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Chemical Orientation Strategies of the Crayfish are Influenced by the Hydrodynamics of their Native Environment

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ABSTRACT.—Crayfish of the species *Orconectes virilis* inhabit two distinct types of hydrodynamic environments: lakes and rivers. Odor cues in these habitats convey chemical information differently due to dispersion by different physical processes. In the laboratory we examined orientation strategies of crayfish collected from lake and river habitats to an odor source dispersed in either a lotic (river) or lentic (lake) manner. Our results showed lake crayfish had variable responses under both flow regimes whereas river crayfish oriented similarly under both flow regimes. Lake crayfish increased walking speeds, decreased heading angles, and decreased turn angles while orienting under lotic versus lentic conditions. Conversely, river crayfish oriented similarly under both flow regimes and reflected lake crayfish behavior in lotic flow. We conclude lake and river crayfish show differences in their orientation strategies due to influences from sensory signals in their source habitat. These results show crayfish show behavioral plasticity with respect to the hydrodynamic and signal structure from their native environments and may be an example of sensory bias.

INTRODUCTION

In freshwater systems two major types of flow environments exist: lakes with low average or inconsistent flow (termed lentic) and rivers consistent uni-directional flow (termed lotic). Because flow characteristics in these habitats differ, fine-scale spatio-temporal patterns of chemical signals contained within odor plumes will be different (Moore et al., 2000), producing produce habitats with distinct “odor landscapes” that affect orientation behavior to chemical sources (Moore and Crimaldi, 2004). Different odor landscapes can influence both type and effectiveness of orientation strategies employed to locate the source of chemical signals. Weissburg and Zimmer-Faust (1993) demonstrated blue crabs altered their orientation behavior in response to varying flow properties. In addition crayfish exhibited different orientation behaviors when challenged with different types of chemical cues (Moore and Grills, 1999). Therefore, organisms may display different orientation behavior based on the structure of sensory information within different habitats (Endler, 1993; Endler and Basolo, 1998).

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Classically, orientation exists as either taxis (where information is sampled spatially) or kinesis (where information is sampled temporally). Fraenkel and Gunn (1961) originally defined these terms with significant modifications by others (Schöne, 1984; Bell and Cardé, 1984; Kennedy, 1986; Dusenbery, 1992). Since the quantification of turbulent odor plumes has revealed the underlying nature of turbulent odor signals (Moore and Atema, 1991; Weissburg et al., 2002; Webster and Weissburg, 2009), chemical orientation has focused on the role that stimulus distributions play in guiding orientation behavior. Lobsters and crayfish appear to use some form of a chemotaxis due to results showing that walking speeds and turning angles depend upon spatial comparisons (Devine and Atema, 1982; Moore et al., 1991; Moore and Grills, 1999). Changes in the temporal structure of odor patterns also alter orientation behavior, including walking speeds (Moore and Grills, 1999; Keller et al., 2001; Kozlowski et al., 2003). In contrast, blue crabs use an odour-gated rheotaxis (Weissburg and Zimmer-Faust, 1994; Finelli et al., 1999). The environmental structure of the odor signal remains important regardless of the exact orientation mechanism in place for aquatic decapod crustaceans.

Sensory systems and behavioral responses may be tuned to differences in flow conditions, specifically between lake and river habitats. Therefore, animals may display distinct behaviors under each condition. Jackson et al. (2007) demonstrated physical characteristics of flow habitat altered orientation behavior of blue crabs by reducing success and increasing the net-to-gross aspect of orientation paths. The crayfish Orconectes virilis from lakes also responded differently to chemical cues under experimental lake and river conditions (Hazlett et al., 2006). These studies focused on behaviors under differential conditions but did not explore the question of whether a sensory bias existed in the same species from different habitats.

Organisms may have sensory filters or behaviors ‘tuned’ or adapted to signal characteristics (e.g., intensity, intermittency) contained within native habitats (Wehner, 1987; Endler, 1993; Endler and Basolo, 1998). Recently, researchers (Moore and Crimaldi, 2004; Webster and Weissburg, 2009) have predicted sensory mediated behavior, orientation in this instance, should be adapted to varying environmental conditions. For example crayfish and blue crabs from high flow areas should exhibit behaviors that allow them to sample high dissipated signals, whereas those from low flow environments should exhibit behaviors adapted to high concentration signals.

We compared orientation strategies of lake and river crayfish of the species O. virilis within river or lake flow regimes. We hypothesized, based on the matched filter hypothesis, river crayfish will be more successful and have more direct paths to the odor source when orienting under lotic conditions compared to lake crayfish. In addition, we hypothesized lake crayfish would perform the orientation task more successfully (higher rate of success and more direct orientation paths) when tested under lentic conditions when compared to lotic conditions.

**METHODS**

**ANIMALS AND COLLECTION SITES**

Between 2100 and 0100, we collected male and female crayfish (Orconectes virilis) from both lake and river habitats near the University of Michigan Biological Station (UMBS) in Pellston, Michigan during the summer of 2011 using either wire nets (lake: Maple Bay, Burt Lake (lat. 45°28′N, long. 84°40′W) or a combination of aquarium nets and baited minnow traps (river: East Branch of the Maple River; lat. 45°33′N, long. 84°44′W). The two collection sites exist within the same watershed, which indicates these two crayfish populations
inhabited environments with similar water chemistries. The carapace (thorax) and chelae lengths of crayfish averaged (mean ± se) 3.77 ± 0.13 cm and 3.64 ± 0.10 cm and 3.02 ± 0.14 cm and 3.05 ± 0.19 cm for lake and river crayfish, respectively. No significant difference in size existed between these two populations (P = 0.442) and sex does not alter does not influence orientation strategy (Moore and Grills, 1999; Keller et al., 2001). We only used crayfish with fully intact antennae.

HOLDING TANKS AND CRAYFISH MANAGEMENT

Lake crayfish.—At the UMBS stream research facility, large metal troughs fed with water from the nearby Maple River (maintained under ambient temperatures that ranged from 20 to 29 C with a natural light/dark cycle that ranged from 15.5 /8.5 h in early Jun. to 14 /10 h in mid-Aug.) housed crayfish for the study. Crayfish fed on the detritus contained within the natural unfiltered water from the Maple River. The troughs with lake crayfish had no continuous flow and water was replaced every 2 d to eliminate the buildup of metabolic waste products. Multiple pieces of PVC pipes either whole or cut in half lengthwise served as shelters to diminish aggressive interactions. Lake crayfish were used only once during trials.

River crayfish.—We kept river crayfish in identical conditions as lake crayfish except continuous flow of unfiltered Maple River water occurred through the troughs. Due to low availability of river crayfish, these crayfish participated in multiple orientation trials but only if the crayfish were unsuccessful in locating the odor source in previous orientation trials. This assured crayfish only contributed a single data run to the lotic trials. If a crayfish was used in more than one trial, a minimum of 3 d (72 h) passed between trials.

ARTIFICIAL CHANNEL SETUP

An artificial channel (18.2 × 1.08 × 0.28 m: l:w:d) consisted of concrete cinder blocks and plastic sheeting (Moore and Grills, 1999; Wolf et al., 2004). The depth of the channel measured slightly deeper than the mean depth of the East Branch of the Maple River where we collected river crayfish. The channel contained a 1.85 m mixing section and 11.21 m flow conditioning section in front of the 1.94 m working section and 3.20 m outflow section. The channel size and sections were chosen to establish an equilibrium benthic boundary layer in the working section (Moore and Grills, 1999; Wolf et al., 2004). An approximately 2 cm thick layer of pea stone lined the channel bottom of the channel (approx. 9.7 ± 0.4 mm × 7.5 ± 0.35 mm × 7.5 ± 0.35 mm: n = 50). Collimators consisting of two sheets of plastic egg crating (fluorescent light covering with 1.7 cm² holes) occurred in the upper part of the conditioning section to promote the formation of the equilibrium boundary layer. Two sheets of plastic egg crating spaced 1.94 cm apart contained the crayfish within the working sections and partitioned off the rest of the channel.

Stream water was mixed with well water to achieve the appropriate flow velocity and depth in the channel, which were measured daily as 7.0 ± 0.5 cm/s and 27.9 ± 0.05 cm respectively. Nylon stockings over the ends of the supply pipes helped filter out fine organic matter and macroinvertebrate fauna. The water exited the artificial channel and re-entered the Maple River approximately 200 m downstream of the intake for the stream research facility. We measured free stream velocity (7.0 ± 0.5 cm/s) at the beginning of each day using a Marsh-McBirney Model 2000 Portable Flow Meter. Daily temperature measurements remained a consistent temperature of 14.4 ± 0.1 C throughout the experimental period.

HYDRODYNAMIC CHARACTERISTICS

We determined hydrodynamic characteristics of the artificial stream by measuring the flow with an acoustic doppler velocimeter (ADV, Nortek U.S.A.) at three down current
positions (relative to the odor source, 30, 60, and 90 cm) within the working section of the channel. We chose the down current positions intentionally to match a corresponding field data set (Wolf et al., 2009). At each down current position, three cross-stream sites and five depths were measured. The cross-stream sites occurred 50 cm from the right wall (midpoint of the channel) and 14.25 cm to the right and left of center of the channel.

For each of the vertical measurements, the measuring volume was suspended five heights off of the substrate. These heights were chosen to match some of the chemosensory appendage heights of an average size crayfish. These heights were 2 cm above the surface (matched for walking legs), 3 cm (maxilipeds), 4 cm, 5 cm (antennules and antennae), and 6 cm. Five heights were chosen to allow for a more accurate quantification of the boundary layer structure. Velocity measurements were taken above each substrate at a rate of 25 Hz for 5 min and each site was repeated 5 times for replication for statistical analysis. Statistical results showed no significant differences between the Batchelor scale, the Kolmogorov scale or Friction Velocity calculated for the artificial channel when compared to the flow at the Maple River field site ($F_{3,22} = 0.1224, P > 0.945$: Wolf et al., 2009).

**ODOR PLUME CHARACTERIZATION**

We measured a chemical tracer, dopamine, with an electrochemical detection system (Epsilon, Bioanalytical Systems, West Lafayette, Indiana) to characterize odor plume structure within the lotic trials. The electrode was calibrated with a series of dopamine concentrations (50–500 mmol/L) in a small beaker. Calibration of the electrode showed a linear relationship between concentration of dopamine in the test solution and electrical output from the sensor ($r^2 = 0.968$). Sampling sites all occurred on the midline of the artificial channel at 30, 60, and 90 cm down current of the dopamine source and at heights of crayfish chemosensory appendages (2, 3, and 5 cm, see above). To place the electrode at the appropriate sampling site, the electrode was attached to a to a glass pipette and micromanipulator.

We prepared 0.1 mol/L dopamine gelatin (to mimic the odor release system used in orientation trials) by dissolving 6.8 g of dopamine and 14 g of Knox unflavored gelatin in 356 mL of Maple River water. We cut the gelatin into $2 \times 2 \times 1$ cm blocks for in situ odor plume measurements and placed two pieces of dopamine gelatin in a mesh bag ($9 \times 9$ cm with 1 mm$^2$ holes) with weights attached at the bottom to keep them in place during trials. Electrochemical recordings were performed at a rate of 25 Hz for 5 min and repeated five times at each site to produce replication for statistical analysis. We chose sampling frequencies to span the resolution frequencies that have been found in chemosensory systems (Gomez and Atema, 1996; Gomez et al., 1999).

**ODOR PLUME ANALYSIS**

We analyzed odor signals recorded from the behavioral arena with an in-house basic program to evaluate various temporal aspects (i.e., intermittency between pulses, maximum height, and the absolute slope of the odor pulses) of the chemical signal (Moore and Atema, 1991; Wolf et al., 2009). The comparison between odor plume parameters and those measured in the field (Wolf et al., 2009) was done using a $2 \times 3$ factorial MANOVA and Tukey’s HSD post hoc test. The two factors in the analysis included location (field vs. stream) and height off substrate (2, 3, and 5 cm). Time series analysis was performed on the epsilon data using Fast Fourier spectral analysis (Statistica V8, Statsoft Inc. Tulsa, Oklahoma).

**FLOW FIELD ANALYSIS**

Three dimensional velocity data from the ADV system were analyzed using the commercial software program, Explore V (Nortek AS, Rud, Norway). Spectral analysis of
velocity measurements within the channel followed standard practices set forth by Sanford (1997). The energy dissipation rate ($\varepsilon$) was estimated using the 5/3 rule on the power spectra calculated in Explore V. The energy dissipation rate for each flow velocity ($v$) measurement was used to calculate the Kolmogorov ($\eta$, equation 1) and the Batchelor microscales ($\eta_s$, equation 2: Sanford, 1997). The Kolmogorov scale is the measure of the smallest eddy size and the Batchelor scale is the measure of the smallest distance for differences in chemical concentrations:

$$\eta = 2\pi \left(\frac{v^3}{\varepsilon}\right)^{1/4}$$  \hspace{1cm} (1)

$$\eta_s = 2\pi \left[ \frac{[vD_s^2]}{\varepsilon} \right]^{1/4}$$  \hspace{1cm} (2)

where $D_s$ is the molecular diffusivity coefficient of dopamine ($2 \times 10^{-5}$ cm$^2$/s).

In addition we used the vertical velocity gradients measured to determine the Friction Velocity ($U^*$) and the roughness Reynolds number ($Re^*$) for water flowing over our orientation test section. The slope obtained from the linear portion of plotting vertical velocity profiles on a log-linear scale plot was used to calculate $U^*$ (Hart et al. 1996; equation 3):

$$U^* = \sqrt{\frac{\tau}{\rho}}$$  \hspace{1cm} (3)

where $\tau$ is shear stress and $\rho$ is the density of water at 20°C (0.998 g/cm$^3$). The Kolmogorov, Batchelor, and Friction Velocities also were compared statistically to those found in field sites using a 2 × 3 factorial MANOVA and Tukey’s HSD post hoc test.

**STIMULUS PREPARATION**

We used four uniform fish gelatin blocks ($2 \times 2 \times 1$ cm) in each trial to simulate the effect of slowly diffusing carrion odors, upon which crayfish feed in natural systems (Willman et al., 1994). Quartered squares of the fish gelatin occurred in mesh bag ($9 \times 9$ cm with 1 mm$^2$ holes) with weights attached at the bottom to keep them in place during trials. We marked bags with reflective tape to allow for visual confirmation of the crayfish finding the source. All filming took place under low light conditions to reduce the possibility of crayfish using visual cues during orientation.

**EXPERIMENTAL PROTOCOL FOR ORIENTATION TRIALS AND SUCCESS CRITERIA**

We marked all crayfish with reflective tape on the back of their carapace to facilitate computer controlled motion (see below). To begin each trial, a crayfish started at one end of the working section in a small cage made from plastic egg crating ($17.5 \times 15 \times 11$ cm) and had 15 min for acclimation. Five minutes into the acclimation period, we placed the mesh bag containing the fish gelatin approximately 1 m upstream. After the final 10 min of the 15 min acclimation period, the crayfish then had 20 min to freely explore the working section to potentially locate the odor source.

We employed a 2 × 2 experimental design with two flow regimes tested (lentic with all river flow stopped and lotic where the flow speed measured 7.0 ± 0.5 cm/s and no background flow) and two home habitats tested (lake and river) that together yielded four treatments. Measurements taken with the Marsh McBirney under the lentic conditions did not register any ambient flow. Successful orientation trials met two basic criteria. First, the major chelae of the crayfish had to contact the odor source. Second, the crayfish’s major chelae could not touch the wall or grates of the working section during the final 50 cm of the orientation pathway. A single crayfish only contributed a single data set to the
orientation trials. All trials were recorded on a Canon XL1 3CCD Digital Video Camcorder mounted above the channel.

**BEHAVIORAL DATA ANALYSIS**

Videotaped trials were digitized 1 frame/sec by using the Peak Motus System (version 8.5) to obtain (X, Y) spatial coordinates of crayfish orientation movements throughout each successful trial. The digitized point marked the center of the reflective tape on the carapace. Because crayfish can walk sideways and backwards without changing overall body orientation, a single reference point allowed us to follow the orientation pathway of the crayfish towards or away from the odor source without regard to body orientation. We inferred orientation by continuing or changing trajectories in successive measurements. From these digitized paths, the parameters analyzed included heading angle relative to the odor source, heading angle relative to directly upstream, turn angle, walking speed, walking speed while moving, walking speed toward the odor source, time spent moving, and time spent turning. Linear statistics were used to analyze angle distributions, which ranged in value from 0 to 180°. The exact definition for these orientation parameters can be found elsewhere (Moore et al., 1991; Kozlowski et al., 2003).

For each orientation parameter, we compared between lake and river crayfish and between the two testing conditions (lentic and lotic) using a 2 x 2 fully factorial MANOVA followed with a Tukey's HSD post-hoc analysis using a confidence level of P < 0.05. For the MANOVA analysis, we used the average values, over the entire trial, of each of the orientation parameters above, which resulted in 11 values for each parameter. To analyze movement parameters as a function of distance from the odor source, the individual parameters of heading angle relative to the odor source and walking speed were each averaged over a 5 cm intervals at different distances from the odor source for each population. These interval averages were then used in either a linear (walking speeds) or 2nd order polynomial regression (walking speed or heading angles) analysis (Moore et al., 1991). To determine if treatment had an impact on the success rate of orientation trials, we conducted a chi-squared analysis. If significant, then we specific differences in habitat/flow regime using a multiple comparisons for proportions contingency table (q 0.05, v, 4 = 3.633) that allows for testing analogous to the Tukey’s MCT or Student-Newman-Keuls tests (Zar, 1999).

**RESULTS**

**QUANTITATIVE COMPARISON OF FIELD FLOW AND CHANNEL FLOW QUANTITATIVE COMPARISON OF FIELD ODOR PLUME DYNAMICS AND STREAM ODOR DYNAMICS**

**Overall MANOVA results.**—Statistical results showed no significant differences between the peak height, intermittency, and absolute slope measured at the Maple River field site compared to those measured in the laboratory odor plume ($F_{3,286} = 0.997, P > 0.8367$).

**QUALITATIVE ANALYSIS OF ORIENTATION BEHAVIOR – SUCCESS RATE**

With a lotic flow, 11 out of 23 lake crayfish (48%) versus 11 out of 29 (38%) river crayfish successfully found the odor source. Under lentic flow conditions, 11 out of 19 (58%) and 11 out of 31 (36%) crayfish, from lentic and lotic habitats, respectively, exhibited successful orientation. The percentage of successful trials did not significantly differ among these conditions ($\chi^2 = 2.93$). Crayfish (both lake and river-sourced animals) typically started their orientation pathways much closer to the odor source while orienting under lentic conditions (although we have included a longer trial for an indication of variability).
Overall MANOVA results.—Native habitat differences in orientation parameters resulted in an overall significant MANOVA effect ($F_{5,36} = 2.75, P < 0.03$) and statistical differences due to test regime ($F_{5,36} = 5.66, P < 0.001$). Finally, we found a significant result from the interaction term in the fully $2 \times 2$ design ($F_{5,36} = 3.45, P < 0.05$; Figs. 1, 2).

Temporal analyses.—Lake crayfish orienting in lentic flow regimes had significantly slower average walking speeds ($1.8 \pm 0.14$ cm/s) than any other condition tested ($3.01 \pm 0.39$ cm/s for lake crayfish in lotic flow; $3.4 \pm 0.27$ cm/s and $3.4 \pm 0.52$ cm/s for river crayfish under lentic and lotic flow regimes, respectively, $P < 0.05$; Fig. 1A). Likewise, lake crayfish orienting in lentic flow regimes showed significantly slower average walking speed toward source ($1.4 \pm 0.13$ cm/s) than any other condition tested ($2.6 \pm 0.37$ cm/s for lake crayfish in lotic flow; $3.0 \pm 0.25$ cm/s and $2.8 \pm 0.50$ cm/s for river crayfish under lentic and lotic flow regimes, respectively, $P < 0.05$; Fig. 1B). None of the other tested conditions differed significantly.

Spatial analyses.—Lake crayfish orienting in lentic flow regimes had significantly higher average turn angles ($34^\circ \pm 5^\circ$) than any other condition tested ($18^\circ \pm 2^\circ$ for lake crayfish in lotic flow; $15^\circ \pm 2^\circ$ and $17^\circ \pm 3^\circ$ for river crayfish under lentic and lotic flow regimes, respectively, $P < 0.05$; Fig. 2A). No other turn angles significantly differed among any other condition. Likewise, the heading angle relative to source where lake crayfish oriented in

**Fig. 1.—**Mean (+se) walking speed (A) and walking speed toward the odor source (B) of crayfish from two different native flow habitats (Lake habitat = left bars; River habitat = right bars) orienting under two different flow regimes (lentic flow = solid black bars; lotic flow = diagonally striped bars). n = 11 for all trials. Letters indicate significant differences using a full factorial MANOVA followed by a Tukey-HSD post hoc test: $P < 0.05$. 

**QUANTITATIVE ANALYSIS OF ORIENTATION BEHAVIOR**
lentic flow regimes (33° ± 3°) had significantly higher average heading angles compared to every other condition (25° ± 2° for lake crayfish in lotic flow; 23° ± 3° and 21° ± 2° for river crayfish under lentic and lotic flow regimes, respectively, $P < 0.05$; Fig. 2B). Finally, crayfish orienting under lentic flow regimes, regardless of their native habitat, had a significant left bias in their respective heading relative to straight upstream angles (−21° ± 3° and −22° ± 2°, for lake and river crayfish respectively) whereas crayfish orienting under lotic conditions had a right bias in their respective heading values (24° ± 2° and 21° ± 4°, $P < 0.05$, Fig. 2C).

**ORIENTATION PARAMETERS AS A FUNCTION OF DISTANCE FROM THE ODOR SOURCE**

Analyzing walking speeds and heading angles relative to the odor source as a function of distance to the odor source revealed significantly different ($P < 0.05$) regressions for each population. Lake and river crayfish had different patterns in walking speed with relation to distance from the odor source and this pattern depends upon the flow regime present during orientation (Fig. 3). Lake crayfish showed a slight increase in walking speed reaching a maximum at a middle distance from the odor source. A decrease in walking speeds follows as the crayfish locate the odor source. Although, river crayfish orienting under lotic conditions show this similar pattern, these same crayfish orienting under lentic conditions showed a significant linear relationship between walking speed and distance from odor source.
When heading angles as a function of distance were analyzed, significant regression relationships only emerged when crayfish were orienting under their native flow regime (Fig. 4). Lake crayfish orienting in a lentic habitat showed a significant increase in heading angles that reached a maximum midway through the orientation pathway and then decreased as the crayfish approached the odor source. Conversely, river crayfish orienting under lotic conditions had an opposite relationship between heading angle and distance. These crayfish decreased their heading angles to a minimum halfway through the orientation pathway and then the heading angles increased as the crayfish approached the odor source. Crayfish orienting under flow regimes different than their native habitat (i.e., lake crayfish in lotic flow regime or river crayfish in lentic flow regime) did not show a statistically significant relationship between heading angles and distance from odor source.

**DISCUSSION**

Lake and river crayfish showed significantly different responses in orientation parameters when challenged to locate odor sources in hydrodynamically different environments. In general crayfish from the lentic habitat had altered orientation responses when placed within the lotic or lentic regimes (Figs. 1–4). Under lentic conditions, crayfish from the lake...
The results of this study show crayfish, *Orconectes virilis*, from lentic and lotic environments demonstrated clear differences in their orientation strategies and in their responses to different flow regimes. Significant differences between the populations occurred in both spatial (e.g., heading angle and turn angle) and temporal (e.g., walking speed) parameters of orientation. Although differences exist between populations, characterization of each type of crayfish’s general orientation strategy is not abundantly clear. Under lentic conditions, the predominant chemical cues are spatial comparisons of odor concentration. Whereas, under lotic conditions, both concentration cues and rheotactic, or flow cues, exist. Crayfish from each population most likely used both types of cues to orient to an odor source although each may do so to varying degrees. Therefore, each population may be simultaneously employing characteristics of both an odor-gated rheotaxis (Dusenbery, 1992) and a chemo-tropotaxis (Payne et al., 1986). Despite the difficulty in labeling an orientation strategy to the crayfish’s behavior, our results seem to suggest that crayfish from

![Fig. 4.—Binned (over a 5 cm interval) averages (+se) of heading angle as a function of distance from the odor source. Curves are from crayfish from a lake habitat (left side) and from a river habitats (right side) orienting under different flow regimes (lentic – top panels; lotic – bottom panel). n =11 for each binned data point.](image-url)
a lotic habitat demonstrated less plasticity in their orientation responses when compared to crayfish from lentic habitats. In some way this may indicate that behavioral search strategies are influenced, or ‘tuned,’ by the sensory information existing within the native habitat of each crayfish population (Wehner 1987; Endler, 1993; Endler and Basolo, 1998). In this instance “tuned” to an environment may mean to the variability in odor signals. If lotic systems have a more consistent odor signal structure given the general unidirectional flow, then crayfish in lotic system may have a single strategy that they adopt for this flow.

Flow velocities in lentic systems can demonstrate more variability in intensity and direction than flows in permanent unimpacted river systems (Imberger and Hamblin, 1982). Because physics of flow environments dictate fine scale structure of chemical signals (Webster and Weissburg, 2009; Wolf et al., 2009), sensory information used for orientation (mechanical and chemical cues) will show habitat specific complexity. The variance in sensory information may strongly influence orientation strategies employed by crayfish in different physical habitats. Closely related crayfish show different orientation strategies that are influenced by the hydrodynamics of the testing arena (Moore and Grills, 1999). Therefore, we suggest that the physics of flow of the native habitat determines, in part, the types of orientation strategies (and its plasticity), that develop within the behavioral repertoire of the crayfish.

This conclusion suggests a sensory bias dictated by the physics of the native habitat may be important for shaping animal behavior. In this instance the bias affecting the sensory drive is the differential flow conditions of each native habitat (i.e., lentic and lotic). Differences in orientation behavior in response to varying flow conditions have also been shown in lake crayfish, _O. virilis_ (Hazlett et al., 2006). Furthermore, differences in flow characteristics have been shown to influence the orientation behavior of the blue crab, _Callinectes sapidus_ (Weissburg et al., 2002; Jackson et al., 2007). Although all of these studies demonstrated orientation responses to different signal structure, this current study suggests a difference in the behavioral strategies developed by different crayfish.

Behavioral variation due to differences in the physics of the organism’s native habitat has also been shown in other mediums (light – Tabor et al., 2004; Karakatsouli et al., 2008; sound – Neuweiler and Fenton, 1988; Huang and May, 1996; Hedwig and Poulet, 2004). These behavioral differences suggest that organisms have sensory or behavioral systems that are adapted, or ‘tuned,’ to effectively extract relevant information in response to the physics of the native habitat. The ‘matched filters’ concept for sensory filters has been shown across many environmental mediums, including those of light (Endler, 1991; Cheroske et al., 2003), sound (Fuzessery et al., 1993; Ramcharttar et al., 2006), and chemical signals (Gardiner and Atema, 2007).

The concept of ‘matched filters’ suggests two possible causes for the phenomena observed in this study. The orientation behavior demonstrated could indicate that crayfish have a sensory bias (Endler, 1993; Endler and Basolo, 1998) dictated by the physics of their native habitat. It is possible that the behavioral plasticity is selected for over many generations or that the behavioral plasticity is learned during a developmental period during exposure to different flow environments. This is the first study to demonstrate a sensory bias phenomenon in the chemical senses and clearly demonstrates that the hydrodynamics of specific habitats (which structures the sensory signal) can dictate the behavioral strategies that development to orientation to chemical signals. The next step to distinguish between these two possibilities would be cross-transplanting young individuals from each habitat and raising them in both lentic and lotic habitats. Animals that use chemical signals to perform ecological functions will have morphological, physiological and...
behavioral adaptations to effectively extract relevant information which are dictated by the physics of signal transmission of their habitat.

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LITERATURE CITED


