SYMPOSIUM

Predator–Prey Pursuit–Evasion Games in Structurally Complex Environments

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Synopsis Pursuit and evasion behaviors in many predator–prey encounters occur in a geometrically structured environment. The physical structures in the environment impose strong constraints on the perception and behavioral responses of both antagonists. Nevertheless, no experimental or theoretical study has tackled the issue of quantifying the role of the habitat’s architecture on the joint trajectories during a predator–prey encounter. In this study, we report the influence of microtopography of forest leaf litter on the pursuit–evasion trajectories of wolf spiders Pardosa sp. attacking the wood cricket Nemobius sylvestris. Fourteen intact leaf litter samples of 1 m × 0.5 m were extracted from an oak-beech forest floor in summer and winter, with later samples having the most recently fallen leaves. Elevation was mapped at a spatial resolution of 0.5 mm using a laser scanner. Litter structuring patterns were identified by height transects and experimental semi-variograms. Detailed analysis of all visible leaf-fragments of one sample enabled us to relate the observed statistical patterns to the underlying geometry of individual elements. Video recording of pursuit–evasion sequences in arenas with flat paper or leaf litter enabled us to estimate attack and fleeing distances as a function of substrate. The compaction index, the length of contiguous flat surfaces, and the experimental variograms showed that the leaf litter was smoother in summer than in winter. Thus, weathering as well as biotic activities compacted and flattened the litter over time. We found good agreement between the size of the structuring unit of leaf litter and the distance over which attack and escape behaviors both were initiated (both ~3 cm). There was a four-fold topographical effect on pursuit–escape sequences; compared with a flat surface, leaf litter (1) greatly reduced the likelihood of launching a pursuit, (2) reduced pursuit and escape distances by half, (3) put prey and predator on par in terms of pursuit and escape distances, and (4) reduced the likelihood of secondary pursuits, after initial escape of the prey, to nearly zero. Thus, geometry of the habitat strongly modulates the rules of pursuit–evasion in predator–prey interactions in the wild.

Introduction The behavioral and physical mechanisms involved in the various strategies used by predators to catch their prey, and by prey to escape their predators, have been investigated for a wide variety of taxa, including fishes (Webb and Skadsen 1980; Domenici and Blake 1997), amphibians (Gans and Gorniak 1982; Deban 1997), mammals (Jones and Rydell 1994; Kalko 1995; Catania and Remple 2005), and insects (Brechbühl et al. 2011). Surprisingly, most studies on the mechanisms involved in predator–prey interactions have considered the viewpoint of the predator and the prey independently. This means that the attack strategies of predators cannot be truly understood in regard to the escape strategies developed by prey, and vice versa. The lack of studies considering predator and prey simultaneously is thus likely to hamper our understanding of co-evolutionary forces that shape the strategies used by both in nature (Abrams 2000; Lima 2002).

Considering the trajectories both of predator and prey jointly over a sequence of moves is within the realm of differential games, as defined by Isaacs (1965). Efforts have been made during the past several decades to classify the different search strategies of predators and escape strategies of prey, but these
have not yet been formulated in a comprehensive theoretical framework. Game theory is the tool of choice for such a purpose, and it has been applied in the past, more so to defense by prey than to attacks by predators (Ruxton et al. 2004; Stevens and Merilaia 2011). However, few of these studies have dealt simultaneously with the trajectories of both actors. The vast majority of studies in this area deal with pursuit–evasion games in a featureless environment, from hunting dragonflies and bats in air, to windhounds dogs on land, to fishes and copepods in water. Pursuit–evasion games, in their pure form, assume that complete information is available to both antagonists, for example, that both have full visibility. Most behavioral studies on predators’ attack strategies deal with that kind of game (as surveyed by Alpern et al. 2011).

Search games are another type of game, similar to hide-and-seek games that in their pure form assume no knowledge of the other party’s whereabouts. Sometimes, partial information is available in a so-called “noisy” search game. The information enables one or both to “hear” the other and gain partial information about the other’s movement pattern without full information about its location (Broom and Ruxton 2005; Alpern et al. 2011, 2013). For example, the interaction between a parasitic wasp and leaf-miner moth has been modeled as a noisy search game. Movements both by predator and prey produce vibrations of the leaf tissues in which the caterpillar lives, which may be sensed by both actors (Meyhöfer et al. 1997; Djemai et al. 2000). The wasp flies toward the visual appearance of the mines, lands on the leaf, and then starts the game. Leaf vibrations of the leaf cause the larvae to cease feeding and become “alert.” On the one hand, vibrations produced by the host during escape are useful to the parasitoid female. These tell her that areas previously searched, which did not contain the host, could (unfortunately for her) contain the host again as soon as the host moves. On the other hand, vibrations produced by a hunting parasitoid at the leaf’s surface are also useful to the host, which knows whether the wasp has searched a large portion of the space. A successful search ends with the wasp laying an egg on the host and the larva being parasitized. Sit and wait strategies, which are well studied for predators (Schoener 1971; Helfman 1990), are another form of search game in which the predator has partial information about the prey whereas the prey has virtually no information about the predator’s position and movements.

In the wild, the architecture of the environment is a key factor influencing the amount of information that each antagonist can obtain and the freedom of movement possible. For example, increasing the complexity of the environment in which predator and prey interact likely diminishes their visibility to each other. The attack trajectory must therefore be carefully adjusted to the architecture of the environment, when predators contend with prey possessing high-performance systems of detection. Crickets, for example, are one of the most challenging prey to catch. Their exquisite sensory system detecting the slightest air movement, as for other Orthopteroids (e.g., cockroaches), is a classic example in textbooks on neuroethology (reviewed in Camhi 1984; Gnatzy 1996). The cerci of these insects possess hundreds of mechanoreceptive hairs that enable them to sense the faintest air movements generated by an approaching predator (Gnatzy 1996). The extreme sensitivity of a cricket’s wind-detecting system allows them to use air-flow patterns to detect predators, even at relatively great distances (up to 30 times their body length) (Gnatzy and Kämper 1990; Dangles et al. 2005). This highly sensitive warning system allows crickets to escape most of the time, conferring an obvious selective advantage (Endler 1986). Given this early warning system, one may expect predators of crickets to approach their prey cautiously until the final strike. This is indeed observed in laboratory studies with wood crickets, Nemobius sylvestris, and wolf spiders (Lycosidae, Pardosa sp.). The spider opts for either a sit-and-wait strategy, until the cricket haphazardly comes very near, or attacks at high speed to overrun the warning system of the cricket (Dangles et al. 2006). However, field conditions might constrain the movements of both antagonists, because the leaf litter of temperate forests is sufficiently rough terrain to warrant complex maneuvers and is not appropriate for long runs. Furthermore, the complex structure of forest leaf litter might provide both predator and prey with opportunities to hide. The impact of the environmental architecture sequences of pursuit and escape has never been studied in detail for any predator–prey pair. This is the aim of the present study.

We first characterized the architecture of temperate forest leaf litter by measuring and analyzing the spatial patterns of leaf litter elevation (see Materials and methods section) at the scale of these small arthropods. We studied the litter’s microtopography both in summer and winter for two reasons. First, we wanted to gain a dynamic perspective on the geometry of the litter, which is not feasible with measurements taken only at a single point in time. Second, while the peak activity of wood crickets and wolf spiders is in the summer, both antagonists
are active from March through November. The leaf litter’s microtopography, which may affect both predator and prey, changes over time; the structural dynamics of leaf litter begin in the winter, after the leaves fall, and litter structure is subsequently changed by the activity of primary decomposing organisms (Berg and McClaugherthy 2008). In addition, plant species may influence the leaf litter’s architecture by supplying the ground with leaves of different sizes and shapes (Berg and McClaugherthy 2008). Therefore, we sampled mixed-forest litter during two seasons to assess the influence of these factors on leaf litter elevation patterns. These litter samples were scanned in 3D using a laser to capture and map elevation patterns at a very fine spatial scale. An estimate of compactness was derived from the laser measurements and height transects (see Materials and methods section) were extracted. An experimental variogram was used to describe the spatial structure of litter elevation. We also deconstructed one litter sample and extracted geometrical characteristics of the visible leaf fragments to relate the statistical structure of leaf litter to the geometry of its elements. Finally, we conducted predation trials with pairs of spiders and crickets in empty arenas containing either a flat bottom or one of the samples of leaf litter, in order to assess the role of habitat microtopography on the rules of the search game.

Materials and methods

Biology of the system and the collection of animals

Wolf spiders (Pardosa sp.) and wood crickets (N. sylvestris; third to fifth-instar) were collected in an oak forest in the vicinity of Tours, France (47°10′00″N, 01°04′60″E). The spiders were probably a mixture of the sibling species Pardosa amentata Clerck and Pardosa lugubris Walckenaer, based upon identification of mature males from the collecting sites. In the laboratory, spiders were isolated individually without food for 40–45 days before behavioral tests began. Withdrawal of food is a common procedure meant to homogenize levels of hunger among individual spiders. Crickets were kept in a separate cage; water and cat food were provided ad libitum.

Wood crickets are widespread and common on deciduous forest floors, reaching high densities over both space and time (Gabbutt 1959). Owing to their small size (~3.5–4 mm for spiders and 7–10 mm for adult crickets) and foraging habits, they are exposed to a wide range of predators that hunt on the ground, including wolf spiders. These spiders hunt either by waiting motionless, ready to snap, or by a fast, active pursuit (Ford 1977). Extensive observations of predation in the field showed that juvenile wood crickets are important prey in the diet of wolf spiders (Gabbutt 1959; Edgar 1969) and that wolf spiders are an important source of mortality in crickets, in particular for the juveniles (Dangles et al. 2006).

Study site and sampling of the litter

Litter was sampled in the forest of Loches (47°10′00″N, 01°04′60″E), located in the vicinity of Tours, France. This is a temperate forest predominantly composed of oak trees (Quercus petraea), mixed with beech (Fagus sylvatica). Litter was sampled by selecting areas in the forest according to four main criteria: (1) accessibility of the area, to facilitate transport of the samples out of the forest, (2) a flat topography to ensure that elevation patterns of the litter are intrinsic properties and not due to the slope of the terrain, (3) a low number of seedlings, as these can disturb geometry of the litter at the time of digging, and (4) the presence of both wood crickets, N. sylvestris, and wolf spiders, Pardosa sp.

Litter consisting of oak and beech leaves was sampled both in summer and winter. Summer samples were collected in June and July, when litter is old and has been partially transformed by macrofauna and microfauna. Winter litter collected in November is relatively young and has not yet decomposed. A total of 14 litter samples were collected, 10 in the summer and 4 in the winter. Collecting litter samples (size: 1 m × 0.5 m = 0.5 m²) without disturbing their initial structure was not straightforward. Several attempts were made to find the best trade-off between a sample big enough to obtain an intact litter area of workable size and the weight of samples (~50 kg). Samples were collected after a period of rain, as litters were much easier to collect when wet. Sampling litter consisted of cutting into the soil along three sides of the chosen area to a depth of 10–15 cm (to obtain samples which are sufficiently rigid and stable), and clearing the surroundings to facilitate extraction (see Fig. A1). Finally, a wooden board (0.5 m × 1 m × 0.01 m) was slid underneath the sample and the fourth side was cut. All litter samples were brought back to the laboratory to be scanned and analyzed.

Microtopography of the litter

Microtopography of litter surfaces was measured using a scanning laser designed by Darboux and Huang (2003). The system measures microtopography with a spatial resolution and accuracy of
approximately 0.5 mm in both the horizontal and vertical directions. Before scanning, all litter samples were cleared of seedlings, and leaves were fixed by being sprayed with a solution of polyvinyl (wood glue diluted with water). This manipulation did not alter the shape of leaves.

The scanner is composed of laser diodes and a charge-coupled device (CCD) camera mounted on the carriage of a motor-powered rail. The lasers project a narrow line of red light on the litter’s surface and the camera views this line from an oblique angle. The laser line appears as pixels of high intensity on the image, and the location of the laser line on the image depends on the height of the microtopography. Based on a calibration, the coordinates of the laser line in the image are converted into a microtopographic profile \((x, z)\). The computer-controlled translation of the carriage allows for the acquisition of successive profiles (moving along the \(y\) direction) every 0.5 mm. The final result is a regular grid (spaced at 0.5 mm \(\times\) 0.5 mm) of vertical heights in the leaf litter.

Unmeasured points occur when the laser is not viewed by the camera because of the obstruction of the light path by a piece of leaf. This shadow effect is not to be confused with litter elements that are not ‘seen’ by the laser due to the opacity of other, overlaid leaves. In other words, the measurement is not a volumetric but a surface measurement. To reduce the number of unmeasured points, each sample was rotated by 180° and measured a second time. The microtopography of each litter sample was reconstructed by merging the two measurements and interpolating the remaining unmeasured points (using custom-built programs). Finally, for each sample, the edges were trimmed slightly to yield microtopographies of a rectangular shape (Fig. 1). The final sizes of the grids ranged from 315 to 394 mm in width and from 833 to 931 mm in length.

**Compaction index of the litter**

The compaction index was defined as the proportion of unmeasured points due to the shadow effect. Indeed, the more compact the litter, the flatter the leaves, leading to fewer unmeasured points and a smaller compaction index.

**Analysis of litter microtopography using geostatistics**

We used the geostatistical method of the experimental semi-variogram (or variogram, see Wackernagel 1995 for an example) to analyze the spatial structure of litter microtopography in our samples, using the freeware VESPER (http://sydney.edu.au/agriculture/pal/software/vesper.shtml). The variogram expresses the degree of spatial variation of a variable as a function of distance. Here, the variable of interest is the height of the litter surface. The difference in height \(z\) between two points separated by a distance \(d\) (\(d\) is also called the lag) is represented by a variogram. The experimental variogram is computed from the variance in height for all pairs of points separated by a lag \(d\), for a selection of lag values, as follow:

\[
\gamma(d) = \frac{1}{2n_d} \sum_{i=1}^{n_d} [z(x_i + d) - z(x_i)]^2
\]

where \(\gamma(d)\) is the variance at lag \(d\) (i.e., the beeline distance between sample locations \(x_i\) and \(x_{i+d}\), \(n_d\) is the number of pairs separated by the lag \(d\), \(z(x_i)\) is the value of the variable of interest (i.e., height) at location \(x_i\), and \(z(x_{i+d})\) is the value of the variable at distance \(d\) from \(x_i\).

Three important features of the variogram can be used for analysis (Fig. A2). The nugget effect corresponds to a variance extrapolated to a lag distance of 0. Theoretically, this variance should be null, but in practice, non-zero values result from errors inherent in the sampling technique or from the existence of structures at spatial scales smaller than the ones investigated. The sill is the variance obtained when the variogram reaches a plateau. Finally, the range corresponds to the lag distance at which the sill is reached. For distances smaller than the range, a spatial structure exists. For distances larger than the range, the variable of interest does not show a spatial structure. When a sill and range are reached, the variogram is said to be bounded. If the variogram is continuously increasing, it is said to be unbounded.

**Elevation transects**

From each leaf litter sample, we extracted 12 height profiles from the elevation maps. Missing data due to the shadow effect were interpolated linearly (Figure C in Appendix). We considered a surface as flat if different contiguous leaf fragments were lower than a given threshold of height. We considered two surfaces as contiguous if the difference in height between them was below a given threshold, varying between 1 and 10 mm. This implies calculating the differences in height between two successive pixels over entire transects, taken every 25 mm along the short axis and running parallel to the long axis of each sample. Therefore, for each given height threshold we obtained the length of all flat pathways along each transect.
Morphometric analysis of leaf fragments

We analyzed the degree to which either entire leaves or leaf fragments contribute to structuring the leaf litter’s surface. This destructive analysis was conducted on a single summer sample. We quantified the dimensions of visible leaf fragments by spraying red paint on the sample from above at a distance of ~20 cm. Therefore, only the parts of the leaf fragments visible from above were painted. Each leaf fragment was then extracted individually and photographed. The maximal chord length of the painted area (i.e., the longest line segment) was estimated using ArcGIS 9.2 (ESRI), as well as the maximal chord length of the entire fragment (Fig. 2). We chose to measure the maximal chord length rather than the surface of leaf fragments, as this characteristic is easier to relate to the pursuit–evasion trajectories displayed during the attacks.

Experimental set-up for recording sequences of pursuit–evasion

The interactions between spiders and crickets were observed in large plastic arenas (20 cm in diameter by 15.5 cm high). For each trial, a single cricket and a single spider were introduced into the arena. The interactions between the animals were observed for a period of 20 min. Crickets could escape spiders either by running or by jumping. Cricket–spider interactions were filmed at 25 frames/s using a high-definition video camera (Panasonic HD-SD200) under 18 W/840 neon illumination. Two different structural types of arena were tested. One structure (called the “empty arena”) had white paper as a ground surface, while the second structure (called the “litter arena”) had a natural leaf litter surface (one of the summer samples). The borders of the litter arena were glued to the litter using silicone sealant in order to keep the cricket and the spider inside the arena during the experiment. The camera was located 31 cm above the empty arena and 36.5 cm above the litter arena (see Fig. 3). We performed experiments on a total of \( N = 25 \) and \( N = 20 \) spider–cricket pairs using the empty arena and the litter arena, respectively.

Video processing and data analysis of pursuit–evasion sequences

We obtained video recordings of the interactions in AVC/H.264 format, with a 1920 × 1080 pixel resolution. Movies were extracted as MPEG-2 video format with a 1280 × 720p resolution using the Elecard Studio Converter v 3.2.39 software. Then the attack sequences were extracted as series of frames (bitmap).
using VirtualDub-MPEG2 v 1.6.19. The position of the front and the back of the two animals (spider and cricket) were measured frame by frame as 2D coordinates using ImageJ 1.43d.

After being placed in the test arena, spiders usually remained motionless while crickets explored the chamber until they were attacked. If a spider launched an attack over a stretch of at least one body length (which usually led to escape movements of the crickets), the behavior was ranked as a “pursuit.” Thus, simply moving accidently towards a motionless prey was not sufficient to be ranked as a pursuit. In contrast, if the cricket itself came very close (within about one spider body length) to the spider, which then responded by attacking, we recorded this behavior as “sit-and-wait.”

After a spider attacked, crickets often escaped by jumping. If the spider moved again in the direction of the landed cricket, we recorded this behavior as a secondary (i.e., subsequent) attack. We characterized each attack using four parameters. First, the distance (between centers of both animals) at which the spider launched its attack was called the “attack distance.” Second, the distance at which the spider’s attack triggered the cricket’s escape was called the “escape distance.” Finally, the velocities of the spider and the cricket during the interaction and the angle between the spider and the cricket during the attack were recorded (180° is where the spider was in front of the cricket, 0° where the spider was behind the cricket). We identified the pursuit angle as the angle at the onset of the pursuit.

All statistical tests were conducted using R 2.6.0 (R Development Core Team 2007). The homogeneity of variances and the Shapiro test for normality were carried out at a significance level of 0.05 before applying other tests. Ranges reported in the text and figures are standard deviations, unless otherwise noted.

Fig. 2 A single beech leaf extracted from the painted sample. The two painted surfaces are outlined, as is the maximal chord length on the largest surface (47 mm).

Fig. 3 Experimental set-up for the behavioral pursuit–evasion study in the litter arena, from the side and from above.
Results

A scan of one sample collected in the summer is shown in Fig. 4.

Compaction, geostatistics, and transects of litter microtopography

The freshly fallen leaves of the winter samples produced a microtopography that was less compact than the leaves of the summer litters (winter compaction index: 23.03% ± 1.37%, N = 4, summer compaction index: 10.59% ± 2.58%, N = 10, t-test = 8.46, P < 0.00001).

All variograms except one were unbounded, hence values for the sill and range could not be estimated (Fig. 5). This also meant that structures existed at scales larger than 22.5 cm in litter collected during both seasons. Variograms of winter litters had higher semi-variances than did summer litter variograms, showing that winter litters are rougher than summer ones. The nugget differed between winter and summer litters (summer = 1.35 mm², N = 4; winter = 3.02 mm², N = 10; t-test, t = 4.9, P = 0.00047). In both cases, the nugget was a small fraction of the scope of the measured variances, suggesting that few spatial structures existed at scales smaller than 0.5 mm.

The mean length of a flat surface as obtained from the transect analysis was larger for summer samples than for winter samples (Fig. 6). This was true irrespective of the height threshold used to define contiguous surfaces (Wilcoxon rank test for the four smallest thresholds, P < 0.0001).

Morphometric analysis of leaf fragments

The longest chord of a painted leaf fragment was much smaller than the maximal chord length of the entire leaf fragment (mean chord length of entire fragments = 5.46 ± 1.72 cm, N = 455; mean chord length of painted fragments = 2.77 ± 1.6 cm, N = 620; Wilcoxon test, W = 250,557, P < 0.0001). This result was also true for each tree species analyzed separately (oak mean chord length entire fragments = 6.39 ± 1.89 cm, N = 183; oak mean chord length painted fragments = 3.03 ± 1.95 cm, N = 277; Wilcoxon test, W = 45,202, P < 0.0001; beech mean chord length entire fragments = 4.84 ± 1.35 cm, N = 275; beech mean chord length painted fragments = 2.47 ± 1.26 cm, N = 351; Wilcoxon test, W = 87,729, P < 0.0001).

Pursuit and escape distances

All pursuit–escape sequences on both substrates ended with a successful escape by the cricket. Among the two arena types, the empty arena showed a higher proportion of attacks. Indeed, attacks occurred in 96% of the trials conducted in empty arenas, as compared to only 45% of the trials in litter arenas (N1 = 25 and N2 = 20 respectively, two-sample test for equality of proportions with continuity correction, P = 0.00045).

The mean pursuit distance of spiders in the empty arena was roughly twice that in the litter arena, as shown in Fig. 7 (5.64 ± 1.7 cm, N = 12, and 2.59 ± 1.1 cm, N = 8, respectively, pairwise t-test with Holm adjustment P-value < 0.0001). The mean fleeing distance of crickets in the empty arena was also roughly twice that of the litter arena (2.8 ± 0.85 cm and 1.32 ± 0.47 cm, N = 12 and 6, respectively, pairwise t-test with Holm adjustment P-value = 0.058). Comparing the distances between both agents in the same environment, we observed
significant differences between the pursuit and fleeing distances in the empty arena, the pursuit distance being twice the escape distance (pairwise $t$-test with Holm adjustment $P$-value $< 0.0001$), but no difference in the litter arena. Spiders launched their pursuits either from the back of the cricket or from the side, irrespective of substrate (mean vector empty arena $= 86.69^\circ$, circular standard deviation $30.13$, $N = 12$; mean vector litter arena $= 53.55^\circ$, circular standard deviation $42.8^\circ$, $N = 8$; Watson–Williams $F$-test, $P = 0.07$).

Due to multiple jumps by the cricket after being pursued by a spider, we sometimes observed up to three subsequent pursuits. Arena types differed in the proportion of subsequent pursuits (47%, $N_1 = 66$ and 15.4%, $N_2 = 13$ primary pursuits, respectively, two-sample test for equality of proportions with continuity correction $P = 0.07$, multiple pursuits from the same experiment counted). Indeed, we observed a secondary pursuit only twice in the litter arena; in both cases, the jumping cricket landed on the same leaf from which it jumped. The mean pursuit distance of secondary pursuits in empty arenas was 8.00 cm ($8.00 \pm 3.06$ cm, $N = 9$), which is different from the first pursuit ($5.64 \pm 1.7$ cm, $N = 12$, $t$-test, $t = 2.24$, $P$-value $= 0.03$). We did not observe a similar trend in the fleeing distances of crickets, as they tended to jump multiple times, irrespective of the behavior of the spider.

Discussion
The link between architecture of the micro-habitat and the biotic interactions at the scale of the organism has mainly been studied in freshwater river systems, although none of these studies deal within differential games theoretical context. These studies indicate a clear effect of habitat structure, such as surface microtopography of the river bed, on the structure of macro-invertebrate assemblages (Robson 1996; Taniguchi and Tokeshi 2004; Shumway et al. 2007). Despite its potential importance, the role of the architecture of forest leaf litter in ecological interactions has largely been neglected except for G. Uetz and collaborators who related variations in different aspects of the forest litter to the spider populations and assemblages, including by creating artificial litter made of polyvinyl leaves (Uetz 1979; Bultman and Uetz 1984 and references therein). Leaf litter structure could interfere with the outcome of predator–prey interactions directly, by providing places to hide or spatial refuges (e.g., Bultman and Uetz 1984; Finke and Denno 2006), or indirectly, by influencing the air flow and temperature regime at the litter’s surface (e.g., Uetz 1979; Finnigan 2000; Poggi et al. 2003). Here we show that the most basic element of leaf litter, fragmented leaves, determine the litter’s spatial structure at a microscale, which sets the spatial rules for the predator–prey interaction. In the following, we discuss the microtopography of the litter over seasons and in the context of the sensory ecology of cricket–spider interactions. We end with general considerations about the need to take into account the architecture of the environment when studying pursuit–escape interactions between predator and prey.
Microtopography of the leaf litter

Estimating the impact of leaf litter on biotic interactions requires characterization of its structure at the scale at which organisms interact, but very little work has been done on this topic. A pioneer study of litter microtopography of tropical and temperate forests, based on visual assessment of curling and flatness of leaves, was carried out by Heatwole (1961), in the context of biogeographical comparisons of types of litter structures in forests. His classification enabled him to rank forest floor litters according to the amount and shape of interstices in which organisms live. A few other studies have reported the effects of soil pits and mounds on local microclimate and bacterial assemblages (Berg and McClaugherty 2008), but they did not characterize the entire architecture of the litter. A clear flattening of the leaf litter was observed in our study in summer as shown by (1) the compaction index, which diminished by half compared with winter samples, (2) the length of contiguous flat surfaces, which was larger in summer litter, and (3) the higher variance of the winter variograms, which show that the surfaces of winter litter were less rough than those collected in summer. This change in the architecture of the leaf litter was most likely caused by weathering and decomposition.

We observed no range on the variograms for lag distance between 0.5 mm and 22.5 cm, meaning that structures existed at all scales within these distances. This underlines the high geometric complexity of the litter’s microtopography, both for the fresh winter litter and the partly-decayed summer litter. The actual range of the litter’s microtopography was likely at distances greater than 22.5 cm. Hence, the actual range of the variograms was invariably much larger than the mean length of a visible leaf fragment. We found good agreement between the size of the smallest structuring unit of leaf litter and the size at which both attack and escape behaviors are initiated (both ~3 cm). The implications of this spatial restriction are discussed in the following section.

Sensory ecology of cricket–spider interactions in leaf litter

The wolf spider–wood cricket interaction is one of the best-understood predator–prey interactions in terms of neuroethology and sensory ecology, but with the exception of one study (Dupuy et al. 2012), this interaction has been studied exclusively in the laboratory. Biomechanical experiments measuring the speed and direction of air flow in front of a running spider (Casas et al. 2008) and neuroethological studies reporting crickets’ fleeing distances (Dupuy et al. 2011) suggest that the detection system of the cricket is able to perceive a spider launching its attack at a distance of up to 5 cm away. Results presented in this article support these earlier conclusions. Spiders in arenas with a flat bottom (i.e., laboratory settings) did indeed attack crickets at a mean distance of approximately 6 cm. Laboratory settings identify what is intrinsically feasible and thus represent the upper boundary of performance, both of predator and prey, without any external disturbances.

The experiments conducted in arenas with litter from field samples, by contrast, show what actually occurs in more complex environments. For example, attacks taking place in summer leaf litter were launched at a mean distance of 2–3 cm, a reduction by half of the distances measured on flat terrain. This distance corresponds nicely with the mean maximal length of a visible leaf fragment, which seems to be the actual scale at which the interaction takes place. Because the border of a leaf fragment is reached within a few body lengths, spiders have either caught their prey by then, or there is no point in pursuing it further. Indeed, the near total absence of subsequent pursuits once the cricket jumped away in litter arenas can be explained by the highly complex architecture of the environment. This makes subsequent localization of the prey a nearly impossible task for the spider, as the cricket has then escaped into a different “world.” By contrast, on flat artificial surfaces, spiders often launch subsequent pursuits, as they can use both vision and vibrations produced by the landing crickets to localize the prey. This may be feasible in the leaf litter as well, but vibrations may not be well-transmitted at leaf junctions and their origin may be difficult to localize due to the complexity of the structure of the leaf litter. Visual feedback might also be precluded by the rugosity of the leaf litter.

Pursuit–evasion and search games in complex environments

The present study focused on the pursuit–evasion sequences resulting from an encounter between predator and prey. The above considerations led us to conclude that these sequences are preceded by hide-and-seek search games in the leaf litter until the spider is within striking distance of its prey, or until the cricket approaches an ambushin spider. The behavioral interactions between spiders and crickets are thus a mixture of search games and pursuit–evasion games, which occur during the attack.
sequences. Furthermore, the relative importance of these two types of games is function of the rugosity of the environment: the more rugose it is, the more important are search games. These different types of games have been mathematically studied nearly independently since Isaacs (1965). The joint occurrence of these games during cricket–spider interactions and most likely during interactions between other predator–prey pairs calls for a conceptual merging between these two kinds of games. Such synthesis would apply not only to predator–prey interactions in general, but more largely to police actions, warfare, and counter-terrorism (Alpern et al. 2011; Bonato and Nowakowski 2011; Alpern and Lidbetter 2013).

The mathematical and theoretical works of pursuit–evasion and search games described in the introduction pay special attention to the geometry of the arena, which can be a network, a star, or a continuous space, bounded or unbounded. These works demonstrate that the geometry of the arena indeed has an immense impact on the value of the games, usually defined as the time until capture or escape, and on optimal solutions for both the searcher and the escaper (Garnaev 2000; Alpern and Gal 2003). By analogy, ecologists, ethologists, and biomechanists might need to consider the architecture of the environment more thoroughly than is currently common. The parasitic wasp–leaf miner interaction described in the introduction was the first interaction to be studied in terms of search games using the princess–monster game as its closest analogue (Meyhöfer et al. 1997; Djemai et al. 2000). The arena (the mine) is not bigger than 2 cm² but is highly structured. In this example, the search region is a planar area between the two surfaces of an apple leaf, where the feeding activity of the larva produces so-called windows. These are small, translucent, and whitish spots in which only the upper leaf epidermis remains, because the plant tissue underneath has been consumed. The wasp violently inserts its ovipositor almost exclusively through the feeding windows, because the rapid escape reactions of the larva implies blazing fast attacks by the wasp, which are not feasible if it has to pierce thick tissues of leaves. The geometrical arrangement of the feeding windows, their increasing numbers during the course of larval development, and the relative size of the larva and the feeding windows are therefore very important. Unfortunately, in previous studies, the positions of both antagonists were not recorded, nor was the exact geometry of the mine. The wolf spider–wood cricket interaction reported here does not suffer from these limitations and seems to be the only one available in the literature for which we have all the appropriate data for modeling the interaction as a pursuit–evasion game (Isaacs 1965), i.e., (1) a high resolution mapping of the location of both antagonists for the whole duration of the interaction at sufficiently high frequency so that trajectories can be faithfully reconstructed, and (2) precise mapping of the arena geometry at the scale of the organisms. This unique dataset and our first, coarse analysis of several statistics of the games shows that the size of nearly flat areas, often corresponding to a single leaf fragment, determines the extent of the arena in which pursuit–evasion games between spiders and crickets occur. We also found that leaf litter has a four-fold topographical effect on pursuit–escape sequences: it (1) greatly reduces the likelihood of launching a pursuit, (2) reduces pursuit and escape distances by half, (3) puts prey and predator on par in terms of pursuit and escape distances, and (4) reduces the likelihood of secondary pursuits to nearly zero. A refined analysis of the trajectories of both predator and prey will be carried out in a subsequent article. These first results show, however, that architecture of the habitat has a profound influence on the rules of the game in biological systems, as it does in theoretical models.

There is a need to obtain datasets similar to ours for larger animals that engage in predator–prey interactions, such as cheetahs chasing antelopes (Hilborn et al. 2012). Unfortunately, none seems to exist (T. Caro, personal communication), because the rate at which collars around the necks of big cats send GPS locations is too low to faithfully represent the trajectories of both antagonists during a chase–fleeing interaction (S. Durant, personal communication). The much higher rate of sampling of accelerometers attached to penguins chasing krill (Watanabe and Takahasi 2013) is a major improvement in this respect, but in this case the geometry of the arena, as well as the trajectory of the prey, remains unknown. Until major advances in telemetric technologies, combined with high-resolution environmental mapping, provide adequate datasets for large animals, encounters between invertebrate predators and prey will provide the bulk of experimental data for future studies of pursuit–evasion and search games.

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**References**


Brechbühler R, Casas J, Bacher S. 2011. Diet choice of a predator in the wild: missed opportunities along the prey capture sequence. Ecosphere 2, art. 133.

Broom M, Ruxton G. 2005. You can run—or you can hide: Pursuit-evasion games in complex habitats 777


Appendix

![Photograph of the mixed oak-beech forest, the leaf litter, and the outline of a sample before extraction.](image-url)

Fig. A1 Photographs of the mixed oak-beech forest, the leaf litter, and the outline of a sample before extraction.
Fig. A2. Definition of the experimental variogram and its characteristics.

Fig. A3. Extraction of transects using reconstructed microtopography.