Research

Phenotypic determinants of inter-individual variability of litter consumption rate in a detritivore population

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The metabolic theory of ecology predicts resource consumption rates of animals from their body mass, but other phenotypic traits might affect individual resource consumption rate. In this paper, we used a hierarchical framework to examine relationships between phenotypic traits thought to constrain variation in per capita resource consumption rate. Physiological and behavioural traits were assumed to be important in mediating the control of morphology and sex on consumption. We conducted a longitudinal study aiming to relate the consumption rate of submerged leaf litter to sex, morphological, physiological and behavioural traits in an aquatic detritivore population. Then, we analysed the pattern of trait covariation using structural equation modelling (SEM). We observed broad and repeatable inter-individual variation in leaf consumption rate and other phenotypic traits. We found that expressing litter consumption rate relative to the time individuals spent feeding revealed and increased the effect of body mass and sex differences, respectively. Accordingly, SEM analyses showed that time allocated to resource acquisition mediated body mass and sex effects on apparent litter consumption rate whose variation was also accounted for by an indicator of activity-specific metabolic rate. Substantial variation in resource consumption rate was due to sex difference whereas body mass was of secondary importance. Individual phenotypic trait variations strongly altered consumer–resource relationships. Therefore, we encourage studies on consumers' intraspecific variability to advance knowledge about phenotypic determinants of individual resource consumption, an important link between individuals and ecosystems.

Keywords: behavioural type, consumer–resource interaction, energetic balance, gammarids, intraspecific variation, leaf litter, morphology, structural equation modelling (SEM)

Introduction

Animals consume resources at rates spanning over several orders of magnitude and a lot of this variability is explained by body mass (Pawar et al. 2012). This makes sense since large organisms require more energy than smaller ones to maintain essential body functions (Brown et al. 2004). Because energy expenditure is not solely driven

by body mass, mass-independent variations in resource consumption rate are also expected between individuals of a same species or population (see Fig. 2 in Careau et al. 2008). Energy requirement, foraging behaviour and resource consumption rates can differ between sexes due to asymmetric contribution of males and females to reproduction, parental care, and sexual dimorphism (Plaistow et al. 2003, Geffard et al. 2010, Becker et al. 2013, Fryxell et al. 2015). In addition, phenotypic traits beyond sex or body mass should explain the remaining variation in resource consumption rate (Bolnick et al. 2003, Sih et al. 2004, Biro and Stamps 2010). Feeding morphological traits could constrain the handling of resources and reflect trophic specialisation (Araújo et al. 2008). There is also ample evidence that animals can display consistent behavioural differences (Sih et al. 2004, Wolf and Weissing 2012) and such an intraspecific behavioural variability can influence consumer–resource interaction through mass-independent effects (Raffard et al. 2017, Start and Gilbert 2017).

A premise of ecology is to predict the resource consumption rates of organisms with their phenotypic traits (Violle et al. 2007, Brousseau et al. 2017). However, current approaches often assume independence among phenotypic traits (Verberk et al. 2013). This raises inferential issues (Shipley 2004), since phenotypic traits could be interdependent or causally related (Arnold 1983, Garland and Losos 1994, Violle et al. 2007, Careau and Garland 2012, Pey et al. 2014, Coelho et al. 2017, Závorka et al. 2017). Here we use a hierarchical approach (cf. Agrawal et al. 2010) to examine relationships among phenotypic traits (Fig. 1). Resource consumption rate could be directly conditioned upon physiological (e.g. metabolic rate in activity and at rest), behavioural (e.g. time budget) and morphological traits (e.g. shape of mouthparts) and, indirectly, by sex difference. Sex difference may impose limits on the range of morphological, physiological and behavioural traits (Fryxell et al. 2015). Morphology (e.g. body size) is assumed to drive variations in physiological and behavioural traits, and thus to have an indirect effect on consumption rate. Although the reverse holds true (i.e. morphological plasticity is induced by change in physiological traits), the processes underpinning morphological control over physiological and behavioural traits conceivably operate within a shorter period than morphological plasticity. The same rationale is applied to the case of allometric scaling relationships between metabolic rate and the size of organisms, as size is viewed as a cause, not a consequence of variation in metabolism (Brown et al. 2004).

To assess the phenotypic determinants of individual variations in resource consumption rates, we measured phenotypic traits in a wild population of the freshwater amphipod *Gammarus fossarum,* which primarily relies on submerged leaf litter as a food source. We used a longitudinal design where litter consumption rate was measured twice over time. As prerequisites to infer hypothesised traits-to-resource consumption rate causation, we expected repeatable interindividual differences, and coordinated variations among the
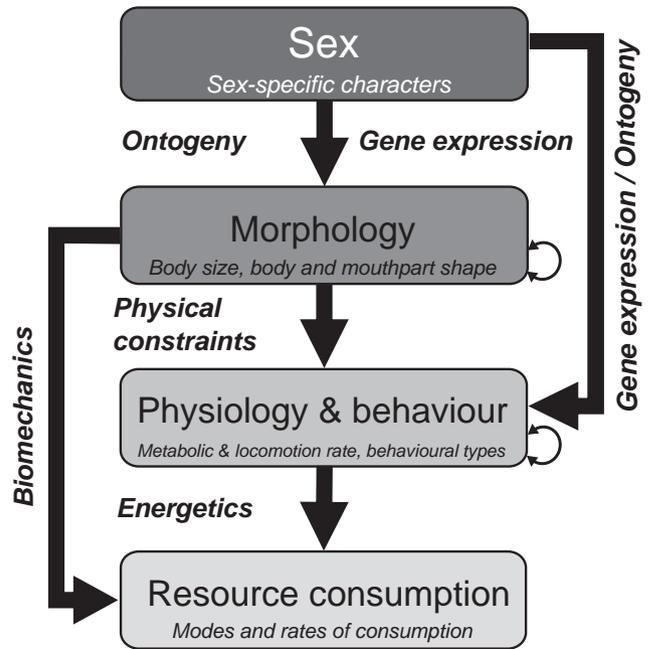

Figure 1. Hierarchical framework for organising the phenotypic traits controlling resource consumption. Each box represents a type of traits (examples are given in italics). Examples of biological mechanisms and processes underpinning causal relationships (arrows) are given in bold italics. Two-headed arrows represent covariations between traits of the same type.

phenotypic traits. Beyond a positive effect of body mass and differences among males and females, we predicted a positive covariation among specific metabolic rate proxies at rest and in activity, alike a positive direct effect of energy expenditure proxies on consumption rates (Careau and Garland 2012). Hierarchical relationships among the traits were examined using structural equation models (SEMs), built relative to our conceptual model and a priori information.

Material and methods

Animal collection and experimental design

We collected gammarids from natural accumulations of submerged leaf litter in a 10 m long reach of a first-order forested stream (Lampy, 43°26′7.3″N; 2°9′56.8″E; southwestern of France) in January 2016. We immediately transported them in a cool box to the laboratory and held them to a constant temperature room set at 9°C (actual mean: 9.28°C, SD = 0.32). We used horticultural LED lightning to create a 11:13 photoperiod light–dark regime with light flux alternating between <1 to 198 lux. Two small light bulbs set in opposite corners of the room ensured that there was sufficient illumination to record videos of the microcosms during dark phases. All video captures done in this study were recorded using a video camera pointed vertically downwards, set at 1.3 m above a white laboratory bench.

After a one-week acclimation period to room conditions, we sorted gammarids into females and males based on primary sexual characters (i.e. presence of oocytes and first stage embryos for females). We did not consider juveniles in this study because of their low reliance on leaf litter as a food source (Felten et al. 2008). A subset of 78 individuals was selected in such a way that sex- and size-dependent variations of phenotypic traits could be teased apart. There were equal numbers (39) of females and males with body length being distributed over ranges of 8.25–12.29 mm and 8.77–13.89 mm, respectively. We placed animals individually in microcosms consisting of food grade plastic containers (diameter: 117 mm, height: 61 mm), filled with 90 ml of spring bottled water, and renewed with 20 ml of water every three days. Gammarids were allowed to feed ad libitum on submerged litter from the stream until five days prior to going through a sequence of two experiments to assess litter consumption rate, time budget, pleopod beat rate, and locomotion velocity. We repeated this sequence twice at a one-week interval to assess the consistency of traits over time. Then, we sacrificed and dissected the individuals before body mass determination and mandible morphometry analyses. Mortality was low (5%) over the study period.

Litter consumption and time budget (experiment 1)

We moved gammarids individually to new microcosms supplied with ash *Fraxinus excelsior* leaf litter as resource, and containing two 2-cm long pebbles underneath which gammarids could hide while not feeding. We took care to ensure minimum variability of the palatability of the food items offered to gammarids. We collected abscised leaves of similar appearance (size, colour and toughness) from one tree and cut 10-mm diameter leaf discs using a cork borer, avoiding the central vein. Following the procedure of Jabiol et al. (2013), we conditioned leaf discs for six days in a nutritive liquid medium containing spores of six species of aquatic hyphomycetes. Batches of four leaf discs were then freeze-dried, weighed to the nearest 0.001 mg (mean mass: 6.24 mg; SD = 0.57) and stored at –20°C prior being offered to gammarids. Elemental C-to-N ratio of the leaf discs exhibited very small variation around the mean (n = 13, mean = 22.4, CV = 8%).

Each gammarid was allowed to feed on a set of pre-weighed and re-wetted leaf discs for two days. We used ten control microcosms without animal to assess leaf mass loss solely due to leaching and microbial decomposition. At the end of experiment 1, we transferred individuals in new microcosms containing water only. Remaining leaf fragments larger than 1 mm were freeze-dried and weighed. We calculated apparent consumption rate (apparent CR, mg d^{-1}) as follows:

$$\text{apparent CR} = \frac{\left(M_i - M_f\right) - \varepsilon}{T}$$

where M_i and M_f are the initial and final dry mass of litter in microcosms with animals, respectively, ε is the mean mass of litter lost in control microcosms (n = 10), and T is the experiment duration (i.e. 2 days). We calculated an effective rate of litter consumption (effective CR) by dividing apparent CR by the fraction of time each individual allocated to feeding.

During the feeding experiment, gammarids allocated their time to feed on ash leaf litter, to shelter underneath pebbles, and to move in the microcosm. The relative amount of time spent on each activity (i.e. time budget) was determined based on 15-min video sequences recorded at four occasions, one at daytime and one at nighttime on two consecutive days. We extracted one frame per 30 s from each video sequence using the software VitualDub (ver. 1.10.4). Then, we analysed images to determine the number of occurrences of each type of behaviour (feeding, sheltering or moving) in light and dark conditions. We estimated the relative time allocated to feed, shelter or move (hereafter referred as 'feeding RD', 'sheltering RD' and 'movement RD', respectively, expressed in % of time), by dividing occurrences by the total number of frames analysed.

Ventilation and locomotion velocity (experiment 2)

Twenty-four hours after the end of the feeding experiments, we placed gammarids individually in petri dishes (diameter: 6 cm, height: 2 cm), filled with 15 ml of water and allowed them to acclimate for 1 h. Ventilation activity of pleopods at rest was used as a proxy of mass-specific resting metabolic rate (Vellinger et al. 2012). Not only metabolism at rest but also metabolism when animals are active might affect energetic demands (Humphries and McCann 2014). Consequently, we designed an index combining the locomotion activity duration (i.e. movement RD) with the intensity of this locomotion activity (i.e. locomotion velocity). Therefore, this index represents a proxy of the mass-specific metabolism in activity (Peters 1983). We made measurements during light phases. We counted pleopod beats visually over three 30-s periods, after animals had stayed ca 5-min at rest. We summed the number of beats over the three counting periods and expressed them as a rate (beat min^{-1}). After 1 h, we determined locomotion velocity based on a 5-min video recording of all petri dishes. We then converted the video record to a sequence of images at a rate of one frame every three seconds and analysed them using Image J (ver. 1.46). We tracked individuals between consecutive frames in order to determine their mean locomotion velocity (cm s^{-1}). The index representing mass-specific metabolism in activity (hereafter referred to 'velocity × movement RD') was calculated as the product of mean locomotion velocity (expressed in cm h^{-1}) and movement RD (expressed in h), the latter being assessed in experiment 1.

Mandible shape and body mass measurements

Morphological traits were measured after having completed all experiments on living organisms. We sacrificed gammarids by placing them in a freezer set at –20°C. The left mandible of each individual was dissected, mounted on a microscopic slide under a glycerol drop, and photographed with a dissecting microscope equipped with a numeric camera at a 40-fold magnification. We then freeze-dried individuals and weighed them to the nearest 0.001 mg.

Morphological analysis

The external shape of mandibles was described by 7 landmarks and 70 semi-landmarks using the software tpsDig2 ver. 2.3.2 (Rohlf 2005, for details about morphometrics, see Webster and Sheets 2010). After digitisation, we converted landmark and semi-landmark coordinates to warp scores after a superimposition stage, and analysed the corresponding shapes using the R package 'geomorph' (Adams et al. 2017). The two first axes of the principal component analysis (PCA) of warp scores accounted for 60% of the variability of mandible shapes among individuals (n = 71). Deformation grids indicated that the first principal component 'mandible PC1' (40% of the variance in the data set) was associated with differences in thickness of the basal part of the mandible, whereas the second principal component 'mandible PC2' (20% of the variance) was associated with differences in curvature of the incisor process (Supplementary material Appendix 1 Fig. A1).

Data analysis

Seven mandibles were broken at the dissection stage, and one and three individuals died during experiment 1 and 2, respectively. Moreover, we excluded one additional individual that displayed an extreme behaviour: it spent 2.1% of its time feeding, while its congeners spent on average 60.3% (± 24.3 SD). Therefore, we used a dataset of 68 observations for multivariate analyses (PCA, PERMANOVA and SEM) as well as for linear models testing for the effects of body mass and sex on other traits. In contrast, we used the totality of observations (147 to 152 observations) available for repeatability analyses.

We evaluated the repeatability of traits measured in the two experiments by the mean of the intraclass correlation coefficient (ICC; Dingemanse and Dochtermann 2013). We estimated ICCs using generalised linear mixed-effects models with no fixed effect and individual identity as a random variable. We obtained ICCs and 95% confidence intervals by bootstrapping 1000 samples, and significance was tested using a likelihood ratio test (LRT). We also assessed the repeatability of traits in terms of covariation pattern. We computed two correlation matrices with trait values determined twice over time, and compared these covariance matrices using the Jennrich test (Jennrich 1970). Trait values and their covariations were consistent over time; therefore, phenotypic variability was assessed based on trait values averaged over trials.

We assessed the main and interactive effects of body mass and sex on phenotypic traits using a two-way permutational multivariate analysis of variance (PERMANOVA), based on the Euclidean distances. We visualised correlations among traits and similarities among individuals using a principal component analysis (PCA). To prevent the influence of trivial correlations on PCA results, we specified sheltering RD and velocity × movement RD as supplementary rather than active variables. The former trait was strongly associated with time spent feeding and moving whereas the latter was intrinsically related with the two traits (i.e. feeding RD and mean locomotion velocity) combined for its calculation. All multivariate analyses were performed using standardised data (mean = 0 and SD = 1).

We analysed traits separately using generalised linear models (Table 1). As the interaction between sex and body mass was not significant in the PERMANOVA, we did not test it in further analyses in order to limit the risk of false discoveries. We assumed a Gaussian error distribution for the

Table 1. Phenotypic traits measured on *Gammarus fossarum*. Intraclass correlation coefficients (ICC) are displayed along with bootstrap 95% confidence intervals (CI 95%, bootstrap: 1000 samples). The log-likelihood ratio test (LRT) was performed to evaluate the significance of ICC (i.e. ICC > 0). ICC was not calculated for morphological traits, as they were measured once. Apparent consumption rate (*) was estimated assuming that individuals spent 100% of their time feeding. Effective consumption rate (**) was calculated based on the actual feeding duration. '–' indicates non-calculated values for composite traits.

Traits	ICC (CI 95%)	LRT (χ^2)	p	Mean	Range	CV (%)	Body mass $F_{1,65}$	p	Sex $F_{1,65}$	p
Time budget										
Feeding RD (% of time)	0.74 (0.66 – 0.80)	4984.2	<0.001	60.34	15.42 – 100	40.3	31.17	<0.001	6.34	0.01
Sheltering RD (% of time)	0.76 (0.69 – 0.81)	5018.2	<0.001	34.74	0 – 80.42	68.6	32.84	<0.001	4.79	0.03
Movement RD (% of time)	0.72 (0.61 – 0.78)	716.8	<0.001	4.92	0 – 20.83	109.3	0.10	0.75	1.92	0.17
Litter consumption										
Apparent consumption rate (mg d^{-1})*	0.35 (0.13 – 0.53)	9.7	<0.001	0.74	0 – 1.49	51.8	0.82	0.39	3.94	0.05
Effective consumption rate (mg d^{-1})**	–	–	–	1.55	0 – 8.56	93.0	13.27	<0.001	6.72	0.01
Energy expenditure proxies										
Pleopod beat rate (beats min^{-1})	0.65 (0.50 – 0.76)	40.8	<0.001	142.70	79.7 – 200.0	20.8	2.65	0.11	3.76	0.06
Locomotion velocity (cm s^{-1})	0.23 (0.02 –0.45)	4.0	0.020	1.02	0 – 3.82	83.2	0.16	0.69	0.49	0.49
Velocity × movement RD (cm)	–	–	–	222.10	0 – 1525	129.6	0.28	0.60	2.36	0.13
Morphology										
Mandible PC1 (thickness)				–	–	73.3	35.10	<0.001	1.19	0.28
Mandible PC2 (incisor process curvature)				–	–	81.2	0.00	0.98	3.91	0.05
Body mass (mg)				4.44	1.06 – 10.11	37.4			15.78	<0.001

statistical analyses of all traits except time budget traits, for which we assumed a binomial distribution. Assumptions of generalised linear models were assessed visually using residuals versus fits plots, which did not reveal serious inferential problems.

Finally, we examined how apparent CR was influenced by phenotypic traits using SEM (Shipley 2004), computed from variance–covariance matrices (function *sem* in package 'lavaan'; Rosseel 2012). First, we constructed a minimal model including sex, body size and other important traits selected based on results from multivariate and univariate analyses. We refrained from testing all phenotypic traits at a time because our dataset was not large enough to properly fit complex SEMs. We rather added one or two variables at a time to the minimal model in order to obtain a model exhibiting the best balance between a high r² of apparent CR versus a low AIC*c*. Total, direct and indirect effects and their standard errors were computed based on the results of the final model using the function *sem* and the delta method (Rosseel 2012). Indirect effects were calculated as the sum of the products of path coefficients along all indirect pathways. Total effects equalled the sum of direct and indirect effects. We performed all statistical analyses using the R software (ver. 3.3.1, <www.r-project.org>).

Data deposition

Results

Evidence for inter-individual phenotypic variability

Gammarids spent on average 60% of the time feeding, 35% sheltering underneath pebbles, and 5% moving in the microcosms (values extrapolated over the 48 h experimental period). They consumed 0.74 mg leaf litter per day. This value was twice as low as the grand mean rate of effective CR (1.55 mg d⁻¹ if individuals spent 100% of their time feeding). Individuals performed, on average, 143 pleopod beats per minute at rest and moved at a rate of 1 cm s⁻¹. The body mass of gammarids determined at the end of the study varied over a ten-fold range. We detected substantial variations around the mean in all traits assessed in this study (CV = 21–130%; Table 1).

ICC always significantly departed from zero with values ranging from 0.23 to 0.76. Mean locomotion velocity (ICC = 0.23) and apparent CR (ICC = 0.35) were moderately repeatable whereas pleopod beat rate and time budget traits were highly repeatable (from ICC = 0.65 to 0.76, respectively). The consistency of traits was also highlighted by the statistically indistinguishable covariance matrices of the traits assessed in the two trials (Jennrich test: $\chi^2_{15} = 9.52$, p = 0.85).

Patterns of trait covariation

A two-way PERMANOVA test indicated that sex ($F_{1,64} = 3.10$, p < 0.01, r² = 0.04) and body mass ($F_{1,64} = 11.50$, p < 0.001, r² = 0.14) accounted for significant variations in other traits. The mass-by-sex interaction was not significant ($F_{1,64} = 1.18$, p = 0.30, r² = 0.02), suggesting that body mass was equally important in determining phenotypic variations in males and females. A PCA of quantitative traits showed that body mass correlated positively with mandible PC1 and sheltering RD (included as a supplementary variable), and negatively with feeding RD (Fig. 2a). These three traits had by far the highest loadings on the first principal component (PC1), which captured 30.3% of the total variance in the traits specified as active variables in the analysis. PC1 also discriminated males and females, the latter having on average lower scores than the former (Fig. 2b). PC2 was largely unrelated to sex and body mass, yet it still captured substantial phenotypic variation
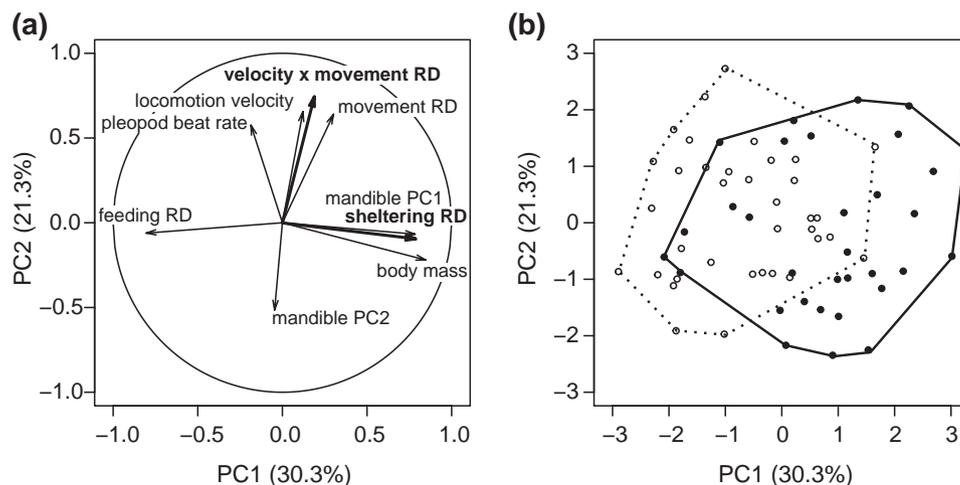

Figure 2. Principal component analysis of phenotypic traits. The correlation circle (a) and ordination plot of the individuals (b) were drawn for the two first principal components, which condensed 51.6% of the total variation in phenotypic traits within the dataset. Traits in regular characters were specified as active variable and those in bold characters were included as supplementary variables (a). Solid and open dots depict males and females, respectively (b). The convex hull of all individuals of the same sex is also displayed.

(21.3%). PC2 was primarily related to specific metabolism proxies. Pleopod beat rate, movement RD, locomotion velocity and their product (velocity × movement RD; included as a supplementary variable) loaded positively on PC2 whereas the scores of the second axis of mandible shapes (mandible PC2) had a negative loading. The product velocity × movement RD contributed the most to PC2 (Fig. 2a).

Explaining inter-individual variation in litter consumption rate

The body mass of animals did not predict their apparent consumption rate ($F_{1,65}=0.82$, p = 0.37). We observed only a small difference between males and females ($F_{1,65}=3.94$, p = 0.05, Fig. 3a). When we took the actual amount of time that individuals allocated to feed into account (effective CR), the effect of body mass became significant and the effect of sex was stronger (Table 1, Fig. 3b). Effective CR increased significantly with body mass ($F_{1,65}=13.27$, p < 0.001) and was on average higher in males than in females ($F_{1,65}=6.72$, p = 0.01; Fig. 3b). These results were not strongly influenced by three outliers displaying extremely high effective CR (4–9 mg d^{-1}). These three individuals were those that spent the least time feeding, explaining their high effective CR. The relationship between apparent CR and body mass did not provide evidence for allometric scaling, since the power-law exponent was close to zero (non-linear estimation: $b = 0.16 \pm 0.15$ SE, $t_{1,65}=1.04$, p = 0.30; Fig. 3a). This was not the case either for the relationship between effective CR and body mass, since the power law exponent was closer to 1 (non-linear estimation: $b = 0.93 \pm 0.31$ SE, $t_{1,65}=3.04$, p < 0.01; Fig. 3b).

We constructed a first SEM based on the hypothesized hierarchical relationships among phenotypic traits (cf. Fig. 1) and abovementioned results. We found that both sex and body mass affected indirectly apparent CR through feeding RD, but also that sex had direct (i.e. mass-independent) effects on feeding RD and apparent CR (Fig. 4a). As this model explained very little variance in apparent CR ($r^2=0.13$), we sought to identify further predictors (Supplementary material Appendix 2). We found that the r^2-value for apparent CR almost doubled when we added the proxy for specific metabolism in activity (velocity × movement RD) into SEMs. This trait had a direct effect on apparent CR whereas, unlike feeding RD, it was independent of sex and body mass (Fig. 4b; Supplementary material Appendix 2). The initial (Fig. 4a) and final (Fig. 4b) models provided comparable estimates of path coefficients, yet the former was more parsimonious than the latter (AICc = 643 versus 826).

Total effect estimates for phenotypic traits revealed that inter-individual variation in apparent CR was primarily due to sex differences (p = 0.02; Fig. 4c). Feeding RD and velocity × movement RD still had a substantial influence on apparent CR (p < 0.01). In contrast, body mass differences did not significantly account for variation in apparent CR (0.06, p = 0.61). Partitioning total effect into direct and indirect components revealed that direct effects were by far the most
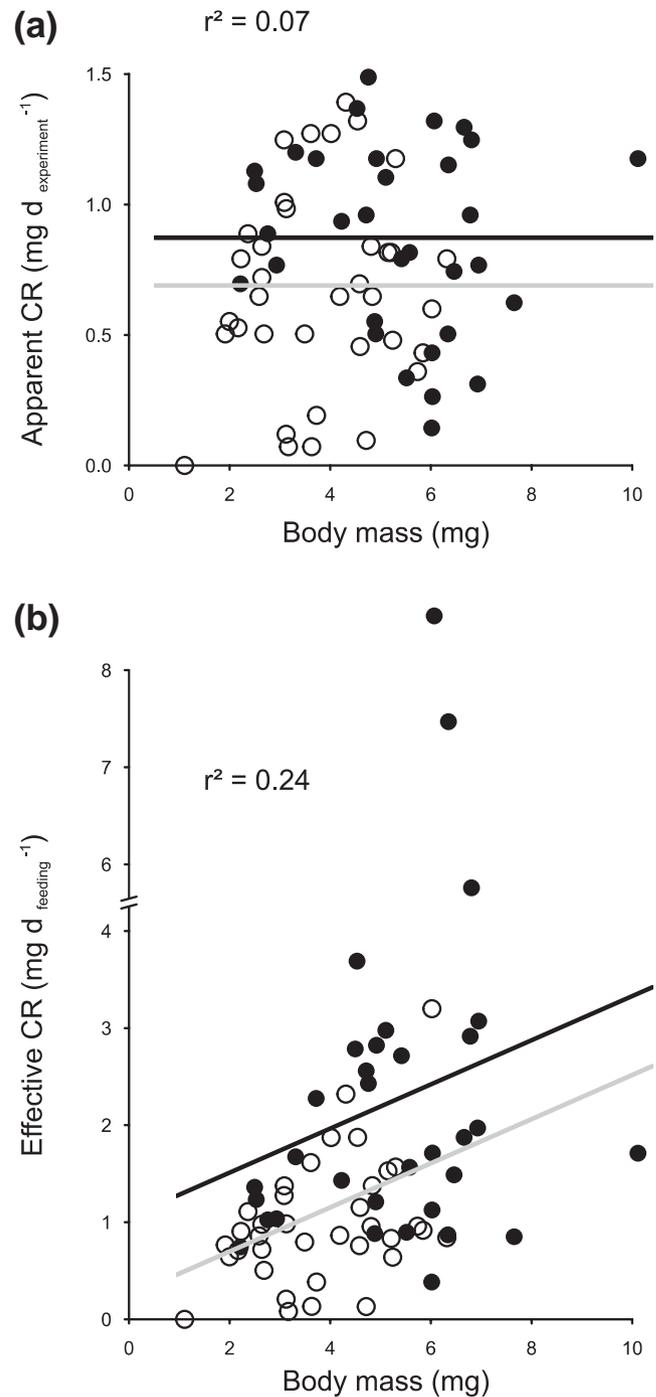

Figure 3. Apparent (a) and effective (b) consumption rate of litter by gammarids as a function of body mass. Solid and open dots depict males and females, respectively. Black and grey lines are intercepts (a) and regression lines (b) for males and females, respectively. r^2-values are computed from a model including body mass and sex as main effects.

important in determining how phenotypic traits controlled apparent CR in this study. In contrast, estimates for indirect effects were not significant for all traits, except for body mass (p = 0.03; Fig. 4c).
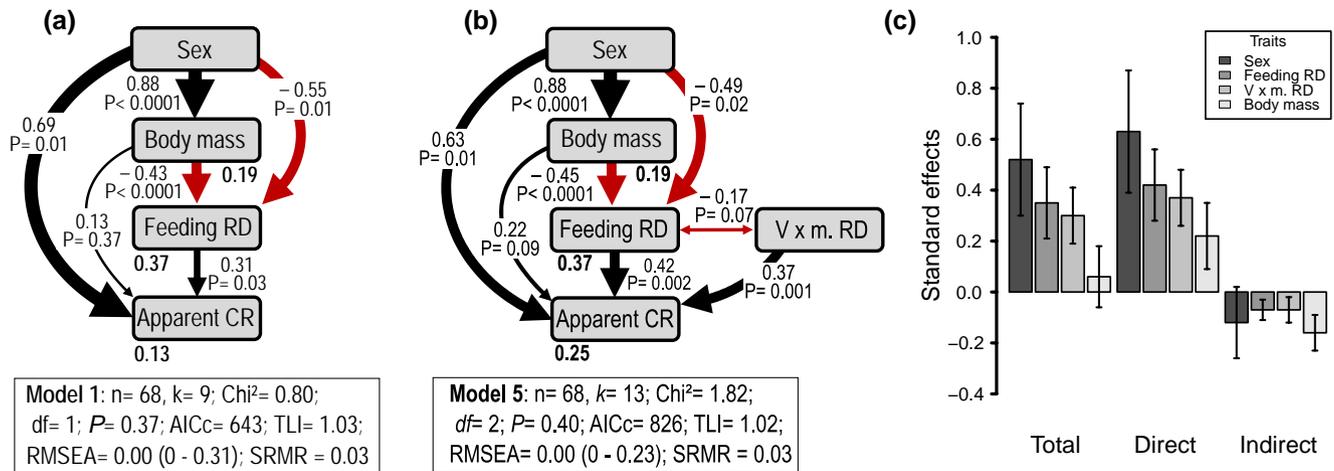
Figure 4. (a) Initial structural equation model describing how a behavioural trait (Feeding RD) constrains the effects of body mass and sex on apparent consumption rate of litter. (b) Final structural equation model including a physiological trait used as a proxy of specific metabolism in activity ('V × m. RD'). Black and red arrows indicate positive and negative relationships, respectively, and the size of arrows is proportional to path coefficients (i.e. beta estimates). The signs of path coefficients of 'Sex' correspond to the effect of male compared to that of female gammarids. The two-headed arrow represents covariances. r^2-values are given in bold. The boxes below the models contain summary statistics. A valid model should have a χ^2 p-value > 0.05, RMSEA < 0.06, TLI > 0.90 and SRMR < 0.08. (c) Barplots of total, direct and indirect effects assessed in the final model shown in panel (b). Error bars are standard errors (SE).

Discussion

The hierarchical framework we designed to assess intrinsic determinants of individual resource consumption rate was useful to organise hypotheses about how phenotypic traits drive variation in resource consumption rate and to assess the relative importance of hypothesised relationships. Two a priori predictions were supported by our data: 1) litter consumption rate was controlled by physiological (a proxy of specific metabolism in activity) and behavioural (feeding RD) traits and 2) the behavioural trait was constrained by sex and body mass. In contrast, we did not expect that a strong influence of sex on litter consumption rate would be transmitted through a direct pathway. As sex had an influence on feeding RD, a significant indirect effect of sex on litter consumption rate was expected to occur. This was not the case, conceivably because the apparent direct effect of sex on resource consumption was, in fact, mediated by unmeasured traits linked to resource consumption.

There are many reasons why female and male gammarids are different in terms of resource consumption. The a priori higher energy demand in females, associated with egg and embryos production as well as their ventilation (Geffard et al. 2010), should be balanced by a higher resource consumption than in males. However, the mate-guarding behaviour of male gammarids may be energetically costly (Plaistow et al. 2003, Becker et al. 2013). In our study, while female gammarids did exhibit higher pleopod beat rates than males, reflecting higher standard metabolic rates, they also ingested resource at lower rates for the same amount of time spent to feed (lower effective CR, Fig. 3b). A possible explanation is that females compensated the energetic cost inherent to

reproduction by selecting the highest quality resource patches, which is consistent with the longer feeding duration observed in females (Fig. 4b). The ability to select the most nutritive patches at the surface of the leaf mosaic (Bärlocher 1985) could thus be higher in females, and be related to subtle differences in mandible shape between sexes (i.e. higher curvature of the incisor process for females). Intuitively, a curved incisor process for females is better suited to graze leaves on a 2d space, while streamlined incisor processes for males might be an advantage for shredding leaves (Supplementary material Appendix 1 Fig. A1). A close examination of the shape of leaf discs at the end of the feeding experiments provided evidence that females indeed grazed the surface of leaf discs, while males shredded at their edge (Supplementary material Appendix 1 Fig. A3).

In this study, resource consumption rate varied over a wide (ca one order of magnitude) range and, as expected, individual differences were repeatable. A recent study has reported similarly large and temporally-consistent individual variation in litter consumption rate in an omnivorous crayfish species (Raffard et al. 2017). Another common thread between these studies was that body size explained little variation in resource consumption rate at the intraspecific level. A tight size-consumption relationship is expected when it is inferred from interspecific data encompassing many orders of magnitude variation (Pawar et al. 2012). As we narrow down the range of body size variation, such as in studies of single species, mass-dependent variation in consumption rate may become less prominent (Maino and Kearney 2015).

Small-sized individuals are known to invest more energy in growth than large individuals, which exhibit small biomass production (Brown et al. 2004, Houston and McNamara

2014). Here, the behaviourally-mediated body mass effect on consumption rates (Fig. 3, 4c), may reveal a tradeoff between survival and energy intake rates. The rationale is that older individuals, which have a high reproductive value, should adopt a behaviour that minimises mortality whereas younger individuals should seek for rapid growth (Biro et al. 2005, Killen 2011, Houston and McNamara 2014). This tradeoff may explain why small individuals spent more time feeding in our study, unlike larger ones, which spent more time in shelters (Fig. 2a). Additionally, the size and shape of mandibles may also determine how much time gammarids spent feeding on leaf litter. However, the biomechanical explanation is not supported by our results, as no significant relationship was found between feeding RD and mandible morphology axes (Supplementary material Appendix 1 Fig. A2b–c).

As behavioural traits measured in our study were repeatable and covaried together, our results lend support for the existence of behavioural types in the gammarid population investigated (Sih et al. 2004). The behavioural type is defined here in term of activity energy expenditure assessed by the mean of the velocity × movement RD index (see PCA axis 2 in Fig. 2a). Moreover, covariations between physiological and behavioural traits (Fig. 2a), as well as the positive effect of the velocity × movement RD index on litter consumption rate (Fig. 4b), indicate that gammarid individuals were distributed along a continuum of energy turnover from slow to fast rates. This is consistent with the POLS hypothesis (Biro and Stamps 2008, 2010, Réale et al. 2010). The POLS hypothesis states that aggressive and bold individuals displaying highest locomotion activity exhibit also higher standard metabolic rate. This is because fast metabolism can sustain energetically costly behaviours, but in turn requires a higher energy intake rate (Careau et al. 2008, 2014, Biro and Stamps 2010, Careau and Garland 2012).

Proxies used to assess standard and in activity specific metabolic rates were not significantly related (Supplementary material Appendix 1 Fig A2d). Biro et al. (2016) found similar results, and observed that swimming activity levels in guppies did not relate significantly with resting metabolic rate, while it was related with peak metabolic rate. In our study, the gammarids expressing high locomotion activity tended to spend a little time feeding on leaf discs, while consuming large amounts of litter. This might indicate that such active individuals adopted a pulse foraging strategy (Biro et al. 1996, 2016).

A commonplace tenet in ecology is that the effects of phenotypic variability on ecosystems are higher among species than between populations or individuals of a same species. However, this postulate should be revised downward, since meta-analyses have shown that intra- and interspecific variability are almost equally important in mediating the biotic control on ecosystems (Palkovacs et al. 2015, Des Roches et al. 2018). Although the present study was not designed to compare magnitudes of biological variations across levels of organisation, it provides evidence that intraspecific variability of consumption rate within a population of litter consumers have phenotypic determinants. Litter consumption is an important mechanism through which litter decomposition occurs (Gessner et al. 2010) and, therefore, this fundamental ecological process may be affected by phenotypic changes in detritivore populations.

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