

RESEARCH ARTICLE

Running away or running to? Do prey make decisions solely based on the landscape of fear or do they also include stimuli from a landscape of safety?

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ABSTRACT

Predator–prey interactions are a key part of ecosystem function, and non-consumptive effects fall under the landscape of fear theory. Under the landscape of fear, the antipredator responses of prey are based on the spatial and temporal distribution of predatory cues in the environment. However, the aversive stimuli (fear) are not the only stimuli prey can utilize when making behavioral decisions. Prey might also be using attractive stimuli that represent safety to guide decision making. Using a novel, orthogonal design, we were able to spatially separate aversive and attractive stimuli to determine whether prey are utilizing safety cues to navigate their environment. Crayfish *Faxonius rusticus* were placed in the center of a behavioral arena. Aversive stimuli of either predatory bass *Micropterus salmoides* cues or conspecific alarm cues increased along the x-axis of the behavioral arena. Safety cues (shelters) increased along the y-axis by decreasing the number of shelter openings in this direction. Crayfish were allowed two phases to explore the arena: one without the fearful stimuli and one with the stimuli. Linear mixed models were conducted to determine whether movement behaviors and habitat utilization were affected by the phase of the trial and the type of aversive stimuli. Crayfish responded more strongly to alarm cues than to fear cues, with only alarm cues significantly impacting habitat utilization. When responding to alarm cues, crayfish used safety cues as well as fear cues to relocate themselves within the arena. Based on these results, we argue that crayfish utilize a landscape of safety in conjunction with a landscape of fear when navigating their environment.

KEY WORDS: Behavioral ecology, Predator–prey interactions, Sensory ecology

INTRODUCTION

Predator–prey interactions are composed of two major impacts on the prey: consumptive effects, where the predator consumes the prey, and non-consumptive effects, where the predator causes alterations in the prey's behavior, physiology, morphology or life history (Matassa and Trussell, 2011; Weissburg et al., 2014). While the consumptive effects are obvious when studying the interactions between predator and prey, the non-consumptive effects can remain more shadowed (Lima, 1998). One well-established concept in the

field of non-consumptive effects is the concept of the landscape of fear (Laundré et al., 2001).

The landscape of fear is the sensory landscape composed of aversive cues associated with the presence of predators (Laundré et al., 2001; Luttbegg and Trussell, 2013). The aversion to these cues has been termed 'fear' and may result in significant changes to a prey's behavior, physiology, morphology or even their evolutionary trajectory (Brönmark and Miner, 1992; Brown and Chivers, 2005; Peckarsky et al., 2008). The landscape element refers to the spatial and temporal distribution as well as the specific dynamics of predatory cues within a habitat (Hernández and Laundré, 2005). Shifts in behavior, such as foraging choices and habitat use, can often have broadscale ecological impacts that can alter ecosystem function and services (Arias-Del Razo et al., 2012; Laundré et al., 2014; Gallagher et al., 2017). These changes, independent of the biological level of response, are dictated by the landscape of aversive signals (Gaynor et al., 2019; Leavell and Bernal, 2019). Yet, the landscape of fear is only one of a number of sensory landscapes from which prey make behavioral decisions (Leavell and Bernal, 2019).

These sensory landscapes include multiple sensory modalities that vary in their spatial and temporal dynamics (Jordan and Ryan, 2015; Kohl et al., 2018). The landscape of fear is often visualized as a three-dimensional plane with peaks and valleys (Fig. 1; Gaynor et al., 2019). Within this plane, the peaks represent some form of aversion or fear. Depending on the specific usage within a paper, the peak can represent the intensity of the predatory cue in nature, the perceived intensity after neural filtering, or even the perceived risk of predation (Fig. 1, left-hand side; Jordan and Ryan, 2015; Gaynor et al., 2019; Leavell and Bernal, 2019). In response to the detection and perception of this landscape, prey can evoke two common options by either hiding in refuges or moving to habitats with lower levels of perceived risk (Lima and Dill, 1990; Lima and Bednekoff, 1999; Martín and López, 1999; Kobak et al., 2014). Of course, other anti-predatory behavior exists such as jamming of bat sonar in moths (Corcoran et al., 2009) or mobbing in magpies (Koboroff et al., 2013). The relocation of prey to areas of lower perceived risk (or movement away from aversive stimuli) led to the coining of the concept of fear (Laundré et al., 2010). Integrated upon this landscape of fear are other sensory landscapes from which animals extract useful ecological knowledge (Luttbegg and Trussell, 2013).

Probably the most commonly researched landscape (beside fear) is that of food resources (Sih, 1982; Sih et al., 1990; Brown et al., 1999). In contrast to the aversive response to predatory cues, food patches or resources are attractive stimuli and create within prey an easily researched decision-making point: foraging versus predation (Sih et al., 1990; Shrader et al., 2008; Iribarren and Kotler, 2012; Luttbegg and Trussell, 2013). By modulating relative risk or resource value, estimates of decision-making paradigms used by prey can be

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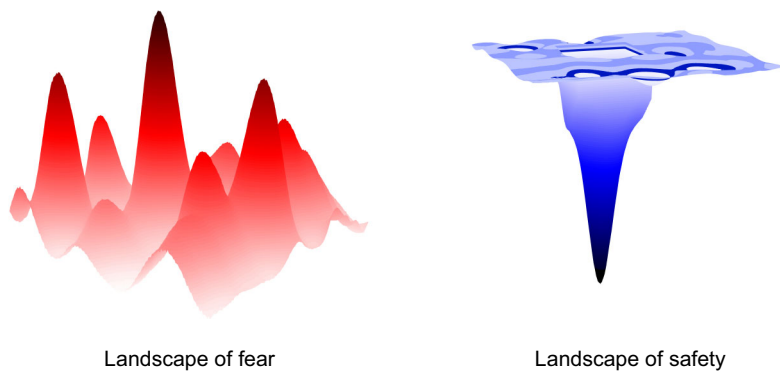


Fig. 1. Visual representation of the landscape of fear (left) and the landscape of safety (right). The perceived intensity of predatory cues is in red, with deeper shades and greater heights indicating a greater intensity of threat. The perceived intensity of safety cues is in blue, with lower levels and deeper blues representing increased safety. These two landscapes (along with others) are part of a prey organism's Umwelt.

produced (Křivan, 2007; Ferrari et al., 2009). At the base of these experimental and theoretical projects is the interplay between the spatial and temporal dynamics of aversive stimuli (landscape of fear) and attractive stimuli (resource patchiness). During predator–prey interactions, prey are faced with far more complex sensory landscapes composed of a multitude of aversive and attractive stimuli, which produce an Umwelt of their habitat (Partan and Marler, 2002; Van Dyck, 2012; Leavell and Bernal, 2019). While prey are unlikely to integrate all aversive and attractive stimuli within a landscape in their decision making, prey are likely to incorporate both multimodal sensory information (vision and olfaction) as well as sensory signals and cues related to both fear and safety.

In relation to predator–prey interactions and the landscape of fear, prey may seek out refuges as sources of safety or protection against predation (Cressman and Garay, 2009; Orrock et al., 2013; Donelan et al., 2017). Just as decision making using information about the landscape of fear and distribution of resources can serve as an experimental model, seeking of refuges by prey is additionally useful as an experimental model of predator–prey dynamics (Sih, 1987; Sih et al., 1988; Wang and Wang, 2012). Integrating safety information may even provide better estimates of predation risk (Luttbeg et al., 2020). In a broader sense, refuges can be defined as any strategy invoked by prey to reduce predation risk (Sih, 1987). In simplistic terms, the cost of safety is a loss of potential energy gained from not foraging weighed against the benefit of reduced predation risk. The spatial distribution of refuges is yet another sensory landscape that prey need to extract meaningful information from to make decisions on behavioral actions (Dill, 1987; Brown and Kotler, 2004; Chivers et al., 2001). Shifts in foraging to less risky habitats are one form of refuge from predation (Hixon and Beets, 1993; Hernández and Landré, 2005). Additionally, changes in activity patterns (Kohl et al., 2018), or even shifts in body morphology such as deeper bodies to escape gape-limited predators (Brönmark and Miner, 1992) can also create refuges from predation.

Some organisms have the ability to create their own physical space of refuge such as burrows, dens or shelters. These distinct locations serve as a safe location to hide themselves or their offspring from predators. Thus, animals with these home bases must have some perception of safety (Bayoumi and Meguid, 2011). For example, snails *Nucella lapillus* utilize rock crevices to hide from predatory green crabs *Carcinus maenas* (Donelan et al., 2017). Similar to the landscape of fear, these physical refuges provide sensory stimuli which prey can utilize to navigate their environment, but unlike the landscape of fear, these burrows could create a landscape of safety. The difference between refuges dispersed throughout an ecosystem, such as habitats with high cover, and

burrows or shelters is the spatial specificity of the landscape because organisms create the refuges in a distinct location.

A landscape of safety with distinct burrows or shelters can provide animals with a sensory landscape that allows a goal orientation toward a known spot of safety (Fig. 1, right-hand side; Hansson and Åkesson, 2014; Schone, 2014). Landscapes of fear are composed of aversive stimuli where behavioral responses involve moving away from regions with a higher intensity predator cues to areas with a lower intensity of cues (Fig. 1, left-hand side; Jordan and Ryan, 2015). As opposed to a general movement ‘downhill’ from predatory peaks, burrows and shelters provide organisms with the opportunity to extract spatial information and perform a navigation strategy to locate a haven of safety (Schone, 2014). The landscape of safety can be visualized as a singular valley in a landscape, where the risk to the prey decreases the closer the prey approaches their refuge (Fig. 1, right-hand side). Signal detection theory within sensory ecology would predict that prey integrate these two landscapes (fear and safety) when responding behaviorally in threatening situations. Yet, in experimental or even field situations, the spatial and temporal representation of these two landscapes relative to each other are either unknown or conflated. In a conflated Umwelt, the ‘downhill’ of the landscape of fear aligns with the ‘downhill’ of the landscape of safety. As such, movement along this path could be guided by aversion to predators, attraction to safety or some combination of those two.

To answer questions regarding the presence of safety cues and whether prey are using the spatial distribution of safety cues for movement, two distinct sensory landscapes that are orthogonal to each other must be created. When done correctly, prey can move along one axis (e.g. fear) independent of the sensory landscape along the other axis (e.g. safety). Movement and behavioral responses can be analyzed along each axis of the landscape separately. We have created just such an environment to evaluate whether crayfish can detect and use a landscape of safety along with a landscape of fear. In addition, we have created these orthogonal landscapes using two different types of aversive cues, one from a predator and one from injured conspecifics. Crayfish have been shown to react to predatory bass and alarm cues as aversive or fearful stimuli (Beattie and Moore, 2018; Wood and Moore, 2020) and both built shelters or used natural crevices as locations of refuge (Martin and Moore, 2008; Florey and Moore, 2019). We hypothesized that crayfish will integrate both the aversive stimuli that compose the landscape of fear and attractive stimuli in the landscape of safety to navigate an experimental arena. We created a novel experimental design, which simultaneously and orthogonally presents both fear and safety stimuli to crayfish, thus allowing us to determine whether crayfish movement was based on either the

aversive stimuli presented through cues or the attractive stimuli presented through shelters.

MATERIALS AND METHODS

Experimental design

Wild-caught rusty crayfish, *Faxonius rusticus* (Girard 1852), were exposed to two different types of fear-inducing chemical stimuli within a landscape of differing safety cues to determine whether behavioral decisions are based primarily on the perception of fear or safety cues. A fear gradient was constructed perpendicular to a safety gradient within a behavioral arena to spatially differentiate between these two cues. The fear gradient was created using chemical stimuli that relayed information of either predator presence or conspecific injury cues, which were delivered at different concentrations across the behavioral arena (Fig. 2). Previous work has shown fear or aversive responses to both of these cues in crayfish (Hazlett, 1994; Jurcak and Moore, 2018). Safety cues were based on a spatial distribution of shelters of varying values based on the number of openings (1–4). Previous research has demonstrated that crayfish prefer shelters with fewer openings (Matin and Moore, 2008). Crayfish were allowed to explore the arena for 15 min (called the exploratory phase) prior to one of the two chemical cue introductions. Crayfish were briefly removed from the arena and the appropriate stimulus was delivered into each of the shelters through a small hole in the top of the shelter. Once the chemical stimulus was delivered, crayfish was placed back into the middle of the arena were allowed an additional 15 min to navigate the arena (called the stimulus phase), now with an altered landscape of chemical cues. Crayfish position within the arena was tracked at a rate of 1 point per second using Xcitex ProAnalyst[®] motion tracking system.

The design of the experiment comprises a fully factorial 2×2 repeated design, as the same crayfish were used in the exploratory phase and given an additional stimulus phase of the experiment. The second factor was the two different fear cues. Treatment: alarm – phase: exploratory, $N=20$; phase: stimulus, $N=20$ (same 20 crayfish used in the previous phase). Treatment: bass – phase: exploratory, $N=20$; phase: stimulus, $N=20$ (same 20 crayfish used in the previous

phase). Henceforth, we will refer to each of the four conditions by combining the phase followed by the treatment. Thus, the experiment consists of these four conditions: exploratory alarm, stimulus alarm, exploratory bass, stimulus bass.

Animal collection and housing

Both male and female F1 (reproductive) and F2 (non-reproductive) rusty crayfish, *F. rusticus*, were collected via kick seining on the Portage River (41.3618, −83.5007) in Bowling Green, OH, USA. After collection, crayfish were brought back to the Laboratory of Sensory Ecology at Bowling Green State University, where experimental crayfish were individually housed in plastic containers (25.2×16.2×11.8 cm, l×w×h). Each container was connected by recirculating aged tap water, but the individuals were mechanically and visually isolated. Crayfish used to make injury cues were communally housed in a modified steel cattle tank (119.4×55.9×77.5 cm, l×w×h). All crayfish were fed Manna Pro[™] Small World[™] Complete guinea pig pellets 3 times a week. Only crayfish with fully intact appendages and chelae were used in the behavioral trials. Crayfish had an average intraorbital carapace length of 2.2 ± 0.1 cm.

Largemouth bass *Micropterus salmoides* were purchased from Hills Trout Farm LLC (Harrietta Hills, MI, USA). Bass were kept in a flume (243.8×58.4×55.9 cm, l×w×h) of aged tap water and fed a fish food diet (Sportsman's Choice TrophyFish Feed, High-Protein, Multi-Species Fish Formula).

Ethical statement

All bass used to collect bass cue were kept following the established animal care and used procedures approved by the Institutional Care and Use Committees at Bowling Green State University (Protocol: 856543-5).

Chemical cue generation

The predator chemical cue was generated by placing three largemouth bass *M. salmoides* in a 102 l plastic storage bin filled with 68 l of tap water that was aged a minimum of 24 h. The total length of the three fish placed within the odor collection bin was 59.8 ± 5 cm (mean±s.e.m.) for the trials. Fish were fed prior to introduction into the storage bin but were not fed within the bin. Water from the bin was collected fresh before each trial in which bass cue was needed. Bass were chosen such that each individual animal exceeded the gap ratio needed to consume the crayfish used in the trial (Wood and Moore, 2020).

The alarm cue was created by macerating 15–18 g wet mass of whole *F. rusticus* crayfish in 400 ml of deionized water (Hazlett, 1994). The alarm cue was used within 6 h of creation, as previous studies have shown that crayfish are less reactive to older chemical stimuli (Hazlett, 1994).

Behavioral assay

Behavioral assays were conducted in a black (6 mm thick) Plexiglas arena (74.3×62×13 cm, l×w×h) (Fig. 2). Aquarium rocks (approximately 0.5 cm in diameter) were attached to the bottom of the arena using silicone to increase traction and aid in crayfish movement. The arena was divided into 16 equally sized quadrants in a 4×4 (rows×columns) fashion using fishing line that was affixed to the top of the arena, 5.0 cm above the waterline. Crayfish shelters were constructed using PVC pipe with an inner diameter of 3.2 cm that had been sawed in half lengthwise. A total of 16 shelters were used for the experiment: 4 with a single opening, 4 with two openings, 4 with three openings and 4 with four openings (Fig. 2).

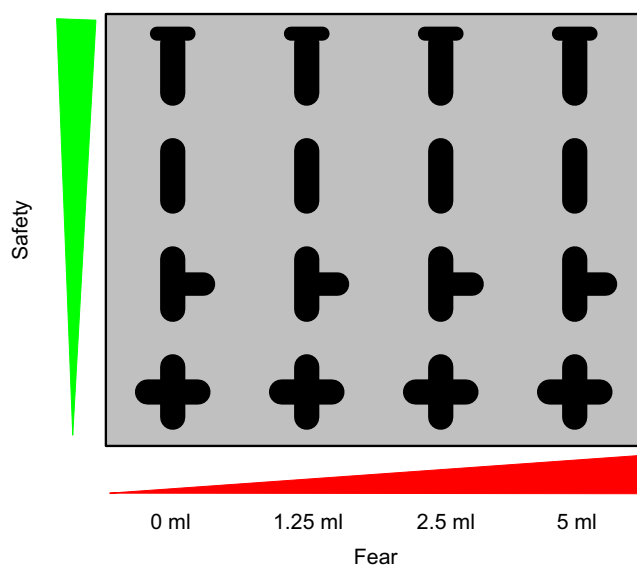


Fig. 2. Schematic diagram of the behavioral assay arena showing the fear gradient along the x-axis and the safety gradient along the y-axis. The numbers along the x-axis indicate the volume of stimulus injected into each shelter through a hole in the top of the shelter.

These shelters were equally placed in four rows of four. This created a pattern such that the shelters in each row had the same number of openings, and the shelters in each column had one more opening than the row above it (Fig. 2). Each shelter also had a small hole (0.6 cm in diameter) drilled in the top for delivery of the appropriate chemical stimulus. Each chemical stimulus was pipetted into these holes so that the stimulus remained within each shelter. The chemical cues were delivered in four different aliquots: 5, 2.5, 1.25 and 0 ml. Chemical stimuli were pipetted into the shelters such that each column of shelters received the same amount of stimulus, thus creating a grid within the arena in which the crayfish could choose between shelters with one to four openings, which were injected with 5 to 0 ml of aversive stimulus (Fig. 2). The placement of the shelters and delivery of the stimuli created two different landscapes with increasing perceptual levels perpendicular to each other. Along the x -axis, the intensity of the predator or alarm cue increased, but was uniform perpendicular to the axis. In a similar manner, the safety of the shelter increased along the y -axis but remained uniform along the x -axis (Fig. 2).

Prior to the assays, the crayfish's carapace was painted white using correction fluid (BIC® White-Out® Quick-Dry Correction Fluid), which does not affect the behavior of the crayfish (Edwards et al., 2018; Wood et al., 2018). One crayfish was placed in the middle of the arena and allowed to explore for 15 min. During the exploration phase, the shelters were in place in the arena, but no chemical stimulus had been added to the shelters. After 15 min, the crayfish was removed from the arena and the chemical stimulus was added to the shelters in the manner described above. Removing crayfish in this fashion has little effect on their behavior (Edwards et al., 2018). The same crayfish was then replaced in the center of the arena and allowed to navigate the arena for an additional 15 min. Both the exploration and stimulus phases were recorded as MP4 files using a Sony Handycam HDR-CX405. Between each trial, the entire arena and all shelters were rinsed to remove any odors from the previous trials.

Data processing

Videos of each trial were analyzed in Xcitex ProAnalyst® software. The videos were digitized at a rate of 1 point per second, as crayfish movement behavior can be analyzed every second (Kamran and Moore, 2015; Moore et al., 2021). The video was calibrated so that the output of the tracking would give an x,y coordinate in centimeters from the origin of the behavioral arena. The origin was set as the corner of the tank which contained the shelter with four openings (lowest safety) and no chemical stimulus (lowest fear). Thus, the origin reflected the part of the behavioral arena where both safety and fear stimuli were the lowest and thus was set to zero. The x -axis represented an increase in either the alarm or predator cues, and the y -axis represented an increase in the safety provided by the shelter. The calibration of each video was set by choosing the edges of the Plexiglas and setting the distance between the two edges as 6 mm. After each video was calibrated in millimeters, the crayfish's carapace was manually tracked for the entire duration of the trial. This tracking gave an x,y coordinate position of the crayfish within the arena. Thus, each individual crayfish had a total of 900 points throughout the 15 min exploration phase and a subsequent 900 points during the 15 min stimulus phase. This track was exported (as calibrated millimeter units) to an Excel file for further processing by an R code (<https://www.r-project.org/>).

After all of the tracks were digitized, each individual track was processed using an R code to extract relevant behavioral parameters.

As the arena was moved and cleaned between all of the trials, the exact distance between the camera and arena was subtly different between trials. Despite trials being calibrated to known locations and distances in the arena, there were small scale differences in the real-world coordinates of the arena. These differences varied no more than 5% of the total arena size. To account for subtle differences between trials and prior to the extraction of any behavioral parameters, both the x - and y -axes were normalized to run from 0 to 100 by subtracting the minimum x -axis value from all x coordinates and the minimum y -axis value from all y coordinates. These new coordinates were divided by the maximum value for the x - and y -axes. This procedure produced x and y values that ranged from 0 to 100 along each axis. After normalizing x,y positions of the crayfish, behavioral parameters were extracted from the digitized pathways. The x - and y -axes were divided into four different zones based on the concentrations of alarm and bass stimulus for the fear axis and based on the safety provided by the number of different shelter openings. Based on this, we created four different fear zones (0–25, 25–50, 50–75, 75–100 along the x -axis) and four different safety zones (0–25, 25–50, 50–75, 75–100 along the y -axis). The increasing numbers also indicate increasing levels of fear (x -axis) and increasing levels of safety (y -axis). Finally, the overall walking speed of the animal, as well as the walking speed in the x dimension (fear) and the y dimension (safety), were calculated. A negative walking speed indicates that the mean walking speed of the animal is toward the origin of the arena or toward lower safety or fear values.

Data analysis – statistical treatment

An initial statistical analysis was done to ensure that there were no significant differences in responses due to sex or reproductive form of the crayfish. No differences were found, so these two factors were ignored in the subsequent analysis.

All data analysis took place within the programming language of R. The beginning steps of the data conditioning follow those typically done in mixed model analysis (Zuur et al., 2009). The first step in the analysis was to produce histograms, Q–Q plots and normality tests of all the behavioral variables. The variance of the overall walking speed and walking speed in the y dimension were not normally distributed. Given that most GLMMs are robust against violations of the underlying assumptions of data distributions, we chose not to transform any of our response variables before running the models (Schielzeth et al., 2020). Cleveland dot plots were used to examine both the behavioral and spatial data for outliers, and none were found. Finally, to check for collinearity within the behavioral variables, independent regressions were performed between all of the (behavioral) variables. None of the behavioral measures showed any significant correlations.

All statistical tests were performed using the generalized linear mixed models approach (Zuur et al., 2009). All statistical models were performed in R used the 'lmer' function from the lmerTest package in R (<https://CRAN.R-project.org/package=lmerTest>). Following model construction, the outputs were extracted using the 'anova' function from the car package in R and the 'summary' function (<https://cran.r-project.org/web/packages/car/index.html>). Within models that showed significant interactions, the 'emmeans' function with a Tukey adjustment was used to investigate where significant differences between treatments occurred (<https://cran.r-project.org/web/packages/emmeans/index.html>).

For the models, the behavioral movement measures (walking speed, walking speed along the fear dimension, and walking speed

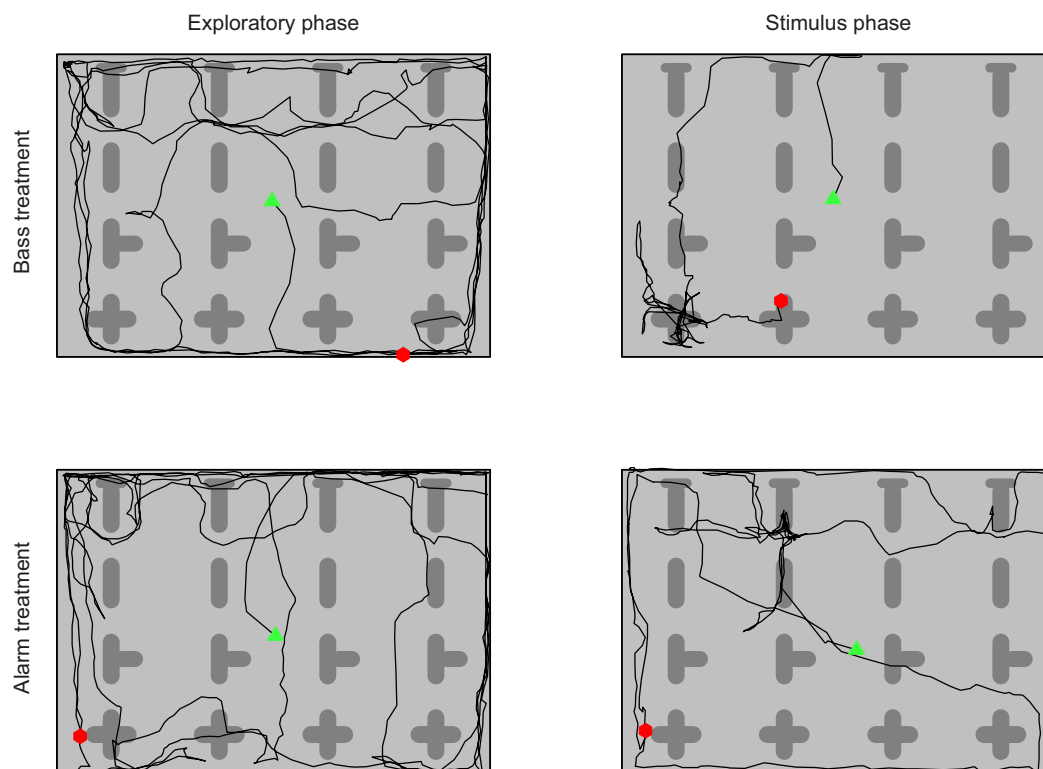


Fig. 3. Example of two crayfish tracks digitized at one point per second under the four experimental treatments. Tracks of crayfish in the exploratory phase (left) and stimulus phase (right) of the experiment are shown, for the bass stimulus (top) and alarm stimulus (bottom). The green triangle indicates the starting point of the track and the red circle indicates the ending point.

along the safety dimension) served as the dependent variable, and the phase of the experiment (exploration or stimuli) and type of stimuli (alarm or bass cue) as independent measures with full interactions between those two variables. Finally, because the exploration and stimulus phase of any individual trial included the same animal, the trial number was used as a random factor within each model. For the spatial data (duration in different fear or safety zones), duration served as the dependent measure, and phase of the experiment, type of stimuli and zone number served as independent measures with full interactions between those three variables. As in the first model, the trial number served as a random factor within each model.

RESULTS

Movement behaviors

Crayfish displayed a wide array of movement tracks in both phases of both stimulus treatments (Fig. 3). Crayfish typically spent a portion of their time traveling along the edges of the arena and exploring the entire tank. In some trials, some crayfish spent most of their time within one or more shelters regardless of the odors present in the arena (Fig. 3, bottom right). A more quantitative and statistical analysis is provided below.

Crayfish walking speed significantly increased in the presence of bass cues compared with their speed without the bass cue present, but walking speed significantly decreased when the alarm cue was

Table 1. Main statistical output of the linear mixed models with significant models with full interactions

Behavioral parameter	Model	F-value	P-value
Walking speed	Phase	$F_{1,38,0.05}=0.17$	0.682
	Treatment	$F_{1,38,0.05}=28.3$	<0.001
	Interaction	$F_{1,38,0.05}=18.9$	<0.001
Walking speed, fear axis	Phase	$F_{1,38,0.05}=0.008$	0.931
	Treatment	$F_{1,38,0.05}=1.05$	0.312
	Interaction	$F_{1,38,0.05}=0.03$	0.854
Walking speed, safety axis	Phase	$F_{1,38,0.05}=2.16$	0.146
	Treatment	$F_{1,38,0.05}=4.62$	0.035
	Interaction	$F_{1,38,0.05}=5.9$	0.017
Duration in fear zones*	Phase zone interaction	$F_{3,304,0.05}=6.85$	<0.001
	Treatment zone interaction	$F_{3,304,0.05}=6.91$	<0.001
	Phase treatment zone interaction	$F_{3,304,0.05}=5.16$	0.002
Duration in safety zones*	Phase Zone Interaction	$F_{3,304,0.05}=7.02$	<0.001
	Treatment zone interaction	$F_{3,304,0.05}=10.1$	<0.001
	Phase treatment zone interaction	$F_{3,304,0.05}=4.45$	0.004

*Univariate models were not significant. Significant findings are in bold.

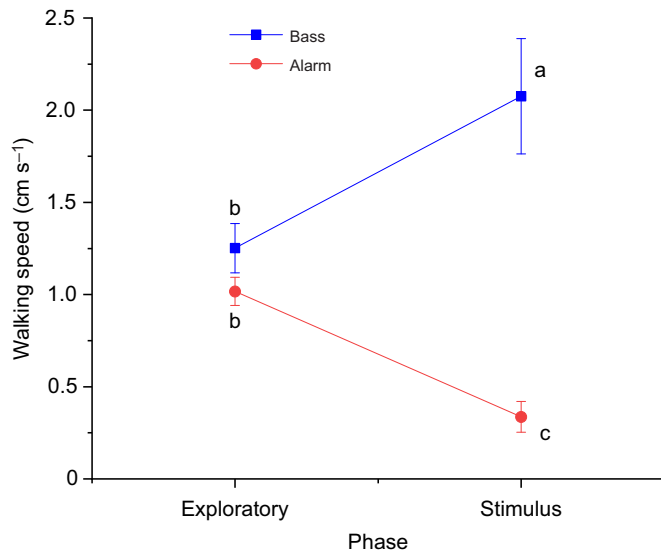


Fig. 4. Mean (\pm s.e.m.) walking speed throughout the entire arena for the different cues (alarm, bass) during the exploratory and stimulus phases of the experiment. Different letters indicate a significant difference using a *post hoc* test (emmeans, see Materials and Methods) with a Tukey adjustment ($P < 0.05$). $N = 20$ for all treatments; the same 20 crayfish used in the exploratory phase were used in the stimulus phase.

added compared with that during the exploratory phase of the alarm treatment (overall model: $F_{1,38,0.05} = 18.9$, $P < 0.001$; Table 1, Fig. 4). When presented with the predatory cue of bass, crayfish increased their walking speed by approximately 68% from 1.25 ± 0.13 cm s⁻¹ during the exploratory phase to 2.1 ± 0.3 cm s⁻¹ during the odor phase (emmeans *post hoc* $P = 0.009$). Conversely, crayfish reduced their walking speed by a third from 1.02 ± 0.08 cm s⁻¹ during the exploratory phase to 0.34 ± 0.08 cm s⁻¹ while the alarm cue was present (emmeans *post hoc* $P = 0.039$). As expected, the walking speed during the two different exploratory phases was not significantly different (emmeans *post hoc* $P = 0.79$), and the walking speed during the bass cue presentation was significantly higher than during the alarm cue presentation (emmeans *post hoc* $P < 0.001$).

An analysis of the walking speeds along either the x-axis (fear) or y-axis (safety) reveals further differences (Figs 5 and 6). Crayfish did not exhibit any significant shift in walking speed along the x-axis under any of the treatments (overall model $F_{1,38,0.05} = 0.03$, $P = 0.854$; Fig. 5). Yet, crayfish significantly altered their walking speed along the y-axis (overall model $F_{1,38,0.05} = 5.9$, $P = 0.017$; Fig. 6). Crayfish exhibited a larger negative walking speed along the y-axis during the bass stimulus phase when compared with the exploratory phase of this experiment (emmeans *post hoc*, $P = 0.04$, Fig. 6). Conversely, the only positive walking speed along the y-axis exhibited by crayfish during any phase of the experiment was when they were presented with the alarm cue in the stimulus phase. Under these conditions, crayfish exhibited a higher and positive walking speed along the y-axis compared with that with the bass odor in the stimulus phase of the experiments (emmeans *post hoc*, $P = 0.0095$, Fig. 6).

Fear and safety movement

Crayfish significantly altered their movement patterns along the fear axis in response to the different odor treatments (overall fear model: $F_{3,304,0.05} = 5.16$; Fig. 7). Crayfish significantly increased their use of the lower alarm cue areas when compared with both exploratory

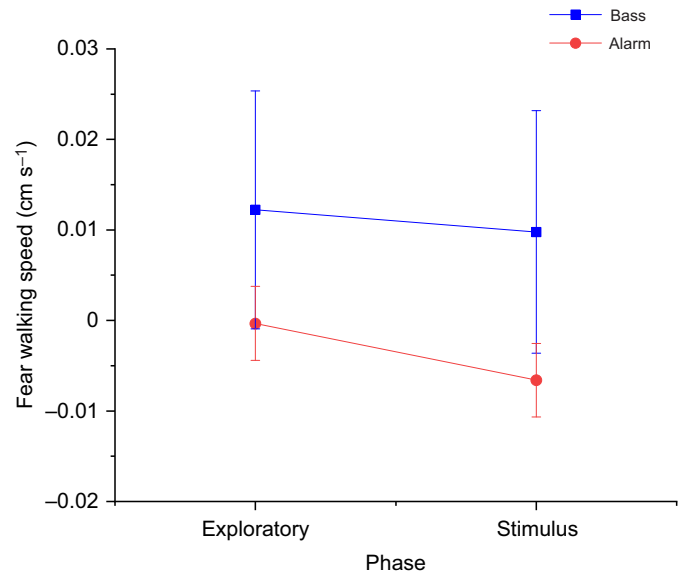


Fig. 5. Mean (\pm s.e.m.) walking speed only along the x-axis (or fear dimension) throughout the entire arena for the different cues (alarm, bass) during the exploratory and stimulus phases of the experiment. Negative values represent a net movement toward lower values along the x-axis (i.e. lower fear). There were no significant differences using a *post hoc* test (emmeans, see Materials and Methods) with a Tukey adjustment ($P < 0.05$). $N = 20$ for all treatments; the same 20 crayfish used in the exploratory phase were used in the stimulus phase.

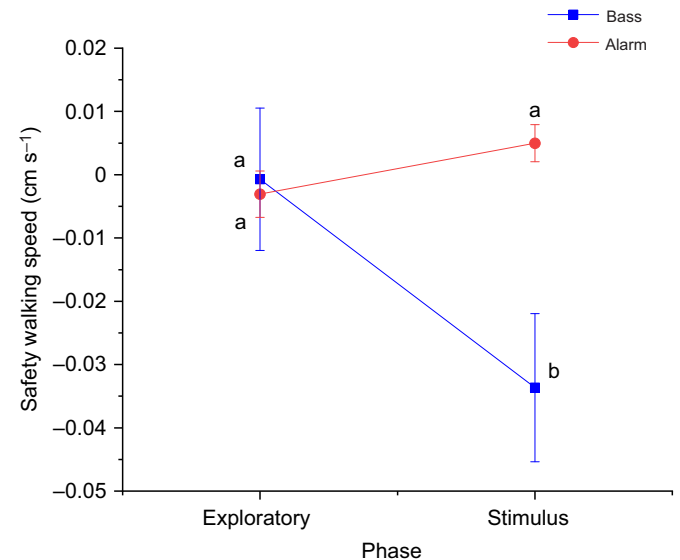


Fig. 6. Mean (\pm s.e.m.) walking speed only along the y-axis (or safety dimension) throughout the entire arena for the different cues (alarm, bass) during the exploratory and stimulus phases of the experiment. Negative values represent a net movement toward lower values along the y-axis (i.e. lower safety). Different letters indicate a significant difference using a *post hoc* test (emmeans, see Materials and Methods) with a Tukey adjustment ($P < 0.05$). $N = 20$ for all treatments; the same 20 crayfish used in the exploratory phase were used in the stimulus phase.

phases as well as the stimulus bass phase (exploratory bass, $P = 0.003$; exploratory alarm, $P = 0.025$; stimulus alarm, $P = 0.001$; Table 2). This change in habitat usage is further supported by a shift away from zones with higher alarm cues to zones with lower alarm cues exhibited by crayfish during the stimulus alarm treatment.

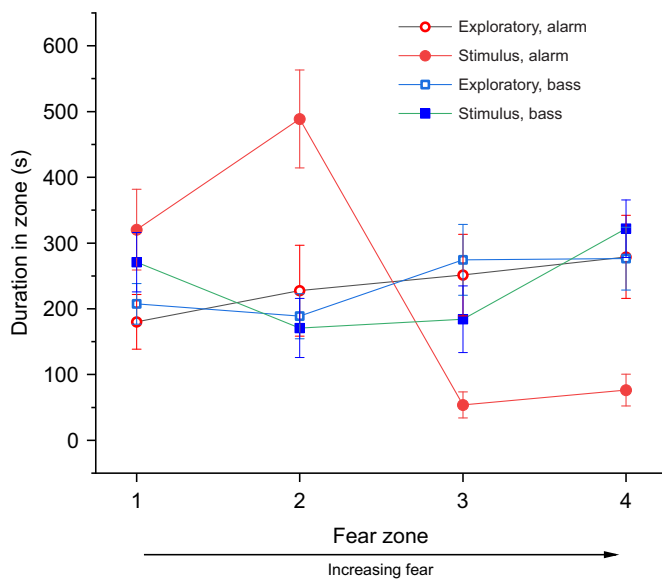


Fig. 7. Mean (\pm s.e.m.) duration in different zones along the fear gradient for the different cues (alarm, bass) during the exploratory and stimulus phases of the experiment. Zones 1–4 are grouped based on the x-axis (fear) of the arena, and increasing zone numbers indicate an increasing concentration of the stimulus (see Materials and Methods for details). Paired significant differences can be found in Table 2 ($P<0.05$). $N=20$ for all treatments; the same 20 crayfish used in the exploratory phase were used in the stimulus phase.

During the stimulus alarm treatment, crayfish spent more time in zone 2 along the fear axis than in zones 3 and 4 ($P<0.001$ for both; Table 2). Crayfish also exhibited an increase in the use of zone 1 of the fear axis as compared with the two higher fear zones 3 and 4 during the stimulus alarm phase ($P=0.055$ for zone 1 compared with zone 4; $P=0.019$ for zone 1 compared with zone 3; Table 2). There were no significant shifts in zone use during any of the exploratory phases or during the stimulus phase with bass treatment.

In a more dramatic result, crayfish shifted their zone usage along the safety axis during the alarm stimulus phase of the experiment compared with the other three treatments (overall model: $F_{3,304,0.05}=4.45$, $P=0.004$; Fig. 8). Crayfish significantly increased their use of the zone with the highest safety when presented with the alarm odor (Table 2). Crayfish exhibited higher use of zone 4

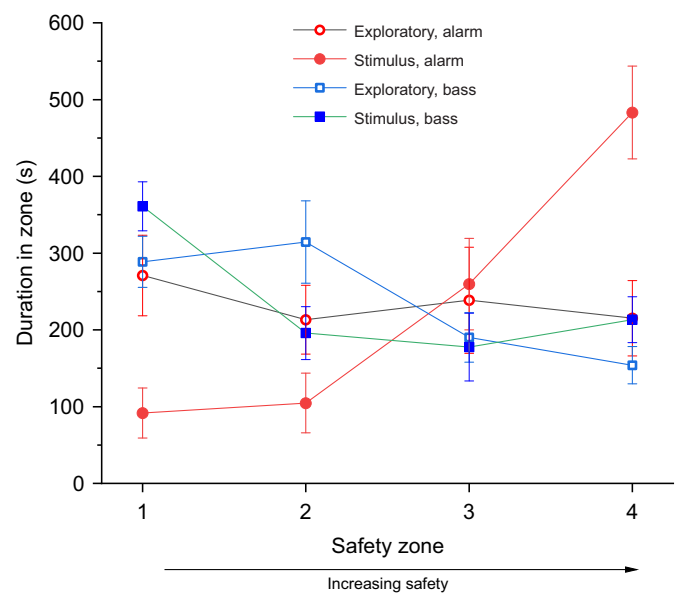


Fig. 8. Mean (\pm s.e.m.) duration in different zones along the safety gradient for the different cues (alarm, bass) during the exploratory and stimulus phases of the experiment. Zones 1–4 are grouped based on the y-axis (safety) of the arena and increasing zone numbers indicate a decreasing number of openings for the shelters, thus increasing safety (see Materials and Methods for details). Paired significant differences can be found in Table 2 ($P<0.05$). $N=20$ for all treatments; the same 20 crayfish used in the exploratory phase were used in the stimulus phase.

compared with zone 3 ($P=0.042$), zone 2 ($P<0.001$) and zone 1 ($P<0.001$) (Table 2). This statistical finding is even more evident in the pairwise comparisons of zone 4 use across the different treatments. Crayfish increased their use of the zone with the highest safety, zone 4, when the alarm cue was present, compared with other treatments (alarm stimulus compared with alarm exploratory, $P=0.004$; compared with bass exploratory, $P<0.001$; compared with bass stimulus, $P=0.003$). This shift in zone use was followed by the expected decrease in zone 1 use compared with the bass stimulus treatment ($P=0.003$).

DISCUSSION

Our results showed that crayfish movement kinetics and habitat use were influenced by the perception of both aversive (fear) and

Table 2. Post hoc significant comparison using 'emmeans' function with the Tukey adjustment within R

Axis	Grouping	Compared zones	<i>t</i> ratio	<i>P</i> -value
Fear (across zones)	Stimulus phase alarm treatment	Zones 1 to 4	3.427	0.055
		Zones 1 to 3	3.744	0.019
		Zones 2 to 3	6.112	<0.001
		Zones 2 to 4	5.794	<0.001
		Stimulus alarm to exploratory bass	4.216	0.003
Fear (within zone)	Zone 2	Stimulus alarm to stimulus bass	4.468	0.001
		Stimulus alarm to exploratory alarm	−3.671	0.025
		Zones 1 to 4	−6.156	<0.001
		Zones 2 to 4	−5.951	<0.001
Safety (across zones)	Stimulus phase alarm treatment	Zones 3 to 4	−3.516	0.042
		Stimulus alarm to stimulus bass	−4.235	0.003
		Stimulus alarm to exploratory alarm	−4.215	0.004
		Stimulus alarm to exploratory bass	5.179	<0.001
		Stimulus alarm to stimulus bass	4.246	0.003

Significant comparisons are in bold. Two selected groupings include comparisons across zones but within a phase, cue type (e.g. time across the different zones for exploratory phase with alarm cue) or within a zone, but across phase, cue type (e.g. duration within zone 1 for the different phase, odor type groupings). This information is visually displayed in Figs 7 and 8.

attractive (safety) stimuli within the behavioral arena (Tables 1 and 2, Figs 4–8). The degree to which both of these sensory landscapes (attractive and aversive) shape movement and habitat choices was based, in part, on the identity of the aversive stimuli (i.e. bass or alarm) (Table 1, Figs 4–8). While predatory cues provide information about the location of potential threats, alarm cues indicate that an immediate injury or predation event of a conspecific has occurred. Because of the differences in perceived risk between these two aversive stimuli for crayfish, alarm cues carry a more threatening message than bass cues (Hazlett, 1999).

In the presence of predatory cues, crayfish increased their overall walking speed and displayed an increased average walking speed toward lower safety environments (Table 1, Figs 4 and 6). There was no statistical change in walking speed along the fear gradient (Fig. 5). Despite these changes, crayfish did not alter their overall habitat use along either the fear or safety gradients when confronted with predator cues (Table 2). In contrast, in the presence of the more threatening cue (alarm), crayfish decreased their overall walking speed and habitat use, which strongly indicates that crayfish were responding to the sensory landscape of alarm cues (landscape of fear) as well as the sensory landscape of attractive shelters (landscape of safety) (Tables 1 and 2, Figs 4, 7 and 8). Thus, crayfish integrated these two related landscapes when making movement and habitat usage decisions. These movement decisions alter how predator and prey interact (Shrader et al., 2008; Iribarren and Kotler, 2012).

Within the field of predator–prey interactions, the theory of the landscape of fear has created room for a better understanding of the non-consumptive dynamics between prey and predator (Laundré et al., 2001; Preisser et al., 2005; Preisser and Bolnick, 2008; Laundré et al., 2010). Prey animals extract relevant information from their entire sensory landscape and use this information to make behavioral decisions (Lima and Dill, 1990; Wisenden, 2000). The spatial and temporal distribution of cues and signals within the landscape can provide information that alters prey behavior, including when and where they forage, mate or inhabit (Sih et al., 1990; Brown et al., 1999; Laundré et al., 2001; Sih and McCarthy, 2002; Hernández and Laundré, 2005). In addition to behavioral alterations, prey respond to the spatial distribution of predatory cues by altering their physiology, morphology or life history (Lima and Dill, 1990; Brönmark and Miner, 1992; Janssens and Stoks, 2013). This series of observations has led to the development of the landscape of fear theory, where prey behavioral, morphological and physiological changes are dictated by the perception of aversive or fearful stimuli within the entire sensory landscape (Peckarsky et al., 2008; for reviews, see Laundré et al., 2014; Gaynor et al., 2019). However, the sensory landscape of the prey contains both aversive cues about predation threats and attractive cues about potential areas of safety (shelters or refuges) that protect prey from predation (Hixon and Beets, 1993; Martín and López, 1999; Donelan et al., 2017). In the present study, crayfish used the landscape of fear differentially depending on the level of threat present in the arena (Figs 7 and 8). The attractive cues and their effect on the sensory ecology of prey have previously been underappreciated and often not integrated into the landscape of fear theory, leaving gaps in the existing predator–prey concepts (Wang and Wang, 2012; Jordan and Ryan, 2015; Donelan et al., 2017). Based on ambiguity and signal detection theory, prey should use multiple sources of information to respond appropriately to the threat of predation (Hazlett, 1999; Brown et al., 2006; Leavell and Bernal, 2019). Empirical evidence also suggests that the use of multidimensional integration, which is the neural integration of multiple stimuli along

multiple dimensions, by prey increases the effectiveness of behavioral responses (Brown et al., 2006; Leavell et al., 2018; Ocasio-Torres et al., 2021). By extension, both theoretical and experimental studies in sensory ecology predict that prey would combine and use the information contained within both the well-established landscape of fear and the understudied landscape of safety (van der Merwe and Brown, 2008; Jordan and Ryan, 2015). Certainly, the results of this study show this is probably occurring in crayfish. During high threat events (alarm cues), crayfish use a combination of fear and safety to guide their movement patterns. In events that are less threatening, safety cues have an important role.

The use of safety cues for prey may be dependent upon habitat use of the prey species and their sensory capabilities (Sih and McCarthy, 2002; Orrock et al., 2013). Many prey species do not build specific protective structures such as burrows or dens but instead utilize natural variations in the landscape to hide from predators (Sih, 1987; Persson, 1993; Cressman and Garay, 2009). However, other prey create or use refuges that provide protection from predation and continually return to these refuges (Kobak et al., 2014; Pustilnik et al., 2021). Warthogs *Phacocoerus africanus* utilize burrows for both predator avoidance and communal nesting, though communal nesting might be a side effect of predator avoidance (White and Cameron, 2009). Golden jackals, *Canis aureus*, build burrows to rear pups and increase their guarding of these burrows at night, when predation risks are highest (Mukherjee et al., 2018). Eastern fox squirrels, *Sciurus niger*, occupy vacated burrows of the gopher tortoise, *Gopherus polyphemus*, to hide from predators and escape extreme temperatures (Potash et al., 2020). With specific and distinct spatial locations indicating safety, prey with refuges may utilize these safe zones and integrate the information into a landscape of safety (Weissburg et al., 2014; Jordan and Ryan, 2015). The sensory landscapes of fear and safety that refuge-building prey utilize to move through habitats is very different from the landscapes of prey that do not consistently return to these protective structures (Wilson and Weissburg, 2013; Gaynor et al., 2019).

The landscape of fear has often been visualized as a spatial distribution of peaks and valleys overlaid upon the three-dimensional habitat of the prey (Fig. 1: Jordan and Ryan, 2015; Gaynor et al., 2019). The peaks indicate intensity of the predatory cues and the valleys indicate lower intensity predatory cues (Relyea, 2003). While there is some confusion within the literature of whether the peaks and valleys indicate intensity of the cues or perception of those cues, the spatial variation remains poignant (Gaynor et al., 2019). Within this type of sensory landscape, prey supposedly move ‘downhill’ away from highly threatening areas to less threatening areas during threatening encounters (Fig. 1, left). This ‘downhill’ movement is driven by decreasing predatory cues as prey move away from a threatening stimulus, but the movement is not a goal-directed movement as defined by orientation literature (Hansson and Åkesson, 2014; Schone, 2014). Movement in any number of directions, as long as the movement is away from the aversive stimuli, results in relocation to a less threatening habitat. This movement can be directly contrasted with the goal-directed movement toward a refuge (Schone, 2014). The landscape of safety can be composed of specific locations of refuges (burrows, nests or shelters), where movement is only beneficial to the organism if that movement is in the specific direction of the refuge (Fig. 1, right). These refuges have distinct spatial locations within a habitat which would require a different set of orientation strategies from the non-goal-directed movement away from predatory cues (Moore and Crimaldi, 2004; Åkesson et al., 2014; Mulheim et al., 2014). In

addition to the different strategies, the extraction of specific spatial locations and directional cues along with some measure of progress toward that location from the surrounding sensory landscape is needed to perform these behaviors (Lohmann et al., 2008; Geva-Sagiv et al., 2015; Kheradmand and Nieh, 2019). For example, insects can often measure distances, and hence progress toward safety, from their burrow during homing events (Wehner, 2003; Mandal, 2018). This distance of safety is often assessed by placing the animal in the center of its immediate landscape and is termed an egocentric frame of reference. For some prey, the movement toward the increased safety of a refuge can provide more certainty of reduced risk than simply moving away from an intense aversive stimulus.

Mapping prey responses onto solely a landscape of fear could create mismatches in predation risk and prey response (Abrams, 2000; Luttbegg and Trussell, 2013; Abom and Schwarzkopf, 2016). These mismatches can be indicators that other sensory stimuli in the environment are involved in the decision making and movement of animals (Ferrari et al., 2010; Neri et al., 2017). In these cases, prey are likely measuring trade-offs based on the sum total perception of risk, reward and safety in other sensory landscapes besides the landscape of fear (Ganson, 2018). The spatial distribution of foraging resources has been the most common landscape measured and assessed when considering prey habitat use under predation threats (Matsuda and Abrams, 1994; Krivan, 2007; Fleischer et al., 2018). Concepts such as giving-up density and resource patchiness are important pieces of information in the sensory landscape that prey utilize to assess risk and reward during foraging (Brown, 1988; Bedoya-Perez et al., 2013). While foraging is the most commonly researched motivator, other sensory landscapes such as water resources, mate distribution and refuges may be as important as the landscape of fear in the process of animal decision making. Indeed, recent modeling evidence has shown that the integration of public information about predation risk, which can be thought of as safety cues, can lead to greater fitness gains (Luttbegg et al., 2020).

The complete sensory landscape that prey experience is a series of different stimuli with varying meaning and intensity as well as spatial and temporal distribution (Wilson and Weissburg, 2013; Jurack and Moore, 2018). The meaning of these landscapes is connected to predation threats, foraging, mating and potentially refuges, and may vary in importance based on the motivational state of the prey (Jordan and Ryan, 2015). The perception of these landscapes may include a prey's major senses (e.g. vision or audition for terrestrial vertebrates) as well as their minor senses (e.g. vibration). These stimuli comprise multiple and potentially disparate landscapes which form a singular Umwelt for the prey (Partan and Marler, 2002; Van Dyck, 2012; Jordan and Ryan, 2015). The landscape of fear and spatial distribution of foraging resources are two critical elements of this Umwelt (Leavell and Bernal, 2019). The work in this paper would indicate that for animals that create spatially distinct refuges, safety is another key landscape that is integrated into that Umwelt (Table 1 and Fig. 8). The degree that the landscape of safety plays in the decision making and movement of prey seems to change based on the type of fear signals that are present (Fig. 8).

The ecological impacts of the landscape of fear have been demonstrated rather thoroughly (Laundré et al., 2010). Alterations in prey behavior, morphology, physiology and habitat use in response to stimuli within the landscape of fear create changing dynamics in ecosystem function (Laundré et al., 2014; Schmitz et al., 2015; Gallagher et al., 2017). The reintroduction of wolves to Yellowstone had profound effects on the spatial distribution of elk,

which led to significant changes in grazing and primary productivity (Laundré et al., 2001). An interesting addition to the landscape of fear concept would be the landscape of safety composed of specific and spatially distinct refuges within habitats. This safety landscape could also help explain non-consumptive effects at the ecosystem level. In these cases, prey may be motivated by the landscape of fear, but the behavioral patterns may be dictated by the landscape of safety. By integrating a landscape of safety with the landscape of fear, as well as other sensory landscapes, a deeper explanation of prey responses, non-consumptive effects and the ecological impacts may arise.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: P.A.M.; Methodology: T.C.W., P.A.M.; Validation: R.N.M., T.C.W.; Formal analysis: T.C.W., P.A.M.; Investigation: R.N.M., T.C.W.; Data curation: P.A.M.; Writing - original draft: R.N.M., P.A.M.; Writing - review & editing: R.N.M., T.C.W., P.A.M.; Visualization: R.N.M., P.A.M.; Supervision: P.A.M.

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Data availability

Raw data are available through the University of Michigan Biological Station's research portal: <https://portal.edirepository.org/nis/mapbrowse?packageid=edi.871.1>

References

- Abom, R. and Schwarzkopf, L. (2016). Differential behavioural flexibility in response to predation risk in native and introduced tropical savannah rodents. *Anim. Behav.* **122**, 117–124. doi:10.1016/j.anbehav.2016.10.005
- Abrams, P. A. (2000). The evolution of predator-prey interactions: theory and evidence. *Annu. Rev. Ecol. Syst.* **31**, 79–105. doi:10.1146/annurev.ecolsys.31.1.79
- Åkesson, S., Boström, J., Liedvogel, M. and Muheim, R. (2014). Animal navigation. In *Animal Movement Across Scales* (ed. L.-A. Hansson and S. Åkesson), pp. 151–178. Oxford University Press.
- Arias-Del Razo, I., Hernández, L., Laundré, J. W. and Velasco-Vázquez, L. (2012). The landscape of fear: habitat use by a predator (*Canis latrans*) and its main prey (*Lepus californicus* and *Sylvilagus auduboni*). *Can. J. Zool.* **90**, 683–693. doi:10.1139/z2012-036
- Bayoumi, A. and Meguid, M. A. (2011). Wildlife and safety of earthen structures: a review. *J. Fail. Anal. Prev.* **11**, 295–319. doi:10.1007/s11668-011-9439-y
- Beattie, M. C. and Moore, P. A. (2018). Predator recognition of chemical cues in crayfish: diet and experience influence the ability to detect predation threats. *Behaviour* **155**, 505–530. doi:10.1163/1568539X-00003501
- Bedoya-Perez, M. A., Carthey, A. J. R., Mella, V. S. A., McArthur, C. and Banks, P. B. (2013). A practical guide to avoid giving up on giving-up densities. *Behav. Ecol. Sociobiol.* **67**, 1541–1553. doi:10.1007/s00265-013-1609-3
- Brönmark, C. and Miner, J. G. (1992). Predator-induced phenotypic change in body morphology in crucian carp. *Science* **258**, 1348–1350. doi:10.1126/science.258.5086.1348
- Brown, J. S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* **22**, 37–47. doi:10.1007/BF00395696
- Brown, G. E. and Chivers, D. P. (2005). Learning as an adaptive response to predation. In *Ecology of Predator–Prey Interactions* (ed. P. Barbosa and I. Castellanos), pp. 34–54. Oxford University Press.
- Brown, J. S. and Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.* **7**, 999–1014. doi:10.1111/j.1461-0248.2004.00661.x

- Brown, J. S., Laundré, J. W. and Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* **80**, 385–399. doi:10.2307/1383287
- Brown, G. E., Rive, A. C., Ferrari, M. C. O. and Chivers, D. P. (2006). The dynamic nature of antipredator behavior: prey fish integrate threat-sensitive antipredator responses within background levels of predation risk. *Behav. Ecol. Sociobiol.* **61**, 9–16. doi:10.1007/s00265-006-0232-y
- Chivers, D. P., Mirza, R. S., Bryer, P. J. and Kiesecker, J. M. (2001). Threat-sensitive predator avoidance by slimy sculpins: understanding the importance of visual versus chemical information. *Can. J. Zool.* **79**, 867–873. doi:10.1139/z01-049
- Corcoran, A. J., Barber, J. R. and Conner, W. E. (2009). Tiger moth jams bat sonar. *Science* **325**, 325–327. doi:10.1126/science.1174096
- Cressman, R. and Garay, J. (2009). A predator–prey refuge system: evolutionary stability in ecological systems. *Theor. Popul. Biol.* **76**, 248–257. doi:10.1016/j.tpb.2009.08.005
- Dill, L. M. (1987). Animal decision making and its ecological consequences: the future of aquatic ecology and behaviour. *Can. J. Zool.* **65**, 803–811. doi:10.1139/z87-128
- Donelan, S. C., Grabowski, J. H. and Trussell, G. C. (2017). Refuge quality impacts the strength of nonconsumptive effects on prey. *Ecology* **98**, 403–411. doi:10.1002/ecy.1647
- Edwards, D. D., Rapin, K. E. and Moore, P. A. (2018). Linking phenotypic correlations from a diverse set of laboratory tests to field behaviors in the crayfish, *Orconectes virilis*. *Ethology* **124**, 311–330. doi:10.1111/eth.12734
- Ferrari, M. C. O., Sih, A. and Chivers, D. P. (2009). The paradox of risk allocation: a review and prospectus. *Anim. Behav.* **78**, 579–585. doi:10.1016/j.anbehav.2009.05.034
- Ferrari, M. C. O., Wisenden, B. D. and Chivers, D. P. (2010). Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Can. J. Zool.* **88**, 698–724. doi:10.1139/Z10-029
- Fleischer, S. R., terHorst, C. P. and Li, J. (2018). Pick your trade-offs wisely: predator-prey eco-evo dynamics are qualitatively different under different trade-offs. *J. Theor. Biol.* **456**, 201–212. doi:10.1016/j.jtbi.2018.08.013
- Florey, C. L. and Moore, P. A. (2019). Analysis and description of burrow structure in four species of freshwater crayfishes (Decapoda: Astacoidea: Cambaridae) using photogrammetry to recreate casts as 3D models. *J. Crust. Biol.* **39**, 711–719. doi:10.1093/jcblol/ruz075
- Gallagher, A. J., Creel, S., Wilson, R. P. and Cooke, S. J. (2017). Energy landscapes and the landscape of fear. *Trends Ecol. Evol.* **32**, 88–96. doi:10.1016/j.tree.2016.10.010
- Ganson, T. (2018). Sensory malfunctions, limitations, and trade-offs. *Synthese* **195**, 1705–1713. doi:10.1007/s11229-016-1298-3
- Gaynor, K. M., Brown, J. S., Middleton, A. D., Power, M. E. and Brashares, J. S. (2019). Landscapes of fear: spatial patterns of risk perception and response. *Trend Ecol. Evol.* **34**, 355–368. doi:10.1016/j.tree.2019.01.004
- Geva-Sagiv, M., Las, L., Yovel, Y. and Ulanovsky, N. (2015). Spatial cognition in bats and rats: from sensory acquisition to multiscale maps and navigation. *Nat. Rev. Neurosci.* **16**, 94–108. doi:10.1038/nrn3888
- Hansson, L. A. and Åkesson, S. (eds.). (2014). *Animal Movement Across Scales*. Oxford University Press.
- Hazlett, B. A. (1994). Alarm responses in the crayfish *Orconectes virilis* and *Orconectes propinquus*. *J. Chem. Ecol.* **20**, 1525–1535. doi:10.1007/BF02059878
- Hazlett, B. (1999). Responses to multiple chemical cues by the crayfish *Orconectes virilis*. *Behaviour* **136**, 161–177. doi:10.1163/156853999501261
- Hixon, M. A. and Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.* **63**, 77–101. doi:10.2307/2937124
- Hernández, L. and Laundré, J. W. (2005). Foraging in the 'landscape of fear' and its implications for habitat use and diet quality of elk *Cervus elaphus* and bison *bison bison*. *Wildl. Biol.* **11**, 215–220. doi:10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2
- Iribarren, C. and Kotler, B. P. (2012). Foraging patterns of habitat use reveal landscape of fear of Nubian ibex *Capra nubiana*. *Wildl. Biol.* **18**, 194–201. doi:10.2981/11-041
- Janssens, L. and Stoks, R. (2013). Predation risk causes oxidative damage in prey. *Biol. Lett.* **9**, 20130350. doi:10.1098/rsbl.2013.0350
- Jordan, L. A. and Ryan, M. J. (2015). The sensory ecology of adaptive landscapes. *Biol. Lett.* **11**, 20141054. doi:10.1098/rsbl.2014.1054
- Jurcak, A. M. and Moore, P. A. (2018). Sensory signals and the reaction space in predator–prey interactions. *Hydrobiologia* **816**, 137–152. doi:10.1007/s10750-018-3574-3
- Kamran, M. and Moore, P. A. (2015). Comparative homing behaviors in two species of crayfish, *Fallicambarus fodiens* and *Orconectes rusticus*. *Ethology* **121**, 775–784. doi:10.1111/eth.12392
- Kheradmand, B. and Nieh, J. C. (2019). The role of landscapes and landmarks in bee navigation: a review. *Insects* **10**, 342. doi:10.3390/insects10100342
- Kobak, J., Jermacz, L. and Piłchowski, D. (2014). Effectiveness of zebra mussels to act as shelters from fish predators differs between native and invasive amphipod prey. *Aquatic Ecol.* **48**, 397–408. doi:10.1007/s10452-014-9492-1
- Koboroff, A., Kaplan, G. and Rogers, L. J. (2013). Clever strategists: Australian Magpies vary mobbing strategies, not intensity, relative to different species of predator. *PeerJ* **1**, e56. doi:10.7717/peerj.56
- Kohl, M. T., Stahler, D. R., Metz, M. C., Forester, J. D., Kauffman, M. J., Varley, N., White, P. J., Smith, D. W. and MacNulty, D. R. (2018). Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* **88**, 638–652. doi:10.1002/ecm.1313
- Křivan, V. (2007). The Lotka-Volterra predator-prey model with foraging–predation risk trade-offs. *Am. Nat.* **170**, 771–782. doi:10.1086/522055
- Laundré, J. W., Hernández, L. and Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, U.S. A. *Can. J. Zool.* **79**, 1401–1409. doi:10.1139/z01-094
- Laundré, J. W., Hernandez, L. and Ripple, W. J. (2010). The landscape of fear: ecological implications of being afraid. *Open Ecol. J.* **3**, 1–7. doi:10.2174/1874213001003030001
- Laundré, J. W., Hernández, L., Medina, P. L., Campanella, A., López-Portillo, J., González-Romero, A., Grajales-Tam, K. M., Burke, A. M., Gronemeyer, P. and Browning, D. M. (2014). The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* **95**, 1141–1152. doi:10.1890/13-1083.1
- Leavell, B. C. and Bernal, X. E. (2019). The cognitive ecology of stimulus ambiguity: a predator–prey perspective. *Trend Ecol. Evol.* **34**, 1048–1060. doi:10.1016/j.tree.2019.07.004
- Leavell, B. C., Rubin, J. J., McClure, C. J. W., Miner, K. A., Branham, M. A. and Barber, J. R. (2018). Fireflies thwart bat attack with multisensory warnings. *Sci. Adv.* **4**, eaat6601. doi:10.1126/sciadv.aat6601
- Lima, S. L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *Bioscience* **48**, 25–34. doi:10.2307/1313225
- Lima, S. L. and Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* **153**, 649–659. doi:10.1086/303202
- Lima, S. L. and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640. doi:10.1139/z90-092
- Lohmann, K. J., Lohmann, C. M. F. and Endres, C. S. (2008). The sensory ecology of ocean navigation. *J. Exp. Biol.* **211**, 1719–1728. doi:10.1242/jeb.015792
- Luttbeg, B. and Trussell, G. C. (2013). How the informational environment shapes how prey estimate predation risk and the resulting indirect effects of predators. *Am. Nat.* **181**, 182–194. doi:10.1086/668823
- Luttbeg, B., Ferrari, M. C. O., Blumstein, D. T. and Chivers, D. P. (2020). Safety cues can give prey more valuable information than danger cues. *Am. Nat.* **195**, 636–648. doi:10.1086/707544
- Mandal, S. (2018). How do animals find their way back home? A brief overview of homing behavior with special reference to social Hymenoptera. *Insectes. Soc.* **65**, 521–536. doi:10.1007/s00040-018-0647-2
- Martín, J. and López, P. (1999). When to come out from a refuge: risk-sensitive and state-dependent decisions in an alpine lizard. *Behav. Ecol.* **10**, 487–492. doi:10.1093/beheco/10.5.487
- Martin, A. L., Ill and Moore, P. A. (2008). The influence of dominance on shelter preference and eviction rates in the crayfish. *Orconectes rusticus*. *Ethology* **114**, 351–360. doi:10.1111/j.1439-0310.2008.01473.x
- Matassa, C. M. and Trussell, G. C. (2011). Landscape of fear influences the relative importance of consumptive and nonconsumptive predator effects. *Ecology* **92**, 2258–2266. doi:10.1890/11-0424.1
- Matsuda, H. and Abrams, P. A. (1994). Timid consumers: self-extinction due to adaptive change in foraging and anti-predator effort. *Theor. Popul. Biol.* **45**, 76–91. doi:10.1006/tpbi.1994.1004
- Moore, P. A. and Crimaldi, J. (2004). Odor landscapes and animal behavior: tracking odor plumes in different physical worlds. *J. Mar. Syst.* **49**, 55–64. doi:10.1016/j.jmarsys.2003.05.005
- Moore, P. A., Edwards, D., Jurcak-Detter, A. and Lahman, S. (2021). Spatial, but not temporal, aspects of orientation are controlled by the fine-scale distribution of chemical cues in turbulent odor plumes. *J. Exp. Biol.* **224**, jeb240457. doi:10.1242/jeb.240457
- Mukherjee, A., Kumara, H. N. and Bhupathy, S. (2018). Golden jackal's underground shelters: natal site selection, seasonal burrowing activity and pup rearing by a cathemeral canid. *Mamm. Res.* **63**, 325–339. doi:10.1007/s13364-018-0356-2
- Mulheim, R., Boström, J., Åkesson, S. and Liedvogel, M. (2014). Sensory mechanisms of animal orientation and navigation. In *Animal Movement across Scales* (ed. L.-A. Hansson and S. Åkesson), pp. 179–194. Exford, U.K: Oxford University Press.
- Neri, D., Ruberto, T., Cord-Cruz, G. and Porfiri, M. (2017). Information theory and robotics meet to study predator–prey interactions. *Chaos: An Interdiscip. J. Nonlin. Sci.* **27**, 073111. doi:10.1063/1.4990051
- Ocasio-Torres, M. E., Crowl, T. A. and Sabat, A. M. (2021). Effect of multimodal cues from a predatory fish on refuge use and foraging on an amphidromous shrimp. *PeerJ* **9**, e11011. doi:10.7717/peerj.11011

- Orrock, J. L., Preisser, E. L., Grabowski, J. H. and Trussell, G. C. (2013). The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology* **94**, 573–579. doi:10.1890/12-0502.1
- Partan, S. and Marler, P. (2002). The Umwelt and its relevance to animal communication: introduction to special issue. *J. Comp. Psychol.* **116**, 116–119. doi:10.1037/0735-7036.116.2.116
- Peckarsky, B. L., Abrams, P. A., Bolnick, D. I., Dill, L. M., Grabowski, J. H., Luttbeg, B., Orrock, J. L., Peacor, S. D., Preisser, E. L., Schmitz, O. J. et al. (2008). Revisiting the classics: considering nonconsumptive effects in textbook examples of predator–prey interactions. *Ecology* **89**, 2416–2425. doi:10.1890/07-1131.1
- Persson, L. (1993). Predator-mediated competition in prey refuges: the importance of habitat dependent prey resources. *Oikos* **68**, 12–22. doi:10.2307/3545304
- Potash, A. D., Murphy, C. M., Pynne, J. T., McCleery, R. A., Conner, L. M., Castleberry, S. B., Smith, L. L. (2020). Eastern fox squirrel (*Sciurus niger*) observed using a gopher tortoise (*Gopherus polyphemus*) burrow. *Southeast. Nat.* **19**, N14–N19. doi:10.1656/058.019.0109
- Preisser, E. L. and Bolnick, D. I. (2008). The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. *PLoS ONE* **3**, e2465. doi:10.1371/journal.pone.0002465
- Preisser, E. L., Bolnick, D. I. and Benard, M. F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* **86**, 501–509. doi:10.1890/04-0719
- Pustilnik, J. D., Searle, J. B. and Curtis, P. D. (2021). The effects of red fox scent on winter activity patterns of suburban wildlife: evaluating predator–prey interactions and the importance of groundhog burrows in promoting biodiversity. *Urban Ecosyst.* **24**, 529–547. doi:10.1007/s11252-020-01056-5
- Relyea, R. A. (2003). How prey respond to combined predators: a review and an empirical test. *Ecology* **84**, 1827–1839. doi:10.1890/0012-9658(2003)084[1827:HPRTCP]2.0.CO;2
- Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allee, H., Teplitsky, C., Réale, D., Dochtermann, N. A., Garamszegi, L. Z. and Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods Ecol. Evol.* **11**, 1141–1152. doi:10.1111/2041-210X.13434
- Schmitz, O. J., Buchkowski, R. W., Burghardt, K. T. and Donihue, C. M. (2015). Functional traits and trait-mediated interactions: connecting community-level interactions with ecosystem functioning. In *Trait Based Ecology – From Structure to Function* (ed. S. Pawar, G. Woodward and A. I. Dell), pp. 319–343. Academic Press.
- Schone, H. (2014). *Spatial Orientation: The Spatial Control of Behavior in Animals and Man*. Princeton University Press.
- Shrader, A. M., Brown, J. S., Kerley, G. I. H. and Kotler, B. P. (2008). Do free-ranging domestic goats show 'landscapes of fear'? Patch use in response to habitat features and predator cues. *J. Arid Environ.* **72**, 1811–1819. doi:10.1016/j.jaridenv.2008.05.004
- Sih, A. (1982). Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. *Ecology* **63**, 786–796. doi:10.2307/1936799
- Sih, A. (1987). Prey refuges and predator–prey stability. *Theor. Popul. Biol.* **31**, 1–12. doi:10.1016/0040-5809(87)90019-0
- Sih, A. and McCarthy, T. M. (2002). Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Anim. Behav.* **63**, 437–443. doi:10.1006/anbe.2001.1921
- Sih, A., Petranks, J. W. and Kats, L. B. (1988). The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. *Am. Nat.* **132**, 463–483. doi:10.1086/284865
- Sih, A., Krupa, J. and Travers, S. (1990). An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *Am. Nat.* **135**, 284–290. doi:10.1086/285044
- van der Merwe, M. and Brown, J. S. (2008). Mapping the landscape of fear of the cape ground squirrel (*Xerus inauris*). *J. Mammal.* **89**, 1162–1169. doi:10.1644/08-MAMM-A-035.1
- Van Dyck, H. (2012). Changing organisms in rapidly changing anthropogenic landscapes: the significance of the 'Umwelt'-concept and functional habitat for animal conservation. *Evol. Appl.* **5**, 144–153. doi:10.1111/j.1752-4571.2011.00230.x
- Wang, Y. and Wang, J. (2012). Influence of prey refuge on predator–prey dynamics. *Nonlin. Dyn.* **67**, 191–201. doi:10.1007/s11071-011-9971-z
- Wehner, R. (2003). Desert ant navigation: how miniature brains solve complex tasks. *J. Comp. Phys. A* **189**, 579–588. doi:10.1007/s00359-003-0431-1
- Weissburg, M., Smee, D. L. and Ferner, M. C. (2014). The sensory ecology of nonconsumptive predator effects. *Am. Nat.* **184**, 141–157. doi:10.1086/676644
- White, A. M. and Cameron, E. Z. (2009). Communal nesting is unrelated to burrow availability in the common warthog. *Anim. Behav.* **77**, 87–94. doi:10.1016/j.anbehav.2008.08.030
- Wilson, M. L. and Weissburg, M. J. (2013). Biotic structure indirectly affects associated prey in a predator-specific manner via changes in the sensory environment. *Oecologia* **171**, 427–438. doi:10.1007/s00442-012-2413-x
- Wisenden, B. D. (2000). Olfactory assessment of predation risk in the aquatic environment. *Philos. Trans. R. Soc. Biol. Sci.* **355**, 1205–1208. doi:10.1098/rstb.2000.0668
- Wood, T. C. and Moore, P. A. (2020). Big and bad: how relative predator size and dietary information influence rusty crayfish (*Faxonius rusticus*) behavior and resource-use decisions. *Can. J. Zool.* **98**, 62–72. doi:10.1139/cjz-2019-0089
- Wood, T. C., Kelley, R. E. and Moore, P. A. (2018). Feeding in fear: Indirect effects of predatory fish on macrophyte communities mediated by altered crayfish foraging behaviour. *Freshw. Biol.* **63**, 1523–1533. doi:10.1111/fwb.13181
- Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. and Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Springer Science & Business Media.