The size dependency of foraging behaviour: an empirical test performed on aquatic amphipods

Francesco Cozzoli1,2 · Milad Shokri2 · Sarah Boulamai2 · Vanessa Marrocco2 · Fabio Vignes2 · Alberto Basset1,2

Received: 18 March 2021 / Accepted: 10 April 2022 / Published online: 9 June 2022
© The Author(s) 2022, corrected publication 2022

Abstract

The behavioural choices made by foragers regarding the use of resource patches have a direct influence on the energy balance of the individual. Given that several individual traits linked to the acquisition of spatially distributed resources increase with body size (e.g., energy requirements, resource ingestion rates, and movement capacity), it is reasonable to expect size dependencies in overall foraging behaviour. In this study, we tested how body size influences the number, duration, and frequency of foraging episodes in heterogeneous resource patches. To this end, we performed microcosm experiments using the aquatic amphipod Gammarus insensibilis as a model organism. An experimental maze was used to simulate a habitat characterised by resource-rich, resource-poor, and empty patches under controlled conditions. The patch use behaviour of 40 differently sized specimens foraging alone in the experimental maze was monitored via an advanced camera setup. Overall, we observed that individual body size exerted a major influence on the use of resource patches over time. Larger individuals had stronger preference for the resource-rich patches initially and visited them more frequently than smaller individuals, but for shorter periods of time. However, larger individuals subsequently decreased their use of resource-rich patches in favour of resource-poor patches, while smaller individuals continued to prefer resource-rich patches for the whole experimental time. With body size being a key organismal trait, our observations support the general understanding of foraging behaviours related to preference, patch use, and abandonment.

Keywords Body size · Foraging behaviour · Patch use · Aquatic amphipods · Microcosm

Introduction

Foraging decisions regarding the selection and abandonment of resource patches are crucial to individual fitness of motile foragers (MacArthur and Pianka 1966; Brown et al. 1988). For instance, optimal foragers should exploit a patch until the ingestion rate of the resources is higher than the average in the foraging area (MacArthur and Pianka 1966; Charnov 1976) or if/until the ingestion rate of resources balances the energy and fitness costs of foraging (Brown et al. 1988). Identifying the drivers of patch-scale foraging decisions is crucial to understanding population dynamics and large-scale patterns of space use (Potts et al. 2014; Van Moorter et al. 2016; Milles et al. 2020; Webber et al. 2020). The importance of body size as a driver of patch-scale foraging decision has long been recognized in ecological theory (Mittelebach 1981). However, the underlying mechanisms that determine the size dependence of foraging behaviour have not yet been fully investigated (Dial et al. 2008; Webber et al. 2020), hampering the mechanistic connection between size scaling and foraging theories (Hirt et al. 2018).

Larger body size implies higher energy costs (Kleiber 1932; West et al. 1997; Kooijman, 2000; Makarieva et al. 2004) which must be supported by higher ingestion of resources per unit of time (Peters 1983; Hendriks, 1999).
It follows that larger foragers have greater ability to manage and ingest large amounts of resources (Vucic-Pestic et al. 2010), and, therefore, are faster in exploiting abundant resource patches (Basset et al. 2012). However, larger foragers are also limited in exploiting patches with (or until reaching) a low resource level, because these patches cannot satisfy their higher energy need (Kotler and Brown 1990; Basset 1995; Cozzoli et al. 2018; Cozzoli et al. 2020). For instance, larger rodents may achieve higher foraging rates due to size-related adaptations (Brown et al. 1994), but they abandon the patch at higher residual resource density (Cozzoli et al. 2019). Furthermore, larger foragers generally have higher dispersal ability (Innes and Houlihan 1985; Hirt et al. 2017) and lower locomotion costs per unit of body mass (Denny 1980; Dial et al. 2008), which make it more convenient for them to seek and move to new and more abundant resource patches than further exploit the patch in use.

Mobile foragers modulate their use of a resource patch mostly by adjusting the duration and the frequency of their foraging episodes (Van Moorter et al. 2016). Generally, the higher the preference for a patch, the more frequently foragers visit it and the more time they spend there. However, longer and more frequent foraging episodes may reduce the locally available amount of resources (Van Moorter et al. 2009). Since larger foragers are expected to: (i) ingest more resource per unit of time when resources are abundant; (ii) abandon resource patches at higher resource levels than smaller individuals due to their higher energy requirements; (iii) have higher dispersal ability, making them more inclined to move and explore the surrounding space; the choice, duration, and the frequency of visits to resource patches are expected to be size-dependent, as well. To test these hypotheses, we performed microcosm experiments using the aquatic amphipod *Gammarus insensibilis* (Stock, 1966) as a model organism. Thanks to a novel methodological approach (Shokri et al. 2021), we were able to accurately describe the patch use behaviour of *G. insensibilis* specimens in a range of sizes (Fig. 1). This allowed us to describe the observed patterns in individual foraging as allometric functions (see Glazier 2021) of the foragers’ body mass.

**Materials and methods**

**Model organism**

The biological model used, *Gammarus insensibilis* (Stock, 1966) (Fig. 1), is a widely distributed crustacean species found in European transitional and coastal waters, reaching a maximal length of 19 mm at adult size (Tillin and White 2017). They disperse over short distances by relatively fast swimming movements (up to 10 cm s⁻¹) that are often interrupted by rest and feeding breaks of a few minutes (Shokri et al. 2021). *G. insensibilis* feed mainly by grazing microscopic fungi growing on submerged decaying plant litter (Nelson 2011). They are selective foragers, feeding preferentially on fungi with high lipid or protein content (Arsuffi and Suberkropp 1989). However, they exploit less palatable microorganisms or even the leaves matrix when their preferred food is in short supply (Rossi 1985; Graça et al. 1993; Aßmann et al. 2011; Mancinelli 2012). While feeding, *G. insensibilis* quickly scroll the surface of leaves for highly valuable resources (Basset 1992; Shokri et al. 2021).

**Experimental maze**

The experimental maze was made of transparent Plexiglas® and was composed of six circular patches (13 cm in diameter, 3 cm high) connected by a network of channels 2.5 cm wide and 3 cm high, of length variable between 5 and 42 cm (Fig. 1). A set of infrared-sensitive cameras (Basler aca1300–60gm) mounted above the maze was used to record
the movement of individual specimens. An infrared light source was placed under the maze to have high contrast and facilitate specimen detection. The video-tracking files were processed automatically by Ethovision XT 14 software to determine which patches were visited, for how long and when. The frame supporting the cameras, the backlight unit, and the analytical software were developed by Noldus Information Technology BV. The mazes were kept in an isolated and temperature-controlled room (18 ± 0.3 °C) to prevent external disturbance that could interfere with the behaviour of the specimens. See Shokri et al. (2021) for further details.

Trophic resource

As a trophic resource, we used leaves of Phragmites australis. The leaves were collected in early spring (at the same collection time as the animal specimens) in a single episode from a single location in the coastal area of the Acquatina lagoon (SE Italy, 40°26′31″N 18°14′19″E). Authorization for collection of the plant material was issued by the competent authority (the University of the Salento). In the laboratory, the leaves were cut into approximately 10 cm lengths, dried in the oven at 60 °C for 72 h, and weighed. The leaves were inoculated with water from the specimens’ collection site and conditioned for 2 weeks in circulating water at 18 °C before the experiment. The nutritional quality of the leaves is known to increase during conditioning because of microbial colonization and the assimilation of nutrients from the leaves by fungi and bacteria (Marks 2019).

Experimental procedures

Specimens’ collection and keeping

The specimens of G. insensibilis used in this experiment were collected in the Le Cesine National Nature Reserve (Vernole, SE Italy, 40°21′38″N 18°19′49″E) 2 weeks before the experiments. They were transferred to the Biodiversity and Ecosystem Functioning Laboratory (BIOforIU) of the University of the Salento in thermo-insulated containers filled with water from the sampling sites and aerated during transport. Authorization for the collection of specimens was issued by the competent authority (World Wildlife Fund Italy). Specimens were maintained in the laboratory’s aquaria for 2 weeks at a temperature of 18 °C and salinity of 7 (i.e., similar to the conditions at the sampling site of the specimens) and fed with decaying P. australis leaves. Given that P. australis is by far the largest contributor to plant organic detritus at the G. insensibilis collection site (Tomaselli et al. 2011), we are confident that the specimens were accustomed to this type of resource. Only males were selected for laboratory experiments, since oocyte production in females may induce non-size-related variability in energy requirements (Glazier et al. 2011; Becker et al. 2016).

Resources patches’ preparation

For each experiment trial, 1 g dry weight (DW) of conditioned leaves was placed in one of the maze’s patches (thereby creating a resource-rich patch) and 0.5 g DW was placed elsewhere (thereby creating a resource-poor patch), leaving the other four empty, thereby creating a heterogeneous environment. The positioning of the resource patches was randomised in each trial to minimize the potential influence of maze geometry on the specimens’ behaviour. We expected that during the experimental time (360 min), the specimens would selectively feed on the fungal biomass growing on the surface of the leaves rather than on the vegetal matrix (Graça et al. 1993; Mancinelli 2012). Therefore, they would explore the maze extensively even if they could theoretically support themselves on the resources present in a single patch (Basset 1992). As instantaneous growth rate of fungal biomass on submerged P. australis detritus is relatively low (ca. 0.7% d−1) and stable (Kominkova et al. 2000), we assumed that the growth of decomposing microorganisms after grazing was either negligible in the experimental timeframe (6 h) or constant across patches. The specific amount of resources used in this experiment to simulate resource-rich and resource-poor patches was determined through preliminary observation of our experimental systems. Lower amounts of resource than used did not allow to clearly distinguish differences in foraging. Greater amounts of resources had the effect of increasing the specimens’ residence time on the patches, making the overall experiment duration impractical.

Experimental trials

Prior to the experiment, specimens of different size were selected on the base of their body length, starved for 24 h to ensure similar starting conditions in individual resource requirements (Shokri et al. 2021). Using a constant starvation time for differently sized individuals might generate uncertainty in our observations due to size dependency in starvation resistance (Gergs and Jager 2014). However, lacking detailed a priori knowledge on the size-dependent behavioural response of G. insensibilis to starvation, we chose a constant time of 24 h, because it generally ensures physiological and metabolic equilibrium among differently sized individuals of aquatic invertebrates (Glazier et al. 2011; Shokri et al. 2019).

Each specimen was tested alone without replication, i.e., 40 separate experiments were conducted, each with a single specimen in the maze. Each trial lasted 6 h and it was carried out at the same time of day (9.00 to 15.00) at controlled
Table 1 Summary of the mixed regression model of the total number of visits to patch types during the complete experimental time (N, left) and the number of the visits to the resource patches only (N, right) with respect to the foragers’ individual body mass (M, mg DW), accounting for random variation in intercept at the level of experimental blocks.

| Predictors     | log(N of visits to all patches) | log(N of visits to resource patches only) |
|----------------|---------------------------------|------------------------------------------|
| (Intercept)    | 2.47                            | 2.06                                     |
| log(M)         | 0.46                            | 0.35                                     |
| Random effects |                                 |                                          |
| σ²             | 0.18                            | 0.22                                     |
| τ₀₀ Block      | < 0.01                          | < 0.01 Block                             |
| N Block        | 40                              | 40                                       |
| Marginal R²/conditional R² | 0.50/0.50             | 0.33/0.33                                |

Table 2 Summary of the mixed regression models of duration of visits to patches (h, left), time to return to the patches (h, centre) and individuals preference for patch typologies (%), right) with respect to the fixed terms experimental time (h), amount of resource originally present in the patch (Rich, Poor or Empty) and forager body mass (M, mg DW), accounting for random variation in intercept at the level of individuals nested within experimental blocks.

| Predictors     | log(Duration of visit) | log(Interval between consecutive visits) | logit(Preference) |
|----------------|------------------------|-----------------------------------------|-------------------|
| Intercept      | −2.21                  | −0.27                                   | 0.09              |
| Rich           | 2.05                   | −3.37                                   | 145.70            |
| Poor           | 0.61                   | −0.33                                   | 0.50              |
| Time           | −0.12                  | −0.25                                   | 1.25              |
| log(M)         | −0.36                  | −0.43                                   | 1.75              |
| Rich × Time    | −0.29                  | 0.56                                    | 0.52              |
| Poor × Time    | −0.06                  | −0.17                                   | 1.20              |
| Rich × log(M)  | −0.19                  | 0.77                                    | 0.33              |
| Poor × log(M)  | −0.06                  | 0.44                                    | 0.79              |
| Time × log(M)  | 0.08                   | −0.03                                   | 1.00              |
| Random effects |                         |                                         |                   |
| σ²             | 0.84                   | 1.49                                    | 3.29              |
| τ₀₀ Block      | 0.08 Block             | < 0.01 Block                            | < 0.01 Block      |
| N Block        | 40 Individual          | 40 Individual                           | 40 Individual     |
| Marginal R²/conditional R² | 0.28/0.28             | 0.22/0.22                               | 0.27/0.27         |

temperature (18 °C). The resource patches were placed in the maze 30 min before introducing the specimen, which were always released in one of the empty patches. During the experiment, we considered a patch “visited” if the tested specimen travelled the whole length of a channel from a neighbouring patch, entered the patch with its whole body, and remained there for at least 30 s. Thus, brief “probes” of patches lasting less than 30 s (which were also sporadically observed) were not considered to be foraging episodes for the purposes of the analysis. During these “probes”, the specimens were probably still able to evaluate the amount of resource present in the patch as they briefly explored the leaves’ surface. After the experiment, the specimens were dried individually in an oven at 60 °C for 72 h and weighed to the nearest ± 0.001 mg. The experiments were conducted in two separate time blocks (spring 2020 and autumn 2021), each block comprising 20 specimens.
Data analysis

The number of visits to type of patches (N) and number of visits to the resource patches only (N) during the whole experiment were used as a proxy for the individual cumulative space use and modelled as a function of the foragers individual body mass (mg DW). Since the relationships between body size and amount of space used are commonly formulated as a power law (Tamburello et al. 2015; Glazier 2021), the response and the explanatory variable were log-transformed. The two time blocks of measurements were fitted as random terms.

To investigate the change in the behaviour of foragers across time, the duration of the visits (h) to the type of patch defined according to the amount of resource originally present (empty, resource-poor or resource-rich) was modelled as a function of the fixed terms individual body mass (mg DW), starting time of the visit (h) and patch(es) type. Similarly, the interval between consecutive visits (h) to the same type of patch (empty, resource-poor or resource-rich) was modelled as a function of the fixed terms individual body mass (mg DW), ending time of the visit (h) and patch(es) type. Two-way interactions were included as fixed terms in both models. To account (i) for variations across the time blocks of measurements and (ii) for the non-independence of observations repeated over time on the same individual, we allowed random variation in intercept at the level of individuals nested within time blocks. The response variables’ duration of visits and interval between visits, and the explanatory variable body mass of the foragers were log-transformed to model the size dependency as a power law.

We quantified overall patch preferences of foragers by dividing the experimental time of 360 min into 72 slots of 5 min each. Each specimens’ foraging behaviour was expressed in terms of type of patch mainly frequented during each time slot. Pooling together observations from all specimens, this approach allows to quantify the overall patch preferences of the foragers, i.e., the fraction of individuals using a certain patch type at a given time during the experiment. Logistic regression was used to model variation in preferred patches with respect to the following fixed terms: experimental time (h), type of used patch (empty, resource-poor or resource-rich), and forager body mass (mg DW). Also in this case, the model was fitted with two-way interactions between fixed terms; the individuals nested within experimental blocks were used as random term; the explanatory variable body mass was log-transformed.

Uncertainty of model estimates was reported as 95% Confidence Interval [lower–upper]. All analyses were performed within the R free software environment (R Core Team 2019) using the lme4 (Bates et al. 2015) and sjPlot (Lüdecke 2018) packages. The full dataset is available as an appendix to this paper (Appendix A) and in the OSF repository (https://doi.org/10.17605/OSF.IO/GHVKN).

Results

Preliminary observations

The specimens used in this experiment (N = 40) had body masses ranging from 0.6 mg DW to 12.4 mg DW (average value 6.2 mg DW [± 4.1 SD]) (Fig. 1). During the experiment, the specimens moved continuously around the maze, alternating periods of exploitation of the resource patches with rapid exploration of the surrounding environment. Although the specimens also carried out activities other than foraging, while in the resource patches (e.g., hiding, resting, and intra-patch movements), much of their time was allocated to feeding. The number and/or duration of foraging episodes can thus be considered a positive measure of the resource patch value perceived by the foragers.

Fixed vs random effects

The mixed regression models were able to explain from 22% (interval between visits) to 50% (total number of
Fig. 3 Model response surfaces of duration of visits to patches (h) (A–C), interval between consecutive visits (h) (D–F), and preference for patch typologies (%) (G–I) with respect to the fixed terms experimental time (h) and forager body mass (mg DW). Regression models are summarised in Table 1.
visited patches) of the observed variance of patch usage behaviour descriptors on the base of the fixed terms. The estimated random variation across experimental blocks (N = 2) and individuals (N = 40) was virtually null (Tables 1–2), implying that our observations are highly replicable and that the behavioural pattern followed by different individuals is constant under the same external conditions.

**Total number of visited patches**

The total number of (re)visits to patches type by each forager ranged from 5 to 60, while the number of visits to the resource patches ranged from 3 to 33. Both the total number of (re)visited patch types and the number of visits to resource patches significantly (p < 0.001) increased as a hypoallometry of the foragers’ body mass (Fig. 2, Table 1).

**Duration of visits to the same patch type**

At the beginning of the experiment, the foragers made significantly (p < 0.001) longer visits to the resource-rich patch (estimated 17 min [14–21] for average-sized individuals) than to the resource-poor patch (estimated 5 min [4–8] for average-sized individuals) and to the empty patches (estimated 3 min [3–4] for average-sized individuals) (Fig. 3A–C, Table 2). The duration of the visits to the same patch type decreased significantly (p = 0.034) over time, in particular for visits to the resource-rich patch (p < 0.001) (Fig. 3A–C, Table 2). The duration of visits to the same patch type also decreased significantly (p < 0.001) at the increase of the body mass of the foragers, in particular for visits to the resource-rich patch (p = 0.032) (Fig. 3A–C, Table 2). However, the decrease over time in duration of visits was slower at the increase of the foragers’ body mass (p < 0.01). At the end of the experiment, the estimated duration of visits was of ca. 4 min independent of the type of patch and of the body mass of the forager (Fig. 3A–C, Table 2).

**Interval between consecutive visits to the same patch typology**

At the beginning of the experiment, the foragers abandoned the resource-rich patch for short intervals before returning to it (estimated 3 min [2–4] for average-sized individuals). The initial estimated time interval between consecutive visits of average-sized foragers to the resource-poor patch and to the empty patches, respectively, was of 63 min [39–101] and 21 min [16–28] (Fig. 3D–F, Table 2). Over time, the time interval between consecutive visits to the resource-rich patch increased significantly (p < 0.001). Simultaneously, the time interval between consecutive visits to the resource-poor patch and to the empty patches decreased (p < 0.001) (Fig. 3D–F, Table 2). The interval between visits to the resource-poor patch and to the empty patches decreased significantly (p < 0.001) at the increase of the forager’s body mass (Fig. 3D–F, Table 2). Conversely, the time intervals between visits to the resource-rich patch increased with the forager’s body mass (p < 0.001) (Fig. 3F, Table 2).

**Preference for patch type**

At the beginning of the experiment, the near totality of foragers preferred the resource-rich patch (Fig. 3G, Table 2). Over time, the foragers’ preference decreased significantly (p < 0.001) for the resource-rich patch (Fig. 3G, Table 2) and, simultaneously, increased significantly their preference (p < 0.001) for the resource-poor patch and for the empty patches (Fig. 3H–I, Table 2). As the foragers’ body mass increased, the preference for both resource patches decreased (p < 0.001) and preference for empty patches increased (p < 0.001) (Fig. 3G–I, Table 2).

**Discussion**

Overall, we detected a clear influence of specimens’ body mass on the use of resource patches. We also observed that the amount of resource present in a patch has a mass-dependent influence on the selection and abandonment of the resource patch.

Independent of body mass, the foragers exploited both the resource-rich and the resource-poor patches in repeated visits interspersed with moments of exploration of the surrounding environment and exploitation of the other resource patch. The vast majority of the long-lasting visits to the resource patches occurred in the early hours of the experiment, when, we assume, the previously starved foragers consumed most of the resource. Subsequent visits were progressively shorter in duration, suggesting that only part of the available resource was consumed during each foraging episode. This pattern could be explained by the fact that *G. insensibilis* are selective feeders, exploiting at first the most palatable part of the resource (Rossi 1985; Âßmann et al. 2011; Mancinelli 2012) and preferentially moving in search of other valuable resources rather than making full use of the patch under exploitation. This also implies that perceived patch value decreases with each foraging episode at a higher rate than can be inferred from the amount of residual resource alone, since a decrease in quality also occurs (Price and Correll 2001). This patch use strategy may have been selected, because it also reduces predation risk (Eccard et al. 2021).
that some of the unexplained variance we observed may result from non-size-related variation in energy requirements (Shokri et al. 2019). It should also be considered that there are interdependencies between individual’s energy requirements and behaviour (Glazier 2015), particularly active behaviours being energetically expensive and resulting in greater resource requirements (Halsey et al. 2015). It is therefore possible that individuals who spent more time on resource patches reduced their energy requirements. Furthermore, small individuals may adopt strategies aimed at reducing activity and diverting energy towards growth (Killen et al. 2007) or may differ in anti-predator behaviour (Gavini et al. 2020), which could also explain the lower frequency and longer stays in the resource patches that we observed with increasing size. New experiments involving accurate measurements of the individual forager’s metabolic rate are needed to better understand the relationship between body sizes, energy requirements, and patch exploitation behaviour. In addition, the role of individual personality (i.e., consistent difference between individuals in their behaviour across time and context, Dingemanse et al. 2010) should be investigated, because it could modulate the effect of size on resource exploitation (Cash-Padgett and Hayden, 2020; Cornwell et al. 2020) and foragers’ movement patterns (DiNuzzo and Griffen 2020; Milles et al. 2020).

**Implications**

The criteria used by foragers of varying size for resource patch selection and abandonment may provide a link between individual energy requirements and spatial and temporal variation in the resource landscape (Van Moorter et al. 2016; Auer et al. 2020). For instance, the extent to which animals are able to locally deplete resources should determine home range size (Mitchell and Powell 2004). Staying longer in one patch before moving to another (as observed with smaller foragers) should favour more systematic coverage and should therefore lead to relatively smaller home ranges (Kodric-Brown and Brown 1978; Paton and Carpenter 1984). In addition, having a higher capacity for movement and larger home ranges leads to fewer returns to individual patches (and longer periods between them), including those incompletely exploited during the first foraging episodes (Seidel and Boyce 2015). Therefore, the pattern observed in our experiment is consistent with the observation of steep positive scaling of home range with individual body size (Ofstad et al. 2016).

Although our experiments were carried out on a single species and on individuals foraging alone, the observed patterns in patch exploitation behaviour support the hypothesis of size-related coexistence mechanisms even with regard to a single resource (Wilson 1975; Basset 1995; Szabó and Meszéná 2006; Basset and DeAngelis 2007). Indeed, the inability of larger foragers to exploit patches down to a low
level of resources may enable smaller foragers to satisfy their requirements with what remains, and therefore to establish home ranges nested within those of their larger competitors (Basset 1995; Basset and DeAngelis 2007).

Our study highlights the importance of body size on foraging behaviours related to preference, patch use, and abandonment. Given the allometric links between body size, metabolism, home range, population density at carrying capacity, and potential coexistence, our observations can be included in a broader conceptual framework and contribute to the general understanding of space and resources use patterns in ecological systems.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-022-05195-8.

Acknowledgements This research was supported by the LifeWatch Italy network, with the contribution of the ECOPOTENTIAL project (H2020, Award Number 641762). We thank the following people and associations: WWF Italy and Giuseppe De Matteis for authorising specimen collections in the Le Cesine National Nature Reserve (Vernole, Italy); George Metcalf for language editing.

Author contribution statement FC, MS, and AB conceived and designed the experiments. MS and FV developed the methodology. MS carried out the experiments. MS and FC analysed the data. FC wrote the first draft of the manuscript; other authors provided editorial advice. AB was in charge of scientific supervision and funding acquisition.

Funding Open access funding provided by IRETI - LECCE DIPARTIMENTO DI SCIENZE E TECNOLOGIE BIOLOGICHE ED AMBIENTALI DELL’UNIVERSITÀ DEL SALENTO STRADA PROV.LE LECCE-MONTERONI SNC within the CRUI-CARE Agreement. This research was supported by the LifeWatch Italy network.

Declarations

Conflict of interest The authors have not disclosed any competing interests.

Ethical approval Ethics approval was not required for this study according to European Directive 2010 63 UE.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Allmann C, Rinke K, Nechwatal J, Elert EV (2011) Consequences of the colonisation of leaves by fungi and oomycetes for leaf consumption by a gammarid shredder. Freshw Biol 56(5):839–852

Arsuﬁ TL, Suberkropp K (1989) Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. Oecologia 79(1):30–37

Auer SK et al (2020) Metabolic rate interacts with resource availability to determine individual variation in microhabitat use in the wild. Am Nat 196(2):132–144

Basset A (1992) Functional aspects of coexistence relationships in aquatic systems. Atti Soc Ital Ecol 15:177–194

Basset A (1995) Body size, coexistence and guild structure: an approach through allometric constraints on home-range use. Ecolgy 76:1027–1035

Basset A, DeAngelis D (2007) Body size mediated coexistence of consumers competing for resources in space. Oikos 116:1363–1377

Basset A, Cozzoli F, Paparella F (2012) A unifying approach to allometric scaling of resource ingestion rates under limiting conditions. Ecosphere 3:2

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Soft 67:1–48

Becker J, Ortman C, Wetzl MA, Koop JH (2016) Metabolic activity and behavior of the invasive amphipod Dikerogammarus villosus and two common Central European gammarid species (Gammarus fossarum, Gammarus roeselii): low metabolic rates may favor the invader. Comp Biochem Phys A 191:119–126

Biro PA et al (2018) Metabolic scope as a proximate constraint on individual behavioral variation: effects on personality, plasticity, and predictability. Am Nat 192(2):142–154

Brown JS, Kotler BP, Smith R, Wirtz W (1988) The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408–415

Brown JS, Kotler BP, Mitchell WA (1994) Foraging theory, patch use, and the structure of a Negev Desert granivore community. Ecology 75(8):2286–2300

Careau V, Thomas D, Humphries MM, Reale D (2008) Energy metabolism and animal personality. Oikos 117:641–653

Cash-Padgett T, Hayden B (2020) Behavioural variability contributes to over-staying in patch foraging. Biol Lett 16(3):20190915

Charnov EL (1976) Optimal foraging: the marginal value theorem. Theor Popul Biol 9:129–136

Cornwell TO, McCarthy ID, Biro PA (2020) Integration of physiology, behaviour and life history traits: personality and pace of life in a marine gastropod. Anim Behav 163:155–162

Cozzoli F, Ligetta G, Vignes F, Basset A (2018) Revisiting GUD: an empirical test on size-dependencies of patch exploitation behaviour. PLoS ONE 13(9):e0204448

Cozzoli F, Gioni V, Basset A (2019) Size dependency of patch departure behaviour: evidence from granivorous rodents. Ecology 100(10):e02800

Cozzoli F et al (2020) Relationship between individual metabolic rate and patch departure behaviour: evidence from aquatic gastropods. Oikos 129(11):1657–1667

Cressman R, Krivan V (2006) Migration dynamics for the ideal free distribution. Am Nat 168:384–397

Denny M (1980) Locomotion: the cost of gastropod crawling. Science 208(4449):1288–1290

Dial K, Greene E, Ischick D (2008) Allometry of behavior. Trend Ecol Evol 23:394–401

Dingemans NJ, Kazem AJ, Réale D, Wright J (2010) Behavioural reaction norms: animal personality meets individual plasticity. Trends Ecol Evol 25(2):81–89
DiNuzzo ER, Griffen BD (2020) The effects of animal personality on the ideal free distribution. Proc R Soc B 287:20201095
Eccard J, Liesenjohann T, Dammhahn M (2020) Among-individual differences in foraging module resource exploitation under perceived predation risk. Oecologia 194:621–634
Gavini SS, Quintero C, Tadey M (2020) Intraspecific variation in body size of bumblebee workers influences anti-predator behaviour. J Anim Ecol 89(2):658–669
Gerger A, Jager T (2014) Body size-mediated starvation resistance in an insect predator. J Anim Ecol 83(4):758–768
Glazier DS (2015) Is metabolic rate a universal ‘pacemaker’ for biological processes? Biol Rev 90:377–407
Glazier DS et al (2011) Ecological effects on metabolic scaling: amphibian responses to fish predators in freshwater springs. Ecol Monogr 81(4):599–618
Glazier DS (2021) Biological scaling analyses are more than statistical line fitting. J Exp Biol. https://doi.org/10.1242/jeb.241059
Graça MAS, Multhy L, Calow P (1993) Importance of fungi in the diet of Gammarus pulex and Asellus aquaticus I: feeding strategies. Oecologia 93(1):139–144
Halsey LG et al (2015) The interactions between temperature and activity levels in driving metabolic rate: theory, with empirical validation from contrasting ectotherms. Oecologia 177(4):1117–1129
Hendriks AJ (1999) Allometric scaling of rate, age and density parameters in ecological models. Oikos 86:293–310
Hirt MR et al (2017) The little things that run: a general scaling of invertebrate exploratory speed with body mass. Ecology 98(11):2751–2757
Hirt MR et al (2018) Bridging scales: allometric random walks link movement and biodiversity research. Trend. Ecol. Evol. 33(9):701–712
Hollling CS (1992) Cross-scale morphology, geometry and dynamics of ecosystems. Ecol Monogr 62:447–502
Innes AJ, Houlihan DF (1985) Aerobic capacity and cost of locomotion of a cool temperate gastropod: a comparison with some Mediterranean species. Comp Biochem Physiol A Physiol 80(4):487–493
Killeden SS, Brown JA, Gamperl AK (2007) The effect of prey density on foraging mode selection in juvenile lumpfish: balancing food intake with the metabolic cost of foraging. J Anim Ecol 76(4):818–825
Kleiber M (1932) Body size and metabolism. Hilgardia 6:315–353
Kodric-Brown A, Brown JH (1978) Influence of economics, interspecific competition, and sexual dimorphism on territoriality of migrant rufous hummingbirds. Ecology 59(2):285–296
Kominkova D et al (2000) Microbial biomass, growth, and respiration associated with submerged litter of Phragmites australis decomposing in a littoral reed stand of a large lake. Aquat Microb Ecol 22(3):271–282
Kooijman SALM (2000) Dynamic energy and mass budgets in biological systems. Cambridge: Cambridge University Press
Kotler BP, Brown JS (1990) Rates of seed harvest by two species of gerbilline rodents. J Mammal 71(4):591–596
Lüdecke D (2018) sjPlot: Data visualization for statistics in social science. [Online] Available at: https://CRAN.R-project.org/package=sjPlot [Accessed R package version 2.6.2]
MacArthur RH, Pianka ER (1966) On optimal use of a patchy environment. Am Nat 100(916):603–609
Makarieva AM, Gorshkov VG, Li BL (2004) Body size, energy consumption and allometric scaling: a new dimension in the diversity-stability debate. Ecol Complex 1:139–175
Mancinelli G (2012) To bite, or not to bite? A quantitative comparison of foraging strategies among three brackish crustaceans feeding on leaf litters. Est Coast Shelf Sci 110:125–133
Marks JC (2019) Revisiting the fates of dead leaves that fall into streams. Annu Rev Ecol Evol Syst 50:547–568
Milles A, Dammhahn M, Grimm V (2020) Intraspecific trait variation in personality-related movement behavior promotes coexistence. Oikos 129(10):1441–1454
Mitchell MS, Powell RA (2004) A mechanistic home range model for optimal use of spatially distributed resources. Ecol Model 177:209–232
Mittelbach GG (1981) Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62(5):1370–1386
Nelson D (2011) Gammarus-microbial interactions: a review. Int J Zool 2011(295026):1–6
Ofstad EG, Herfindal I, Solberg EI, Sæther BE (2016) Home ranges, habitat and body mass: simple correlates of home range size in ungulates. Proc R Soc B 283(1845):20161234
Paton DC, Carpenter FL (1984) Peripheral foraging by territo- rious rufous hummingbirds: defense by exploitation. Ecology 65(6):1808–1819
Peters RH (1983) The ecological implications of body size
Potts JR et al (2014) Predicting local and non-local effects of resources on animal space use using a mechanistic step selection model. Met Ecol Evol 5(3):253–262
Price MV, Correll RA (2001) Depletion of seed patches by Merriam’s kangaroo rats: are GUD assumptions met? Ecol Lett 4(4):334–343
R Core Team (2019) R: A language and environment for statistical computing. [Online] Available at: https://www.R-project.org/
Rossi L (1985) Interactions between invertebrates and microfungi in freshwater ecosystems. Oikos 44(1):175–184
Seidel DP, Boyce MS (2015) Patch-use dynamics by a large herbivore. Mov Ecol 1(1):7
Shokri M et al (2019) Components of standard metabolic rate variability in three species of gammarids. Web Ecol 19(1):1–13
Shokri M et al (2021) A methodological approach to assess the space use behavior of macroinvertebrates by using automated video tracking. Ecol Evol 11(7):3004–3014
Spaargaren DH (1999) Shape and hydrodynamic properties in relation to size in marine macro-Crustacea. Crustaceana 72:203–214
Szabó P, Meszéna G (2006) Spatial ecological hierarchies: coexis- tence on heterogeneous landscapes via scale niche diversification. Ecosystems 9(6):1009–1016
Tamburrello N, Côté IM, Dulvy NK (2015) Energy and the scaling of animal space use. Am Nat 186(2):196–211
Tillin H, White N (2017) Marine Life Information Network: Biology and Sensitivity Key Information Reviews. Plymouth: Marine Biological Association of the United Kingdom.
Tomasselli V, Di Pietro R, Sciandrello S (2011) Plant communities structure and composition in three coastal wetlands in southern Apulia (Italy). Biologia 66(6):1027–1043
Van Moorter B et al (2009) Memory keeps you at home: a mechanistic model for home range emergence. Oikos 119(1):1027–1043
Van Moorter B et al (2009) Memory keeps you at home: a mechanistic model for home range emergence. Oikos 119(1):1027–1043
Van Moorter B, Rolandsen CM, Basille M, Gaillard J-M (2016) Movement is the glue connecting home ranges and habitat selection. J Anim Ecol 85:21–31
West G, Brown JH, Enquist B (1997) A general model for the origin of allometric scaling laws in biology. Science 276:122–126
Wilson DS (1975) The adequacy of body size as a niche measure. Am Nat 109:769–784