DECISION MAKING IN CHANGING SENSORY LANDSCAPES

Ana M. Jurcak

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Committee:
Paul Moore, Advisor
Shannon Pelini
C. Eric Hellquist
ABSTRACT

Paul Moore, Advisor

Animals make many ecological decisions such as foraging, mating and predator avoidance based on the information they extract from the sensory signals in their environment. Environmental stimuli which include the information animals’ use for decision making can be called a sensory landscape. To investigate ecological decision making in complex sensory landscapes, we presented a crayfish with a choice of resource rich and resource poor habitats under different predatory conditions within a y-maze setting. A simulated predatory event (alarm odor) was alternately placed in either the resource rich or poor habitat to observe the impact of the predation event on the habitat choice and use. Habitats consisted of multiple food resources, multiple shelter resources or combined food and shelter resources. Trials were videotaped and crayfish behavior was analyzed for time spent in each habitat under different predatory and resource conditions. Results show that crayfish avoided the location of alarm odors, regardless of resource presence. Resource preference of crayfish differed among resources depending on the alarm odor location. Female and male crayfish made different decisions based on resource type and alarm odor location. Information from an animal’s sensory landscape drives the decision making of an animal. Researchers need to understand the sensory environment of an animal in order to make the most accurate prediction on an animal’s decision making and behavior. We suggest using a sensory landscape model, instead of a landscape of fear model, because organisms use the entire umwelt of stimuli to guide their decision on habitat and resource use.
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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>INTRODUCTION</td>
<td>1</td>
</tr>
<tr>
<td>METHODS</td>
<td>6</td>
</tr>
<tr>
<td>Animal collection and holding</td>
<td>6</td>
</tr>
<tr>
<td>Experimental design</td>
<td>6</td>
</tr>
<tr>
<td>Experimental areas</td>
<td>7</td>
</tr>
<tr>
<td>Resource types</td>
<td>8</td>
</tr>
<tr>
<td>Shelters</td>
<td>8</td>
</tr>
<tr>
<td>Food</td>
<td>8</td>
</tr>
<tr>
<td>Combination of shelters and food</td>
<td>9</td>
</tr>
<tr>
<td>Alarm odor</td>
<td>9</td>
</tr>
<tr>
<td>Experimental protocol</td>
<td>10</td>
</tr>
<tr>
<td>Data analysis</td>
<td>10</td>
</tr>
<tr>
<td>RESULTS</td>
<td>12</td>
</tr>
<tr>
<td>Overall effects</td>
<td>12</td>
</tr>
<tr>
<td>Alarm odor location impacts crayfish behavioral choices</td>
<td>12</td>
</tr>
<tr>
<td>Predatory effects on time spent in resource area by alarm odor treatment and resource types</td>
<td>12</td>
</tr>
<tr>
<td>Sex differences on time spent in resource rich area by resource type when alarm odor was present in resource rich area</td>
<td>13</td>
</tr>
<tr>
<td>Sex differences on time spent in different areas of the y-maze testing arena</td>
<td>14</td>
</tr>
<tr>
<td>DISCUSSION</td>
<td>15</td>
</tr>
</tbody>
</table>
REFERENCES ............................................................................................................. 20
APPENDIX A. FIGURES .............................................................................................. 29
APPENDIX B. IACUC LETTER OF APPROVAL .............................................................. 33
INTRODUCTION

Animals extract information from environmental stimuli in order to make important ecological decisions regarding foraging, predator avoidance, and mating (Dill 1987; Keller & Moore 1999). Bright colors on poison frogs serve as warning to potential predators and provide predators with information on the toxicity of the frogs (Darst et al., 2006). Western toads can identify predators using chemical cues to detect if a predator has recently consumed conspecifics (Keisecker et al., 1996). Female wolf spiders will emit chemical cues which male wolf spiders use in order to gain information on the females’ reproductive status (Rypstra et al., 2003). Black capped chickadees will use alarm calls to warn others of potential predators. Researchers found that alarm calls of the black capped chickadees will vary depending on the size of the predators (Miller, 2005). Although the examples above focus on single sensory signals, natural habitats are complex environments that contain an array of environmental stimuli that consist of signals, noise and sensory pollution. Often organisms are simultaneously exposed to multiple stimuli and need to extract the relevant information (Hazlett, 1999; Bytheway et al., 2013). Sensory systems have evolved to extract information from a noisy or complex environment (Endler, 1992).

Complex signals can be conflicting when some of the stimuli are from attractive sources (i.e. food and mates: Moens et al., 1999; Martin & Lopez, 2000; Pearl et al., 2000) while other signals convey danger (i.e. predator and alarm odors: Hazlett, 2000; Rosell, 2001; Kaliszewicz & Uchmanski, 2009). These stimuli can include visual signals, auditory signals, chemical signals, abiotic and biotic factors. Within an aquatic habitat, a complex landscape may contain an odor plume generated by a food patch mixing with the body odor of a predatory fish and a pheromone from a female conspecific (Willman et al., 1994; Cummins & Bowie, 2012; Nelson et al., 2013).
Essentially, this complex environment has been called a sensory landscape (Wilson and Weissburg 2013).

We formally define a sensory landscape as the spatial and temporal distribution of various stimuli within an organism’s environment. The spatial and temporal structure of the landscapes is determined by the movement of stimuli through the environment and the information within the landscape is determined by the type of stimuli present. Biotic structures (i.e. trees that provide shading and sound barriers) and flow of water or air can affect how these sensory stimuli are distributed throughout the landscape (Evenden et al., 2000; Abrahams et al., 2007; Fairhurst et al., 2013; Wilson & Weissburg, 2013). Wind speed and wind direction can affect odor plume structure of pheromones from lepidopterans (Evenden et al., 2000). An overcast night may prevent migratory birds from using celestial cues for orientation, causing the birds to rely on their magnetic compass (Poot et al., 2008). The sensory landscape is constantly being altered by different interactions between different biotic and abiotic factors. In addition to the movement and transmission of stimuli within a landscape, the type of stimuli relative to the needs of the organism can alter the attractiveness of different aspects of the landscape.

In a simplistic way, stimuli can be grouped into those that are attractive for the focal organism (i.e. mating signals) (Resink et al., 1989; Rodriguez et al., 2012; Wilgers & Hebets, 2012) and those that are aversive (i.e. predatory signals, alarm signals) (Chivers et al., 2001; Mirza & Chivers, 2001; Gall & Brodie Jr, 2009). Within natural habitats, these two types of signals often coexist within a single landscape even though the spatial and temporal dynamics of those signals could differ (Vickers, 2000; Moore & Crimaldi, 2004; Weissburg, 2011). For example, stimuli from a food source may be relatively consistent while visual or chemical cues from a predator may periodically overlap with stimuli from the food source as the predator
passes through the area (Bytheway et al., 2013). These conflicting (attractive and aversive) and temporally variable stimulus distributions construct the sensory landscape from which organisms need to extract spatial and temporal information.

Recent research within predator-prey dynamics has focused on indirect or non-consumptive effects and how these effects can construct a sensory landscape called “landscapes of fear”. The “landscape of fear” or “ecology of fear,” states that fear (aversion) drives behavioral decisions based on the information contained within the sensory landscape (Ripple & Beschta, 2004; Tolon et al., 2009; Laundrè et al., 2010). Fear can be expressed as elk (*Cervus elaphus*) fleeing from predation by wolves (*Canis lupis*) or Mule deer (*Odocoileus hemionus*) avoiding open areas that are patrolled by pumas (*Puma concolor*) (Laundrè et al., 2010). The foraging of the atlantic dogwhelk (*Nucella lapillus*) is inhibited in risky habitats which contain the predatory green crab (*Carcinus maenas*) (Matassa & Trussell, 2011). Landscapes of fear are often part of a more complex sensory landscape.

Within natural habitats, landscapes of fear overlap other landscapes (possibly attractive or other aversive landscapes) to create a more composite and dynamic sensory landscape (Martin et al., 2003; Iribarren & Kotler, 2012). The umwelt of a sensory landscape and a landscape of fear is constantly changing throughout space and time (i.e. light levels throughout a day, alterations in background sound levels, natural movements of prey and predators: Endler, 1987; Lehtiniemi, 2005). As stimulus sources change location or the intensity of signals being generated, the environmental stimuli of the sensory landscape changes as well (Bytheway et al., 2013). Organisms in these overlapping sensory landscapes use the information present in the stimuli to make ecological decisions (Derby & Steullet, 2001; Kulahci et al., 2008; Wolf et al., 2009). These overlapping sensory landscapes are typically conflicting, causing organisms to face trade-
off situations (Strobbe et al., 2011). Through adaptation, sensory systems and behavioral responses have evolved to operate within complex and often conflicting sensory landscapes (Moore & Crimaldi, 2004; Cappe et al., 2010).

During predator-prey interactions, animals make decisions about the relative risk of predation compared to the relative reward of resource acquisition and often this decision is made from information extracted from the dynamic sensory landscapes within natural habitats (Dill, 1987; Corcoran et al., 2013). In theory, both predator and prey should make decisions using tradeoffs that result in the greatest payoff or benefit (Sih, 1982; Brown & Kotler, 2004). These payoffs are important to the ecological and evolutionary success of both predator and prey (Rohr et al., 2002; Rossong et al., 2011). Higher payoffs have greater benefits such as more food, more mates and more safety (Nicholson et al., 1997; Barash, 2003). These benefits will lead to a higher rate of successful reproduction which will in turn lead to a generation of individuals who will make the same “high-paying” decisions (Barash, 2003). “Profitable strategies” are favored in a population and less “profitable strategies” are less selected for and decrease in a population (Barash, 2003). Prey that make more precise anti predatory decisions will be selected for by natural selection (Shave et al., 1994). Natural selection will favor the most accurate information gathering techniques (Brown, 2003). The ability to gather accurate information will lead to the best decisions being made resulting in the highest payoffs and benefits achieved (Arnott & Elwood, 2009).

In order to investigate how prey animals make decisions about resource acquisition within dynamic sensory landscapes, we challenged animals with three distinct landscapes which featured overlapping and conflicting sensory signals. These stimuli included two attractive signals (a visual and tactile resource [shelters], a chemically detected resource [food]), and an
adverse chemical stimuli (alarm odor). We analyzed the decision making of virile crayfish

(Orconectes virilis) in these multiple sensory landscapes. We found that the decision making of

crayfish is dependent on the sensory stimuli and how the sensory landscapes overlapped.
METHODS

Animal collection and holding

Male and female crayfish, *Orconectes virilis*, were collected from Maple Bay in Burt Lake in Cheboygan County MI (N45.48°, W -84.70°) during the summer of 2013. All crayfish used in this study were in the non-reproductive form (Form II). Crayfish were housed in metal horse troughs and were provided broken clay pots and PVC half pipes (11.43 x 3.81 cm, L:H) as shelters to reduce aggression. Unfiltered river water from the Maple River was pumped into the troughs to provide fresh oxygenated water as well as detritus for food. Crayfish were used only once in the trials. The carapaces of all crayfish used in the experiment were measured and only crayfish with intact appendages were used in trials (average size 3.69 ± 0.03cm). Crayfish were returned to separate metal horse troughs after trials were completed.

Experimental design

All trials occurred at the Experimental Stream Research Facility of the University of Michigan Biological Station in Pellston, MI. To investigate the habitat choices crayfish make under predation pressures, a fully 3 x 3 x 2 factorial experimental design was run with resource type, alarm odor location, and sex as the three factors. Resource type had three different conditions: shelters, food, and shelters and food combined. Alarm odor location; consisted of three different conditions: no alarm odor, alarm odor on the side of the y-maze with resources, and alarm odor on the side of the y-maze without resources. The third factor was sex of the crayfish. Each combination of resource type, alarm odor location, and sex consisted of 10 replicates.

Experimental conditions were as follows:
• Shelters:
  o No alarm odor in habitats N = 10
  o Alarm odor in habitat with shelters N = 10
  o Alarm odor in habitat without shelters N = 10

• Food:
  o No alarm odor in habitats N = 10
  o Alarm odor in habitat with food N = 10
  o Alarm odor in habitat without food N = 10

• Combination:
  o No alarm odor in habitats N = 10
  o Alarm odor in habitat with combination N = 10
  o Alarm odor in habitat with no combination N = 10

*Male and female were each run under all conditions above for a total of 18 different conditions and 180 total different crayfish*

**Experimental arena**

An experimental arena (122 cm x 122 cm x 41 cm L:W) was created using cinder blocks (30.5cm) with a 4mL polyethylene plastic sheeting. A 5 cm layer of pea gravel covered the bottom of the arena. A 1.27 cm thick wooden T structure (30.5 cm across and 62.23 cm down) was placed in the arena to create a Y maze with two different arms. (Figure 1). Four y-maze arenas were constructed sided by side each other.

Unfiltered water taken from the Maple River was pumped into a 208.2 L constant head tank which allowed detritus to settle out. Water flowed from the head tank to the upper part of
the y-maze arena through 1.59 cm diameter hoses and exited the testing arena from the center portion of the downstream end. Three hoses were placed on either side of the y-maze to create equal flow down the arms of the maze. Water flowed through the system at a rate of 0.006 L/s. The water level in the y-maze arenas was 20.32 ± 5 cm.

Low light security cameras (Model # CVC6995CL) were mounted on wooden frames 1.78 m above the arenas. Cameras were connected to a monitor and DVR security system (Model # CV502-4CH) in the Stream Research Facility building to view while trials were running. Videos were at a record frame rate of HDI 30.

Resources types

Shelters

Shelters were constructed from 7.62 cm diameter PVC pipes cut in half and attached to a Plexiglas base with silicone. Two shelters were 11.43 cm long and the third shelter was 13.97 cm long. The first small shelter was placed at the end of the wooden divider and the second small shelter was placed 39.4 cm away from the first shelter, along the wooden divider. The larger shelter was placed across from the two smaller shelters, along the testing arena wall. Shelter construction and use was based on Martin & Moore (2008).

Food

Food consisted of squares (2.54 cm x 2.54 cm L:W) of Pollock filets (Walmart ® brand fish: Hazlett, 2003). Pollock fillets were placed within a mesh pouch (8.89 cm x 7.62 cm) containing a 3.81 cm x 5.08 cm tile to provide weight so that the pouches did not move or float. To replicate the shelter locations, the first food pouch was placed at the end of the wooden
divider and the second food pouch was placed 39.4 cm away from the first food pouch, along the wooden divider. The last food pouch was placed across from the two food pouches, along the testing arena wall. Fresh pieces of Pollock filets were used for each trial. The last food pouch was placed across from the two food pouches, along the testing arena wall. Fresh Pollock was used for each trial.

*Combination of shelters and food*

The combination trial set included one side with 3 food squares of Pollock filets (2.54 cm x 2.54 cm L:W) and 3 shelters constructed from 7.62 cm diameter PVC pipes cut in half and attached to a Plexiglas base with silicone. Two shelters were 11.43 cm long and the third shelter was 13.97 cm long on the opposite side without any resources. In one arm, the first small shelter was placed at the end of the wooden divider and the second small shelter was placed 39.4 cm away from the first shelter, along the wooden divider. The larger shelter was placed across from the two smaller shelters, along the testing arena wall. The three food pouches were placed directly across from the shelters (Figure 1). Fresh pieces of Pollock filets were used for each trial. Shelter construction and use were based on Martin & Moore 2008 and food use was based on Hazlett 2003.

*Alarm odor*

In order to simulate a predatory event, a single female crayfish had both chelea clipped off with a wire cutter (Hazlett, 2000) and the crayfish along with both removed chelea were placed in a 40.64 cm long mesh bag in the arena to allow the crayfish being tested to sense alarm odors from an injured conspecific. Female crayfish (3.61 ± 0.05 cm) was used for all of the female as well as male trials so all tested crayfish were exposed to the same type of alarm odor.
Experimental protocol

All trials were run from 09:00 to 17:00 and recorded using a DVR system. Shelters and food pouches were placed in one arm of the y-maze arena prior to the beginning of the trial. Each experimental treatment had 5 trials with the resources in the left arm and 5 trials with the resources in the right arm. Before each trial, crayfish were randomly selected from holding tanks and marked with white out (Bic ® White Out brand) to increase visibility for subsequent post trial analysis.

Crayfish were placed individually at the downstream end of the y-maze arena (neutral area) and allowed to acclimate for 15 minutes. Once the acclimation period finished, the crayfish was removed from the arena. An injured crayfish (described above) was placed in a 40.64 cm mesh bag. The mesh bag with the injured crayfish was clipped onto the back part of wood divider with a plastic tarp clip and hung on either side of the upstream end y-maze with the injured crayfish under the water.

Once the injured crayfish was placed into the arena, the tested crayfish was placed back into the beginning of the y-maze by the outflow. The 15 minute trial began once the tested crayfish entered the arena for a second time. The tested crayfish was free to move about the arena and make a choice on which habitat to enter. Once the 15 minute trial was over, the crayfish was removed from the arena as well as the injured crayfish. There was 1 hour in between trials in order for all odors from previous trials to be flushed out.

Data analysis

For all trials, videos were analyzed to calculate total amount of time in seconds that each crayfish spent in each section of the y-maze testing arena (resource, non-resource, and neutral
areas). This was calculated by recording the time crayfish would enter and leave an area of the
arena, converting the time to seconds, and then adding the amount of time together to find the
total for each area of the arena. Once the total amount of time spent in each area of the testing
arena was calculated for all trials, the average time in each area of the testing arena was
calculated, as well as the standard deviation, and standard error mean. Effect of alarm odor
location on average time spent in each section of the y-maze, resource type, and sex were
statistically analyzed using a three way MANOVA's followed with a Fisher-LSD to test for
significant differences across variables. Predation event location, sex of crayfish, and resource
type were the three factors for the MANOVA (Statistica 9.0 StatSoft, Tulsa, OK).
RESULTS

Overall Effects

There were significant differences in crayfish behavior as a result of the presence of alarm odor (Three way MANOVA, $F_{(6,320, 0.05)} = 3.4, p < 0.05$) and there was a significant interaction between the alarm odor and resource type (Three way MANOVA, $F_{(12,423, 0.05)} = 3.2, p < 0.05$). There were no significant differences between sex, alarm odor treatment, sex and alarm odor treatment, sex and resource type, and sex, alarm odor treatment, and resource type.

Alarm odor location impacts crayfish behavioral choices

Crayfish avoided the y-maze arm with the alarm odor present regardless of resource distribution (Fisher-LSD, $p < 0.05$; Figure 2). Crayfish spent significantly more time in the non-resource area when compared to the resource area when the alarm odor coincided with the resources (Fisher-LSD, $p < 0.05$). Crayfish spent an average of $206.9 \pm 43.5$ s in the resource area and an average of $331.9 \pm 46.2$ s in the non-resource area when the alarm odor coincided with the resources. Crayfish also spent significantly more time in the resource area compared to the non-resource area when the alarm odor was opposite of the resources (Fisher-LSD, $p < 0.05$). Conversely, crayfish spent an average of $360.2 \pm 46.2$ s in the resource area and an average of $227.3 \pm 42.8$ s in the non-resource area when the alarm odor was opposite of the resources. There was no difference between the amount of time crayfish spent in the resource or non-resource area when there was no alarm odor present in the y-maze.
Predatory effects on time spent in resource rich area by alarm odor treatment and resource type

Crayfish altered their response to an alarm odor as a consequence of resource type (Fisher-LSD, \( p < 0.05 \); Figure 3). Under control situations, crayfish spent significantly more time with food and the combination of food and shelter resources as opposed to just shelter resources (Fisher-LSD, \( p < 0.05 \)). Crayfish spent 100.0 ± 34 s in the resource area with shelters, 368.0 ± 86.0 s in the resource area with food, and 298.0 ± 95.0 s in the resource area with a combination.

With alarm odor and resources together, there was no difference between the amount of time crayfish spent in the resource area between resource type. Crayfish spent 265.0 ± 78.0 s in the resource area with shelters, 128.0 ± 61.0 s in the resource area with food, and 199.8 ± 93.0 s in the resource area with a combination of resources. When there was an alarm odor present in the area without resources, there was no difference between the amount of time crayfish spent in the resource area between resource type. Crayfish spent 512.0 ± 78.0 s in the resource area with shelters, 334.0 ± 79.6 s in the resource area with food, and 351.5 ± 77.5 s in the resource area with a combination of resources.

Sex differences on time spent in resource rich area by resource type when alarm odor was present in resource rich area

There were no significant differences between the amount of time female and male crayfish spent in the resource area by resource types when the alarm odor was in the resource area (Figure 4). Females spent 195.7 ± 108.0 s and males spent 332.6 ± 136.1 s in the resource area with shelters. Females spent 163.9 ± 108.1 s and males spent 149.6 ± 93.73 s in the resource area with food, and 298.0 ± 95.0 s in the resource area with a combination.
area with food. Females spent $288.2 \pm 125.6$ s and males spent $111.3 \pm 62.3$ s in the resource area with a combination of resources.

**Sex differences on time spent in different areas of the y-maze testing arena**

Female and male crayfish spent significantly different amount of times in different areas of the y-maze (Fisher-LSD, $p < 0.05$; Figure 5). Female crayfish spent significantly more time in the non-resource area compared to male crayfish (Fisher-LSD, $p < 0.05$). Females spent $320.8 \pm 37.0$ s and males spent $250.5 \pm 35.8$ s in the non-resource area. There was no difference between the amount of time that female and male crayfish spent in the resource area. Females spent $275.2 \pm 37.0$ s and males spent $263.6 \pm 37.0$ s in the resource area. There was no difference between the amount of time that female and male crayfish spent in the neutral area of the y-maze. Females spent $301.6 \pm 32.8$ s and males spent $386 \pm 37.8$ s in the neutral area.
DISCUSSION

The interaction between resource type and alarm odor location influences the decision making in crayfish. Crayfish avoided areas with alarm odors regardless of resource distribution (Figure 2). Yet, this response was altered depending on the type of resource present (shelter or food: Figure 3). Crayfish showed a preference for food over shelters when no alarm odor was present and this preference was not seen when alarm odor was present (Figure 3). There was no difference in resource preference between sexes (Figure 4). Finally, female and male crayfish made different decisions in resource use based on the location of the alarm odor (Figure 5). Crayfish choices and subsequent behaviors were dependent upon the sensory landscape present in the testing arena.

The crayfish umwelt of the sensory landscape tested in this study consisted of sensory signals with potentially conflicting information. This sensory information contained a positive visual signal (shelter), a positive chemical signal (food), and an aversive chemical signal (alarm odor). In natural systems, sensory landscapes often contain a wide variety of stimuli which are temporally and spatially distributed in the landscape (Endler, 1987; Vickers, 2000; Moore & Crimaldi, 2004; Weissburg, 2011). For example, the presence and the quality of food sources changes throughout the seasons (Orpwood et al., 2006) and at the same time, visual and olfactory signals from predators move through the environment in conjunction with the predator movements (Endler, 1987; Lehtiniemi, 2005). Organisms need to extract the appropriate information from these complex sensory landscapes in order to guide effective ecological decisions and interactions (Nelson & Maciver, 1999; Derby & Steullet, 2001; Moore & Crimaldi, 2004; Wolf et al., 2009).
Organisms may be using a cost-to-benefit calculation based on information extracted from the complex sensory landscapes. For example, organisms would need to calculate the spatial location of predators or a predation event and resources in order to determine the costs and benefits of using a resource versus the cost of a potential predation event. Previous work has shown that the behavioral impact of alarm odors on crayfish depends upon the spatial location of other sensory stimuli in the test arena (Hazlett, 1994, 1999, 2000; Mitchell & Hazlett, 1996; Bouwma & Hazlett, 2000; Tomba et al., 2001). Virile crayfish reached food sources significantly less when an alarm odor was present with a food source compared to the food source alone (Tomba et al., 2001). Red back salamanders (Plethodon cinereus) foraged less in waters that contained cues from predatory garter snakes that had fed on red back salamanders (Maerz et al., 2001). Verplancke et al. (2010) found that blank voles increased foraging in areas where conspecific odors were located and decreased foraging when terrestrial predator odors were located. In each of these examples, organisms are faced with conflicting sensory signals, usually between attractive stimuli and a stimulus warning of predation, and the information extracted from all of the sensory signals present were used to make effective behavioral decisions. Our study demonstrated that crayfish made decisions on which area of the y-maze to inhabit based on the location of the alarm odor and resources.

Predator and alarm odors have an effect on the behavior and spatial use of organisms (Friesen & Chivers, 2006; Briones-Fourzan et al., 2008; Lautala & Harivonen, 2008). Fathead minnows (Pimephales promelas) and fine scale dace (Chrosomus neogaeus) exhibit avoidance behavior when exposed to alarm odors of conspecifics (Friesen & Chivers, 2006). Spiny lobsters (Panulirus guttatus) will avoid shelters when conspecifics in those shelters are emitting alarm odors (Briones-Fourzan et al., 2008). Lautala & Harivonen (2008) found that juvenile arctic char
exhibited a greater level of avoidance of areas which included both predator odors and conspecific alarm cues compared to those areas with cues from predators which had been recently fed char. Recent work has developed the “the landscape of fear” model to explain the spatial distribution of prey in response to a sensory landscape consisting of non-consumptive predator signals (Laundrè et al., 2010; Schrader et al., 2008).

Under the “landscapes of fear” model, prey are exposed to sensory landscapes with an attractive stimuli (food) and an aversive stimuli (predator signal), and the averse stimuli drives prey behavior (Altendorf et al., 2001; Hernàndez & Laundrè, 2005; Searle et al., 2008; Laundrè et al., 2009; Matassa & Trussell, 2011). The results from these studies demonstrate that foraging decisions and habitat use are altered supposedly based solely on the spatial distribution of predator signal within the habitat (Altendorf et al., 2001; Hernàndez & Laundrè, 2005; Searle et al., 2008 Laundrè et al., 2009; Matassa & Trussell, 2011). Specifically, these studies show that prey perform a cost-to-benefit analysis that results in choosing safety over foraging in lesser quality habitats with no predation risk (Hernàndez & Laundrè, 2005; Laundrè et al., 2009; Arias-Del Razo et al., 2012). Elk were found to have a lower quality of diet due to predation pressure by wolves (Hernàndez & Laundrè, 2005). In our study, crayfish avoid habitats with and without resources when alarm odors are present which supports the concept of landscape of fear model.

Although this work (Altendorf et al., 2001; Hernàndez & Laundrè, 2005; Laundrè et al., 2009; Matassa and Trussell, 2011) has clearly demonstrated that the conceptual model of “landscape of fear” predicts prey behavior, natural environments contain a mixture of sensory landscapes including attractive as well as aversive stimuli (Tomba et al., 2001). Organism’s choices, in the face of complex sensory landscapes, are driven by information extracted from
both attractive sensory sources and aversive sources. In our study, crayfish change their choice of resource use in the presence of the alarm signal, but still use resources (Figure 3). Our results demonstrate that information from both attractive and aversive stimuli are used for behavioral decisions whereas under the landscape of fear concepts, behavioral decisions are primarily or solely driven by the aversive stimuli (Hernández & Laundrè, 2005). Since stimuli from a landscape fear are often combined with stimuli from other sources, a concept of a sensory landscape, rather than a landscape of fear, more accurately captures the decision making paradigm for organisms in natural habitats.

Thus, we suggest using a sensory landscape model, instead of a landscape of fear model, because organisms use the entire umwelt of stimuli to guide their decision on habitat and resource use. In natural systems, organisms are faced with a host of sensory stimuli containing information about a number of different ecological decisions (Moore & Crimaldi, 2004). For example, within an aquatic habitat, crayfish are faced with a mixture of chemical plumes that contain information about the spatial location of food (Moore & Grills, 1999), potential mates (Stebbing et al., 2003), agonistic encounters (Bergman et al., 2005; Moore & Bergman, 2005), and predators (Hazlett & Schoolmaster, 1998; Tomba et al., 2001). In addition, natural habitats have visual signals that contain information about shelters, predators, and other ecologically important resources (Hughes, 1996; Murphy, 2006). In addition, the sensory landscape of odors (Vickers, 2000; Weissburg, 2011) and visual signals (Endler, 1987) is constantly changing in space and time. To begin to predict the behavioral decisions of organisms based on cost to benefit analyses, the entirety of the stimuli present within natural systems must be accounted for. Not only does the interaction between predator and prey change the layering of these landscapes, but other factors such as resources, conspecifics, and heterospecifics.
Knowing the sensory landscape organisms are in is important when studying decision making within the predator-prey relationship. By recognizing the sensory landscapes, researchers will be able to understand how the environmental stimuli are presenting information to the organism. The information within the environmental stimuli drives the decision making of organisms. Just as animals need to gather the best set of information in order to make the best set of decisions, researchers need to understand how the sensory environment relays information to the organism in order to make the most accurate predictions on animal decision making in behavior. When moving forward with the landscape of fear, considering the sensory landscapes which overlap with the landscape of fear is important for predicting the behavior between predator and prey.
REFERENCES


from the seminal vesicle of African catfish, Clarias gariepinus. – Aquaculture 83:137-151.


APPENDIX A. FIGURES

**Figure 1:** Y-maze setup for decision making in changing sensory landscapes experiment.

**Figure 2:** Mean (± SEM) time spent in the resource and non-resource area of the y-maze when there was no alarm odor (Control), alarm odor in the resource area (AO+), and alarm odor in the non-resource area (AO-). Different shaded bars represent the mean time crayfish spent in an area of the y-maze: resource area (light grey) and non-resource area (white). N = 60 for control, N = 60 for alarm odor in resource area, and N=60 for alarm odor in non-resource area. Bars with different letters are significantly different from each other (Three-way MANOVA Fisher’s LSD post-hoc, p < 0.05).
**Figure 3:** Mean (± SEM) time spent in the resource area of the y-maze when there was no alarm odor (Control), alarm odor in the resource area (AO+), and alarm odor in the non-resource area (AO-) by resource type. Different shaded bars represent the mean time crayfish spent in the resource area by resource type: shelters (white), food (diagonal stripe), and combo (cross-hatched). Each bar contains an N = 20. Bars with different letters are significantly different from each other. Capital letters indicate differences among resources type within a treatment. Lowercase letters indicate differences among resource types across treatments (Three-way MANOVA Fisher’s LSD post-hoc, p < 0.05).
**Figure 4:** Mean (± SEM) time spent in the resource area of the y-maze with an alarm odor by resource type (shelter, food, and combo) and sex. Different shaded bars represent the mean time crayfish spent in the resource area by sex: females (white) and males (dark grey). Each bar contains an N = 30. (Three-way MANOVA Fisher’s LSD post-hoc, p > 0.05).
Figure 5: Mean (± SEM) time spent in the resource area (R), non-resource area (NR), and neutral area (N) of the y-maze by sex. Different shaded bars represent the mean time crayfish spent in the area by sex: females (white) and males (dark grey). N = 90 females and N = 90 for males. Asterisk indicates differences. (Three-way MANOVA Fisher’s LSD post-hoc, p < 0.05).
March 25, 2013

Dr. Paul Moore  
Biological Sciences  
Bowling Green State University  

Re: IACUC Protocol 12-016

Title:  
Behavorial mechanisms of rusty crayfish, (orconectes rusticus) used to determine between predator and prey of channel catfish (ictalurus punctutas)

Dear Dr. Moore:

On March 25, 2013 the above referenced protocol received final approval after review of the requested modifications by the IACUC. The modifications have been incorporated into the official copy of your protocol (see attached).

This approval expires on March 24, 2014, by which time renewal must be requested if you wish to continue work on the protocol. The Office of Research Compliance will send notification reminding you of the need for renewal in advance of that date.

Please have all members of your research team read the approved version of the protocol. Please also remember to keep a copy of the approved protocol in the animal facility room(s) in which your animals are housed and in any associated procedure rooms (contact the UAF staff for assistance in this regard).

Please consult with the staff of the Animal Facility about your requirements to get started on this project. Good luck with your project.

Sincerely,

Hillary Harms, Ph.D.  
IACUC Administrator

Comments:
Summary of approved modifications (page 2)

All modifications have been addressed and are incorporated into the final version of the IACUC protocol.