Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Seeking water while avoiding predators: moisture gradients can affect predator–prey interactions

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ARTICLE INFO

Water is an essential resource that can affect the distribution and abundance of species across ecosystems. However, how water availability and its spatial heterogeneity affect animal movement, and associated predator–prey encounter and predation rates, is still poorly understood. Using predatory centipedes and springtails (prey) from the leaf litter of a beech forest, we conducted two laboratory experiments in which we manipulated water availability to test (1) whether centipedes and springtails decrease their mobility when moisture is limiting, (2) whether centipedes and springtails aggregate in patches were moisture is high, and, if so, (3) whether springtails tend to avoid these otherwise suitable areas when predators are present. Overall, average water availability did not affect levels of mobility, and both animal taxa were equally attracted to the moistest spots. Springtails, however, switched to slightly drier spots when predators were present, and as expected from physiological constraints in water loss, smaller springtails spent more time in wet spots, incurring higher predation risk. Larger animals were more active regardless of taxonomic affiliation, although springtails switched to a much higher mobility under predation risk. This size-dependent antipredator behaviour could explain why predation rates were similar across treatments. Since spatial heterogeneity in moisture is widespread in terrestrial ecosystems, our findings may be relevant to understanding predator–prey dynamics, not only in arid environments, but also in temperate ecosystems, such as beech forests.
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Water is an essential resource in terrestrial ecosystems that can often become limiting (McCluney & Sabo, 2009; Noy-Meir, 1974; Wolf & Walsberg, 1996). Water availability can actually be used to predict species richness and organism abundance (Hawkins et al., 2003), as well as the spatial distribution of taxonomic and functional groups (Chown & Nicolson, 2004; Grear & Schmitz, 2005; Levings & Windsor, 1984; Melguizo-Ruiz, Verdeny-Vilalta, Arnedo, & Moya-Laraño, 2012). Thus, water availability appears to strongly affect the spatial coupling of species and the potential for biotic interactions to occur. However, although the effects of water availability on plant interactions are well studied (e.g. Dawson, 1993; Maestre & Cortina, 2004; Pugnaire, Armas, & Valladares, 2004; Scholes & Archer, 1997; Soliveres et al., 2011; Weigelt, Rottgermann, Steinlein, & Beyschlag, 2000), studies on water-mediated interactions in animal communities have received much less

attention, with most of the studies based on drylands and desert ecosystems (McCluney et al., 2012; McCluney & Sabo, 2009; Noy-Meir, 1974, but see Lensing & Wise, 2006; Spiller & Schoener, 2008).

Variation in the amount of water can directly affect animal interactions by altering their physiology and water balances (Stenseth et al., 2002). This, in turn, may alter the consumption behaviour (McCluney & Sabo, 2009; Walter et al., 2012) and foraging games of animals (McCluney et al., 2012). Moreover, experimentation has shown that water availability can indirectly alter animal interactions through changes in the composition and number of links among species (e.g. in freshwater food webs: Ledger, Brown, Edwards, Milner, & Woodward, 2013). Yet, it remains poorly understood how in terrestrial ecosystems the availability and distribution of water influence animal interactions through changes in movement patterns of individuals and populations. Unravelling the effects of water on patterns of animal movement will provide essential clues on how altered precipitation may affect encounter rates and subsequent predator–prey and food web dynamics.

In terrestrial ecosystems, water availability is often heterogeneously distributed at the microscale level (Herbst & Diekkruger,

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2003; Jost, Schume, & Hager, 2004; Melguizo-Ruiz et al., 2012; Schume, Jost, & Katzensteiner, 2003). Moreover, altered precipitation regimes could result in longer dry periods (Easterling et al., 2000), which increases soil water evaporation, leading to the formation of stronger water gradients for longer periods. Soil invertebrates that face such changes in water availability have evolved different physiological, morphological and behavioural traits to diminish water loss during dry periods (Chown, 2011; Chown & Nicolson, 2004). Behavioural responses involving the rate and direction of movement can potentially modify the rates at which animals encounter each other and the opportunity for predation. However, to our knowledge these potentially important consequences of water scarcity have been barely studied.

In general, animals can, by behavioural means, avoid water loss either by reducing their movement and metabolic rates, or by increasing their movement rate to find resources with high water content or suitable wet areas (McCluney & Sabo, 2009; Moya-Laraño, 2010). In fact, most invertebrates must actively search for water sources in excess of that ingested with food (e.g. Walter et al., 2012). As a consequence, most invertebrates migrate vertically and horizontally to find suitable moistened areas (Hassall, Visser, & Parkinson, 1986; Swift, Heal, & Anderson, 1979), which probably contributes in part to the positive correlations between water availability and invertebrate numbers (Badejo, Nathaniel, & Tian, 1998; Ferguson & Joly, 2002; Melguizo-Ruiz et al., 2012). The point of interest for the present work is that water-mediated changes in movement behaviour may alter encounter rates among individuals and thus the opportunity for predation. On the one hand, if individuals become more active due to increases or decreases in the availability of water (Lensing, Todd, & Wise, 2005; Shultz, Lensing, & Wise, 2006), they must encounter each other more frequently (Gurarie & Ovaskainen, 2013; Moya-Laraño, 2010; Scharf, Nulman, Ovadia, & Bouskila, 2006; Werner & Anholt, 1993). On the other hand, if water is heterogeneously distributed, and the animals are attracted to the wettest areas during dry periods, higher encounter rates could be the result of an aggregative response. However, if both prey and predators are attracted to wet areas, prey will have to trade off the risk of desiccation with the risk of predation. Since larger arthropods can retain water more efficiently either because of their lower surface-to-volume ratio, or because they can store proportionally more water (Chown, 1993; Renault & Coray, 2004), smaller prey would face a stronger trade-off and would have to deal with higher predation risk to avoid desiccation.

Here, we tested the hypothesis that the distribution and amount of water largely determine encounters and predator–prey interactions of two major groups of leaf-litter invertebrates: predatory centipedes and fungivorous (prey) springtails. First, we tested (1) whether a gradient of water potentially increases predator–prey encounter rates because both groups are attracted to the wettest areas and (2) whether individuals alter their movement rate when exposed to a low, uniformly distributed amount of water either by moving more frequently to find a wet spot, or by decreasing their movement rate to avoid water loss (McCluney & Sabo, 2009; Moya-Laraño, 2010; Shultz et al., 2006). Second, we assessed whether these water-mediated movement patterns (i.e. microhabitat selection and rate of movement) affect in turn the encounters between predators and prey and, importantly, the probability that predators feed on prey. We also assessed the role of body size on movement rate, and we tested the trade-off hypothesis: larger prey are more likely to avoid wet areas when predators are present, but smaller prey, owing to stronger water physiological constraints, are forced to expose themselves to higher predation risk to balance their water budgets.

METHODS

Field Site and Animal Taxa

The experiments were conducted using two well-represented invertebrate groups from the leaf litter of European beech, *Fagus silvatica*, forests: centipedes (*Lithobius* sp.) as the predator, and surface-dwelling springtails (*Tomocerus* sp.) as prey (Schaefer & Schauermann, 2009). Voucher specimens of the animals have been deposited in the EEZA-CSIC museum (*Lithobius*, INV-134-1; *Tomoceurs*, INV-134-2). Springtails are widely distributed arthropods across most biomes, and can be found throughout the upper part of the soil profile, where they feed mainly on the fungal hyphae associated with the decaying vegetation (e.g. leaf litter, twigs and trunks). Lithobiid centipedes, which also occur in a wide range of biomes, are flat centipedes and common generalist, highly active predators that live in the upper soil layers pursuing prey such as springtails (Coleman, Crossley, & Hendrix, 2004; Hopkin, 1997).

Springtails and centipedes were manually collected during October 2010 from a beech forest near Vielha in Catalonia, Spain (42°35′49″N, 0°45′11″E), by sifting the leaf litter (e.g. Lensing & Wise, 2006). Animals were collected from the field and used for the experiments within 3–4 days. Individuals were individually kept in petri dishes with moistened plaster of Paris and activated charcoal (in a proportion of 9:1) to maintain humidity, and provided with water ad libitum. Springtails were fed yeast ad libitum. Centipedes received no prey other than those caught during the experiments. Therefore, predators were deprived of food (within 3–4 days), but not water, prior to experimentation. We measured body length of all individuals twice to the nearest 0.01 mm using a calliper (correlation between measures: springtails: $r = 0.91$; centipedes: $r = 0.94$) and used the mean between measures in our analysis.

Experimental Set-up

During the laboratory experiments the mean ± SD temperature was 10.69 ± 0.51 °C ($N = 160$) and the mean ± SD ambient relative humidity (RH) was 68.59 ± 1.13% ($N = 160$). Both environmental variables were within the natural ranges experienced by these invertebrates (6.5–12.1 °C, $N = 15$; 79.8–95.3% RH; $N = 25$), based on opportunistic measurements of microsites taken by placing a thermo-hygrometer probe (DeltaOHM HD2301.0) approximately 10 cm into the leaf litter. Although RH was slightly lower, our experimental manipulations allowed us to approach the lowest RH in the natural range (see below).

Each experimental unit consisted of a 35 × 12 × 7.5 cm stainless steel container. We applied liquid Teflon to the walls to prevent animals from climbing up and escaping from the containers. The bottom of each container was filled (to a depth of 5 mm) with a 9:1 mixture of plaster of Paris and activated charcoal, which served to retain the humidity applied in each water treatment. We divided the longitudinal space of each container into four areas of equal size (8.75 × 12 cm) by painting a series of marks on the walls of the container. This subdivision delimited a one-dimensional grid that allowed us to identify easily the area in which individuals were positioned at any given time. Although the animals moved in two dimensions (containers were 12 cm wide), with this space subdivision we aimed to simplify the animals' movement to one dimension. The experimental units were spatially arranged and oriented at random within the experimental room. After this initial set-up we performed two sequential experiments.
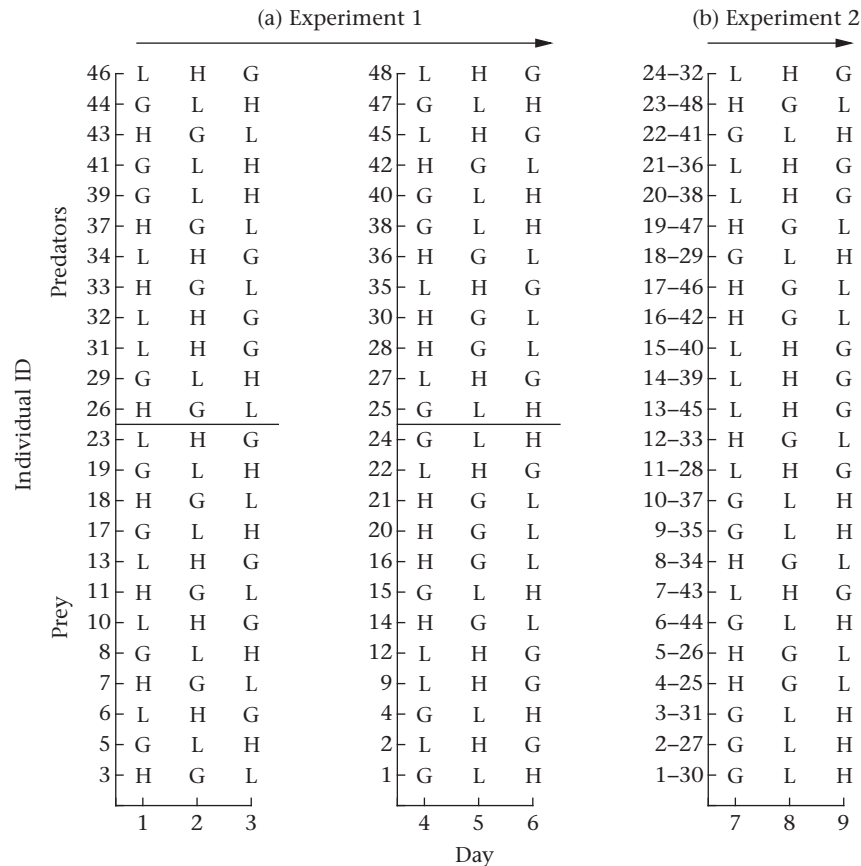
(a) Experiment 1 →   **(b) Experiment 2** →

Individual ID — Predators (top) / Prey (bottom)

Days 1, 2, 3:

ID	1	2	3
46	L	H	G
44	G	L	H
43	H	G	L
41	G	L	H
39	G	L	H
37	H	G	L
34	L	H	G
33	H	G	L
32	L	H	G
31	L	H	G
29	G	L	H
26	H	G	L
23	L	H	G
19	G	L	H
18	H	G	L
17	G	L	H
13	L	H	G
11	H	G	L
10	L	H	G
8	G	L	H
7	H	G	L
6	L	H	G
5	G	L	H
3	H	G	L

Days 4, 5, 6:

ID	4	5	6
48	L	H	G
47	G	L	H
45	L	H	G
42	H	G	L
40	G	L	H
38	G	L	H
36	H	G	L
35	L	H	G
30	H	G	L
28	H	G	L
27	L	H	G
25	G	L	H
24	G	L	H
22	L	H	G
21	H	G	L
20	H	G	L
16	H	G	L
15	G	L	H
14	H	G	L
12	L	H	G
9	L	H	G
4	G	L	H
2	L	H	G
1	G	L	H

Days 7, 8, 9:

ID	7	8	9
24–32	L	H	G
23–48	H	G	L
22–41	G	L	H
21–36	L	H	G
20–38	L	H	G
19–47	H	G	L
18–29	G	L	H
17–46	H	G	L
16–42	H	G	L
15–40	L	H	G
14–39	L	H	G
13–45	L	H	G
12–33	H	G	L
11–28	L	H	G
10–37	G	L	H
9–35	G	L	H
8–34	H	G	L
7–43	L	H	G
6–44	G	L	H
5–26	H	G	L
4–25	H	G	L
3–31	G	L	H
2–27	G	L	H
1–30	G	L	H

Day

Figure 1. Schematic representation of the experimental design. Each letter indicates the experimental unit and water treatment (G: gradient; H: high water; L: low water) that an individual (with its unique ID) experienced in a given day. (a) In experiment 1 we used 24 springtails and 24 centipedes, which were randomly and individually placed in separate containers. All individuals experienced the three water treatments during the experiment, making a total of 144 animal–treatment replicates. All treatments and taxa were well dispersed among the experimental trials. The order in which an individual entered each treatment was randomly assigned. To obtain the 144 replicates we established six trial blocks (1 block = 1 day) of 24 animals. (b) In experiment 2 we used the same individuals as in experiment 1 plus replacements when predation occurred. In this case, each container had a randomly picked centipede and springtail, also making a total of 144 animal–treatment replicates. The water treatment that a given pair of individuals experienced each day was assigned randomly. However, to assess predation rate we had 72 + 17 observations (i.e. 72 predator–prey pairs + 17 springtail replacements owing to predation). At the beginning of both experiments, when an individual entered a container, it was randomly placed in one of the four areas.

Experiment 1

In experiment 1 we tested whether water availability and its distribution influence encounter rates between prey and predators through rates of mobility and microhabitat preferences (e.g. aggregation in the wettest areas) when no interactions were allowed (we placed a single individual per experimental container). We established three water treatments (low, high and gradient). The low water and high water treatments received a total of 12 ml and 48 ml of water, respectively, uniformly distributed along the four areas. The gradient treatment received 12 ml of water in one of the outermost areas. We measured RH using the same device as in the field (see above), but by putting the probe in contact with the experimental surface. Within the gradient treatment, areas with supplied water had an RH range of 85.7–89.2%, and the dry areas (in the opposite extreme of the container from where the water was supplied) had an RH range of 68–80.3% ($N = 4$). These ranges of RH are similar to those experienced by these animals in wet (ca. 85–95% RH) and dry (ca. 75–85% RH) microsites in the field, respectively (Melguizo-Ruiz et al., 2012). The water used in the laboratory experiments was from a natural fountain, to which we added 0.5 ppm of chlorine. Before applying the water to the experimental units we let it rest in an opened recipient for 24 h to facilitate evaporation of chlorine. Figure 1a details the experimental design and how individuals were assigned to each treatment. To ensure that cues from previous trials did not influence the behaviour of the individuals, we cleaned each container between individual replicates and replaced the plaster of Paris.

Experiment 2

In experiment 2 we assessed the effect of the amount and distribution of water on predation rates through water-mediated changes in individual behaviour. Thus, for this experiment we placed one centipede and one springtail in each container. If springtails do not display antipredator behaviour, we predicted that rates of predation would be higher in situations where the potential encounter rates in experiment 1 were higher. If, on the other hand, springtails do assess the risk of predation and avoid risky areas, we predicted that, owing to the constraint imposed by body size and water budget, individuals that avoided the wettest areas in the gradient treatment would be the largest individuals and as a consequence, predation rates would not match the potential encounter rates estimated in experiment 1. The water treatments were the same as in experiment 1. If a centipede killed a springtail, we gently removed the dead body without disturbing the predator by using soft forceps, and introduced a new individual in a random position. Because we used the same individuals in both experiments, the springtails that replaced the killed ones in experiment 2 had not previously been exposed to the water treatments. We tested whether the new added individuals showed differences in behaviour (e.g. from assessing the cues of a recent

predation event) relative to those that were killed in the containers, and found no differences ($\chi^2_2 = 0.97$, $P = 0.62$). Details of the experimental design of experiment 2 are given in Fig. 1b.

Behavioural Measures

At 30 min intervals, for a total of 10 h, we recorded the area of the experimental unit where each individual was positioned in each container. The experiments were conducted in complete darkness, and the observations were made with a red LED lamp to minimize disturbance. We think that this approach best mimics the light conditions of invertebrates living within the leaf litter while still allowing us to observe them. We randomly placed each individual in the container 30 min before we began to record behaviour. With the data on the position within each area, we estimated three variables for analysis: (1) location preference, (2) rate of movement and (3) encounter rate.

Location preference

We estimated location preference as the mean across individual locations (areas in the container) over the period of observation (i.e. 10 h, 20 observations). When an individual sat on or crossed over a dividing line, we scored the preferred location as the one with the greater amount of the animal's body area. The four areas of each experimental unit were scored as −0.75, −0.25, 0.25 and 0.75, and for the water gradient, maximum water availability was arbitrarily established to be 0.75. This scoring corresponds to the centre of each of the four sectors, assuming that the dimension of the container goes from −1 to +1. Thus, if the average location for a given individual equals 0, it means that the individual expended the same amount of time in each half of the container (expected in the two uniformly distributed water treatments). On the other hand, if the average location within the gradient treatment approaches either 0.75 or −0.75, it means that the individuals were attracted to or repelled from the water area, respectively.

Rate of movement

As in the analysis of discrete random walks (Turchin, 1998), we interpreted a single movement as a change in position between the four areas of the container. We scored a switch in area (transition) as 1 and recorded a 0 if the animal had not changed the area within the 30 min interval. The rate of movement of an individual was simply calculated as the fraction of transitions across the observation period. Even though these estimates of movement rate were not obtained without error (e.g. movements away from and back to the original area within a 30 min interval would have been missed), our preliminary observations showed that this was almost never the case, as once an animal started moving it was highly likely to move to a different area of the container thereafter.

Encounter rate

We assumed that a predator and a prey encountered each other if (1) they shared the same area in a given 30 min interval and if (2) they switched areas reciprocally (e.g. when the prey moved from area 0.25 to area −0.25 and the predator moved from area −0.25 to area 0.25 in the same 30 min interval). We differentiate between two types of encounter rates: 'potential' and 'actual'. We calculated potential encounter rates by pairing all combinations of predators and prey of experiment 1 as if they were located in the same container, even though they were in different ones (see above). We calculated actual encounter rates by considering the pairs of individuals of experiment 2 that were confined to the same container. Note that we assumed that the predator and prey encountered each other even though the distance between them within an area, or even the distance when they reciprocally switched areas, could be

long enough to prevent a real encounter. Although this approach overestimates encounter rates, we emphasize that the probability of encounter in these instances is relatively much higher than when animals are in separate areas or do not reciprocally switch areas.

Data Analyses

For the statistical analyses of location preference, rate of movement and encounter rates, we used generalized linear mixed models (GLMM) with Gaussian errors and identity link functions. Water treatment and taxon identity were included as fixed factors, and individual identity was included as a random factor to account for the repeated use of individuals among water treatments. To explore whether uniformly distributed water quantity alone affects mobility of prey and predators, we specifically tested for differences in the responses between high and low treatments.

Since we had a limited number of specimens, we sacrificed interdispersing the predation replicates (experiment 2) among the separate-container replicates of experiment 1 and performed two sequential experiments. The order of the experiments was forced to minimize loss of springtails and to ensure completion of experiment 1 before starting experiment 2. To test whether observed differences between experiments were due to experimental treatment (i.e. prey and predators in different or in the same containers) and not to the order of the experiments, we analysed whether the three response variables (area location, movement rate and encounter rate) differed between experiments in a model with time and experiment as fixed factors. With severe temporal pseudoreplication, time would absorb most of the variability in the response variable. Moreover, time was included as a random factor in all models to account for changes in individual motivation as the experiments progressed (e.g. predators were starved until they were able to catch a prey in the experiments). Including time as a random factor served to minimize the problem of temporal pseudoreplication of our forced experimental design and allowed comparison of the results between experiments. By using the variable experiment as a fixed factor, we compared whether location preferences, rates of movement and encounter rates differed between the experiments.

To analyse predation rates we also used GLMM but with a binomial error and logit link function. Body size (length in mm) of both predator and prey were included when we analysed the location preference of individuals within the gradient treatment, the rate of movement and the predation rate. Individual identity was also included as a random factor in all the analyses. To test whether predator-to-prey size ratios (Brose et al., 2006) or the absolute relative sizes of predators and prey were better at predicting the probability of predation, we used Akaike's information criterion corrected for small sample sizes (AICc) to decide between models. We tested this hypothesis because, for instance, it could be that size-dependent mobility in the different treatments could affect predator–prey encounters differently. Thus, predation success based on predator–prey ratios, which relies mostly on the ability of predators to chase and subdue prey, could be a less appropriate estimate of predation success.

We calculated P values using likelihood ratio tests (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). All analyses were performed using the library lme4 in the statistical software R (R Development Core Team, 2012).

RESULTS

Experiment 1

Location preference

When individuals of each taxon, either centipedes or springtails, were placed in separate containers, we found that the water

treatment affected their location preference ($\chi_2^2 = 54.23$, $P < 0.001$), and that the response did not differ between prey and predators (treatment*taxon: $\chi_2^2 = 2.04$, $P = 0.361$). Thus, the wet areas of the gradient treatment tended to attract both groups of animals equally and, as expected, when water was uniformly distributed, neither centipedes nor springtails showed any preferences for a particular area (i.e. location preference did not differ from 0; Fig. 2a).

Within the gradient treatment, we detected a negative but nonsignificant relationship between body size and location preference ($\chi_1^2 = 3.51$, $P = 0.06$), where smaller individuals stayed in wet areas for longer periods than larger individuals. This tendency did not differ between prey and predators (size*taxon: $\chi_1^2 = 2.77$, $P = 0.10$).

Movement rate

Both the water treatment ($\chi_2^2 = 19.3$, $P < 0.001$) and taxon ($\chi_2^2 = 29.3$, $P < 0.001$) affected the movement rate of individuals, although the two taxa behaved differently across treatments (treatment*taxon: $\chi_2^2 = 7.4$, $P = 0.025$). Centipedes, in general, had higher movement rates than springtails, but the difference was less in the gradient treatment (Fig. 2b).
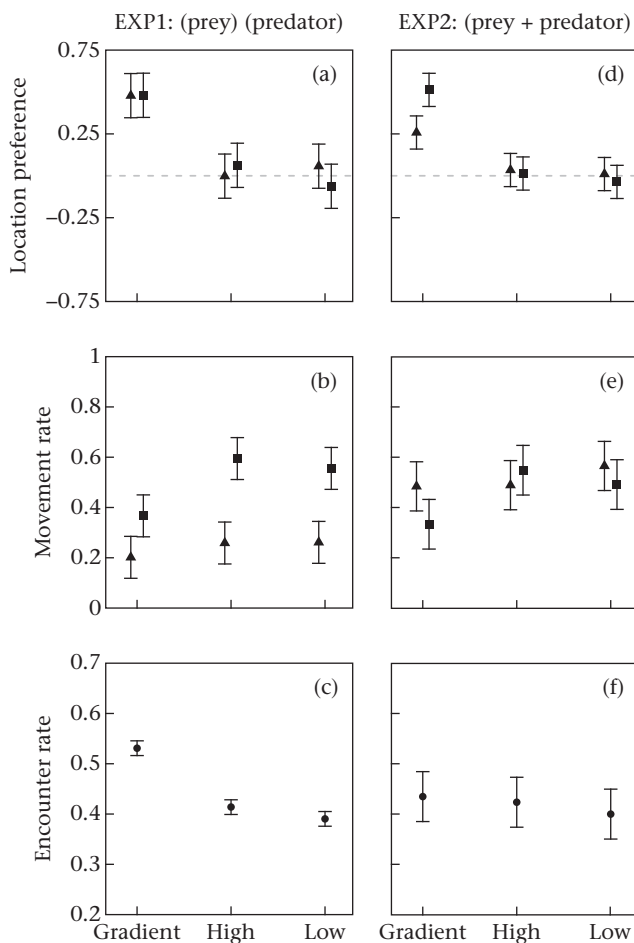

Figure 2. Response variables (mean ± 95% CI) for experiment 1 (a, b, c), in which prey (springtails: ▲) and predators (centipedes: ■) were in different containers, and for experiment 2 (d, e, f), in which prey and predators were in the same container. (a, d) Location preference, where 0.75 represents the wettest area in the gradient treatment and −0.75 the driest. The horizontal dashed grey line represents the midpoint of the gradient (0). If the CIs do not overlap zero (the dashed horizontal grey line), we can conclude that there is a significant nonrandom preference for a given container section. (b, e) Rate of movement. (c, f) Potential and actual encounter rates, respectively, between centipedes and springtails.

However, including body size in the model showed that, regardless of taxon or treatment (treatment*taxon*size: $\chi_2^2 = 2.7$, $P = 0.256$; treatment*size: $\chi_2^2 = 0.51$, $P = 0.776$; taxon*size: $\chi_2^2 = 0.66$, $P = 0.417$), larger individuals moved at a higher rate (size included in a model retaining treatment*taxon: estimate = 0.028, $\chi_1^2 = 9.0$, $P = 0.003$). Movement rates did not differ significantly between the high and low water treatments ($\chi_1^2 = 0.33$, $P = 0.565$; Fig. 2b).

Potential encounter rate

We found differences in potential encounter rates between water treatments ($\chi_2^2 = 208.39$, $P < 0.001$). As animals were in the wettest areas most of the time, the highest potential encounter rates were found in the gradient treatment (Fig. 2c). In addition, when we compared high versus low water treatments, the high water treatment had slightly higher encounter rates than the low water treatment, although the difference was not significant ($P = 0.055$).

Experiment 2

Location preference

In contrast to experiment 1, when prey and predators were placed in the same container, prey spent less time in the wet area of the gradient treatment than predators (treatment*taxon: $\chi_2^2 = 10.96$, $P = 0.004$; Fig. 2d). Moreover, for the gradient treatment, the location preference of springtails was significantly different between the two experiments ($\chi_1^2 = 4.58$, $P = 0.032$), indicating that prey switched the use of space when predators were present (Fig. 3). This was not the case for centipedes ($\chi_1^2 = 0.51$, $P = 0.473$). As in experiment 1, the location preference of centipedes and springtails did not differ from 0 when water was uniformly distributed (Fig. 2d).

Also, for the gradient treatment, smaller individuals had a stronger preference for the wet area than larger ones ($\chi_1^2 = 11.79$, $P < 0.001$), and the pattern tended to be stronger for springtails (size*taxon: $\chi_1^2 = 3.7$, $P = 0.054$; Fig. 3). However, although there seemed to be a clear pattern in Fig. 3, we detected no significant differences in location preference and relative body size of each taxon between experiments (experiment*size*taxon: $\chi_1^2 = 0.03$, $P = 0.859$).

Movement rate

As in experiment 1, the water treatments affected the movement rate of each taxon differently ($\chi_2^2 = 9.79$, $P = 0.007$; Fig. 2e). However, the pattern also differed greatly between experiments. Prey ($\chi_1^2 = 15.11$, $P < 0.001$; Fig. 2b, e), but not predators ($\chi_1^2 = 2.08$, $P = 0.149$; Fig. 2b, e), switched to a much higher mobility in experiment 2. However, the three-way interaction was not significant, indicating no differences in these patterns across treatments (experiment*treatment*taxon: $\chi_2^2 = 1.16$, $P = 0.559$).

Considering both experiments together, larger individuals were more active (size was included in a model retaining treatment*taxon and experiment*taxon: estimate = 0.024, $\chi_1^2 = 9.28$, $P = 0.002$). Furthermore, regardless of body size, and perhaps because springtails showed a greater increase in mobility in experiment 2, springtails were more active in general in the gradient treatment than centipedes (treatment*taxon: $\chi_2^2 = 15.64$, $P < 0.001$).

Actual encounters and predation rate

Encounter rates did not differ between water treatments ($\chi_2^2 = 1.02$, $P = 0.601$). However, experiments affected how water treatments determined encounter rates (experiment*treatment: $\chi_2^2 = 10.24$, $P = 0.006$): encounters in the gradient treatment were
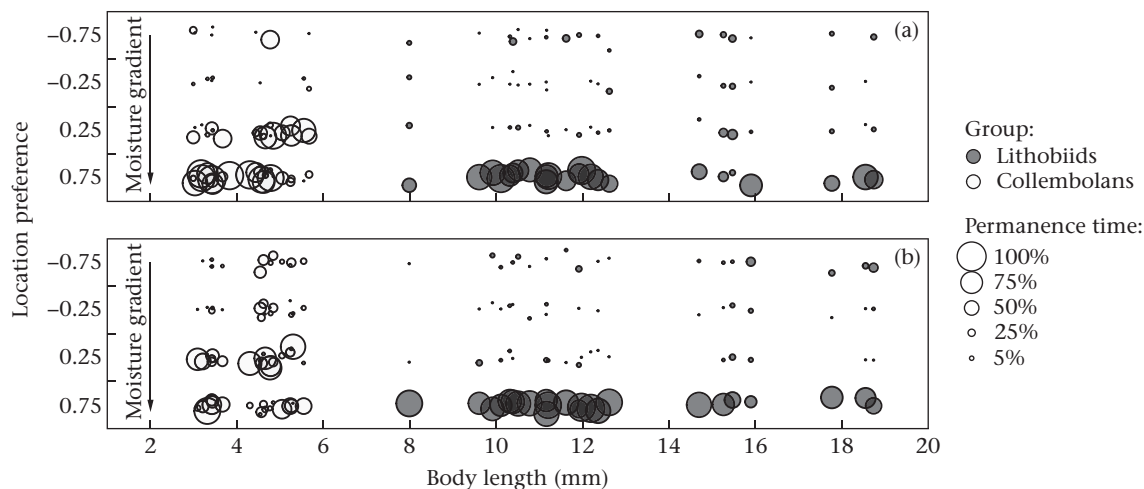
Figure 3. Patterns of space use of centipedes and springtails of different body sizes in the gradient treatment of (a) experiment 1 and (b) experiment 2. The diameter of each circle indicates the percentage of time that an individual spent in one of the four sections of the container.

significantly lower in experiment 2 than in experiment 1 ($\chi^2_1 = 5.14$, $P = 0.02$; Fig. 2c, f).

Seventeen of 41 springtails were killed by a total of eight centipedes. The probability of predation was positively affected by predator size ($\chi^2_1 = 11.79$, $P < 0.001$) and negatively affected by prey size ($\chi^2_1 = 6.73$, $P < 0.01$; Fig. 4). Predation, however, was not affected by the water treatment ($\chi^2_2 = 0.93$, $P = 0.629$), nor by the interaction with prey or predator body sizes (both $P > 0.05$). A model including predator-to-prey body size ratios alone produced a worse fit (AICc = 90.6) than a model including predator and prey body sizes separately (AICc = 80.8). Fitting a spline to the ratio model (e.g. to search for optimal body size ratios predicting predation) did not substantially improve the fit (AICc = 89.3).

When we analysed whether animals changed their location preference, movement rates or encounter rates in a model containing both time and experiment as fixed factors, we still found that, regardless of time, springtails in experiment 2 preferred less humid areas (experiment*taxon: $\chi^2_1 = 8.32$, $P = 0.004$), moved at

higher rates (experiment*taxon: $\chi^2_1 = 45.03$, $P < 0.001$) and had lower encounters in the gradient treatment (experiment*treatment: $\chi^2_1 = 0.33$, $P = 0.005$).

DISCUSSION

Our results show that both predators and prey respond to artificial moisture gradients mimicking those found in the wild (Jost et al., 2004; Melguizo-Ruiz et al., 2012; Schume et al., 2003). The wettest areas in gradients, such as the ones we experimentally established, can potentially increase predator–prey encounter rates because both springtails and centipedes were attracted to these patches. However, when predator and prey shared the same container, there was a clear tendency for prey to avoid the wettest areas, and this was more apparent in larger prey, which can potentially resist desiccation better. This could partially explain why predation risk was lower for larger prey (Fig. 4), as all prey increased their movement rate, but larger prey tended to remain away from the wettest areas in the gradient treatment. In addition, when predator and prey sizes were entered into a model predicting predation, they resulted in a better fit than predator-to-prey size ratios as single predictors in a model. This may indicate that size-dependent mobility and antipredator behaviour, in addition to the ability of relatively larger predators to chase and pursue prey (predator-to-prey size ratios alone), were relevant to predict the probability of predation. Moreover, prey moved at substantially higher rates when predators were present. These two behavioural switches in experiment 2 are evidence of antipredator behaviour directed towards the centipedes, which could explain why predation rates were similar among treatments (experiment 2) despite the higher potential encounter rates in the water gradient treatment (experiment 1). This behavioural switch by which prey avoided areas used by predators may also explain why encounter rates were similar among treatments in experiment 2.

Since many soils exhibit a heterogeneous distribution of moisture (Herbst & Diekkruger, 2003; Jost et al., 2004; Schume et al., 2003), and this positive hydrotaxis of animals has been documented in other soil systems (Badejo et al., 1998; Grear & Schmitz, 2005; Hopkin, 1997; Lensing et al., 2005), our findings could be extrapolated to most terrestrial ecosystems and to other soil taxa. Moreover, aggregations of individuals driven by the heterogeneous distribution of moisture could have important consequences for the functional responses of predators and subsequent predator–prey
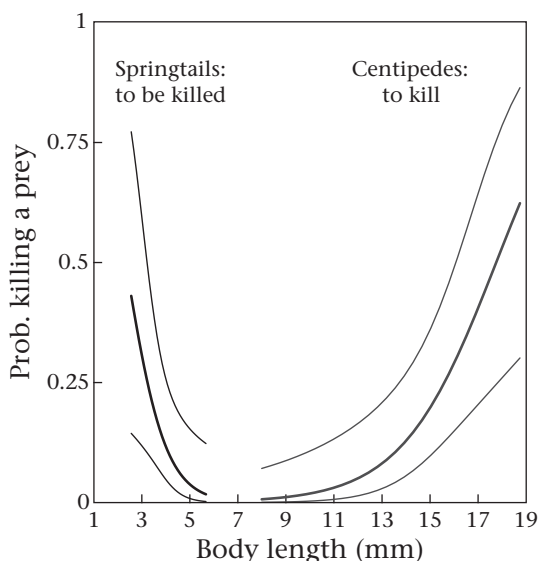

Figure 4. Probability of predation (effects ± 95% CI) in experiment 2 as a function of the body size of springtails (in black) and centipedes (in grey).

dynamics (Hassell & May, 1974; Vucic-Pestic, Birkhofer, Rall, Scheu, & Brose, 2010).

Moisture-dependent Rates of Mobility

Contrary to what other studies have found or have suggested to occur across terrestrial ecosystems (Moya-Laraño, 2010; Shultz et al., 2006), we found that a uniformly distributed amount of water did not have a major direct effect on the rates of movement or on the encounter rates of individuals. This result suggests that, at least within the range of moisture that we used, springtails and centipedes do not change their movement rate as a function of relative humidity. Instead, it seems that the behavioural strategy is rather to move towards patches of increased humidity. Alternatively, the two taxa studied might need to experience water shortages for longer periods before they alter their mobility to prevent desiccation.

Physiological Constraints, Antipredator Behaviour and Predation Rates

In experiment 2, when both the predator and the prey were placed in the same container, we found that prey changed their movement behaviour by switching to an area where the predator was absent. Although the wet areas of the gradient treatment biased the movement of the individuals by attracting them, springtails seemed to assess the predation risk and be less attracted to wet areas, where the predators were more likely to be present. But importantly, this predator avoidance behaviour of prey was guided by the body size of individuals in such a way that smaller prey spent more time on the wettest but more dangerous sections of the gradient. Larger individuals could resist desiccation better because they have a lower surface-to-volume ratio and can store relatively higher amounts of water than smaller individuals (Chown, 1993; Renault & Coray, 2004).

Additionally, the springtails significantly increased their movement rate when exposed to predators and did so to a larger extent in the gradient treatment. Thus, in the gradient treatment, where potential predator–prey encounter rates were highest, springtails reduced their encounter rates with centipedes to a similar degree as in the other treatments, leading to similar predation rates across treatments. Some researchers have reported that, in the presence of predators, prey decrease mobility to minimize encounter rates (e.g. Beckerman, Uriarte, & Schmitz, 1997; Lima & Dill, 1990; Schmitz, Beckerman, & Obrien, 1997; Werner & Peacor, 2003), but others have also shown that prey show an increase in mobility to migrate to safer areas (Wooster & Sih, 1995). In addition, note that, in both of our experiments, prey were presented singly and the arena was rather simple, without the structural complexity of the leaf litter. Since springtails are known to form aggregations, which are supposed to be a dilution risk strategy (Grear & Schmitz, 2005; Vucic-Pestic et al., 2010), and it has been found that some springtails decrease activity when they are aggregated (Mertens & Bourgoignie, 1975), it could be that springtails increased their activity to find a cluster. Also, in more realistic situations in the wild, prey actively search for shelter and decrease their mobility once safely hidden; thus, prey without access to a refuge may have no other choice but to increase activity. Future experiments should manipulate shelter availability and the density of prey to explore their consequences on prey mobility. Nevertheless, our experiments suggest that the differential antipredator behaviour of springtails (i.e. higher mobility and settling in suboptimal patches in terms of water availability) in the gradient treatment probably served to lower predation rates to the levels observed in the other treatments, pointing to the adaptive value of this behaviour.

Predator and Prey Sizes versus Size Ratios in Heterogeneous Environments

We found that, rather than body size ratios (e.g. Brose et al., 2008; Brose et al., 2006; Cohen, Pimm, Yodzis, & Saldana, 1993), including the body size of the prey and the predator separately in the model had better explanatory power for predicting predation rates. A model (Persson, Leonardsson, de Roos, Gyllenberg, & Christensen, 1998) and a recent study testing it (Brose et al., 2008) demonstrated that even when predators and prey are allowed to interact freely in laboratory arenas, there is an optimal predator-to-prey body size ratio predicting predator attack rates. However, the above model did not take habitat heterogeneity and antipredator behaviour into consideration.

By monitoring antipredator behaviour in a heterogeneous environment (gradient treatment), we found that smaller prey incurred a higher predation risk in the gradient treatment than in the other treatments, and that prey moved at higher rates in this treatment. In addition, both larger prey and predators moved at higher rates, which probably contributed to an increase in the probability of encounter multiplicatively. These patterns may largely explain why the body sizes of both prey and predators additively contributed to explain predation rates, and why they predicted predation rates better than predator-to-prey size ratios. We believe that more studies like the one we present here will help to disentangle how body sizes of predators and prey and traits associated with them can influence predator–prey dynamics.

In conclusion, we have shown how the horizontal distribution of water has the potential to affect encounter rates between different trophic levels and alter predator–prey interactions such as the two soil invertebrate taxa in our study. Thus, water may not only play a central role in typically water-limited ecosystems, such as deserts and semiarid areas, but it can also alter predator–prey interactions of invertebrates inhabiting the leaf litter of temperate deciduous forests, such as in European beech forests, where water is not as limiting. Further studies of this type in other ecosystems will provide a better understanding of the complex role of water availability in the functioning of detrital food webs and associated ecosystem processes.

Acknowledgments

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