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Population consequences of behaviour in the European bitterling (*Rhodeus sericeus* Cyprinidae)

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Abstract – The European bitterling is a freshwater fish with an unusual spawning symbiosis with freshwater mussels. Female bitterling possess long ovipositors that they use to place their eggs onto the gills of a mussel. Males fertilise the eggs by releasing sperm into the inhalant siphon of the mussel. The embryos develop inside the mussel for approximately a month, eventually leaving the mussel as actively swimming larvae. Because they use a discrete spawning site that can be readily manipulated they represent an ideal model for linking reproductive decisions with population dynamics. Bitterling have been used in field and large-scale pool experiments, in combination with modelling and population and genetic studies to investigate the population consequences of behaviour. Here we show how male mating tactics, female mate and oviposition decisions, and aggressive interference competition among juveniles, may have significant impacts on bitterling population size and population genetics.

C. Smith[1], M. Reichard[1,2], A. Douglas[3], P. Jurajda[2]

[1]Department of Biology, University of Leicester, University Road, Leicester, UK, [2]Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno, Czech Republic, [3]School of Biology, Zoology Building, University of Aberdeen, Aberdeen, UK

Key words: juvenile; male–male competition; model; oviposition choice; population dynamics; territoriality

C. Smith, Department of Biology, University of Leicester, University Road, Leicester LE1 7RH, UK; e-mail: cs152@le.ac.uk

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Introduction

Behavioural ecology is founded on the principle that natural and sexual selection favours behavioural decisions that maximize the inclusive fitness of individuals (Hamilton 1972; Williams 1975). However, the population consequences of this paradigm are unclear (Smith & Sibly 1985). A central goal in ecology has been to link the behaviour of individuals with population dynamics (Ebling & Stoddart 1978; Smith & Sibly 1985; Łomnicki 1988; Sutherland 1996). Yet despite acceptance that population dynamics and behaviour may be mutually dependent processes, progress in linking the two has been slow, possibly because population ecologists tend to focus on schedules of birth, death, immigration and emigration without questioning the underlying behavioural contributions to these processes. In contrast, behavioural ecologists have primarily concerned themselves with the adaptive significance of behaviour for individuals while ignoring the possibility of population consequences of behaviour (Hassell & May 1985; Sutherland 1996). Here, we review the research that attempts to link the behaviour of European bitterling (*Rhodeus sericeus* Pallas, Cyprinidae) with their population dynamics, using a combination of field, mesocosm and aquarium experiments, in combination with population and genetic studies, and modelling. Research to link behaviour with population processes has focused on male and female reproductive behaviour and the behaviour of juveniles during early life stages.

The European bitterling is a freshwater fish belonging to a cyprinid sub-family (Acheilognathinae) with an unusual spawning symbiosis with freshwater mussels. During the spawning season, males develop bright nuptial colouration and defend territories around mussels. Female bitterling develop long ovipositors

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that they use to place their eggs onto the gills of a mussel through the mussel's exhalant siphon. Males fertilise the eggs by releasing sperm into the inhalant siphon of the mussel, so that water filtered by the mussel carries the sperm to the eggs (for a review see Smith et al. 2004). Developing embryos reside inside the mussel for approximately 1 month during which time they develop into actively swimming larvae (Aldridge 1999). After emergence from a mussel the larvae enter shallow, vegetated margins of lakes and rivers that serve as nursery areas, where they remain until the end of their first summer (Przybylski & Zięba 2000; Reichard et al. 2002). At this life stage, the principal predator of bitterling appears to be the European perch (*Perca fluviatilis*) (Smith et al. 2000a). At approximately 6 months of age, juvenile bitterling recruit to the adult population and overwinter in areas of deep water with spent adults. Bitterling rarely live beyond 2 years, and the majority of individuals survive only a single breeding season (Smith et al. 2000a). Bitterling display remarkable morphological, physiological and behavioural adaptations for using mussels as spawning sites, and they represent a valuable model in behavioural, population and evolutionary ecology. The value of the bitterling as a model for linking behaviour with population processes arises from it having a spawning site that can be easily manipulated and assessed for quality. They can also be observed in nature and adapted readily to laboratory conditions.

Female oviposition decisions

Four species of unionid freshwater mussel (*Anodonta anatina*, *Anodonta cygnea*, *Unio pictorum* and *Unio tumidus*) are commonly used as spawning hosts by bitterling in Western Europe (Smith et al. 2004). Smith et al. (2000b) used field experiments to show that female bitterling have preferences for spawning in *A. anatina*, *U. pictorum* and *U. tumidus*, while avoiding spawning in *A. cygnea*. Female bitterling were further shown to avoid mussels that already contained large numbers of bitterling embryos. The mortality rates of bitterling embryos while incubated in mussels were found to be strongly density dependent; the strength of density dependence varying among mussel species and strongest in *A. cygnea*, the species of mussel avoided by bitterling. The oxygen content of the water emerging from the exhalant siphon of the mussel may serve as the cue for mussel choice (Smith et al. 2001a). Because female preferences for mussels match the survival of their embryos this raises the prospect that oviposition choices by females might have an impact on population size.

In a study to test this hypothesis, Smith et al. (2000a) incorporated these behavioural preferences for spawning sites by female bitterling into a population model and demonstrated that, whereas discrimination by bitterling among mussel species as hosts for their young had a minor effect on population size, discrimination against mussels already containing high numbers of embryos had the potential to reduce populations by 6% compared with random spawnings (Table 1). This effect arose because a random (Poisson) distribution of eggs among mussels led to enhanced survival of embryos in those mussels that received few spawnings, ultimately resulting in better recruitment. The weak effect of species discrimination stemmed from the fact that differences among mussels in the density-dependent survival of embryos was less than the strength of density dependence within mussels (Smith et al. 2000b). Thus, female spawning decisions were shown to play a significant, though relatively minor, role in the population dynamics of bitterling, while other variables, such as predation and habitat structure, were of much greater significance.

Table 1. Importance of model components to the correlation between the full and partial models for predicted bitterling population sizes.

Model component removed	*r*	Per cent deviation from full model
Discrimination against mussel fullness with embryos	0.99	+6
Discrimination among mussel species	1.00	+1
Refuges	0.68	−48
Perch predators	0.73	+23

r is the correlation coefficient for the fit of the partial model versus the full model. Percentage deviation from the full model is the percentage increase or decrease in population size that results due to the removal of a model component from the full model. This was obtained as the per cent change from a slope of 1 of the gradient from a linear regression of the fitted population size of the partial model as a function of the full model. The intercept has been forced through the origin.

Male reproductive behaviour

Alternative male mating behaviours are common in European bitterling (Smith et al. 2002, 2003, 2004; Reichard et al. 2004a,b). While some males defend territories and attract females, other males adopt sneaking behaviour. Both males that do not defend territories and those in adjacent territories attempt to release their sperms over the inhalant siphon of mussels guarded by territorial males, before and after a female has spawned (termed pre- and postoviposition ejaculation, respectively). Territorial males respond to the presence of competing males by varying sperm expenditure and directing aggression towards competitors (Smith et al. 2004).

Reichard et al. (2004a) examined the mechanisms by which competition for fertilisations affect spawning rate and the spatial scale at which these effects are manifested. Using a mesocosm, they experimentally tested whether the number of eggs spawned by females was dependent on the number of available spawning sites, and if so, whether male behaviour, mussel spatial distribution and operational sex ratio (OSR) had any effect on spawning rate. For details of materials and methods, see Reichard et al. (2004a).

Reichard et al. (2004a) established that the number of available spawning sites affected spawning rate; the total number of eggs spawned was positively correlated with the number of mussels available (Fig. 1). In addition, the OSR in the immediate vicinity of a mussel ('local' OSR) correlated with the number of mussels available for oviposition, with local OSR male biased at low mussel densities and female biased at high mussel densities (Fig. 2). It was also shown that territorial male aggression and the number of territorial male ejaculations were positively correlated with the number of rival male ejaculations.

These results could be explained on the basis that the number of eggs spawned by bitterling might be limited by mussel capacity to accommodate eggs. However, the average number of eggs per mussel (41 eggs) recorded in the study was far below the known carrying capacity of mussels. Indeed, up to 132 eggs were found in a single mussel during the experiment and much higher egg densities have frequently been encountered in field studies (Smith et al. 2004).

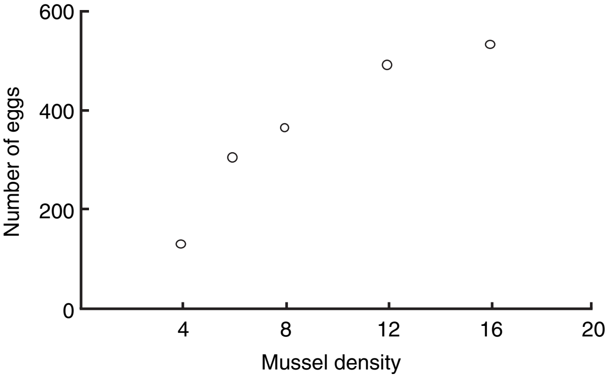

Fig. 1. The relationship between the total numbers of bitterling eggs spawned over 24 h by the study population and the number of mussels available for oviposition.

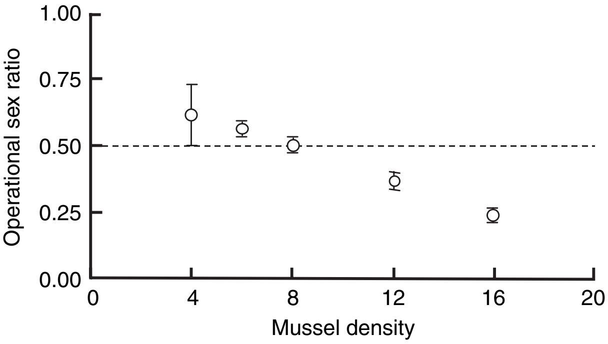

Fig. 2. Local male to female operational sex ratio (OSR) across different mussel densities. OSR was calculated according to Kvarnemo & Ahnesjö (2002) as: OSR = males/(males + females). The dashed line indicates equal OSR; values from 0 to 0.49 indicate female-biased and from 0.51 to 1 male-biased OSR.

Local OSR changed significantly with mussel density and OSR is known to affect male behaviour (Kvarnemo & Ahnesjö 2002), with increased male–male interference competition for matings under male-biased OSR (Emlen 1976; Enders 1993; Jirotkul 1999). Territorial male bitterling were shown to adjust their aggression across mussel densities according to the change in local OSR, which influenced the success of spawning attempts by females. Based on these results, Reichard et al. (2004a) proposed that male–male competition might affect the total oviposition rate of the experimental population.

In a second mesocosm experiment, Reichard et al. (2004a) partitioned the effects of 'total' male density (total number of males in the population) and 'local' male density (manipulated by a proximity between adjacent territories) while holding the number of spawning sites constant. For details of materials and methods, see Reichard et al. (2004a). High total male density was correlated with the number of rival males involved in spawning and rival male ejaculation rate. At the high total male density, territorial males increased their aggression towards competing males (Fig. 3a), which resulted in a significant interaction between total male density and the rate of interruption to female spawning attempts (Fig. 3b).

When total male density was low, territorial males aggressively defended their territories against rivals, and the rate of aggressive interactions increased as a function of local male density. Consequently, the number of unsuccessful spawning attempts by females significantly increased, with females abandoning spawning as males interrupted courtship to engage in aggressive attacks against rivals. Oddly, at high total male density, territoriality appeared to break down with an increase in local male density. Territorial male aggression decreased, with the effect that courtship interruptions were considerably reduced and females were able to spawn with fewer interruptions. Thus, the highest male density in the study, which resulted in territoriality being relaxed, may have been at the point at which territoriality was no longer adaptive; high investment in defence by territorial males may have been uneconomic in terms of male reproductive success. Fish densities in this experiment were within the range already recorded for bitterling in the wild (Smith et al. 2000a), and the same response was observed by Smith et al. (2002) under natural conditions, with territorial males unable to defend a mussel

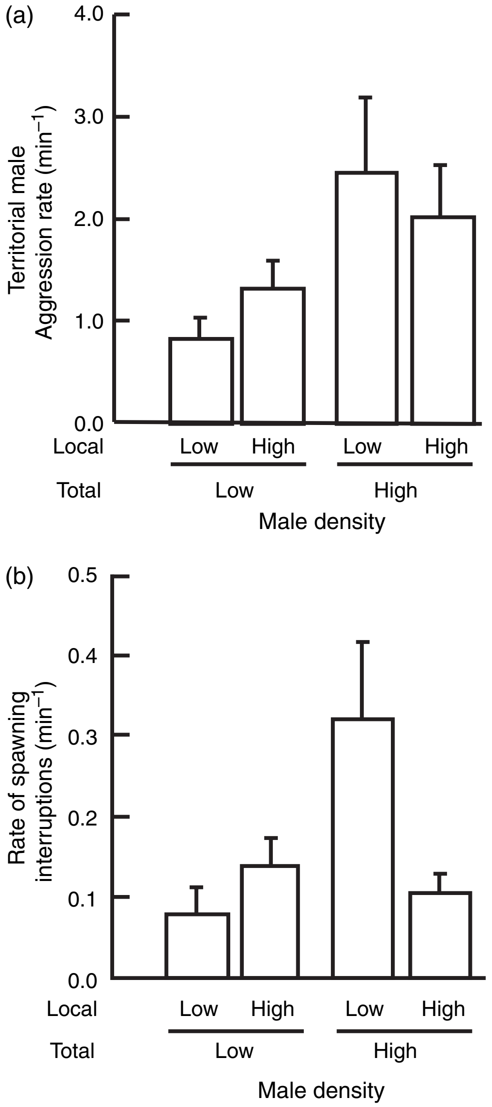

Fig. 3. Male behaviour: (a) rate of aggressive attacks by territorial males towards rival males; (b) rate of spawning interruptions. Error bars are 1 SE.

against large groups of rival males that attempted to participate in spawnings.

To address the question of why territoriality declined and female spawning rate increased at the highest male densities, a separate genetic study was conducted using fin tissue collected during the density experiment. See Reichard et al. (2004b) for materials and methods. Paternity analysis established that the proportion of offspring sired by territorial males decreased with an increase in total male density (Fig. 4). The proportion of embryos sired by an individual sneaker male was significantly higher at high total, but not high local male density. Territoriality conferred a higher reproductive success than sneaking when total or local male density was low, but at high local and total density territorial males had the same reproductive success as sneakers, and at this point territoriality broke down.

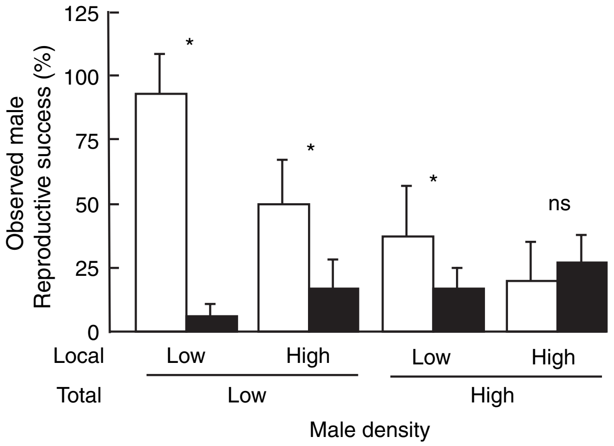

Fig. 4. Mean observed relative reproductive success of territorial (white) and sneaker (black) males among four male density treatments in the pool experiment. Asterisk indicates statistical differences between alternative behaviours. Error bars are 1 SE.

In these two studies, male–male interference competition significantly reduced bitterling spawning rates, and this effect was detectable at the population level. However, it does not necessarily follow that this effect has the potential to alter recruitment patterns. The failure of female bitterling to spawn may have been temporary, and females with eggs in their ovaries might have been able to spawn eventually, though with the result that the spawning season was more protracted. However, female fish that fail to spawn tend to reabsorb their eggs through the process of ovarian atresia (Tyler & Sumpter 1996; Wootton 1998). For example, female seabream (*Sparus aurata*) showed high levels of atresia within 1 week of isolation from males (Meiri et al. 2002), and in rainbow trout (*Oncorhynchus mykiss*) up to 50% of the eggs in the ovaries of some females may undergo atresia (Tyler et al. 1990). Thus, the repeated failure to spawn as a result of male–male competition could reduce total population egg production for a spawning season. Because bitterling embryo mortality inside mussels is density dependent (Smith et al. 2000a), a decrease in spawning rate may result in an improved survival of spawned eggs in mussels, with a positive effect on population size. Consequently, although male competition over spawnings was shown to significantly reduce spawning rates, the long-term effect on population size is ambiguous and warrants further investigation.

Competition among juveniles

Douglas (2003) conducted field surveys, field experiments and field-based behavioural observations to identify density-dependent interactions among juvenile bitterling that might have an impact at the population level. Smith et al. (2000a) demonstrated that during their first summer the availability of shallow vegetated habitat, interacting with predatory perch abundance, was significantly related to juvenile bitterling abundance, raising the prospect that juvenile bitterling use these areas as refuges from predators. Smith et al. (2000a) also illustrated that both mortality and growth of juvenile bitterling were strongly density dependent during their first summer and winter. Further, both density-dependent growth and overwinter mortality had direct consequences for bitterling population size. Douglas (2003) showed that juvenile bitterling used vegetated habitat in preference to unvegetated habitat [for details of materials and methods, see Douglas (2003)]. As bitterling density increased, unvegetated habitat was used more frequently. Juvenile bitterling inhabiting the vegetated margins of lakes were larger than juveniles in the unvegetated margins suggesting competitive exclusion of small juveniles from preferred habitat. Examination of daily growth increments in the otoliths of juvenile bitterling revealed that this difference in size was not the result of differences in growth rate or size-dependent mortality associated with each habitat. Rather, a difference in the age structure of juvenile bitterling in each habitat offered the most likely explanation, with a higher proportion of older juveniles in the vegetated habitat (Douglas 2003).

In a field experiment, juvenile bitterling were shown to display clear differences in individual feeding and agonistic behaviour that were habitat-, size- and density dependent. Strong interference competition was observed between juvenile bitterling, with smaller juveniles suffering the highest rate of interference in vegetated habitat. Smaller juveniles also suffered higher rates of aggression directed towards them by larger individuals, which was believed to reduce their feeding rate. Interference competition in vegetated margins appeared to result in smaller juvenile bitterling being forced to forage in unvegetated areas, where the intensity of intraspecific competition was lower, but the risk of predation higher.

In a second field experiment, juvenile bitterling that were prone to both exploitative and interference competition were shown to suffer density-dependent growth and mortality as zooplanktons became depleted in experimental enclosures. Mortalities recorded in the study were probably caused by starvation, and were found to be density dependent over the duration of the experiment. Bitterling subjected only to interference competition also exhibited density-dependent growth, but at a reduced level.

The results of this study indicate that recruitment in bitterling is determined between larval emergence from their mussel host and autumn. Mortality at this stage was strongly density dependent, and arose either through starvation or predation, which were directly related to intraspecific competition among juveniles. The strength of density dependence was mediated by the availability of vegetated nursery areas. Because events in early life history appear to be most important in determining recruitment success, its behavioural interactions at this stage appear to be of most significance for bitterling demography. Behaviours we have identified that may play a role in the population dynamics of bitterling are summarised in Fig. 5.

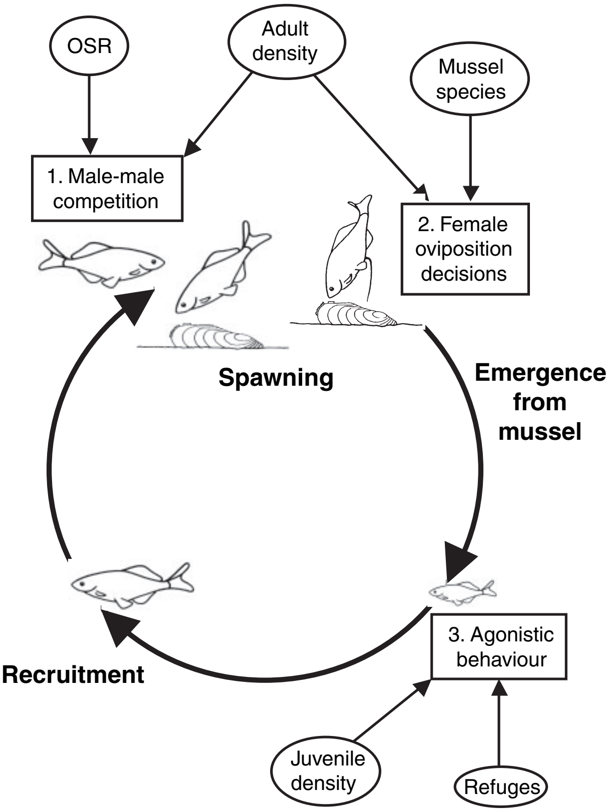

Fig. 5. This figure summarises the three stages during which behaviour has been identified as playing a role in the population dynamics of bitterling.

Conclusions

The European bitterling is a freshwater fish that lays its eggs in the gill chamber of freshwater mussels. This review identifies the possible role of behaviour in population dynamics of this species. The identification of population consequences of behaviour is an important goal in attempts to unify ecology with behaviour (Hassell & May 1985; Parker 1985; Sutherland 1996).

Although bitterling have an unusual reproductive ecology, which makes them amenable to studies aimed at understanding links between spawning decisions and population dynamics, they are not unique in this respect. For example, many fishes use discrete sites for spawning, and many are choosy with respect to oviposition decisions. European perch select substrates on which to deposit their eggs (Gillet & Dubois 1995), which may have consequences for embryo survival (Smith et al. 2001b). Alternative male mating tactics are diverse in fishes (Taborsky 1994), and may have implications for population-level processes in a range of fish species (Avise et al. 2002). Early life stages are probably crucial in determining year class strength in many fish species (Wootton 1998), and behavioural interactions that underpin recruitment success are likely to have significant population consequences. Consequently, although bitterling have served as a model to understand how individual behaviours are the mechanisms that may ultimately shape population parameters, these are not the only species with which the links between behaviour and population dynamics can be investigated.

Another species that may represent a valuable model for investigating population consequences of behaviour is the threespine stickleback (*Gasterosteus aculeatus*). Sticklebacks are small fishes that live in streams, ponds, lakes and coastal waters in the northern temperate zone. For more than 50 years, the threespine stickleback has been at the forefront of research in several areas of biology, most particularly as a model organism in ethology, behavioural ecology and evolutionary biology. The great value of the threespine stickleback lies in its distinctive and well-described behavioural repertoire (Wootton 1976). Sticklebacks are amenable to field (Le Comber et al. 2003), population (Wootton & Smith 2000) and genetic (Largiadèr et al. 2001) studies. Another distinctive feature of this species is the rapid adaptive radiation among populations; it is a species complex of striking phenotypic diversity. Researchers may be able to exploit population differences in behaviour to investigate the consequences of behaviour at the population level.

An extension of the concept of linking behaviour to populations is to develop an understanding of connections among all levels of biological organisation, linking molecular and developmental processes with an organism's physiology, behaviour, ecology and evolution. This more ambitious goal requires a model organism for which there is not only an understanding of the population consequences of behavioural decisions, but also of the links between genetic variation, gene expression, physiology and adaptive behaviour. Few of the model organisms currently used in biology offer the opportunity to undertake such studies, though two fishes, the zebrafish (*Danio rerio*) and the threespine stickleback (*G. aculeatus*), may prove worthy candidates.

Further fruitful areas of research on European bitterling aimed at linking behaviour with population dynamics might address behavioural responses to the temporal and spatial distribution of receptive females in response to the availability of spawning sites. Interspecific comparisons among the 40 or so bitterling species, predominantly found in East Asia, could also prove illuminating (Smith et al. 2004).

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