# Reports

# The little things that run: a general scaling of invertebrate exploratory speed with body mass

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*Abstract.* Speed is a key trait of animal movement, and while much is already known about vertebrate speed and how it scales with body mass, studies on invertebrates are sparse, especially across diverse taxonomic groups. Here, we used automated image-based tracking to characterize the exploratory (voluntary) speed of 173 invertebrates comprising 57 species across six taxonomic groups (Arachnida, Chilopoda, Diplopoda, Entognatha, Insecta, Malacostraca) and four feeding types (carnivore, detritivore, herbivore, omnivore). Across all individuals, exploratory speed (mm/s) scaled with body mass (g) following a power-law relationship with a scaling exponent of $0.19 \pm 0.04$ (mean $\pm$ SE) and an intercept of $14.33 \pm 1.2$. These parameters varied substantially with taxonomic group and feeding type. For the first time, we provide general empirically derived allometric scaling relationships of exploratory speed across broad taxonomic groups of invertebrates. As exploratory speed drives key components of species interactions, such as encounter and attack rates, or competition, our study contributes to a deeper understanding of the role of individual movement in population and community level processes.

*Key words:* allometry; automated tracking; behavior; body size; computer vision; encounter rate; movement.

## INTRODUCTION

Relative to their high diversity, invertebrates are often underrepresented in ecology as they are more difficult to study than the much larger vertebrates. Nevertheless, they are "the little things that run the world" (Wilson 1987) not only by sheer abundance and diversity but also by contributing to key ecosystem structure, functions, and services (Wilson 1987, Hochkirch 2016). Thus, information on invertebrate ecology is crucial in all ecological fields, including movement ecology. The metabolic rate of animals determines the overall average rates of energy requirements (comprising resource consumption, biomass production, and reproduction; Brown

et al. 2004, Savage et al. 2004). For mobile animals, the movement in time and space transforms these rates into interactions with their environment, such as finding resources or mating partners, escaping predators, reaching breeding/oviposition sites, or dispersing. Uncovering the factors that constrain animal movement is thus essential for a mechanistic understanding of how animals survive and reproduce in the real world, including species' interaction strengths (Pawar et al. 2012), spatial distributions (With et al. 1997, Fryxell et al. 2004), and meta-community structures (Davies et al. 2001, Massol et al. 2011). While these relationships have partially been identified for vertebrates (Peters 1983, Domenici 2001, Hedenström and Rosén 2001, Hirt et al. 2017), additional research on invertebrate movement is needed (Kissling et al. 2014, Kalinkat et al. 2015).

The high diversity of invertebrates hinders systematic measurement of the movement of every species, but allometric scaling relationships can be used to generate

general predictions based on individual body masses. Similar to many physiological and ecological parameters (Brown et al. 2004), movement speed has also often been shown to follow a power-law relationship with body mass (Peters 1983, Hedenström 2003, Bejan and Marden 2006). Most of these studies focused on vertebrates, especially mammals, reptiles, and birds (Pennycuick 1997, Van Damme and Vanhooydonck 2001, Iriarte-Díaz 2002, Bejan and Marden 2006, Clemente et al. 2009). These studies comprise several types of speed, including movement where the animal is working at maximum or near maximum capacity (e.g., during attack or escape) and where movement is less strenuous (e.g., during habitat exploration, foraging, dispersal, or migration). Theory derived from metabolic and biomechanical first principles assumes that the metabolic power expended for movement ($\propto B_0 m^\beta$, where $B_0$ is a coefficient that depends upon taxon, metabolic state, and body temperature, and $m^\beta$ represents body mass and its scaling exponent) equals the product of body speed ($v$) and force ($F$) applied by the locomotory appendage (leg, wing, tail, etc.) onto the environmental medium yielding $v \propto B_0 \, m^\beta / F$. Since force is proportional to the cross-sectional area of body and appendage muscles, it scales with body mass as $F = F_0 M^{\beta_F}$, with $\beta_F$ typically varying between 0.50 and 0.67 (Peters 1983, Schmidt-Nielsen 1984, Pawar et al. 2012). This results in

$$v = aM^b \qquad (1)$$

where $a = B_0/F_0$ and $b = \beta - \beta_F$. Using the scaling of field to maximal metabolic rate (0.8–0.9; Pawar et al. 2012), $v$ should scale with mass to an exponent between 0.13 ($\beta = 0.8$, $\beta_F = 0.67$) and 0.4 ($\beta = 0.9$, $\beta_F = 0.5$; Pawar et al. 2012). Most empirically derived (mostly vertebrate) scaling exponents fall within this range (Peters 1983, Van Damme and Vanhooydonck 2001, Bejan and Marden 2006, Clemente et al. 2009). The few empirical studies that include more than two invertebrate species either do not report allometric equations (e.g., Forsythe 1983) or focus on a single taxonomic group (e.g., ants, whose foraging speed scales with mass to an exponent between 0.14 and 0.32 with a central tendency around 0.25; Hurlbert et al. 2008). A general empirical analysis of the allometry of invertebrate speed across broad taxonomic and functional groups is still lacking.

A key contributor to this dearth of comparative empirical studies of invertebrates is probably the technical difficulty of measuring speed for small animals. Here, we used automated image-based tracking (Dell et al. 2014a) to analyze terrestrial invertebrate movement under laboratory conditions across diverse taxonomic groups and feeding types. Our measurements of exploratory speeds for 173 individuals from 57 species across six classes spanning three orders of magnitude in body mass yielded the largest and most diverse database on invertebrate movement compiled so far. Exploratory (voluntary) speed characterizes an animal exploring landscapes for food or shelter, and so is of key ecological importance. Based on theory and data we describe above, we hypothesized that exploratory speed should follow a general allometric scaling relationship with an exponent between 0.13 and 0.4. Exploratory speed is at least partially fueled by metabolism, and it constrains the strength of consumer–resource energy flows. As the allometric scaling of both of these parameters differs across phylogenetic groups and feeding types of invertebrate species (Ehnes et al. 2011, Lang et al. 2017), we also tested for similar effects on the allometric scaling of exploratory speed.

## METHODS

### Animal collection

All animals were manually collected in 2014 in deciduous forest litter layers near Göttingen, Lower Saxony, Germany (51.5546° N, 9.9289° E). Animals were housed individually in small plastic containers (with sediment and leaf litter from their habitat) in an environmental chamber at 15°C and ~60% relative humidity. Animals were kept for a maximum of 50 h prior to experimental trials, with the time spent in captivity prior to filming recorded as a co-variable for statistical analyses. We collected movement and weight data (precision scale with animal weighing mode) from 173 individuals comprising 57 species from six classes (Arachnida, Chilopoda, Malacostraca, Diplopoda, Arachnida, Entognatha), which we henceforth refer to as taxonomic groups (Table S1). These 57 species span 16 orders and 41 families, but replication within these lower taxonomic levels was insufficient for detailed analyses. Each animal was also classified into one of four feeding types: carnivores, detritivores (including microbivores and microbi-detritivores), herbivores, and omnivores.

### Experimental setup

Animals were filmed individually in the same walk-in environmental chamber in which they were stored after collection (see *Animal Collection*), using a custom-designed experimental set-up that allows video recording of movement and behavior of a wide range of taxa (see Barnes et al. [2015] for more detail). Our setup (see Barnes et al. 2015: Fig. 1b) used infrared backlighting to maximize contrast between the animal and its background. Light was provided by an infrared LED light panel (850 nm; Smart Vision Lights, Muskegon, Michigan, USA). Circular glass arenas with three different diameters (543, 293, and 80 mm) were used, depending on the size of the animal (larger animals were filmed in larger arenas). Arena size was used as a covariable in statistical analyses. The sides of the filming arena were lined with a random gray-scale checkerboard pattern, providing a non-uniform background devoid of directional bias. The top of the filming chamber was made of white cloth, above which four LED bulbs (LifeLite daylight mirror

lamp, 5 W at 9.2 V and 0.54 A, LifeEnergy Systems GmbH, Alzenau, Germany) were placed to imitate natural twilight in the filming chamber. A CCD camera (Prosilica GX1920, Allied Vision Technologies GmbH, Stadtroda, Germany) with a 25 mm lens (Fujinon, Fujifilm Europe GmbH, Düsseldorf, Germany) and an infrared pass filter (850 nm, Midwest Optical, Palatine, Illinois, USA) were positioned through a hole in the middle of the cloth. Prior to filming, all animals spent 30 min in a small acclimatization chamber within the filming chamber, open only to infrared light from below. Once the acclimation chamber was removed, filming started as soon as the animal moved with a speed of >1.5 mm/s and continued for a total of 60 min. StreamPix (Norpix, Montréal, Canada) was used to record the videos at 15 frames per second and 1,936 × 1,456 spatial resolution.

### Automated tracking

EthoVision 10.1 (Noldus Information Technology, Wageningen, The Netherlands) was used to identify the position (mid-point of the body) of the animal in each video frame. Each frame was individually time-stamped, permitting calculation of body speed. Random variations in brightness or color information (noise) can lead to tracking errors, although EthoVision produced accurate tracks as long as animals were moving. To exclude artificial changes in position and orientation that were registered even when animals were stationary, we defined a true bout of movement to begin when speeds were higher than 0.6 mm/s and to end when speeds were lower than 0.3 mm/s (these thresholds were defined based on pre-experiments with non-moving animals). Every frame that was outside such a period of movement was excluded from the analyses.

### Statistical analyses

We excluded 12 tracks in which the animals spent less than 30% of the filming time moving, as it is difficult to calculate accurate means of exploratory speed over short periods of movement. For each of the remaining 173 trajectories, we calculated the average speed of each individual during periods of movement. Subsequently, we used linear models to test for effects of $\log_{10}$(body mass) (measured in g) on $\log_{10}$(mean exploratory speed) (measured in mm/s). As the body masses were weighed with a precision scale with animal weighing mode, the error was assumed to be marginal, and we used model-1 regressions (Warton et al. 2006). Based on a priori model choice, we tested for three relationships: (1) the simple allometric speed model without cofactors (speed ~ mass), (2) the taxonomic-allometric speed model (speed ~ mass × taxonomy) with taxonomic group (Arachnida, Chilopoda, Diplopoda, Entognatha, Insecta, and Malacostraca) as fixed co-factor, and (3) the trophic-allometric speed model (speed ~ mass × feeding type) with feeding type (carnivore, detritivore, herbivore, and omnivore) as fixed

co-factor. While more complex models with full or partial interactions between these factors are statistically feasible, we refrained from including them in our study as (1) we were lacking explicit hypotheses on their interactions, and (2) many combinations of these factors are not realized in nature (e.g., all Arachnida are carnivores and all Diplopoda are detritivores). Model comparison by AIC suggests that the trophic-allometric model was the most appropriate for predicting the speeds of invertebrates (AIC = 67.096, $R^2 = 0.43$), whereas the taxonomic-allometric model (AIC = 84.175, $R^2 = 0.40$) and the simple allometric model (AIC = 128.82, $R^2 = 0.13$) had lower explanatory power. Additional comparisons with more complex models showed that including either arena size or time spent in captivity as co-factors was unwarranted, thus we did not include these factors in the main analyses. All statistics were performed using R 3.2.3 (R Core Team 2015).

### Results

We analyzed the exploratory speed of 173 invertebrates across six classes: Arachnida (number of individuals $n_i = 52$, number of species $n_s = 16$), Chilopoda ($n_i = 12$, $n_s = 5$), Diplopoda ($n_i = 26$, $n_s = 10$), Entognatha ($n_i = 8$, $n_s = 5$), Insecta ($n_i = 55$, $n_s = 17$), and Malacostraca ($n_i = 20$, $n_s = 4$) (Table S1). These groups are distributed across four feeding types: carnivores, detritivores, herbivores, and omnivores. Across our entire data set, body mass ranged over three orders of magnitude from 0.22 mg (*Mesentotoma dollfusi*, Entognatha) to 460 mg (Scarabaeidae indet., Insecta), and mean exploratory speed ranged over almost two orders of magnitude from 0.64 mm/s (*Damaeus onustus*, Arachnida) to 56.6 mm/s (Carabidae indet., Insecta). On average, larger invertebrates moved significantly faster than smaller ones (Fig. 1a), with exploratory speed (*v*) following a power-law relationship with body mass (*M*, Eq. 1) with a constant $a = 14.33$ and an exponent $b = 0.19$ ($P < 1 \times 10^{-5}$, $R^2 = 0.51$; Fig. 1a).

Despite finding a significant relationship between body mass and exploratory speed, substantial unexplained variation remains (Fig. 1a). Taxonomy partly explains this variation as the mass–speed relationship is significantly affected by taxonomic group (interaction term taxonomic group × body mass: $P = 0.01$). Arachnida, Chilopoda, and Malacostraca have exploratory speeds that are strongly influenced by body mass, with scaling exponents of 0.43 (95% CI = 0.25–0.61), 0.53 (95% CI = 0.22–0.83) and 0.47 (95% CI = 0.33–0.61), respectively (Fig. 1b, c, g). Moreover, Chilopoda are mostly faster than expected by the overall trend (colored compared to gray regression line, Fig. 1c) while Malacostraca are on average slower (colored and gray line, Fig. 1g). In contrast, the body mass dependence of exploratory speed is less strong for Diplopoda and Insecta, with slopes of 0.12 (95% CI = −0.05 to 0.28) and 0.19 (95% CI = 0.06–0.32), respectively (Fig. 1d, f), and weakest for Entognatha (e.g., collembolans), with a scaling exponent of only 0.07 (95% CI = −0.06 to 0.2,
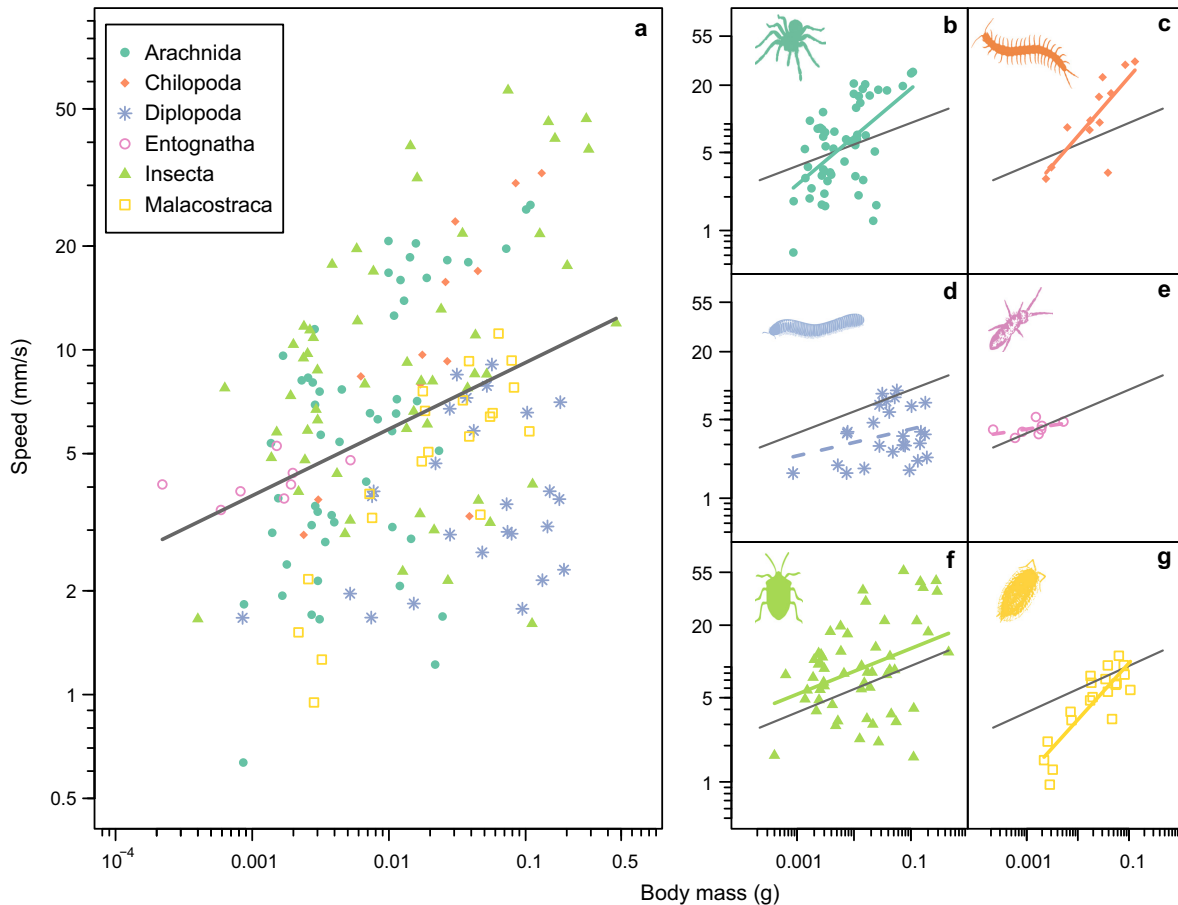
FIG. 1. Scaling of speed with body mass across phylogenetic groups according to Eq. 1 for (a) all species ($a = 14.33 \pm 1.2$ [mean $\pm$ SE], $b = 0.19 \pm 0.04$, $P < 1 \times 10^{-5}$), (b) Arachnida ($a = 50.14$, $b = 0.43 \pm 0.09$, $P < 1 \times 10^{-4}$), (c) Chilopoda ($a = 79.85$, $b = 0.53 \pm 0.14$, $P = 0.003$), (d) Diplopoda ($a = 5.40$, $b = 0.12 \pm 0.08$, $P = 0.15$), (e) Entognatha ($a = 6.60$, $b = 0.07 \pm 0.05$, $P = 0.23$), (f) Insecta ($a = 19.83$, $b = 0.19 \pm 0.07$, $P = 0.005$), and (g) Malacostraca ($a = 28.64$, $b = 0.47 \pm 0.07$, $P < 1 \times 10^{-5}$). Note that intercepts $a$ give speeds at body masses of $10^0 = 1$ g. The gray line shows the simple allometric scaling relationship, colored lines show the group-specific scaling relationship of the taxonomic-allometric model. Dashed lines indicate non-significant regressions.

Fig. 1e). However, Insecta are on average faster than the overall trend (colored and gray line, Fig. 1f) while Diplopoda are generally slower (colored and gray line, Fig. 1d). Based on 95% confidence intervals, only Malacostraca have a higher slope than Insecta, Entognatha, and Diplopoda, and Entognatha have a lower slope than Chilopoda and Arachnida.

We also found significant effects of feeding type on the allometric scaling relationship (interaction term with body mass, $P = 0.005$). The allometric scaling of exploratory speed is steepest for carnivores ($b = 0.42$, 95% CI = 0.32–0.53, Fig. 2b), followed by omnivores ($b = 0.18$, 95% CI = −0.065 to 0.43, nonsignificant, Fig. 2c) and then detritivores ($b = 0.1$, 95% CI = 0.015–0.19, Fig. 2d). Surprisingly, herbivores show a negative but nonsignificant trend ($b = -0.19$, 95% CI = −0.5 to 0.12, Fig. 2d). As tested by an ANCOVA (speed ~ mass × carnivory, with carnivory separating species in carnivores and non-carnivores) and similar to the 95%

confidence intervals, carnivores have a significantly higher slope than the other feeding types ($P < 1 \times 10^{-6}$). Moreover, carnivores are mostly faster compared to the overall trend (colored and gray line, Fig. 2b). In contrast, detritivores are on average slower than expected (gray and colored lines, Fig. 2c).

## DISCUSSION

In contrast to vertebrates, little was previously known about general patterns in the allometry of speed in invertebrates, as the few studies that include more than one or two species are restricted to specific taxonomic groups (Forsythe 1983, Hurlbert et al. 2008). We contribute to filling this gap by providing the first general empirical estimates of the scaling of invertebrate exploratory speed with body mass across 173 individuals from 57 species and six taxonomic groups. We show that exploratory speeds of invertebrates follow a power law
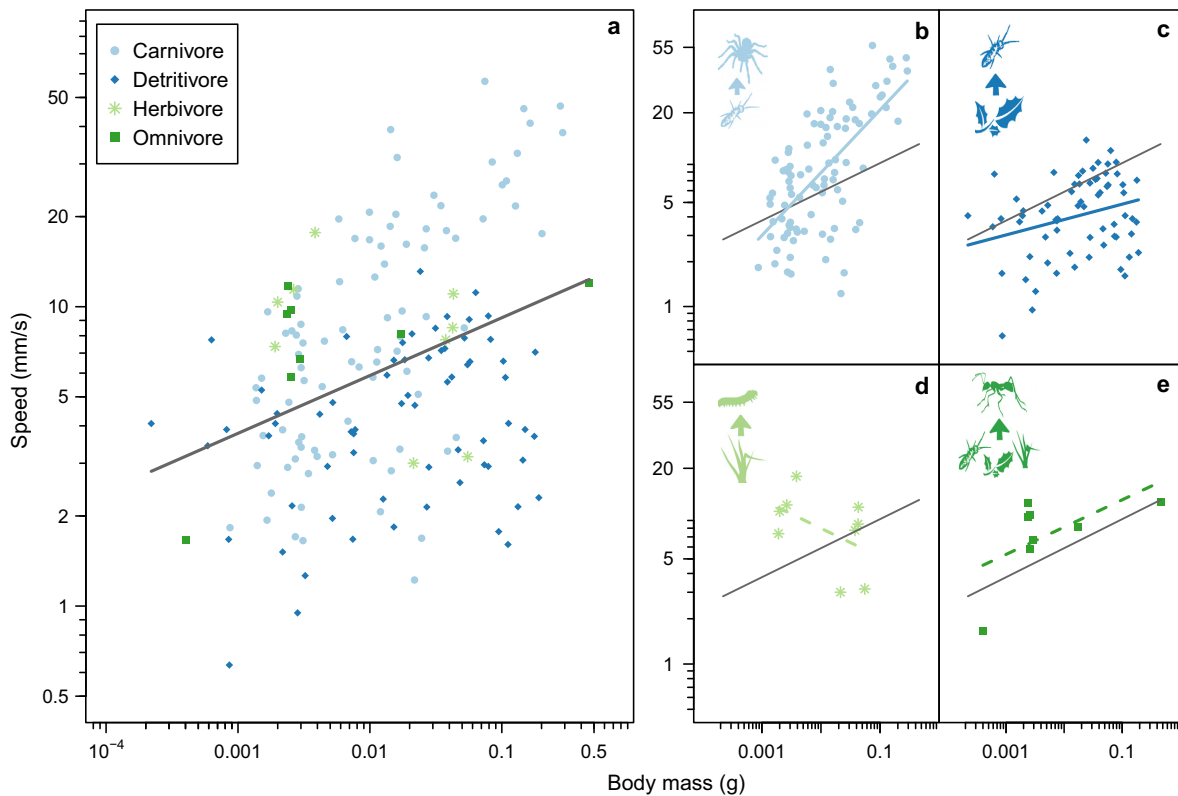
Fig. 2. Scaling of speed with body mass across feeding types according to Eq. 1 for (a) all species ($a = 14.33 \pm 1.2$ [mean $\pm$ SE], $b = 0.19 \pm 0.04$, $P < 1 \times 10^{-5}$), (b) carnivores ($a = 55.20$, $b = 0.42 \pm 0.05$, $P < 1 \times 10^{-11}$), (c) detritivores ($a = 6.17$, $b = 0.10 \pm 0.04$, $P = 0.02$), (d) herbivores ($a = 3.32$, $b = -0.19 \pm 0.13$, $P = 0.19$), and (e) omnivores ($a = 18.75$, $b = 0.18 \pm 0.1$, $P = 0.12$). Note that intercepts $a$ give speeds at body masses of $10^0 = 1$ g. The gray line shows the simple allometric scaling relationship, colored lines show the group-specific scaling relationship of the trophic-allometric model. Dashed lines indicate non-significant regressions.

relationship with body mass with a scaling exponent of $0.19 \pm 0.04$ (mean $\pm$ SE), which is similar to prior estimates for 24 ant species (0.25, Hurlbert et al. 2008). These allometric exponents of exploratory speed are much lower than those for resting metabolic rates of terrestrial invertebrates (0.69; Ehnes et al. 2011) or field and maximum metabolic rates of vertebrates (0.8–0.9; Pawar et al. 2012). Although metabolism provides the fuel for biological activities, these differences among exponents support the assumptions of our theoretical derivations that body morphologies also limit movement capacities. Moreover, our empirical scaling exponent of speed (0.19) is on the lower end of the predicted range (0.13–0.4, see *Introduction* and Pawar et al. [2012]), probably because we focused on exploratory speed where the animal is not working at full capacity.

We found substantial variation between groups in their scaling of body speed, which can arise from a number of sources affecting both the intercept and exponent. Most variation should be captured by the normalization factors, which account for the effects of taxon, metabolic state, body temperature, and locomotory type. Thus, difference in the scaling between taxonomic groups

probably arises due to differences in body shape and other functional traits related to locomotion. Our results on group-specific scaling relationships facilitate future research on how different morphological characteristics across these groups and their allometric scaling limit invertebrate movement. As most ecological studies, our analyses are slightly biased by phylogenetic effects and the different number of individuals measured across the species groups. Future studies could include additional species groups such as mites, which would allow phylogenetically controlled analyses of speed, morphology, and metabolism. Our study showed striking differences between the allometric scaling relationships of metabolism and speed across taxonomic groups, which indicates a need for more mechanistic research on constraints of invertebrate movement, integrating metabolic, morphological, and other phylogenetic factors.

Exploratory speed is also an important component of encounter rates, with higher average speeds generally leading to higher encounter rates, and thus higher attack rates (Mittelbach 1981, Pawar et al. 2012, Polidori et al. 2013, Dell et al. 2014b) and stronger effects of competition (Lang et al. 2012, van Gils et al. 2015). Our

allometric exponent of exploratory speed (0.19) is similar to that of terrestrial invertebrate attack rates (0.24; Rall et al. 2012), supporting prior assumptions that attack rates depend more strongly on movement capacities than on metabolic rates alone (Pawar et al. 2012, Rall et al. 2012), which have a much higher allometric exponent. Although differences in the length of foraging bouts across species also affect realized attack rates, the higher allometric exponent of metabolism compared to exploratory speed and attack rates suggests that with increasing body masses, species become increasingly limited by resource supply. This could explain the higher allometric exponent of carnivore exploratory speed (0.42; Fig. 2b) in comparison to other feeding types (<0.18; Fig. 2c–e), as carnivores often depend on attacking active resources. These differences across feeding types may thus represent different evolutionary selection pressures.

Comparison of the group-specific regression lines to the overall trend (colored and gray lines, Fig. 2) revealed a slower than expected exploratory speed of detritivores (Diplopoda and Malacostraca) relative to the other feeding types. We anticipate three, mutually non-exclusive explanations for this finding. First, detritivores feed on a sessile resource (litter) and, hence, there is no evolutionary pressure on developing high speeds to capture prey, compared to predators that hunt active prey (e.g., spiders). Second, detritivores mainly move within litter and soil, which impedes high speed movements. Third, the dominant detritivorous groups in our study (Diplopoda and Malacostraca) have evolved strong exoskeletons as defenses against predation, which reduces the need for high speed movements. As none of the three hypotheses alone can explain our finding, a combination of all three factors may be the most suitable explanation for the pattern that detritivores are systematically slower than the other feeding types.

Due to their vast diversity, high abundance and important role in ecosystems, invertebrates are indeed "the little things that run the world" (Wilson 1987), yet we know so little about them that we are facing a "scientific insect crisis" (Hochkirch 2016). This crisis starts with characterizing the sheer number and species richness of invertebrates, through to information on their behavior, physiology, or movement. In this vein, it is essential that we develop general scaling laws that incorporate the vast diversity of invertebrates. As this diversity inhibits a measurement of speed that is similarly representative as for vertebrates (Kissling et al. 2014), the scaling relationships we present here can be used to generally predict the speeds of invertebrates depending on their individual body mass, taxonomic group, and feeding type. As exploratory speed should also be a good predictor of the distances that can be covered by animals, gaining a better understanding of invertebrate speed also contributes to predictions of meta-population structure and network connectivity by providing information on the species-specific movement capacities

linking habitat patches. Our study, therefore, represents an important step towards a wider understanding of the ecology of the most diverse group of animals on our planet and how they run the world.

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## Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2006/suppinfo

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