Modeling the role of stage-structured agonistic interactions in ontogenetic habitat shifts

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Ontogenetic habitat shifts are often associated with habitat-dependent changes in competition and/or predation risk. Although inter- and intraspecific interactions are known to influence the distribution of size classes among habitat types, the mechanistic role that agonistic behaviors play in driving apparent ontogenetic habitat shifts has yet to be rigorously examined. We used an individual-based, correlated random walk model which permitted behavioral interactions among individuals to test whether spatial variation in juvenile occupancy of different habitat types can be produced by (1) mortality (i.e., agonistic interactions between adults and juveniles result in juvenile mortality) or (2) escape responses during agonistic interactions (i.e., juveniles fleeing after interactions with adults). We used the signal crayfish (Pacifastacus leniusculus Dana), a well-studied stream invertebrate that experiences an ontogenetic habitat shift from riffles to pools, as a model organism. When modeled juveniles experienced mortality during adult-juvenile agonistic interactions or when interactions produced escape behaviors, the population distributions became size-structured (juvenile occupancy of riffles greater than pools). Although both mortality and escape behaviors produced size-structured distributions, the effect of escape behaviors was greater than the effect of mortality on the distribution of juveniles. Furthermore, maintenance of an asymmetric distribution of juveniles between the habitat types was strongly dependent on a lack of underlying preferences for the pool habitat in juveniles. Our results suggest that juvenile escape responses during agonistic interactions with adults may be a key mechanism contributing to observed ontogenetic habitat shifts, particularly in species for which the juveniles show greater niche flexibility than the adults. 

Key words: body size, correlated random walk, escape behavior, habitat selection, ontogenetic niche shift, size-structured population.

INTRODUCTION

Ontogenetic habitat shifts (OHS) occur when a species occupies different habitats at different developmental stages, resulting in spatially stage-structured population distributions. Spatial structuring associated with OHS can have population- and community-level effects, including population regulation (Mittelbach and Osenberg 1993), stabilization of predator–prey systems (Takimoto 2003), competition dynamics (Osenberg et al. 1994), and the creation and maintenance of biodiversity (Claessen and Dieckmann 2002). OHS are generally attributed to changes in the trade-offs between growth potential and mortality risk that organisms experience as they develop. OHS generally coincide with morphological, physiological, and/or behavioral changes, which may alter the growth potential and/or risk of mortality in a given habitat. Individuals that seek to maximize the ratio of growth potential to mortality risk will move to a new habitat if the ratio of growth potential to mortality risk becomes greater than that of the previously occupied habitat (Werner and Gilliam 1984; Holbrook and Schmitt 1988; Nonacs and Dill 1990).

Although changes in resource requirements during development may drive OHS in some species, habitat shifts may also result from the changes in predation and competition dynamics that occur as individuals increase in size. In many systems, predation rates tend to increase up to a threshold prey size, after which predation declines with further increases in body size (Triplet and Perrin 1994; Lundvall et al. 1999; Woodward and Hildrew 2002). This is consistent with a cost-benefit trade-off between the increasing nutritive benefits of larger prey and the increasing energetic costs and chance of injury for the predator. Shifts in competitive ability with size can also influence habitat selection; when size correlates with dominance within a population or community, larger individuals often have greater access to scarce resources such as food, shelter, and mating opportunities (Raben 1985; Nakano 1995; Pavey and Fielder 1996). Furthermore, increasing size asymmetries between competitors may result in a greater probability of injury or mortality during interference competition, leading to avoidance of such interactions (Olsson and Nyström 2009). This suggests that smaller-bodied individuals may choose poorer quality foraging habitats (e.g., habitats with lower quality or less abundant food sources, habitats with higher energetic demands for foraging movements) in the presence of larger-bodied predators or competitors; although the accumulation of energetic reserves may be reduced relative to higher quality foraging habitats, this is balanced by the increased access to resources and reduced risk of predation or injury (Rosenfeld and Boss 2001).

Although the role of body size in OHS is well documented and shifts have often been attributed to a behavioral response by smaller-bodied individuals, (e.g., Stein and Magnnuson 1976; Magoulick 2004), the mechanistic role that agonistic interactions play in OHS has not yet been rigorously examined. Optimal escape theory predicts that the decision to flee...
from a potential agonistic interaction balances the costs of flight (e.g., energetic expenditure, loss of foraging opportunities) with the risk of mortality, and this trade-off results in flight at some threshold distance (flight initiation distance [FID]; Cooper and Frederick 2007). The distance to which an individual flees (retract distance [RD]) may similarly reflect this balance (Hoover and Richardson 2010). Body size differences among crayfish have been shown to influence flight decisions (Stankovich and Blumstein 2005), suggesting escape behavior occurs in response to the perceived risks of interaction with larger-bodied individuals. Size-structured escape responses to avoid agonistic interactions may contribute to the apparent habitat preferences of smaller-bodied individuals. Habitat-dependent differences in the density of larger individuals are likely to translate into habitat-dependent differences in the frequency of escape responses, and a greater frequency of escape movements in the preferred habitat of larger individuals may lead to a net movement of smaller individuals into an alternative habitat.

An alternative mechanism by which agonistic interactions may influence OHS is through juvenile mortality resulting from adult–juvenile interactions. Spatially structured distributions may be produced when mortality rates differ substantially among habitat types. For example, juvenile threespine stickleback (Gasterosteus aculeatus), which show an OHS from vegetated shallows to deeper regions with size, experience lower rates of cannibalism by adults in the presence of vegetation, suggesting decreased mortality in shallow relative to deeper waters (Foster et al. 1988). Similar habitat-dependent mortality rates have been found for other stream-dwelling species (Harvey and Stewart 1991; Blake et al. 1994). Habitat-dependent mortality rates may result in apparent habitat preferences for smaller-bodied individuals, with increased mortality (and lower densities) associated with the habitat type where the larger individuals are more efficient and/or rates of encounter are higher.

The signal crayfish (Pacifastacus leniusculus Dana) is a large freshwater crustacean that experiences a size-dependent OHS, with adults and juveniles generally occupying pools and riffles, respectively (Guan and Wiles 1996; Harrison et al. 2006). Escape responses to avoid intraspecific agonistic interactions with adults may provide a mechanistic explanation for juvenile avoidance of deeper habitats. Signal crayfish readily engage in agonistic interactions with conspecifics to compete for shelter and foraging areas (Ranta and Lindström 1992; Peere et al. 1995). Size is a major determinant of an interaction’s outcome (Ranta and Lindström 1992; Edman and Jonsson 1996) and crayfish respond to this size-dependent change in mortality risk, with smaller individuals consistently choosing to escape rather than engage in potentially costly combat (Pavey and Fielder 1996; Harrison et al. 2006). This suggests that escape responses by juveniles to avoid interactions with adults may result in apparent habitat preferences for juveniles, with an increased number of escape responses in pools (where adults are more prevalent) resulting in a net movement of juveniles to riffles. Although observed OHS in crayfish have not been fully explained by either shifts in diet (Guan and Wiles 1998; Bondar et al. 2005) or interspecific predation (Englund and Krupa 2000), and size-structured responses to intraspecific interactions have been observed in this species, no study to date has explicitly or causally investigated escape behaviors as a mechanism driving this size-structured population distribution.

Although escape responses to avoid intraspecific agonistic interactions may provide an explanation for the distribution of crayfish, spatially structured distributions may also be produced if juvenile mortality rates differ substantially between pools and riffles. Crayfish will cannibalize vulnerable conspecifics (Guan and Wiles 1998; Ahvenharju and Ruohonen 2007) and, as detailed above, size differences between adults and juveniles are likely to make juveniles vulnerable to mortality during interactions with adults. Prior study suggests the environmental context can influence juvenile signal crayfish mortality, as juvenile mortality rates from adult–juvenile interactions were shown to decline with increasing available cover (Blake et al. 1994). Habitat-dependent mortality rates may result in apparent habitat preferences for juveniles, with increased mortality (and lower densities) associated with pools.

In this study, we used an individual-based, correlated random walk model which permitted behavioral interactions among individuals to investigate the mechanistic role that agonistic interactions may play in driving apparent OHS and creating size-structured population distributions. First, we used the model to determine if higher rates of juvenile mortality (due to higher encounter rates with adults) in the putatively preferred adult habitat type (pools) can produce a size-structured population distribution (i.e., greater juvenile densities in riffles than pools). Second, we used the model to determine if juvenile escape responses to agonistic interactions create a size-structured distribution, where adults aggregate in the preferred pool habitat and juveniles are displaced into the alternative riffle habitat. Third, we conducted a series of model iterations in a factorial design to investigate the relative effects of juvenile mortality and escape behavior on the distribution of juveniles between pools and riffles. Finally, sensitivity analyses were conducted to determine the extent to which the effects of agonistic interaction on juvenile habitat occupancy depended on behavioral and population parameters, specifically the apparent habitat preferences of adults and juveniles, threshold interaction distance, probability of mortality, RD, population density, and tortuosity of movements. To observe the individual effects of each parameter, we varied the value of the parameter while holding all others constant. To determine the relative importance of parameter effects on the juvenile habitat occupancy, we simultaneously varied all parameters within the model, using the standardized partial regression coefficients (β) from linear regression as a measure of relative importance.

METHODS

To examine the mechanisms by which agonistic interactions may create size-structured population distributions, we created 3 versions of an individual-based, correlated random walk model using NetLogo (Wilensky 1999): (1) a “null” model (which featured no agonistic interactions between individuals), (2) a “mortality” model (where adult–juvenile interactions result in juvenile mortality), and (3) an “escape” model (where juveniles retreat to avoid interactions with adults). In the model, a population of smaller-bodied “juvenile” and larger-bodied “adult” crayfish moved within a spatially heterogeneous landscape consisting of 2 habitat types (“pools” and “riffles”). Although individual movement patterns are the result of complex interactions between the internal state of an individual and its environment and are thus highly variable, random walk models are a common and robust tool for modeling movements (for review see Börger et al. 2008) and can realistically approximate invertebrate movements (Turchin 1991; Wallin 1991; Schtickzelle et al. 2007). Our model extended the random walk paradigm, such that individual movement paths followed a state-dependent correlated random walk, where the behavior of each modeled individual depended on its size class (adult or juvenile), habitat occupancy (pool or riffle), and proximity...
to conspecifics (foraging or fleeing). The parameters used to
determine crayfish movements were based on published
studies of the agonistic and foraging behaviors of crayfish (see
Model parameterization). In this study, extending the random
walk models used in previous studies (e.g., Turchin 1991)
allowed us to examine the population-level consequences of
individual-level changes in movement behavior.

Model details
The “foraging” movements of individuals across the mod-
eled landscape were based on 2 movement parameters, step
length and turn angle (Figure 1A,1B). We used a Cartesian
coordinate system to track the movements of each individual
through time, transposing a step length ($L_t$) and turn angle
($\theta_t$) into 2D vectors and calculating the position at the end of
a given time step $p_{t+1}(x,y)$ by adding the vectors to the current
lateral ($x$) and longitudinal ($y$) position:

$$
P_{t+1}(x,y) = P_t(x,y) + [L_t \times \sin(\theta_t), L_t \times \cos(\theta_t)].
$$

Stochasticity was incorporated into the modeled movements
using a gamma and a Gaussian distribution (see Table 1 and
Model Parameterization) to represent the range of possible
values for step length and turn angle, respectively; values
were drawn from these distributions for each individual at
each time step.

The modeled landscape consisted of a 2D stream segment
with a series of alternating habitat types (3 pools and 3 rif-
fles), each 3-m wide and 2-m long (i.e., pool and riffle habi-
tats were equal in area). To create realistic movements and
conserve rates of intraspecific interactions, we constrained
movements to the stream using reflecting boundaries at
streambanks (Figure 1C) and a closed loop at stream segment
ends. Individuals moving either upstream or downstream out
of the modeled segment entered the other end at an equiva-
 lent position.

To initialize each run of the model, an equal number of
adult and juvenile individuals were randomly distributed
within the modeled stream, disregarding habitat preferences,
and initial movement directions were selected at random.
For each subsequent time step, state-dependent behavior was
implemented by using different means and standard devia-
tions (SDs) for the step length distribution of adult and juve-
nile size classes and for the 2 habitat types (pools and riffles).

The null model described above (model 1) was then
extended to include agonistic interactions between adult and
juvenile size classes. After new positions were calculated for
all individuals in a given time step, the distances between
all possible adult–juvenile pairs were calculated and, if
the distance between any adult and juvenile was less than
a threshold distance, an agonistic interaction occurred
between the 2. For the mortality model (model 2), a mortality
probability parameter described the likelihood that juveniles
would be killed during agonistic interactions with adults.
Adults and surviving juveniles remained stationary after
the interaction, and deceased juveniles were removed from
subsequent time steps. To maintain a constant juvenile
population size and thus a constant overall rate of interaction
over time, deceased juveniles were replaced at the end of each
time step by simulating immigration into the stream segment,
randomly assigning a juvenile to either the upstream or
downstream edge. For the escape model (model 3), juveniles
within the threshold distance (i.e., the FID) initiated an
escape response directly away from the adult (Figure 1D),
and a new juvenile position was calculated. The distances
that juveniles retreated from adults (i.e., the RD) were
drawn from a gamma distribution. To simplify the model,
we assumed there were no within-size class interactions (i.e., adult–adult or juvenile–juvenile), adults remained stationary during adult–juvenile interactions, and only 1 adult–juvenile interaction was permitted per time step.

In each iteration, the model was run for 200 time steps to reach an equilibrium distribution (based on preliminary analyses). For the mortality and escape models, the models initially ran for 100 time steps without adult–juvenile interactions (i.e., as the null model) to allow the population to become spatially structured based on the apparent habitat preferences of the adults and juveniles. Then the model was run for 100 time steps allowing adult–juvenile interactions. After each run of the model, the degree to which the population had become spatially size-structured was estimated by recording the number of adults and juveniles present in both pool and riffle habitats after the final time step.

Model parameterization

To the greatest degree possible, we parameterized the model with empirical values drawn from observational and experimental studies of crayfish ecology (Table 1). Estimates of signal crayfish densities vary widely (e.g., 1.3 ± 0.6 adults/m² and 1.4 ± 0.9 juveniles/m², Light 2003; to greater than 20 crayfish/m², Bubb et al. 2006). Densities of signal crayfish in their native habitat in British Columbia range from approximately 1 to 4 adults/m² and 4 to 12 juveniles/m² (Bondar et al. 2005). Thus we chose a conservative population density of 2.5 crayfish/m².

Mean and error estimates from Harrison et al. (2006) were used to parameterize the gamma distributions for the step lengths of adults and juveniles in pools and riffles, where a step represents the distance moved over a period of 1 min. A search of the literature did not return any potential mean and error estimates for the turn angle distribution; however, evidence from studies of other crayfish species indicated that a mean angle of 0° was appropriate (McMahon et al. 2003; Shuranova 2008). Movement lengths and turn angles were not directionally biased toward upstream or downstream movements; the literature describing directional movements in crayfish is inconclusive, with various studies reporting no bias (Robinson et al. 2000; Bubb et al. 2004), upstream bias (Bubb et al. 2006), or size-dependent bias (Light 2003) in the frequency of movements, and either no (Robinson et al. 2000) or downstream bias (Bubb et al. 2004, 2006) in movement rates.

To examine the potential role played by mortality resulting from agonistic interactions in OHS (model 2), we selected the probability of mortality for juveniles during interactions with adults based on the results of a high-density communal rearing experiment (8 crayfish in an area of 0.4 m²), where the mortality rate over a 146-day trial averaged 29.2% (Ahvenharju and Ruohonen 2007). We note that this rate may be an overestimate of the actual mortality rate, as this study did not distinguish between mortality resulting from agonistic interactions and mortality from other sources and reported only the overall mortality for the 146 days rather than a per-interaction mortality rate. The threshold interaction distance was kept consistent with the FID used in the escape model (see below).

To examine the potential role of size-structured escape responses during agonistic interactions in apparent OHS (model 3), we chose realistic FID and RD parameter values, based on the available literature. Results of a study of the escape response of juvenile crayfish to simulated predator attacks suggested an average FID of between 15 and 21 cm (Blake and Hart 1995); for this study, we chose the more conservative value (FID = 15 cm). Values for the juvenile RD distribution were obtained from Harrison et al. (2006), which also showed that adults remain stationary during adult–juvenile interactions.

Experiments and statistical analysis

To compare differences in the degree of spatial structuring (i.e., apparent OHS) among the null, escape, and mortality models, the model was run using each set of parameters for 1000 iterations (Table 1). The model output was expressed as the mean proportions of adults and juveniles occupying pools after the final time step. Expressing the occupancy of both habitat types was unnecessary, as the proportion of individuals of the size class in riffles equals 1 – (proportion of individuals of the size class in pools).

To further evaluate the relative strengths of effect of juvenile mortality and escape behavior on the degree of spatial structuring of juvenile crayfish, we conducted a series of model iterations, varying the probability of mortality and RD simultaneously. Six levels for the probability of mortality (0, 0.2, 0.4, 0.6, 0.8, and 1.0) and the RD (0, 5, 10, 15, 20, and 25 cm) were evaluated in a factorial design (200 iterations for each combination of mortality and RD). Linear regression was used to fit the parameter values to the proportion of juveniles in pools after the final time step, and the relative importance of mortality and escape behavior was inferred from the effect sizes, measured by the β.

To assess the conditions under which mortality (model 2) or escape behavior (model 3) can produce a size-structured population distribution we further manipulated key parameters in a series of model iterations, varying each individual parameter value while holding all other values at the default parameter values. Five levels for each of 6 key behavioral and population parameters (preference of adults for pool habitats, preference of juveniles for pool habitats, probability of mortality, threshold interaction distance, population density, and tortuosity) were evaluated for the mortality model (200 iterations for each level). An apparent preference for pools in adults was implemented by holding the mean step length for pools constant (20.9 cm) and increasing the mean riffle step length to 1, 1.5, 2, 2.5, and 3 times this value. The apparent preference for pools in juveniles was also tested, holding the mean step length for pools constant (8.6 cm).
and increasing the mean riffle step length to 1, 1.5, 2, 2.5, and 3 times this value. We varied the mortality response to adult–juvenile interactions as the probability of mortality (values = 0.2, 0.4, 0.6, 0.8, and 1.0) and threshold interaction distance (values = 5, 15, 25, 35, and 45 cm). Population density was modeled as 2.5, 5, 10, 15, and 20 crayfish/m². Tortuosity was varied by varying the SD of the adult and juvenile turn angle distributions (values = 15, 30, 60, 90, and 120). Five levels for each of 6 key behavioral and population parameters (preference of adults for pool habitats, preference of juveniles for pool habitats, RD, FID, population density, and tortuosity) were evaluated for the escape model (200 iterations for each level). Values for the preference of adults for pool habitats, preference of juveniles for pool habitats, threshold interaction distance (i.e., FID), population density, and tortuosity were the same as those used for the mortality model sensitivity analysis. We varied the mean RD as 5, 10, 15, 20, and 25 cm.

We conducted an additional sensitivity analysis for these 6 key parameters in the mortality model (model 2) and the escape model (model 3) to determine the relative importance of different behavioral and population parameter effects on the spatial size-structuring of the modeled crayfish, based on the regression method developed by McCarthy et al. (1995). A uniform probability distribution was used to generate values for the 6 model parameters for each iteration, selecting a range of values for each parameter where there was a linear relationship with the proportion of juveniles in pools (based on the results of the sensitivity analysis described above), and the model was run 5000 times. For the mortality model, the ranges we investigated were mean riffle step lengths of 1–3 times that in pools for adults and juveniles, probabilities of mortality of 0–1, threshold interaction distances of 0–25 cm, densities of 1–10 crayfish/m², and SD of the adult and juvenile turn angle distributions of 0–120°. For the escape model, we investigated mean riffle step lengths of 1–3 times that in pools for adults and juveniles, RD of 0–20 cm, FID of 0–35 cm, densities of 1–20 crayfish/m², and SD of the adult and juvenile turn angle distributions of 0–120°. Linear regression was used to fit the 6 parameter values to the proportion of juveniles in pools after the final time step, and the relative importance of parameters was inferred from the β.

RESULTS
Simulated foraging movements (based on published movement rates for adult and juvenile signal crayfish in pools and riffles) coupled with agonistic interactions—through juvenile mortality during adult–juvenile interactions or juvenile escape responses (a feature of adult–juvenile agonistic interactions)—created size-structured population distributions. In all 3 formulations of the model (null, mortality, and escape), the final densities of adults were greater in pools (on average, 0.85 adults/m²) than in riffles (0.40 adults/m²) due to between-habitat differences in movement rates. Juveniles were evenly distributed between the pools and riffles in the null model (on average, 0.50); however, models incorporating juvenile mortality or escape responses during adult–juvenile interactions produced uneven distributions of juveniles between the 2 habitat types, with lower proportions of juveniles in pools than expected by chance (on average, 0.43 and 0.44, respectively).

Varying the strength of the escape response (i.e., the mean RD) had a greater influence on the distribution of juveniles between pools and riffles than varying the probability of mortality. Increasing the mean RD and increasing the probability of mortality tended to decrease the proportion of juveniles in pools in the final time step in an asymptotic manner (Figure 2). Effect sizes, as measured by the β, indicate that the effect of changing the mean RD (β = −0.15) was 1.9 times greater than the effect of changing the probability of mortality (β = −0.08).

Mortality model sensitivity analyses revealed that the maintenance of an uneven juvenile distribution depended largely on the lack of apparent habitat preferences of juveniles for pools; all else being equal, increasing juvenile step lengths in riffles relative to pools increased the proportion of juveniles in pools (Figure 3A). Effect sizes, as measured by the β, indicate that the apparent habitat preference of the juvenile size class was the factor that most strongly influenced the final proportion of juveniles in pools (Table 2). This regression coefficient was approximately 1.1 times larger than the coefficient of the next most important variable, the threshold interaction distance, 1.8 times larger than the coefficient of the probability of mortality, and 2.4 times larger than the coefficient of population density. The apparent habitat preferences of adults for pool habitats and the tortuosity parameter (i.e., the SD for the turn angle distribution) had the weakest effects on the proportion of juveniles in pools. Increasing the preferences of adults for pools (i.e., increasing adult step lengths in riffles relative to pools), threshold interaction distance, probability of mortality, population density, and SD for the turn angle distribution all decreased the proportion of juveniles in pools, with an asymptotic pattern of decline observed with changes in the threshold interaction distance and population density (Figure 3A–D).

Similar to the mortality model sensitivity analyses, the escape model sensitivity analyses revealed that the maintenance of an uneven juvenile distribution depended largely on the lack of apparent habitat preferences of juveniles for pools. All else being equal, increasing juvenile step lengths in riffles relative to pools increased the proportion of juveniles in pools
Effect sizes, as measured by the $\beta$, indicate that the apparent habitat preference of the juvenile size class was the factor that most strongly influenced the final proportion of juveniles in pools in the escape model (Table 2). This regression coefficient was approximately 1.3 times larger than the coefficient of the next most important variable, FID, and at least 1.8 times greater than adult habitat preferences, juvenile RD, and population density, whereas the tortuosity parameter (i.e. the SD for the turn angle distribution) had the weakest effect on the proportion of juveniles in pools (Table 2). Increasing the apparent preferences of adults for pool habitats reduced the proportion of juveniles in pools (Figure 4A), and increasing the FID and mean RD decreased the proportion of juveniles in pools in an asymptotic manner (Figure 4B). Increasing population density similarly decreased the proportion of juveniles in pools (Figure 4C), whereas there was a slight positive trend for the tortuosity parameter, with increasing proportions of juveniles in pools observed with increases in the SD of the turn angle distribution (Figure 4D).

**DISCUSSION**

**Insights from the model**

Our model shows that mortality and escape behaviors may play a critical role in creating OHS in species that experience agonistic interactions between size classes. Our correlated

<table>
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<th>Parameter</th>
<th>Mortality model</th>
<th>Escape model</th>
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<tr>
<td>Mean adult riffle:pool step length</td>
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<td>Mean juvenile riffle:pool step length</td>
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<tr>
<td>Probability of mortality</td>
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<td>Threshold interaction distance</td>
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<td>RD</td>
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<tr>
<td>Population density</td>
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<td>−0.19</td>
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<tr>
<td>SD of turn angle distribution</td>
<td>−0.11</td>
<td>0.10</td>
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random walk-based simulations, which used published behavioral (foraging movements and adult–juvenile agonistic interactions) and population density data for signal crayfish, showed that both mortality (resulting from agonistic interactions with adults) and post-encounter escape behaviors of juveniles were sufficient to create an asymmetric distribution of juveniles between the 2 habitat types (pools and riffles). However, escape behaviors had a stronger effect on the distribution of juveniles between the 2 habitat types than direct mortality.

Increasing the strength of the escape response (i.e., the mean RD) had a greater effect on the distribution of juveniles between the 2 habitat types than direct mortality. Although our model focuses on the spatial distribution of adult and juvenile size classes that develops over a relatively short time period (i.e., 100 min) and does not directly examine the dynamics of the spatial distribution, with demographic shifts of juveniles into the adult size class and births replenishing the juvenile size class, we expect that the asymmetric distribution of juveniles and adults in this model would produce an apparent OHS (e.g., Stein and Magnuson 1976; Magoullick 2004).

Figure 4
Effects of varying escape model parameters on the mean proportion of juveniles in pools (±SD, 200 simulations) after the final time step. (A) Varying the apparent pool preferences of adults and juveniles, by changing the ratio of the mean step length in riffles to that in pools. (B) Varying the escape behavior, as the mean RD and the FID. (C) Varying population density, as the number of crayfish per square meter. (D) Varying movement tortuosity, as the SD of the Gaussian distribution for turn angles. In each case, all other parameter values were held at default values. Dashed lines indicate the proportion of individuals that would be found in pools as expected by chance.
associated with the interaction’s outcome, with the probability of survival increasing for the smaller-bodied individual as the size asymmetry declines (e.g., Marshall et al. 2005). Thus as juveniles grow and size asymmetries with adults decline, the resulting reduction in the probability of mortality, coupled with a shift in the apparent adult preference for pools suggested by the increased step length in riffles relative to pools for that size class (Harrison et al. 2006), may result in an OHS toward the preferred adult habitat.

Instead of interacting with adults, juveniles may avoid the risk of injury or mortality by retreating from agonistic interactions with adults (Pavey and Fielder 1996; Harrison et al. 2006), and our model suggests that behaviors of this kind can contribute to the apparent OHS. Higher densities of adults in pools increased the probability of adult–juvenile interaction in that habitat; escape movements associated with these interactions produced a net movement of juveniles from pools to riffles (an adjacent alternative habitat). Escape responses may decrease with declines in size asymmetries between competitors (Cooper and Stankowich 2010; but see Harrison et al. 2006); thus as juveniles grow and size asymmetries with adults decline, the resulting reduction in escape responses, coupled with a shift in the apparent adult preference for pools, may result in an OHS toward the preferred adult habitat.

Apparent habitat preferences of adults and juveniles, implemented as increases in step lengths in riffle habitats relative to pools, were essential for the creation of an asymmetric juvenile distribution through responses to agonistic interactions. Differences in step lengths between habitat types are generally indicative of habitat preferences; shorter step lengths per unit time (i.e., lower rates of movement) generally suggest superior foraging grounds, with individuals stopping frequently to feed or scan for resources (Zach and Falls 1977; de Knegt et al. 2007), or a lower perceived risk of mortality, as animals often increase speed of movements to reduce time spent in risky environments (Gilliam and Fraser 2001; Schtickzelle et al. 2007). Adult habitat preferences were an expected prerequisite for an asymmetric distribution of juveniles, as a uniform distribution of adults throughout the stream would result in juveniles facing roughly equivalent risks from adults in both habitat types. Adult habitat preferences were relatively more important for maintaining an asymmetric distribution of juveniles in the escape model than in the mortality model; in the escape model, the apparent adult preference for pools was the third most important parameter (after the apparent juvenile habitat preference and FID), whereas in the mortality model, this was only more important than the tortuosity parameter. Less intuitive was the strength of effect of apparent habitat preferences in juveniles, which was the most important factor influencing the distribution of juveniles in both the mortality and escape models; when juvenile crayfish were modeled with a preference for pools, their density increased over that in riffles despite the higher densities of adults (and rates of agonistic interactions) in pools. This suggests that preference of juveniles for the preferred adult habitat may mitigate the influence of agonistic interactions on juvenile distributions.

Our model suggests that juvenile responses to agonistic interactions (i.e., mortality or escape behavior) may drive size-structuring of juvenile distributions to the greatest extent when juveniles have more niche flexibility than adults. This supports previous observations of greater niche flexibility in the juveniles of species known to have spatially size-structured distributions. For example, stream-dwelling cutthroat trout (Oncorhynchus clarkii) exhibit a spatially size-structured distribution, with young of the year (YOY) being found in greater densities in riffles and adults in pools. YOY trout show greater niche flexibility than adults; although both YOY and adult trout have greater growth rates in pools relative to riffles, only YOY can maintain positive growth in riffles (Rosenfeld and Boss 2001). The ability of YOY to maintain positive growth in both habitat types provides greater flexibility than adults, and YOY may trade-off enhanced growth potential in pools for the decreased risk of competition and/or predation from adults that they experience in riffles. Flexibility has been observed in YOY golden crayfish (Oncorhynchus limus) and juvenile signal crayfish, which will distribute themselves evenly between 2 available substrate types in the absence of adult crayfish but shift toward the habitat less favorable to the adults after introduction of adults (Rabeni 1985; Harrison et al. 2006). Thus, the effects that the juvenile responses to agonistic interactions have on their spatial distribution may interact with other morphological or physiological attributes of juveniles, such as generalized diets.

Changes in the frequency of adult–juvenile interactions and risk of mortality resulting from those interactions influenced the distribution of juveniles between the 2 habitat types. Increasing the threshold interaction distance increased the frequency of interactions; this in turn increased the likelihood of juveniles being removed from pools more than the likelihood of juveniles being removed from riffles, as higher adult densities in pools resulted in an asymmetric increase in the frequency of interactions (and thus frequency of mortality) in pools relative to riffles. Although increasing the threshold interaction distance had a relatively larger effect than increasing the probability of mortality, increasing the probability of mortality similarly increases the frequency of juvenile mortality in the 2 habitat types in an asymmetric manner.

Changes in both the sensitivity to perceived risk and the strength of response (implemented as changes in the FID and mean RD, respectively) influenced the degree to which escape behaviors produced an apparent OHS. Although the effect of increasing FID was greater than the effect of increasing RD, increasing either parameter reduced the proportion of juveniles in pools. Increasing FID increased the frequency of escape responses, which in turn increased the likelihood of juveniles being displaced from pools into riffles, as higher adult densities in pools resulted in an asymmetric increase in the rate of escape responses between the 2 habitat types. Increasing RD similarly increased the probability that an escape response would result in the juvenile crossing the edge of the habitat patch and movement from one habitat type into the other. Increased movement of juveniles out of pools relative to riffles in our escape model is consistent with observations of killifish (Rivulus hartii) movements; fish introduced into pools had greater upstream and downstream movement rates in the presence of predators than in their absence, but showed no differences in movement rates between these predation conditions if introduced into riffles (Gilliam and Fraser 2001).

Although less important than apparent habitat preferences of juveniles, mortality parameters (threshold interaction distance and probability of mortality), escape behavior (FID and RD), and, in the case of the escape model, the apparent habitat preferences of adults, the degree to which agonistic intraspecific interactions contributed to apparent OHS was density dependent. Increasing population density resulted in a reduction in the proportion of juveniles occupying pools. The influence of density on the juvenile distribution is supported by theories of habitat selection. Habitat selection based on trade-offs between growth potential and mortality risk between alternative habitats (Morris 2003) is ubiquitous across size-structured communities. Increases on a habitat-dependent trade-off between fitness and density, as density-dependent changes in resource availability, competition, and predation

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risk varies between habitats (Morris 1988). Variable influences of density between habitats can result in a “switched preference” pattern, where one habitat is preferred at low density and another at higher density (Morris 1988; Bult et al. 1999; Laurel et al. 2007). In our model, the decreasing proportion of juveniles in pools as population density increased can be interpreted as a possible mechanism by which habitat “switches” occur, as the probability of agonistic interactions disproportionately increases in pools relative to riffles as adult densities increase.

Empirical observations suggest OHS can be flexible for many species. The ability of individuals to detect and respond to changes in resource availability and mortality risk may mediate OHS, with individuals adaptively altering habitat use in response to the environmental context. Predator introduction or removal experiments suggest OHS may be less evident when size-dependent risks associated with competition or predation are removed, with juveniles showing little preference among available habitats (Rabeni 1985; Koczaja et al. 2005; Harrison et al. 2006). Timing of OHS can be delayed by increases in predator density (Werner and Hall 1988; Byström et al. 2003), suggesting that increasing predation risk strengthens apparent preferences of smaller-bodied individuals for the less risky habitat. Similar patterns were observed in our model. Eliminating the risk of mortality or escape responses to avoid perceived risks of mortality caused juveniles to become evenly distributed among habitat types, and higher adult densities strengthened the asymmetrical distribution of juveniles.

Although the tortuosity of movements, modeled as the change in the SD for the turn angle distribution, had the weakest effects on the distribution of juveniles in both the mortality and escape models, this parameter has the distinction of being the only parameter tested in the sensitivity analyses that had opposite effects on the distribution of juveniles in the mortality and escape model formulations. Increasing the SD for the turn angle distribution decreased the proportion of juveniles in pools in the mortality model and increased the proportion of juveniles in pools in the escape model. Increasing the SD of the turn angle distribution increases both the chance of the individual changing direction and the chance of the individual turning back in the direction they previously came from in a given time step. Thus increasing the underlying tortuosity of individual movements tends to reduce the proportion of movements moving from one habitat type to another. Thus when juveniles experience mortality during adult–juvenile interactions, higher tortuosity can be expected to result in fewer movements of juveniles from the riffles (where chance of mortality is lower due to lower adult densities) to pools (where chance of mortality is higher due to higher adult densities), strengthening the effect of mortality on the distribution of juveniles. Alternatively, when juveniles avoid interactions with adults through escape behaviors, although escapes may tend to produce a net escape of juveniles from pools to riffles, increasing tortuosity increases the chance of an individual changing direction and returning to the pool.

Although we have focused on intraspecific agonistic interactions between size classes, the results of this study can be extended to understand the population-level consequences of interspecific agonistic interactions. Larger-bodied species may displace individuals of a smaller-bodied species from superior foraging habitat, if there is a size-dependent risk of mortality and/or the smaller-bodied species initiates escape movements in a risk-sensitive fashion and flees after encounters. For example, displacement of smaller-bodied species into suboptimal habitat has been observed in crayfish. Introduction of rusty crayfish (Orconectes rusticus) displaced smaller-bodied native clearwater crayfish (O. propinquus) and northern crayfish (O. virilis) from refugia during the daytime, exposing these species to increased risk of predation (Hill and Lodge 1994). Similarly, invasive signal crayfish are known to dominate in interactions with many native crayfish species, leading to eventual replacement (Söderbäck 1995; Usio et al. 2001).

Model limitations

Though simulation models are necessarily simplifications of real-world processes, it is nevertheless important to recognize that the assumptions underlying models may influence the outcome and limit how the results can be generalized. In our model, the movement of crayfish between pools and riffles was unrestricted. In the sensitivity analysis, increases in the threshold interaction distance and population density (for the mortality model) and the FID and RD (for the escape model) decreased the proportion of juveniles in pools in an asymptotic fashion. This asymptote reflects the random nature of the modeled crayfish movements; although strong rates of interaction with adults at higher densities and increased sensitivity and response to agonistic interaction increased the proportion of juveniles in pools relative to riffles, there was always some movement of juveniles into pools in any given time step. It is reasonable to assume that in natural systems juvenile crayfish will never be completely excluded from pools, and some juveniles will continue to cross boundaries into pools during daily movements despite the risk of agonistic interactions. However, it is important to recognize that this asymptote is a conservative lower limit. juveniles may learn to avoid patches of adult-dominated habitat, a behavioral process that would increase the asymmetry in juvenile distribution between habitat types and the strength of apparent OHS. Furthermore, the free movement between habitat types modeled here may underestimate effects of habitat-dependent mortality rates for species with boundary responses (e.g., Ross et al. 2005), where reduced rates of movement for juveniles across boundaries are likely to translate into reduced juvenile density in the preferred adult habitat.

A second major simplification made by our model was that flight was the only behavioral response to an agonistic interaction. In crayfish, risk of predation has been observed to decrease active behaviors (e.g., walking and feeding), increase defensive behaviors (e.g., burrowing), and alter substrate use within the given habitat (Stein and Magnusson 1976; Blake and Hart 1995; Olsson and Nyström 2000), and similar behavioral responses have been seen in other species (Dill and Fraser 1984; Rudolf 2006). Such behaviors may reduce the influence of mortality or escape behavior on the spatial structuring of populations, as reduced foraging activity and/or alteration of microhabitat use is likely to reduce the probability of encounter.

We also simplified our model by assuming constant habitat sizes for pools and riffles (3-m wide by 2-m long), and ignoring differences in within-habitat complexity between habitat types. The strength of effect of agonistic interactions is likely to be modified by the habitat spatial extents found in nature; for example, decreasing the sizes of habitat patches is likely to decrease the apparent effects of escape behavior, as at some point the movement rates of juvenile crayfish across boundaries will become so high that they swamp out any other effects. However, we note that the pool and riffle sizes we used in the model closely approximated the lengths of the habitat units in East creek (Hoover T, unpublished data), the original habitat of the signal crayfish used to determine escape behavior (Harrison et al. 2006). Habitat sizes were realistic for the model study system. Rates of encounter within and among size classes will also depend on
habitat complexity. Stream pools often have accumulations of large wood and/or coarse bouldery bed material; this habitat complexity may reduce rates of agonistic interactions, permitting higher densities of crayfish to exist in pool habitats.

A final assumption was the division of the population into 2 discrete size classes with clearly defined between-class interactions (i.e., behaviors during agonistic interaction were constant, with juveniles always responding with an escape response and adults always remaining immobile). Real-world populations feature a continuous range of body sizes, which likely influences the behavior of individuals during interactions. As size differences between interacting individuals decline, the probability of the smaller individual engaging rather than escaping increases. Furthermore, when body sizes are similar the larger individual may initiate an escape response (Cooper and Stankowich 2010). Future studies that incorporate a continuous range of body sizes, and where the response to agonistic interaction is based on the degree of size asymmetry between individuals, may allow for greater understanding of the role of agonistic interaction and the size at which habitat shifts occur.

CONCLUSIONS

The use of a state-dependent correlated random walk that allowed individuals to respond to both the presence of conspecifics and heterogeneity in the model landscape proved to be a powerful tool to investigate the population-level consequences of individual behavior. This model suggests that agonistic interactions between size classes may contribute to OHS, especially in taxa—such as crayfish—that exhibit size-dependent risk of mortality or escape behaviors to avoid injury or mortality. Furthermore, our model suggests that although both juvenile escape responses and mortality during adult–juvenile interactions may play a role in the size structuring of a population, species that produce an escape response to avoid adult–juvenile interactions may display a more pronounced asymmetric distribution of juveniles relative to species which do not display escape behavior. Even when isolated from other processes (e.g., physiological, movement constraints), juvenile responses to agonistic interactions produced spatially structured juvenile distributions, although other processes may act synergistically with these responses to produce stronger asymmetries than modeled here. Our model provides hypotheses as to the relative effects of apparent habitat preferences, characteristics of mortality or escape behavior, population density, and tortuosity of movements on the strength of agonistic interaction effects. In our model, the degree of inherent habitat preference for a particular habitat for juveniles had a relatively large impact on the model outcome. This suggests that one may expect OHS to be more frequently observed in species for which the juveniles show greater niche flexibility than predators or larger-bodied conspecifics.

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