A Stochastic Model for Shelter Use in a Mobile Fish Population: the Effect of Intraspecific Competition

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EXTENDED ABSTRACT

Shelter, or cover, is an important resource for mobile animals, providing refuge from a hostile physical environment and predation. The functional relationship between shelter availability and population abundance depends upon how effectively shelter is utilised, which in turn depends upon the behavioural processes that control access to shelter. Using a benthic stream fish, the bullhead *Cottus gobio*, as a model system, this study investigates how intraspecific competition influences shelter use.

The bullhead is a small fish of swift-flowing, well-oxygenated, shallow streams. Bullheads hide from predators during the day, selecting coarse substrates that provide interstitial shelter. Bullheads are generally solitary animals and agonistic behaviour between non-breeding individuals is common, involving threat displays, chasing and occasionally fights. Competition for shelter occurs in two main ways. First, sheltered individuals defend their shelters to try and prevent sharing with others. Second, agonistic or avoidance behaviours reduce the rate at which shelters are colonised, independently of shelter availability. Both forms of interaction may be considered as interference competition, but here we define occupation of shelter as exploitation and other interactions that reduce colonisation rate as interference.

A series of field experiments were conducted, in which shelter availability and population density were controlled. For each experiment the location of each fish was observed regularly over a period of 10 days. We then constructed a continuous-time Markov chain model for the movement of fish between shelters and the open stream, which explicitly parameterised exploitation and interference competition.

For a given experiment, let s be the number of available shelters. If there are currently n_i fish in shelter i, then we suppose that a given unsheltered fish moves into shelter i at rate

$$c_I \cdot \frac{1}{s}(1-a)^{n_i}$$

where c_I represents interference competition, and $a \in [0,1]$ is the probability that a fish currently using shelter i successfully repels an incoming fish. The term $1/s$ is included so that the total rate at which a given unsheltered fish moves into shelter is $c_I \cdot \sum_{i=1}^{s}(1-a)^{n_i}/s$, which we can interpret as the product of an interference term c_I and an average exploitation term. Formally, the interference term gives the rate at which the fish finds a shelter and attempts to use it, and the exploitation term gives the chance of successfully gaining the shelter. The coefficient a represents the strength of exploitation competition.

A number of different forms of the interference term c_I were compared using the Akaike Information Criterion (AIC). Interestingly, we found that interference competition was best modelled as an increasing function of average shelter occupancy, rather than using the population density directly:

$$c_I = \frac{c}{0.001 + (\sum_{i=1}^{s} n_i/s)^m},$$

for $m \geq 0$.

To complete the model, we suppose that a sheltered fish leaves shelter i at rate dn_i^f, where d is the base departure rate and $f \geq 0$ allows sharing to increase the departure rate. The model was fitted using maximum likelihood, and the parameters a, m and f were all seen to be significantly different from 0, showing strong evidence of exploitation and interference competition, which limited the ability of unsheltered fish to colonise vacant shelters at high population densities.

We also considered a refinement of the above model, which made allowance for the effect of size on intraspecific competition. Fish were classified as juvenile or adult, depending on their size, then the probability a, that a sheltered fish repels an incoming fish, was allowed to depend on the types of the incumbent and incoming fish. Fitting the refined model indicated significant differences between the repulsion probabilities, showing that exploitation competition is highly dependent on size.

1 INTRODUCTION

Using a benthic stream fish, the bullhead *Cottus gobio*, as a model system, this study investigates how intraspecific competition influences shelter use. Like other freshwater sculpins, bullheads hide from predators during the day, selecting coarse substrates that provide interstitial shelter. Use of interstitial shelters is common amongst benthic fish and many salmonoid species also seek refuge in the stream bed during winter (Allouche 2002; Brown 1991; Cunjak 1988; Cunjak & Power 1986; Davey et al. 2005; Gries & Juanes 1998; Harwood et al. 2002; Mullen & Burton 1998; Valdimarsson & Metcalfe 1998). Positive correlations between abundance of shelter and population abundance or biomass are well documented in stream fish (see Allouche 2002 for review). Moreover, experiments in which shelter is supplemented confirm that shelter density is an important determinant of fish density in the field and suggest that competition for shelter may limit population size (Boussu 1954; Saunders & Smith 1962; Eklv & Greenberg 1998).

The functional relationship between shelter availability and population abundance will depend upon the behavioural processes that control access to shelter. But, although shelter clearly influences population dynamics, little is known about the mechanisms that link individual behaviour to population level patterns (Allouche 2002). Bullheads are generally solitary animals and agonistic behaviour between non-breeding individuals is common, involving threat displays, chasing and occasionally fights (Brown 1991; Davey et al. 2005; Ladich 1989; Mills & Mann 1983; Smyly 1957; Welton et al. 1983). Competition for shelter may occur in two main ways. First, sheltered individuals may defend a shelter and prevent further colonisation by unsheltered individuals (Mullen & Burton 1998; Figler et al. 1999). Second, agonistic or avoidance behaviours may reduce the rate at which shelters are colonised, independently of shelter availability. Both forms of interaction may be considered as interference competition, but here we define occupation of shelter as exploitation and other interactions that reduce colonisation rate as interference. A further complication is that if asymmetries in colonisation efficiency or competitive ability exist, then individuals may not have an equal probability of shelter use. For example, body size and species identity can influence individual success in one-on-one contests for shelter (Baltz et al. 1982; Dubs & Corkum 1996; Figler et al. 1999; Greenberg 1988; Guan & Wiles 1997; Mullen & Burton 1998; Sloman & Armstrong 2002; Soderback 1994; Vorburger & Ribi 1999).

Quantifying the effect of population density on the overall exploitation rate has rarely been attempted for resources that are exploited by occupation rather than consumption (Doncaster & Gustafsson 1999; Goss-Custard et al. 1995; Stillman et al. 1997; van der Meer & Ens 1997). This is the first study to quantify the different effects of exploitation and interference competition on shelter use.

2 FIELD EXPERIMENT

The field experiment was conducted on the Brandy Stream, Hampshire, U.K., during June and July 2002. Water temperature ranged from 12.9 to 17.4 C (mean 14.8 C) during the experiment (Seamon mini temperature recorder, Hugrn, Reykjavik, Iceland).

Experiments were performed in situ using 10 cage enclosures, each 2.8 m long, 0.8 m wide and 0.3 m high. Enclosures had solid metal sides and base and 6 mm wire-mesh on the up- and down-stream ends to permit water to flow through. The enclosures were established on 5 June in a broad riffle (water depth 0.17 - 0.22 m; water velocity 0.13 - 0.24 m/s) and filled with gravel to a depth of 25 mm. To protect fish from avian predators, the open top of each enclosure was covered with plastic netting. The up- and down-stream wire meshes were removed for several weeks prior to the start of each experiment to allow invertebrates to colonise the enclosures. Once replaced to enclose fish, the wire meshes were cleaned every 12 hours to remove accumulated plant debris and maintain water flow through the enclosures.

A factorial experimental design was used, crossing two levels of shelter density with five levels of fish density. Four or eight hollow bricks were placed in each enclosure to provide shelter (internal dimensions: 90 x 75 x 30 mm). To avoid confounding availability of shelter with changes in flow heterogeneity or visual connectivity, four additional solid bricks were placed in the low shelter density treatments to hold habitat complexity constant. Enclosures were stocked with 2, 4, 6, 8 or 10 bullheads, corresponding to densities of 0.89 - 4.46 fish/m^2 that are within the natural range observed for bullheads in the Brandy stream. Two replicate trials were performed sequentially for each combination of treatments.

All bullheads used in the study were collected from the Brandy Stream by electrofishing. For each set of trials, 60 fish were weighed to 0.01 g, measured to 0.1 mm and individually marked using subcutaneous elastomer tags (Northwest Marine Technology Inc., WA, USA). Bullheads ranged in initial mass from 2.17 to 9.88 g (mean 3.50 g) and in length from 56.8 to 89.2 mm (mean 64.5 mm). Fish were randomly assigned to treatments, and treatments randomly assigned to enclosures. New fish were used for each set of trials to ensure independence. For each trial, bullheads were

allowed to acclimatise for 48 h, after which use of shelter and longitudinal position of each individual were recorded by visual inspection twice daily (0730–0900 h and 1830–2100 h) for ten consecutive days. Enclosures were inspected in random order for each observation period. Two fish that died during the experiment were replaced with spare fish from a stock enclosure to maintain the treatments. Between trials, shelters were scrubbed and dried to remove any scent of previous occupants, and randomly reallocated to enclosures. The substrate in each enclosure was also redistributed.

3 STOCHASTIC MODEL

We construct a continuous-time Markov-chain model for the movement of fish between shelters and the open stream, which explicitly parameterises individual level competition for shelter (exploitation competition) and population level competition (interference competition). In modelling the observed fish populations we need to make a trade off between the complexity of the model and the degree of certainty with which it can be fitted. In our case we can identify individual fish, but we do not have enough data to model each fish individually. Instead we consider two models: in the first all fish are considered to behave in the same way statistically; in the second we split the fish into two groups based on their size, and allow for statistically different behaviour between each group. We consider the one-size model first.

Exploitation competition will depend on the precise distribution of fish across shelters, not just the average shelter use, so our model must reflect this. At any given point in time the state of the system will be described by a vector $(n_0, n_1, \ldots, n_s)$ where s is the number of shelters, n_0 is the number of unsheltered fish, and for $i = 1, \ldots, s$, n_i is the number of fish in shelter i. We remark that if you consider only average shelter use, then you can construct a solvable differential model for the system, analogous to the stochastic model we describe here. However we found that the differential model gave a poor fit to the data, reinforcing the need to explicitly model the distribution of fish across shelters.

Diurnal observations provided an accurate measure of shelter use since bullheads were never observed to be active outside shelter during daylight hours. However, since they are active at night, night-time observations do not allow us to determine if a fish can be regarded as using a shelter, and were not used for fitting the model. Also it was observed that individual fish were often found in the same shelters a number of nights in a row. That is, shelter use on day $t + 1$ is dependent on shelter use on day t, and we can not regard observations from one day to the next as independent. This leads us naturally to a Markov model

For a given trial let $s \in \{4, 8\}$ be the number of shelters and $k \in \{2, 4, 6, 8, 10\}$ the total number of fish. We suppose that the system dynamics are given by a continuous-time Markov chain, with time measured in days. We use a continuous- rather than discrete-time model, even though we observe the system at regular (daily) time-points, because this simplifies the dynamics. A continuous-time model only requires us to define transitions involving the movement of a single fish; a discrete-time model allows direct transitions from any state to any other, all of which must be defined.

We suppose that a given unsheltered fish moves into shelter i at rate

$$c_I \cdot \frac{1}{s}(1 - a)^{n_i},$$

where $c_I = c_I(k, n_0, s) > 0$ represents interference competition, and $a \in [0, 1]$ is the probability that a fish currently using shelter i successfully repels an incoming fish. The term $1/s$ is included so that the total rate at which a given unsheltered fish moves into shelter is

$$c_I \cdot \frac{1}{s} \sum_{i=1}^{s}(1 - a)^{n_i},$$

which we can interpret as the product of an interference term c_I and an average exploitation term $s^{-1} \sum_{i=1}^{s}(1 - a)^{n_i}$. Formally, the interference term gives the rate at which the fish finds a shelter and attempts to use it, and the exploitation term gives the chance of successfully gaining the shelter. The coefficient a represents the strength of exploitation competition. The form of the interference term c_I is not obvious, so we started with a very general form, then later used the Akaike Information Criterion (AIC, Akaike 1974) to choose a simpler more informative form. We put

$$c_I = \frac{c}{0.001 + (k - n_0)^{m_1} s^{-m_2} k^{m_3} n_0^{m_4}},$$

for $c > 0$, $m_1, \ldots, m_4 \geq 0$. The term 0.001 is included in the denominator so that $c_I \neq \infty$ when $n_0 = k$. In practice we never observed $n_0 = k$ so including the 0.001 has a negligible effect on model fitting, but does make coding it easier. The other terms allow c_I to depend on the total number of fish, unsheltered fish and/or sheltered fish, and the total number of shelters.

We suppose that a sheltered fish leaves shelter i at rate

$$dn_i{}^f,$$

where $d > 0$ is the base departure rate and $f \geq 0$ allows sharing to increase the departure rate.

We fitted the model using maximum likelihood. Write $\theta = (a, c, m_1, m_2, m_3, m_4, d, f)$ for the parameter

vector and let $\Omega^{(i)}$ be the state-space for experiment i and $Q^{(i)} = Q^{(i)}(\theta)$ the rate-matrix of the corresponding Markov chain. The time-t transition matrix is then $P_t^{(i)} = \exp(tQ^{(i)})$. Let $\omega^{(i)} = (\omega_1^{(i)}, \ldots, \omega_{10}^{(i)})$ be the day-time observations from trial i, then the log-likelihood is

$$l(\theta; \omega^{(i)}) = \sum_{i=1}^{10} \sum_{j=2}^{10} \log P_1^{(i)}(\omega_{j-1}^{(i)}, \omega_j^{(i)}).$$

By explicit enumeration we can show that for $s = 8$ and $k = 10$, $|\Omega^{(i)}| = 43{,}758$. In this case calculating $\exp(Q^{(i)})$ and thus l becomes very expensive. However, we can dramatically reduce the size of the state space by observing that the system dynamics, as given by the model, depend only on the relative numbers of fish in each shelter. That is, we can lump together all states for which the ordered values $n_1, \ldots, n_s$ are the same. For example, in the case $s = 4$ and $k = 2$ we lump together states $(n_0, n_1, n_2, n_3, n_4)$ as follows

$$
\begin{aligned}
(2,0,0,0,0) &\equiv (2,0,0,0,0) \\
(1,0,0,0,1) &\equiv (1,0,0,0,1); \ (1,0,0,1,0); \\
& \quad (1,0,1,0,0); \ (1,1,0,0,0) \\
(0,0,0,0,2) &\equiv (0,0,0,0,2); \ (0,0,0,2,0); \\
& \quad (0,0,2,0,0); \ (0,2,0,0,0) \\
(0,0,0,1,1) &\equiv (0,0,0,1,1); \ (0,0,1,0,1); \\
& \quad (0,1,0,0,1); \ (0,0,1,1,0) \\
& \quad (0,1,0,1,0); \ (0,1,1,0,0).
\end{aligned}
$$

In the case $s = 8$ and $k = 10$ the size of the state space drops from 43,758 to 136.

A number of different forms were considered for the factor c_I, by setting the exponents $m_1, \ldots, m_4$ to 0 or 1 or equal to each other, in various combinations. To choose a parsimonious form for c_I we minimised the AIC, given by $2p - 2l^*(\theta)$, where p is the number of free parameters and l^* is the maximised log likelihood. The minimum AIC was 367.67, for

$$c_I = \frac{c}{0.001 + ((k - n_0)/s)^m}.$$

That is, interference competition was best described using the average number of fish per shelter $(k - n_0)/s$.

The likelihood was maximised numerically using sequential quadratic programming (see e.g. Powell 1978; Gill et al. 1991), as implemented in Matlab R2006b (The MathWorks, Inc.) The maximum likelihood parameter estimates are

$$
\begin{aligned}
a &= 0.7525 \ \pm \ 0.2152 \\
c &= 0.9175 \ \pm \ 1.4462 \\
m &= 2.3635 \ \pm \ 0.8693 \\
d &= 0.1725 \ \pm \ 0.1268 \\
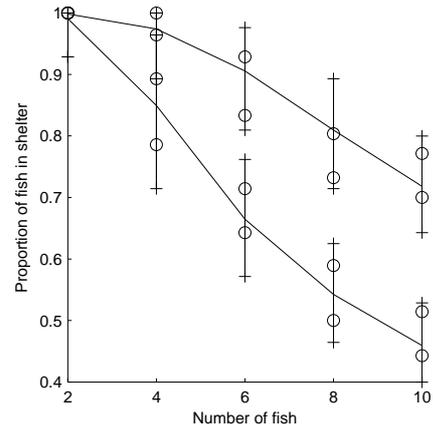f &= 1.4598 \ \pm \ 1.1562
\end{aligned}
$$

Figure 1. Comparison of observed and fitted values for average proportion of fish in shelter. Observed values are given by circles and expected values from the model are given by the two solid lines (corresponding to 4 or 8 shelters). Model based 95% confidence-intervals are given by the vertical lines. There are two observations for each combination of shelter and fish numbers.

The error estimates in the final column are twice the estimated standard deviation, taken from the Fisher information matrix (approximate 95% confidence intervals). We see that a is significantly different from 0 and 1, and m, d and f are all significantly different from 0. By definition we must have $c > 0$; its relatively large error bound indicates that the model is not very sensitive to small changes in c. A discussion of the fitted model is given in Section 4.

To illustrate the fit of the model we plot in Figure 1 the average proportion of fish in shelter for each trial and for the model. For the model we give a mean and 95% confidence-interval obtained by simulation. We see that all the observed values lie within the 95% confidence-intervals given by the model, indicating a good fit.

3.1 Two-size model

Figure 1 indicates that our one-size model is giving a good fit to the data. The confidence-intervals for the model parameters are relatively large, indicating that there may not be enough data to support a more complex model. None-the-less, because we know size is such an important factor in intraspecific competition, it is worth trying to incorporate this.

We classify fish < 63 mm as juvenile and fish > 63 mm as adult. This splits the bullheads into roughly two equal groups of 56 juveniles and 64 adults. In two of the trials, one of the original fish died during the course of the experiment and was replaced by another

fish. For simplicity we have let the replacement fish take on the identity of the original.

For a given s and k, the state of our model is now a $2 \times (1 + s)$ array

$$\left(\begin{array}{cccc} \alpha_0 & \alpha_1 & \cdots & \alpha_s \\ \beta_0 & \beta_1 & \cdots & \beta_s \end{array} \right)$$

where α_0 is the number of unsheltered adults, α_i is the number of adults in shelter i, and similarly using β for the juveniles. Let k_α be the total number of adults and k_β the total number of juveniles. The state space is again reduced by removing any distinction between the ordering of shelters. However, because we have two types of fish this is much less effective than before, and in the case $s = 8$, $k_\alpha = 5$ and $k_\beta = 5$ we still have 1,475 states, which is too large for effective use of maximum likelihood. Observing that there were never more than three fish sharing a shelter, and that happened only once, we further restricted the state space to states for which $\alpha_i + \beta_i \leq 3$ for $i = 1, \ldots, s$. The probability of finding the Markov chain in one of these discarded states is very small, so their removal has very little impact. In the case $s = 8$, $k_\alpha = 5$ and $k_\beta = 5$ this reduces the state space to size 732. With these modifications we were able to numerically maximise the likelihood for the two-size model in around an hour on a desktop PC.

The transition rates for the two-size model are analogous to those of the one-size model. An unsheltered adult fish moves into shelter i at rate

$$\frac{c_\alpha}{0.001 + (k - \alpha_0 - \beta_0)/s} \cdot \frac{1}{s}(1 - a_{\alpha\alpha})^{\alpha_i}(1 - a_{\beta\alpha})^{\beta_i}.$$

An unsheltered juvenile moves into shelter i at rate

$$\frac{c_\beta}{0.001 + (k - \alpha_0 - \beta_0)/s} \cdot \frac{1}{s}(1 - a_{\alpha\beta})^{\alpha i}(1 - a_{\beta\beta})^{\beta_i}.$$

Here $a_{\alpha\alpha}$ is the probability a sheltered adult repels an adult, $a_{\beta\alpha}$ is the probability a sheltered juvenile repels an adult, $a_{\alpha\beta}$ is the probability a sheltered adult repels a juvenile and $a_{\beta\beta}$ is the probability a sheltered juvenile repels a juvenile. For $d, f \geq 0$, we suppose that both adult and juvenile fish leave shelter i at rate

$$d(\alpha_i + \beta_i)^f.$$

A variety of more complex forms were considered for the interference component of the rate of moving into shelter, with the final form being chosen on the basis of the AIC. Similarly more complex size-dependent forms for the rate of leaving a shelter were considered, but they also did not produce better models. Essentially there is not enough data to support more complex forms for these rates; in particular we could not accurately fit the parameter m that appears in the one-size model and instead have fixed it at

1. The AIC for our final fitted model was 735.58. Fitted parameter values, with errors given by twice the standard deviation, are

$$\begin{array}{rcrcr} a_{\alpha\alpha} & = & 0.7458 & \pm & 0.1542 \\ a_{\beta\alpha} & = & 0 & \pm & 0 \\ a_{\alpha\beta} & = & 0.8845 & \pm & 0.1490 \\ a_{\beta\beta} & = & 0.6359 & \pm & 0.3193 \\ c_\alpha & = & 1.4498 & \pm & 0.5506 \\ c_\beta & = & 0.6714 & \pm & 0.3051 \\ d & = & 0.1438 & \pm & 0.0830 \\ f & = & 1.8196 & \pm & 1.0066 \end{array}$$

The variation in the values of $a_{\alpha\alpha}$, $a_{\beta\alpha}$, $a_{\alpha\beta}$ and $a_{\beta\beta}$ confirm that exploitation competition is strongly dependent on size. That $c_\alpha > c_\beta$ also indicates that adults are less effected by interference competition than juveniles. ($a_{\beta\alpha}$ is significantly different to $a_{\alpha\alpha}$, $a_{\alpha\beta}$ and $a_{\beta\beta}$ at the 99% level. c_α and c_β are significantly different at the 90% level.)

4 DISCUSSION

This study adds to a small body of literature showing that shelter use may be density dependent as a result of intraspecific competition or density dependent anti-predator tactics (Armstrong & Griffiths 2001; Rangeley & Kramer 1998). Both of our Markov chain models successfully distinguished between exploitation and interference competition. Although shelter is known to be an important resource for many mobile animal species this is the first study to distinguish between, and quantify the strength of, contrasting competitive processes driving patterns of shelter use.

The detection of strong exploitation competition confirms previous anecdotal evidence that bullheads are solitary animals that defend shelters against colonisation by conspecifics (Smyly 1957). Exploitation competition for shelter appears to be a widespread phenomenon in aquatic animals. Monopolising behaviour has been reported in a variety of taxa, with individuals displacing both conspecifics and heterospecifics from shelter (Baltz et al. 1982; Dubs & Corkum 1996; Figler et al. 1999; Greenberg 1988; Gregory & Griffith 1996; Guan & Wiles 1997; Harwood et al. 2002; Mullen & Burton 1998; Soderback 1994; Vorburger & Ribi 1999). This study advances current understanding, however, by quantifying the probability that a shelter can be occupied by more than one individual. We also see that, as $f > 0$, sharing a shelter is undesirable to the fish, since such fish leave the shelter at a greater rate than if they were on their own.

The two-size model shows clearly that large fish are more successful at defending and acquiring shelter than small fish, with $a_{\alpha\beta}$ close to 1 and $a_{\beta\alpha}$ equal to 0.

This finding is in agreement with previous studies that show that body size is a good predictor of success in one-on-one contests for shelter and space (Figler et al. 1999; Mullen & Burton 1998; Sloman & Armstrong 2002).

Bullheads also exhibited strong interference competition for shelter. Shelters were widely spaced within enclosures, so providing a conservative test of the strength of interference competition. Aggressive interactions between bullheads outside of shelters are common and take the form of threat displays, chasing and occasionally fights (Ladich 1989; A. Davey, personal observation). Density dependence in the colonisation efficiency of benthic shelters by bullheads is therefore thought to be an indirect consequence of territorial competition for foraging space at night. Interference competition is often considered to be a non-linear function of competitor density, with no or negligible interference at low density and stronger interference at higher densities as conspecifics come into closer proximity (Goss-Custard et al. 1995; Stillman et al. 1997). This is analogous to our finding that $m > 1$ in the one-size model.

In this study the form of interference competition that best matched the data was an increasing (non-linear) function of the average number of fish per shelter. Explaining this satisfactorily will require further experimentation, however a possible explanation is that individual fish only try and access a fixed number of shelters before giving up (and then possibly emigrating). None-the-less we note that the average number of fish per shelter increases as population density increases, so it is still correct to say that interference competition increases as population density increases. Our results also show that size mitigates the effect of interference, since $c_\alpha > c_\beta$. More specifically, large fish find and attempt to use a shelter at roughly twice the rate small fish do.

Most previous experimental manipulations of shelter density have confounded shelter availability with habitat complexity. More complex habitat structure may also increase local carrying capacity in territorial species by visually isolating conspecifics and thereby reducing intraspecific competition (Kalleberg 1958; Imre et al. 2002). By holding habitat complexity constant, this study demonstrates that shelter availability per se can affect local density of mobile animals, although structural complexity cannot be eliminated as a factor influencing the spatial distribution of bullheads.

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