

Distinguishing between interference and exploitation competition for shelter in a mobile fish population

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June 2008

Abstract

Understanding the functional significance of shelter for animal populations requires knowledge of the behavioural mechanisms that govern the dynamics of shelter use. Exploitation of shelters may be impeded by mutual interference, yet interference competition can be difficult to distinguish from exploitation competition. We used Bullheads (*Cottus gobio*) as a model system of mobile fish to investigate the effect of intraspecific competition on shelter use. A series of field experiments was conducted under controlled conditions of shelter availability and population density. For each experiment the location of each individual fish was observed 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 competition and interference competition for shelter, and which accounted for two different size classes of fish. By using a stochastic rather than a deterministic model, we were able to account for the distribution of fish across shelters, and not just the average occupation. Analysis of the model showed strong evidence of exploitation competition, which was highly dependent on body size, and an increased departure rate from shared shelters. Over and above exploitation, interference competition limited the ability of unsheltered fish to colonise vacant shelters at high population densities. Different formulations of the interference competition were compared using the AIC information criterion. The formulation that best fitted the observations modelled interference competition as an increasing function of average shelter occupancy, rather than population density per se.

Keywords: attraction versus production; cover; habitat complexity; Markov chain; multiple occupancy; refuge; refugia; resource monopolisation; resource sharing.

1 Introduction

One of the primary goals in ecology is to understand the factors that determine the distribution and abundance of animals. Shelter, or cover, is an important resource for mobile animals, providing refuge from hostile components of the physical and biotic environment. Shelter availability thus influences the spatial distribution of individuals (Allouche 2002; Valdimarsson & Metcalfe 1998). It may limit population abundance through exploitation competition; additionally, as an occupied rather than consumed limiting resource it is particularly susceptible also to interference competition for access (Lessells 1995; Doncaster & Gustafsson 1999).

In streams, shelter may take a variety of forms including interstitial spaces in the stream bed, undercut banks and coarse woody debris. Use of interstitial shelters is common amongst benthic fish and many salmonid 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). It is often uncertain, however, whether addition of shelter affects demographic parameters such as survival or recruitment, or simply causes the redistribution of existing fish.

The functional relationship between shelter availability and population abundance will depend upon the behavioural processes that control access to shelter. Although shelter clearly influences population dynamics, little is known about the mechanisms that link individual behaviour to population level patterns (Allouche 2002). 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; here we define occupation of shelter as exploitation and other interactions that reduce colonisation rate as interference. 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 in a mobile fish population.

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; Soderback 1994; Vorburger & Ribi 1999).

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. Like other freshwater sculpins, 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 (Brown 1991; Ladich 1989; Mills & Mann 1983; Smyly 1957; Welton et al. 1983).

In Section 2 we describe the field experiments used to observe bullhead behaviour, then in Section 3 we model bullhead behaviour using two related continuous-time Markov chains. Both models explicitly parameterise exploitation and interference competition, while the second also allows for two sizes of fish.

Two simplifying assumptions were required to be able to fit a model to the observed data: we assumed that no one shelter was seen as more desirable than the others, and that fish (of a given size class) behaved statistically identically. We note that to capture the effect of exploitation competition on shelter use, it is not sufficient to consider a model system where the state is the average number of fish in shelter. Rather you must consider the distribution of fish across the shelters. For example, consider a fish looking for shelter: in case (a) it is faced with two shelters each already containing one fish, while in case (b) it is faced with one shelter containing two fish and an empty shelter. In each case the average number of fish in shelter is the same, but we expect, and thus our model should allow, the chance of obtaining shelter to be different in the two cases. This consideration leads naturally to a stochastic model, where the state of the system is the distribution of fish across shelters.

An interpretation of the fitted models is given in the discussion in Section 4. Both of our Markov chain models successfully distinguish between exploitation and interference competition, and quantify the probability that a shelter can be occupied by more than one individual. Moreover the two-size model shows clearly that large fish are more successful at defending and acquiring shelter than small fish. There is also evidence that interference competition is a non-linear function of competitor density, with stronger interference at higher densities.

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. See Figure 1. Enclosures were stocked with 2, 4, 6, 8 or 10 adult bullheads, corresponding to densities of 0.89 to 4.46 fish/m² 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.

The experimental results analysed in this paper can be downloaded from www.ms.unimelb.edu.au/~odj

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 modeling 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, \dots, n_s) where s is the number of shelters, n_0 is the number of unsheltered fish, and for $i = 1, \dots, s$, 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 days 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

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

(in units of fish per unit time) 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 $c > 0$, $m_1, \dots, m_4 \geq 0$. The term 0.001 is included in the denominator so that $c_I \neq \infty$ when $n_0 = k$. 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. When $n_0 = k$ we get $c_I = 1000c$. It is tempting to interpret this as the rate at which fish colonise shelter in the absence of interference, however in practice we never observed $n_0 = k$, and we should *not* extrapolate the functional form of c_I beyond the range of observed values of k , s and n_0 .

We suppose that a sheltered fish leaves shelter i at rate

$$dn_i^f,$$

(in units of fish per unit time) where $d > 0$ is the base departure rate and $f \geq 0$ allows sharing to increase the departure rate. The total rate at which fish leave shelter i is thus dn_i^{1+f} .

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 $\omega^{(i)} = (\omega_1^{(i)}, \dots, \omega_{10}^{(i)})$ 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, \dots, 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

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

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, \dots, 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 given in Table 1. We see that 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. Note that a , m and f are all dimensionless, c has dimension fish^{m+1}/t and d has dimension fish^{1-f}/t . 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 2 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 2 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. This change effects only 9 out of 1000 observations, so should have a negligible effect on the analysis.

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

$$\begin{pmatrix} \alpha_0 & \alpha_1 & \cdots & \alpha_s \\ \beta_0 & \beta_1 & \cdots & \beta_s \end{pmatrix}$$

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 $i = 1, \dots, s$. 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 given above 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 significantly 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 are given in Table 2. 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 in fish.

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 1996a; 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).

Factors that affect the level of aggression and hence the strength of exploitation competition will have a strong influence on the carrying capacity of the environment. For example, hatchery-reared Atlantic salmon (*Salmo salar*) share shelters with much greater frequency than wild-reared fish (Griffiths & Armstrong 2002). Although shelter defence is a common phenomenon, the benefit of monopolising a shelter is unclear. The probability of prey in structurally complex refuges being detected by predators is predicted to be positively density dependent (Rangeley & Kramer 1998), and so solitary shelter use may minimise the chance of being detected by predators that use olfactory cues (Armstrong & Griffiths 2001; Griffiths & Armstrong 2002) and employ area-restricted searching (Rangeley & Kramer 1998). Defensive behaviour is therefore thought to be a strategy to reduce predation risk, but further studies are needed to test this hypothesis.

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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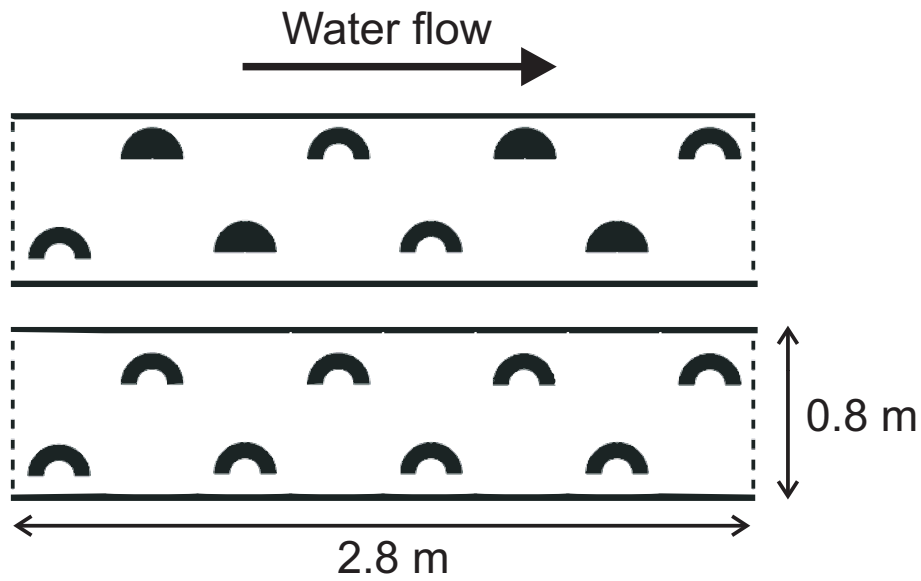


Figure 1: Flow-through stream enclosures were used to experimentally manipulate shelter density and fish density in situ. Enclosures contained either four or eight shelters (hollow bricks), with four solid additional bricks in low shelter treatments to hold habitat complexity constant. Enclosures were then stocked with 2, 4, 6, 8 or 10 individually marked bullheads, and the position of each fish recorded twice daily for 10 days.

Table 1: Maximum likelihood parameter estimates for the one-size model. The error estimates in the final column are twice the estimated standard deviation, taken from the Fisher information matrix (approximate 95% confidence intervals).

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

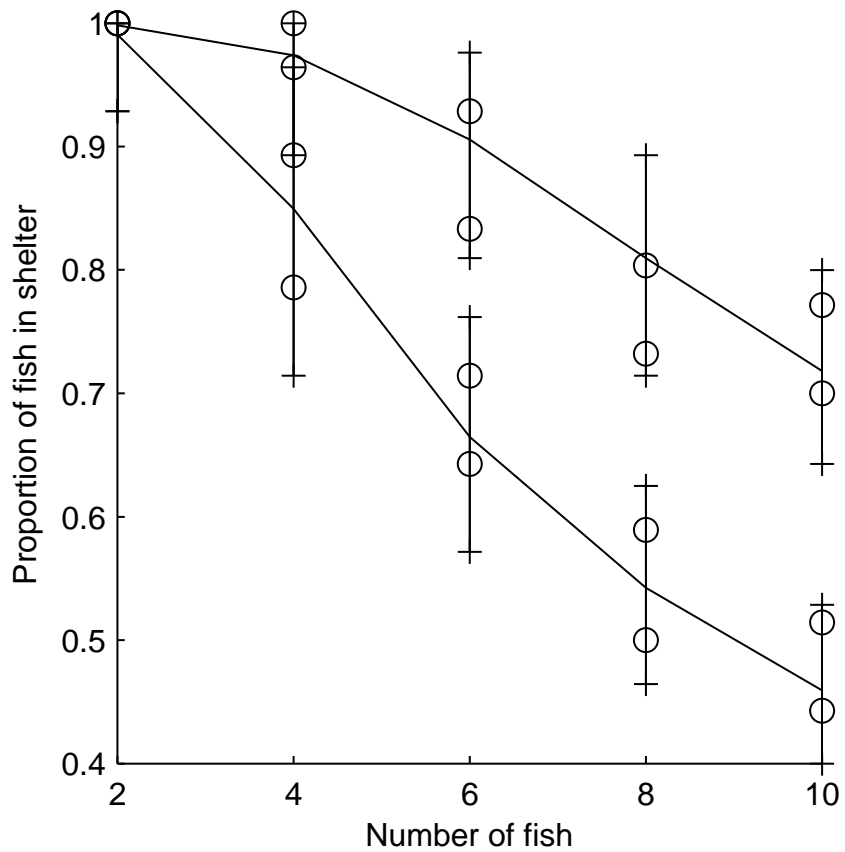


Figure 2: Comparison of observed and fitted values for average proportion of fish in shelter. Observed values are given by circles and expected values from the model are given by the two solid lines (corresponding to 4 or 8 shelters). There are two observations for each combination of shelter and fish numbers. Model based 95% confidence-intervals are given by the vertical lines, with the top and bottom of each interval given by a small horizontal bar (the intervals overlap for the experiments with 2 and 4 fish). In every case the observed values are well within their corresponding confidence intervals, indicating a good fit.

Table 2: Maximum likelihood parameter estimates for the two-size model. The error estimates in the final column are twice the estimated standard deviation, taken from the Fisher information matrix (approximate 95% confidence intervals).

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