14.85 mg dry weight in body mass (on
242 average 6.59 mg [\pm 4.46 SD]). The body mass distribution of the analysed specimens was similar across
243 the three temperature treatments (ANOVA; $F_{2,72} = 0.07$, $p = 0.93$).

244 - *Size scaling SMRs across temperatures*

245 Overall, specimens’ individual Standard Metabolic Rates (SMR) ranged from 0.40 to 8.39 J day⁻¹ (on
246 average 3.15 J day⁻¹ [\pm 1.81 SD]) and increased with temperature, with an average of 2.09 J day⁻¹ [\pm 1.19
247 SD] at 13 °C, 2.79 J day⁻¹ [\pm 1.28 SD] at 18 °C and 4.57 J day⁻¹ [\pm 1.90 SD] at 25 °C. 76.1 % of the
248 variation in individual SMRs was explained by the positive dependency on M (48% of explained
249 variance, scaling exponent 0.62 [0.50 – 0.74 95% CI]) and T (28.1% of explained variance, scaling
250 exponent 0.69 [0.48 – 0.91 95% CI]) (Table 1, Fig. 1). An additional 2.9% of the observed variance in
251 SMR was explained by the marginal negative interaction between M and T (Table 1, Fig. 1), implying
252 that the rate of increase of SMR with temperature decreased slightly as body mass increased.

253 - *Space use*

254 49.7% of the observed variation in foragers’ cumulative space use was explained by its positive allometric
255 scaling with M (21.9 % of explained variance, scaling exponent 0.47 [0.27 – 0.67 95% CI], Table 2, Fig.
256 2a), the positive exponential relationship with T (27.8% of explained variance, exponent 0.72 [0.36 – 1.08

257 95% CI], Table 2, Fig. 2a). The interaction of M and T was not significant (Table 2). Additionally,
258 cumulative space use scaled positively with the foragers' M-T independent SMR, with a scaling exponent
259 of 0.84 [0.44 – 1.24 95% CI] (Table 2, Fig. 2b). This explained an additional 10.1% of the variation in
260 cumulative space use, beyond what was accounted for by body mass and temperature combined (Table 2,
261 Fig. 2b). The significant relationship between cumulative space use and M-T independent SMR, along
262 with its explained variation, indicates that SMR, when considered as a single descriptor in its entirety,
263 explains a greater amount of variance than that explained by body mass and temperature combined.

264 - *Temporal trends in patch use*

265 At the beginning of the experiment, the specimens displayed a marked preference for the Rich patch,
266 spending most of their time there, while the Poor and Empty patches were largely ignored (Table 3, 4,
267 Fig. 3). The initial preference for Rich patch was pronounced at increased temperature (Table 4, Fig 3c),
268 and was also observed among specimens with a higher M-and T-independent SMR (Table 4, Fig. 3d).
269 As the experimental time progressed, the time spent in the Rich patch decreased significantly, while it
270 increased in the Poor patch (Table 3, Fig. 3c, d). The shift from time spent in the Rich patch to time spent
271 in the Poor patch occurred earlier as body mass and temperature increased (Table 4, Fig. 3c). Moreover,
272 this shift from the Rich towards the Poor patch occurred earlier in individuals with higher M-and T-
273 independent SMR (Table 4, Fig. 3d). This implies that individuals with higher-than-average metabolic
274 rates for their size and the given temperature, those having higher M-and T-independent SMR, were more
275 prone to change their residency from Rich to Poor patch as experimental time continued.
276 Towards the end of the experimental time, the percentage of time spent by specimens with larger body
277 mass and by all specimens at the higher temperature decreased in patches with resources (Table 3, Fig.
278 3a). Similarly, specimens with higher M-T independent SMR exhibited a decrease in patches with
279 resources towards the end of the experimental time, corresponding to an increase in time spent in Empty
280 patches (Table 3, Fig. 3b).

281 The fixed effects including M, T, and M-T independent SMR, explained a significant and comparable
282 amount of variation in patch use behaviour (Table 3, 4). They collectively explained 24.1% of the
283 variance in the proportion of time spent in patches with resources and 30.3% in the proportion of time
284 spent in Rich patches relative to resource patches (Table 3, 4). Furthermore, the estimated random
285 variation across specimens was 18.1%, for the proportion of time spent in patches with resources and
286 19.8% for the proportion of time spent in Rich patches relative to resource patches, highlighting the
287 substantial individuality in patch use behaviour (Table 3, 4).

288 **Discussion**

289 Overall, we observed that foragers modulate their resource and space use behaviour in response to
290 variations in body mass, temperature and M- and T-independent SMR, highlighting the role of Standard
291 Metabolic Rate (SMR) in its entirety as the key predictor of foraging patterns. This is likely because SMR
292 (i) is mechanistically related to the individual's energy balance and resource needs, rather than being a
293 proxy of it, (ii) encompasses mass and temperature variations, (iii) is able to capture variations in energy
294 needs beyond size and temperature, linked for example to life style and phenotype (Killen et al. 2010),
295 and (iv) is intimately intertwined with informational control such as hormones (see Glazier, 2015).

296 - *Size scaling SMRs across temperatures*

297 In accordance with MTE expectations (*sensu* Brown et al., 2004), we observed that individual SMR
298 increased allometrically with body mass and exponentially with temperature. However, the mass scaling
299 exponents of SMR marginally decreased as temperature rose, implying that temperature-induced
300 increases in metabolic rate are less pronounced in large-sized individuals than smaller ones. The latter
301 observation accords with the Metabolic-Level Boundaries hypothesis (*sensu* Glazier, 2005; Glazier, 2020;
302 Glazier, 2014) and with empirical evidence e.g. (Hoefnagel and Verberk 2015, Shokri et al. 2022) that the
303 effect of temperature on metabolic rate is body mass-dependent.

304 - *Space use*

305 Individual cumulative space use was found to scale allometrically with body mass, implying that larger
306 individuals used more space than smaller ones. This is consistent with the classical framework of (McNab

307 1963) and with empirical studies e.g. (Minns 1995, Cozzoli et al. 2022, Udyawer et al. 2022). On the
308 other hand, we observed that individuals increased their space and resource use as a function of increasing
309 temperature (within thermal tolerance), likely via kinetic effects (*sensu* Abram et al., 2017). Furthermore,
310 we observed a marginal negative interaction between body mass and temperature in relation to SMR, but
311 this was not reflected in the cumulative space use behaviour of the specimens. This discrepancy may
312 indicate an adaptive behavioural response to warming. In response to temperature rise, organisms,
313 especially the larger ones, face depletion of somatic energy resources from increased metabolic
314 maintenance costs (see Glazier, 2015). As a result, they likely explored a greater cumulative space to
315 access new resources and intensified their foraging effort to fulfill these demands.

316 We observed that individuals with a high SMR, after accounting for body mass and temperature,
317 cumulatively explored a larger proportion of the space. This implies that individuals with higher M-and
318 T-independent metabolic rates are able to collect, process and invest more energy and explore a greater
319 space and resource in order to meet their requirements (since more energy would be needed to maintain
320 this level of metabolism (see also Metcalfe et al., 1995)). The observed positive correlation between SMR
321 and cumulative space use supports and extends the prediction from the performance model (*sensu* Biro &
322 Stamps, 2010), demonstrating that higher metabolic rates require a larger area to explore for resource
323 gathering in a patchy distributed environment.

324 - *Temporal trends in patch use*

325 Specimens at increased temperatures, as well as those with higher M-and T-independent SMR (beyond
326 those dictated by body mass and temperature), exhibited a marked preference, spending more time in the
327 Rich patch during the early hours of the experiment. This is likely because a more profitable patch offers
328 a higher energy gain per unit of time, enabling foragers to achieve their optimal ingestion rate in a
329 heterogeneous environment (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). As the experimental
330 time progressed, we observed that the time spent in the Rich patch decreased. This trend was sharper for
331 larger foragers, at increase of temperature, and those with higher M-and T-independent SMRs. The

332 specimens that left the resource-rich patch were observed to move and spend time in the Poor patch. Our
333 observations on patch use align with the theoretical frameworks (MacArthur and Pianka 1966, Charnov
334 1976) and extend these concepts by empirically demonstrating that foraging decisions are intimately
335 linked to an individual's metabolic rate. This connection provides a mechanistic understanding of how
336 metabolic processes influence the resource acquisition strategies, adding a new dimension to our
337 understanding of foraging behaviour. The findings on these temporal trends of patch selection and use
338 may potentially be explained by the combined effect of three mechanisms: (i) A higher SMR requires
339 higher ingestion rates (Rosenfeld et al. 2015); foragers with higher SMRs thus deplete the resource patch
340 more rapidly, resulting in shorter giving-up times than foragers with lower SMRs. (ii) Foragers with
341 higher SMRs leave the patch when the amount of resource reaches a level (the marginal value (Charnov
342 1976)) that can no longer fulfil their energy requirement rapidly enough, even though it would still be
343 economically viable for foragers with lower SMRs. This suggests that foragers with high metabolic rates
344 are less able to exploit patches until reaching a low level of resource (or patches that are resource-poor to
345 begin with), leading to a higher giving-up density than individuals with lower SMRs (see Cozzoli et al.,
346 2018; Kotler et al., 1993; Kotler & Brown, 1990). (iii) Individuals' resource specialization increases with
347 energy requirement (e.g., intrinsically or with warming), because resources with higher energy content
348 provide more energy per unit of processing time (Schoener 1974, Petchey et al. 2010). It follows that
349 foragers with high SMRs exploiting a resource patch should also perceive a faster decrease in the
350 available resource. Based solely on body mass, larger individuals are thought to be more selective of
351 resources, as they have a higher total energy requirement per unit of time than smaller ones (Cozzoli et al.
352 2022). However, as temperature increased, speeding up metabolic rates, we found that individuals with a
353 smaller body mass began to be more selective and perceive resource shortages in a similar way to larger
354 ones at lower temperatures. This finding highlights the synergistic effects of body mass and temperature
355 on resource specialization and perception via metabolic pathways. Moreover, while this observation
356 supports the size dependency of foragers' perception of available resources (*sensu* Basset et al., 2012;
357 Basset & De Angelis, 2007), it extends this framework from body size to metabolic dependence.

358 In light of our findings and the urgent concerns over the effects of climate change, further studies of
359 species and populations across latitudes under various climate change scenarios are needed. This would
360 further our knowledge of these mechanisms and the adaptive behavioural responses to global warming.

361 - *Ecological implications in the face of climate change*

362 The mechanistic link between metabolic rates and resource and space use behaviour raises the prospect of
363 understanding higher-order ecological processes, e.g. consumer-resource interaction, in the context of
364 climate change. Under global warming scenarios, the equilibrium resource density is expected to decrease
365 due to the temperature-driven rise in consumer metabolic and feeding rates being greater than any
366 corresponding rise in resource growth and turnover rates (Bruno et al. 2015). This is expected to lead to
367 stronger intraspecific competition among foragers owing to declining resource density, as well as
368 increased top-down control in the food web (Lindmark et al. 2018). As a result of lower resource
369 availability and increasing energy requirements with warming, animals are expected to range farther
370 afield, leading to larger home ranges and niche overlap (Börger et al. 2008). This can expose animals to
371 greater predation risk (Biro et al. 2009, Metcalfe et al. 2016, Balaban-Feld et al. 2022) and lead to stunted
372 growth over time (Huey and Kingsolver 2019, Lackey and Whiteman 2022), as the organism may not be
373 able to replace the energy it expends, because ingestion increases at a slower rate than metabolic rate as
374 temperature rises (Basset et al. 2012, Réveillon et al. 2022).

375 In summary, this study offers insights that contribute to bridging metabolic and foraging theories. It
376 showed that warming may have a profound influence on space/resource use and foraging decisions of
377 individuals of different sizes, which have far-reaching consequences for higher-order ecological
378 processes. Our results further highlighted the role of metabolic rate as the key predictor of behavioural
379 patterns which encompasses variations that extend beyond those attributed to body mass, temperature, or
380 their combination.

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555 Gammarus Pulex under Laboratory and Field Conditions with a Note on the Feeding of Young in
556 the Brood Pouch. *Oikos* 41:133–138.
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559 **Tables**

560 Table 1. Output of the linear regression model of the variation in standard metabolic rate (SMR, J day⁻¹)
561 across body mass (M) and temperature (T) gradients.

<i>Predictors</i>	log (SMR)					<i>df</i>
	<i>Estimates</i>	<i>CI</i>	<i>t value</i>	<i>p</i>		
(Intercept)	-0.40	-0.61 – -0.19	-3.81	<0.001	71	
log (M)	0.62	0.50 – 0.74	10.33	<0.001	71	
T	0.69	0.48 – 0.91	6.45	<0.001	71	
log (M) × T	-0.12	-0.24 – -0.00	-2.03	0.046	71	
Observations	75					
R ² / R ² adjusted	0.791 / 0.782					

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563

564 Table 2. (a) Output of the linear regression between the total number of visits to all patches, i.e.
565 cumulative space use, with respect to individual body mass (M), temperature (T) and M-T independent
566 SMR (residual).

<i>Predictors</i>	<i>Estimates</i>	log (total visits)			<i>df</i>
		<i>CI</i>	<i>t value</i>	<i>p</i>	
(Intercept)	3.16	2.81 – 3.52	17.75	<0.001	70
log (M)	0.47	0.27 – 0.67	4.64	<0.001	70
T	0.72	0.36 – 1.08	3.96	<0.001	70
SMR (Residual)	0.84	0.44 – 1.24	4.21	<0.001	70
log (M) × T	-0.06	-0.27 – 0.14	-0.63	0.528	70
Observations	75				
R ² / R ² adjusted	0.601 / 0.578				

567
568

569 Table 3. Output of binomial generalized linear mixed-effects model, where the response variable is the
 570 proportion of specimen's time spent in patches with resources within the 5-minute time interval. The
 571 explanatory variables include body mass (M), temperature (T), M-T independent SMR (residual) and
 572 experimental time as the continuous explanatory variables.

<i>Predictors</i>	%Time in resource patches			
	<i>Odds Ratios</i>	<i>CI</i>	<i>z value</i>	<i>p</i>
(Intercept)	14.40	6.29 – 32.95	6.31	<0.001
Time	1.00	1.00 – 1.00	0.13	0.897
log (M)	1.08	0.69 – 1.69	0.34	0.735
T	0.53	0.24 – 1.15	-1.61	0.107
SMR (Residual)	3.60	0.77 – 16.89	1.62	0.104
Time × log (M)	1.00	1.00 – 1.00	-6.65	<0.001
Time × T	1.00	1.00 – 1.00	-2.46	0.014
Time × SMR (Residual)	0.99	0.99 – 1.00	-5.56	<0.001
log (M) × T	0.94	0.62 – 1.42	-0.29	0.772
log (M) × SMR (Residual)	1.05	0.35 – 3.09	0.08	0.936
T × SMR (Residual)	0.58	0.15 – 2.26	-0.79	0.432
Random Effects				
σ^2	3.29			
τ_{00} individual	1.07			
ICC	0.25			
N individual	75			
Observations	5400			
Marginal R ² / Conditional R ²	0.241 / 0.422			

573

574

575 Table 4. Output of binomial generalized linear mixed-effects model, where the response variable is the
 576 proportion of time spent in Rich patch relative to resource patches over 5-minute time intervals. The
 577 explanatory variables include body mass (M), temperature (T), M-T independent SMR (residual) and
 578 experimental time as the continuous explanatory variables.

<i>Predictors</i>	%Time in Rich / Resource patches			
	<i>Odds Ratios</i>	<i>CI</i>	<i>z value</i>	<i>p</i>
(Intercept)	1.87	0.42 – 8.33	0.82	0.410
Time	1.00	1.00 – 1.00	3.03	0.002
log (M)	2.28	0.98 – 5.29	1.92	0.053
T	20.93	4.63 – 94.57	3.95	<0.001
SMR (Residual)	28.49	1.49 – 543.73	2.23	0.026
Time × log (M)	1.00	1.00 – 1.00	-10.46	<0.001
Time × T	0.99	0.99 – 0.99	-34.99	<0.001
Time × SMR (Residual)	0.98	0.98 – 0.99	-25.82	<0.001
log (M) × T	0.31	0.14 – 0.72	-2.73	0.006
log (M) × SMR (Residual)	3.55	0.38 – 32.91	1.12	0.264
T × SMR (Residual)	0.16	0.01 – 2.69	-1.27	0.205
Random Effects				
σ^2	3.29			
τ_{00} individual	1.29			
ICC	0.28			
N individual	75			
Observations	5400			
Marginal R ² / Conditional R ²	0.303 / 0.501			

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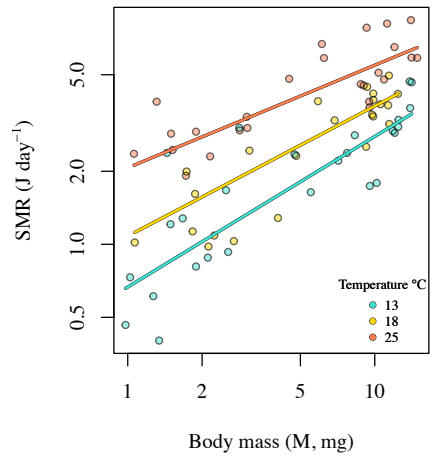
580 **Figure captions**

581 Figure 1. Standard metabolic rate (SMR, J day^{-1}) in relation to body mass (M, mg) across temperature
582 levels.

583 Figure 2. (a) Total number of visits to all patches in relation to body mass (M, mg) across temperature
584 levels. (b) Total number of visits to all patches in relation to M and T-independent standard metabolic rate
585 (residual SMR). Positive values of M-T independent SMR indicate individuals with higher-than-average
586 metabolic rates for their size and the given temperature, while negative values indicate the converse. The
587 secondary y-axis shows cumulative space use (m^2), calculated as the overall surface area of patches that
588 individuals visited.

589 Figure 3. (a-b) Model surfaces of time spent (%) in patches with resources within 5 min time intervals (a)
590 with respect to experimental time, body mass and temperature, and (b) with respect to M- and T-
591 independent SMR. Positive values of M-T independent SMR indicate individuals with higher-than-
592 average metabolic rates for their size and the given temperature and negative values indicate the converse.
593 (c-d) Model surfaces of time spent (%) in Rich patch relative to resource patches (c) with respect to
594 experimental time, body mass and temperature, and (d) with respect to M- and T-independent SMR.

595 Figure 1.

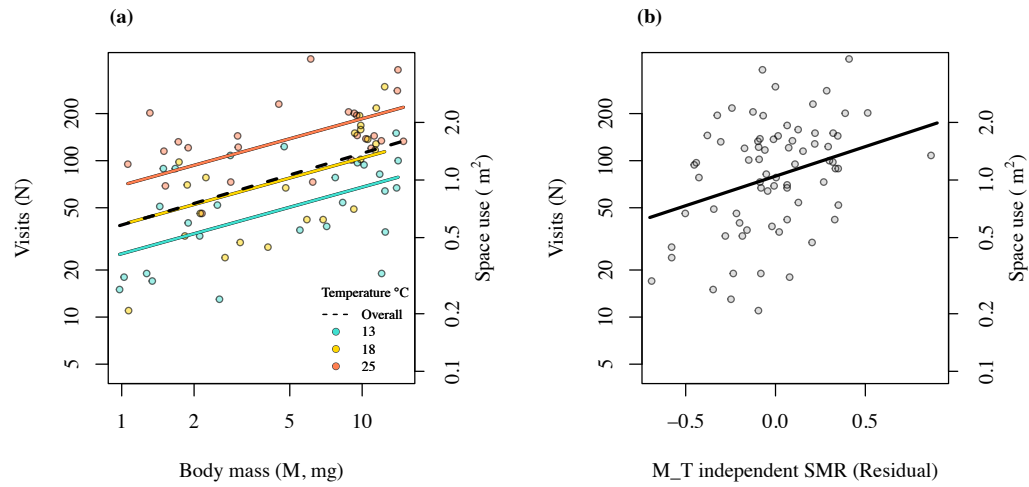


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600 Figure 2.



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603 Figure 3.

