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Mussel ventilation rates as a proximate cue for host selection by bitterling, *Rhodeus sericeus*

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Abstract A range of cues may be used by parasites in selecting hosts, yet few studies have examined multiple cues simultaneously. We investigated the proximate cues involved in spawning decisions of the European bitterling, *Rhodeus sericeus*, a species of fish which lays its eggs in four species of freshwater mussel. When offered a choice of both live and artificial mussels within a single species, females preferred mussels that have high flow speeds and that pump a large volume of water per unit time. Furthermore, the time taken to spawn for a second time in a mussel was accurately predicted from a mussel's ventilation rate. These bitterling preferences based on mussel ventilation rates may benefit the embryos through enhanced oxygenation. We found no preferences for mussel species based on visual or olfactory cues, though the latter cannot be ruled out entirely. Ventilation rates should indicate the quality of host species for offspring survival.

Keywords *Anodonta* · Coevolution · Host–parasite interaction · *Unio* · Unionidae

Introduction

Host selection by parasites may be approached from either an evolutionary or a mechanistic perspective (Godfray 1994). The first approach examines oviposition behaviour in terms of relative fitness returns to the female, whereas the second examines the proximate causes involved in the location and acceptance of a host. Natural

selection should favour the use of proximate cues that allow parasites to recognise the most suitable hosts (reviewed in Majerus et al. 2000). Cues may be based on host criteria such as the quality of sites for offspring development and growth, for adult feeding sites, or for the rate at which oviposition may be achieved (Mayhew 1997; Sadeghi and Gilbert 1999; Scheirs et al. 2000; Mayhew 2001). Olfactory, visual, sensory and acoustic cues are widely used by parasites to select among potential hosts, yet few studies have examined several potential host properties simultaneously (Dorn et al. 2001).

A species where host selection is critical for offspring survival is a freshwater fish, the European bitterling, *Rhodeus sericeus* (Cyprinidae). Male bitterling court females and lead them towards mussels in their territory. Over much of their range, the mussel species available are *Unio pictorum*, *U. tumidus*, *Anodonta anatina*, and *A. cygnea* (Reynolds et al. 1997; Smith et al. 2000). A female bitterling in reproductive condition with a long ovipositor inspects mussels by facing downwards over the top of the mussel with her mouth just above the exhalant siphon. If she accepts a host she inserts her ovipositor into the gills of the mussel and lays between 2 and 4 eggs. Males release sperm over the inhalant siphon which is drawn into the mussel with the respiratory current and fertilises the eggs. The eggs are then incubated within the gills for 3–6 weeks (Reynolds et al. 1997). Offspring survival depends on the species of mussel selected, as mussels are able to eject eggs prematurely (Mills and Reynolds 2002). There are also varying rates of density dependent mortality of embryos in the different mussel species (Smith et al. 2000).

Females have been shown to exhibit adaptive host preference, choosing host species that show the lowest rate of egg ejection (Mills and Reynolds 2002), and they avoid ovipositing into mussels that already contain bitterling embryos (Smith et al. 2000; Candolin and Reynolds 2001). Therefore, females are somehow able to evaluate the quality of the mussel as a suitable host from cues picked up during host inspection. The European bitterling has been shown to respond to mussel smell and ex-

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halant water velocity from dummy mussels (Heschl 1989). Smith et al. (2001) provided circumstantial evidence that the oxygen content of water emerging from a mussel may be a cue for oviposition site choice.

This paper uses host experiments covering a range of potential host properties, including species smell, species shell type and ventilation rate, to determine which host traits govern a female's spawning decision. We compare the proximate cues determined here with host preference and performance results from previous studies under different environmental conditions, to establish the host traits that are important for offspring performance.

Materials and methods

In March and April 2000 we collected adult bitterling and individuals of the four mussel species: *U. pictorum*, *U. tumidus*, *A. anatina* and *A. cygnea* from Reach Lode, a tributary of the River Cam, Cambridgeshire, at the point of confluence with Wicken Lode, 52°18'N, 00°15'E, (NGR: TL545696). The mussels were collected by hand and the fish were caught using high frequency (600 Hz) pulsed DC Electracatch WFC 12 electrofishing equipment. The mussels were maintained in outdoor pools and were fed daily with a live algal suspension derived from an outdoor pool that had been seeded with *Chlorella vulgaris*. The bitterling were maintained in stock aquaria aerated continuously and illuminated by a fluorescent aquarium lamp on a 16L:8D photoperiod. The fish were fed a mixed diet of live *Daphnia pulex*, *Chaoborus* pupae, *Culex* and *Chironomid* larvae, frozen *D. pulex*, *Tubifex* sp., *Artemia salina*, dried protein mix and trout pellets.

Water velocity and ventilation rate

The velocity (flow speed; cm s⁻¹) of water in the exhalant streams of mussels was determined by a small thermistor probe that we built according to the principle described by La Barbara and Vogel (1976) and Vogel (1981) and following the methods described by Meyhofer (1985) and Tankersley and Dimock (1993a). The thermistor probe is heated electrically and cools at a rate proportional to the speed of the mussel's exhalant water flow. The temperature change is recorded as a voltage. Each trial consisted of placing an individual mussel in a sand-filled glass jar (10×6 cm high) within a 300 l aquarium and allowing it to adjust to the experimental conditions for 30 min. Flow speeds were measured by placing the tip of the thermistor probe (3 mm diameter) in front of the exhalant siphon of the mussel using a micro-manipulator. While the mussel was ventilating (i.e. valves open and siphons extended), 10 measurements of voltage output were taken manually from the voltmeter over 10 min and averaged for each mussel. Mean rates at which mussels process the ambient water (ventilation rate; l h⁻¹) were calculated from flow speeds by simultaneously determining the cross sectional area of the exhalant siphon from a grid (0.5×0.5 mm) held next to the mussel's siphon. The flow probe was calibrated by inserting it into the middle of tubing of varying cross sectional areas (0.710, 0.126, 0.283, 0.385, 0.503 cm²) and measuring the voltage output over a range of known flow speeds and temperatures (16–22°C).

Experiment 1: choice of artificial mussels

Artificial mussels were made using the shells of *U. pictorum* and *A. cygnea*. A hole was drilled through one of the valves near to the edge into which we glued a 40 cm length of rubber tubing (0.196 cm² cross-sectional area). This tubing acted as the inhalant siphon for water flowing from a water pump and was not visible when the mussels were buried at their natural depth, approximate-

ly 3 cm into the sediment. Another piece of tubing 2 cm long (0.196 cm² cross-sectional area) was glued between the two valves in the natural position of the exhalant siphon and the two valves were glued together over their entire length to make a water-tight seal. Two artificial mussels were used in each trial, connected to two water pumps with variable flow speeds. The two flow speeds produced a mean high ventilation rate of 1.04±0.13 l h⁻¹, and a mean low ventilation rate of 0.37±0.17 l h⁻¹. These rates are representative of ventilation rates measured from mussels in their natural habitat (see Results). The water that pumped through each mussel came from header tanks containing 3 l of water and live mussels (*U. pictorum* or *A. cygnea*) that had been actively filtering water for at least 3 h.

Two artificial mussels were placed 20 cm apart in the centre of a 300 l experimental aquarium. We varied the flow speed and volume of water pumped per hour (sensory cue), the species of mussel shell used for the artificial shell (visual cue) and the species of mussel filtering water in the header tank (olfactory cue). Only one parameter was varied in each trial. Each trial consisted of adding a fish of each sex in reproductive condition to the aquarium and recording the following behaviours for 10 min: male and female mussel inspection (bitterling approach and face the top of a mussel), sperm release (a white sperm cloud is visible), failed spawning attempt (female misses the mussel siphon with ovipositor), and successful spawning (ovipositor momentarily rigid inside exhalant siphon). The trial was repeated with the parameter under investigation switched between mussel positions. Each of the three parameters was measured using the same fish pair. We performed 11 replicates of this experiment using new fish each time.

Differences in preference between the artificial mussels were tested using the chi-square distribution with a theoretical distribution based on random preference. The data were pooled together and a chi-square analysis was carried out on the pooled data and the Yates correction for continuity was applied (Zar 1984).

Experiment 2: intra-species choice with *Anodonta anatina*

Four *A. anatina* mussels were placed in sand-filled glass containers (10×6 cm high) and arranged in a square formation 20 cm apart within a 300 l aquarium. When the flow speeds and volume of water pumped per hour of all four mussels had been measured a bitterling of each sex in reproductive condition was added to the aquarium. The bitterling were observed until they had spawned twice in each mussel. We performed 18 replicates of this experiment using new fish and mussels each time, however, in one replicate we were only able to obtain spawnings in two of the four mussels. Mussel preference was recorded as the order in which females spawned into the four mussels. Fish pair was used in the analysis as a covariate.

Experiment 3: intra-species choice in *A. anatina* and *U. pictorum*

The volume of water pumped per hour by 40 *U. pictorum* and 30 *A. anatina* was measured and the mussels were then allocated to one of two groups: high ventilation rate (*U. pictorum* >0.3 l h⁻¹; *A. anatina* >0.4 l h⁻¹) and low ventilation rate (*U. pictorum* <0.2 l h⁻¹; *A. anatina* <0.3 l h⁻¹). In each trial two sand-filled glass containers (10×6 cm high) were arranged within a 300 l aquarium. Two mussels of the same species (one from each ventilation rate group) were placed in each of the glass containers. A bitterling of each sex in reproductive condition was added to the aquarium and the fish were observed until a female was about to spawn in one of the mussels. This was easy to determine because the fish adopt a characteristic posture above and in front of a mussel just prior to inserting their ovipositor into the exhalant siphon. We interrupted the spawning and recorded a preference for this mussel. Either the preferred or non-preferred mussel was then covered with a perforated plastic bottle to prevent spawning. We varied which mussel was covered between replicates. The behaviour of the fish was observed until two spawnings occurred in each mussel. The time tak-

Table 1 Repeatability of ventilation rate in four species of freshwater mussel. Repeatability was calculated according to Lessells and Boag (1987). $P < 0.001$ for all species

| | <i>F</i> ratio (<i>df</i>) | Repeatability |
|-------------------------|------------------------------|---------------|
| <i>Unio pictorum</i> | 103.8 (22,23) | 0.98 |
| <i>U. tumidus</i> | 10.7 (45,46) | 0.83 |
| <i>Anodonta anatina</i> | 31.3 (78,79) | 0.94 |
| <i>A. cygnea</i> | 9.4 (19,20) | 0.81 |

en until a spawning occurred was calculated as the period of time from either the start of the experiment or from the last spawning until a successful spawning. The trial was repeated using the same fish pair but with two mussels of the other species. We performed 12 replicates of this experiment using new fish and mussels each time. Differences in preference between the two mussels for each species were tested using paired *t*-tests.

Experiment 4: ventilation rates of the four species of mussel

Mussels of all four species were taken from the study site and flow speeds and volume of water pumped per hour were measured on the following day. The relationship between mussel shell length (mm) and ventilation rate in terms of $l\ h^{-1}$ was calculated. Differences in the ventilation rates among mussel species were tested using an analysis of covariance with ventilation rate as the dependent variable, mussel species as the factor and mussel length as the covariate. We did not log-transform the original morphological data as they were normally distributed within and among species.

A repeatability analysis was carried out on ventilation rates of mussels measured one hour apart. The ventilation rates of mussels measured one hour apart were highly repeatable (Table 1).

The results are presented by a mean \pm SE throughout the paper.

Results

Experiment 1: choice of artificial mussels

Bitterling preferred to spawn in artificial mussels that had high ventilation rates: 10 fish pairs preferred high versus low ventilation rates in both trials and 1 fish pair preferred a high ventilation rate in one trial and a low ventilation rate in the other (heterogeneity chi-square analysis: $\chi^2_{1,10} = 9.18$, $P = 0.002$). However, we found no difference in preference for artificial mussels that differed in the species of mussel that was in the header tank (olfactory cue) nor for mussels differing in the species used for the mussel shell (visual cue) (olfaction: $\chi^2_{1,10} = 0.91$, $P = 0.34$; visual: $\chi^2_{1,3} = 0.94$, $P = 0.33$).

Experiment 2: intra-species choice with *Anodonta anatina*

Choice tests with four live mussels provided further confirmation that female bitterling prefer mussels with high ventilation rates (Fig. 1; General Linear Model using fish pair as a covariate, $F_{3,67} = 6.06$, $P = 0.001$). In pairwise comparisons, significant differences were found between the ventilation rates of 1st and 3rd choice mussels, 1st and 4th choice mussels, and 2nd and 4th choice mussels (Tukey HSD, all $P < 0.01$).

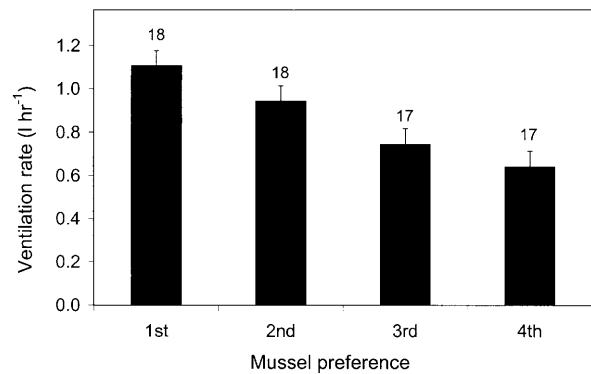


Fig. 1 Ventilation rate ($\bar{x} \pm 1\ SE$) of *Anodonta anatina* mussels in order of spawning preference by bitterling when four mussels were presented simultaneously. Numbers above bars refer to sample size

Experiment 3: intra-species choice in *A. anatina* and *U. pictorum*

The ventilation rates ($l\ h^{-1}$) by mussels that we allocated to the high ventilation rate treatment were about 3.5 times higher than in the low ventilation rate treatment for both species of mussel (*U. pictorum*: low= 0.15 ± 0.02 SE, high= 0.54 ± 0.05 $l\ h^{-1}$; *A. anatina*: low= 0.20 ± 0.04 , high= 0.73 ± 0.10 $l\ h^{-1}$; paired *t*-test on mean ventilation rates, *U. pictorum*: $t_{12} = 8.6$, $P < 0.001$; *A. anatina*: $t_9 = 5.8$, $P < 0.001$).

Female bitterling took longer to spawn in mussels from the treatment with low ventilation rates ($l\ h^{-1}$) than in mussels from the high ventilation rate treatment (paired *t*-test on the mean time taken until a spawning event, *U. pictorum*: $t_{12} = 9.5$, $P < 0.001$; *A. anatina*: $t_9 = 5.1$, $P = 0.001$; Fig. 2). Low flow speeds ($cm\ s^{-1}$) were also associated with longer times until spawning (paired *t*-test on the mean time taken until a spawning event, *U. pictorum*: $t_{12} = 7.6$, $P < 0.001$; *A. anatina*: $t_9 = 5.3$, $P = 0.001$).

Analyses of individual mussels that were the first mussels of each species presented to each fish pair also confirmed that female bitterling spawned more quickly in mussels with high ventilation rates ($l\ h^{-1}$) (Fig. 3A). This was true for both mussel species (generalised linear model with a log-link function of ventilation rate on time until a spawning event, *U. pictorum*: $\chi^2 = 30.2$, $P < 0.0001$; *A. anatina*: $\chi^2 = 23.7$, $P < 0.0001$). Time until spawning was also negatively related to flow speeds ($cm\ s^{-1}$) for both mussel species (*U. pictorum*: $\chi^2 = 12.9$, $P < 0.001$; linear regression, *A. anatina*: $\chi^2 = 21.0$, $P < 0.0001$).

To test our results we used the relationship in Fig. 3A to predict how long bitterling should take to spawn into the same mussel after the 1st spawning. To account for the reduction in ventilation rate due to the presence of 3.2 embryos deposited during the 1st spawning (average number of embryos per spawning, Mills and Reynolds 2002), we used the linear regression $Y = 0.016X + 0.184$, where Y = reduction in ventilation rate and X = number of embryos (Mills and Reynolds, unpublished data). This yielded a significant positive relationship between the

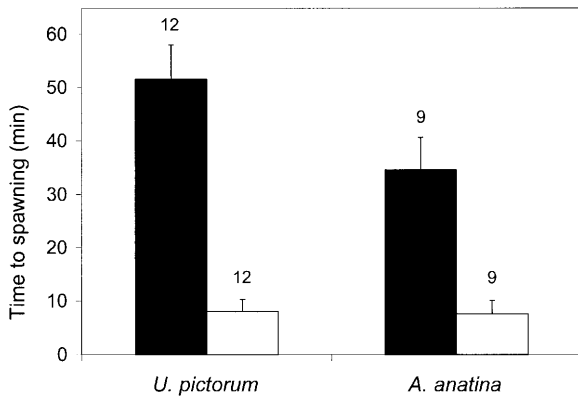


Fig. 2 Time taken (\bar{x} min+1 SE) until a spawning event by bitterling offered live *Unio pictorum* and *A. anatina*. Numbers above bars refer to sample size. *Black bars* low ventilation rate treatment, *white bars* high ventilation rate treatment

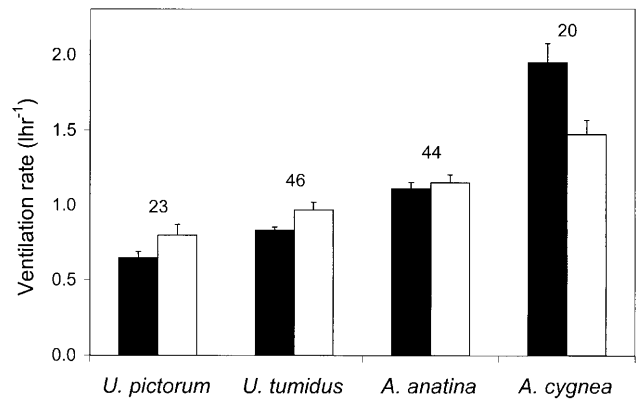


Fig. 4 Ventilation rate (\bar{x} l h⁻¹+1 SE) of the four mussel species. *Black bars* original data, *white bars* data corrected for size. Numbers above bars refer to sample size

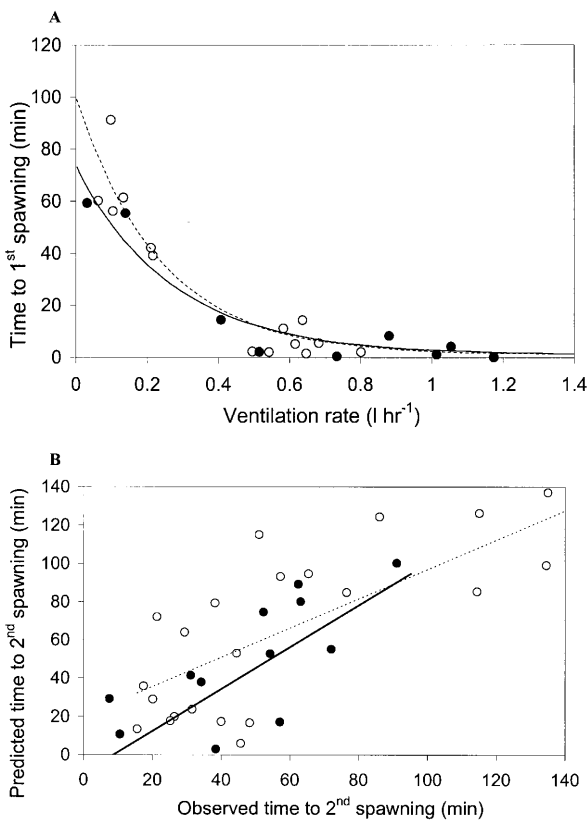


Fig. 3 Relationship between the ventilation rate of mussels and the time taken until the 1st spawning event (**A**) and relationship between the predicted time to second spawning and the observed time to second spawning (**B**). *Open circles* *U. pictorum* (*dotted regression line*), *closed circles* *A. anatina* (*solid regression line*)

Table 2 Ventilation rates (V , l h⁻¹) in mussels as a function of size (L , mm shell length). Linear equation: $V=aL+b$, n =sample size, R^2 =coefficient of determination, P =probability

| Species | n | L (mm) | Slope, $a \pm SE$ (l h ⁻¹ mm ⁻¹) | Intercept, $b \pm SE$ (l h ⁻¹) | R^2 | P |
|--------------------|-----|----------|--|---|-------|--------|
| <i>U. pictorum</i> | 23 | 60–93 | 0.0169±0.004 | -0.684±0.31 | 0.48 | <0.001 |
| <i>U. tumidus</i> | 46 | 58–92 | 0.0159±0.003 | -0.416±0.24 | 0.40 | <0.001 |
| <i>A. anatina</i> | 44 | 64–104 | 0.0278±0.005 | -1.262±0.44 | 0.41 | <0.001 |
| <i>A. cygnea</i> | 20 | 73–146 | 0.0276±0.007 | -0.954±0.79 | 0.43 | 0.002 |

predicted and observed time until the second spawning (Fig. 3B). The intercepts do not differ significantly from zero, but the slopes are significantly greater than zero for *U. pictorum* and *A. anatina* (*U. pictorum*: linear regression of observed time until a second spawning event: $Y=0.77X+20.2$, $R^2=0.60$, $F=31.17$, $P<0.001$, 95% CI slope=0.5–1.1, 95% CI intercept=-1.4–41.7; *A. anatina*: $Y=1.11X-7.35$, $R^2=0.63$, $F=21.9$, $P<0.001$, 95% CI slope=0.6–1.6, 95% CI intercept=-32.2–17.5). Thus, ventilation rates predict time to a second spawning accurately in both *U. pictorum* than *A. anatina*.

Experiment 4: ventilation rates of the four species of mussel

The ventilation rates of all four species of mussel increased with increasing shell length according to the equations shown in Table 2. There is considerable variation among species in ventilation rate (Fig. 4). Differences among species remained significant when controlling for differences in mussel shell length (ANCOVA: $F_{3,130}=10.94$, $P<0.001$). With shell length controlled, all mussel species were significantly different from each other (post hoc tests: $P<0.002$) except for *A. anatina* and *A. cygnea* (post hoc tests: $P=0.125$).

Discussion

Female bitterling preferred to spawn in artificial mussels that pumped a greater volume of water per hour and had

higher flow speeds. They still preferred to spawn in live mussels according to their ventilation rates and flow speeds when other mussel differences were present (Figs. 1, 2, 3A). The time taken by bitterling to spawn a second time in *U. pictorum* and *A. anatina* was accurately predicted from mussel ventilation rates (Fig. 3B). We did not detect preferences for mussel species based on visual or olfactory cues, though these cannot be ruled out. We also cannot rule out a role for oxygen concentration as a cue, except in the test with artificial mussels, in which oxygen concentration should have been the same in high and low ventilating mussels. Smith et al. (2001) suggested that a drop in oxygen concentration between the inhalant and exhalant siphon may be important in the discrimination of bitterling against the least preferred mussel species, *A. cygnea*.

We suggest that mussel ventilation rates and flow speeds are used by female bitterling as important proximate cues in host selection. Increases in ventilation rates have been associated with increases in mantle cavity oxygen tensions in the marine mussel, *Mytilus edulis* (Davenport and Woolmington 1982). Ventilation rates may therefore provide a reliable indication to adult bitterling of the oxygen available in a mussel for uptake by their offspring. The flow speeds of freshwater mussels used in this study ranged from 1 to 4 cm s⁻¹. These speeds are well within the range detected by other fish species for migration, feeding, microhabitat preferences and escape responses, using the inner ear, vision, tactile sense and mechanosensory systems (Montgomery et al. 2000). Montgomery et al. (1997) have shown that the velocity of water movements over the skin of fish are detected by superficial neuromasts of the lateral-line system. Blind cave-fish, *Astyanax fasciatus*, detect flow speeds of 2–3 cm s⁻¹ and even as low as 0.4 cm s⁻¹ and the New Zealand long-fin eel, *Anguilla dieffenbachii*, detects flow speeds ranging from <0.5 to 4 cm s⁻¹ (Montgomery et al. 1997, 2000).

Are these spawning decisions adaptive to female bitterling in terms of offspring survival? High ventilation rates may be associated with a lack of super-parasitism, as bitterling embryos reduce mussel ventilation rates (Mills and Reynolds, unpublished data). Thus, bitterling may be able to avoid the negative effects of high numbers of eggs on offspring survival (Smith et al. 2000) by using ventilation rate as a proximate cue for host choice. Furthermore, if super-parasitism did occur, high ventilation rates would increase the amount of oxygen available to competing embryos. High ventilation rates also indicate that mussel gills are not brooding glochidia (Tankersley and Dimock 1993b). Bitterling preferring non-brooding individuals and non-marsupial gills have higher numbers of offspring (Mills and Reynolds, unpublished data). Finally, preference for high ventilation rates could be advantageous in adverse environmental conditions. For example, at high concentrations of phosphate, mussels reduce their ventilation frequency and increase the rate of premature bitterling ejection (Reynolds and Guillaume 1998). Therefore, there are several reasons why spawning decisions based on ventilation rates should be adaptive for offspring survival.

Although female bitterling prefer high ventilation rates *within* species (e.g. Fig. 1), the rank order of ventilation rates *among* species (Fig. 4) is the opposite of the fish's among-species preferences, which we have shown to be adaptive in terms of avoidance of egg ejections (Mills and Reynolds 2002). These preferences are not confounded by mussel shell length, as the rank order of host preferences among mussel species reported in Mills and Reynolds (2002) is upheld when mussel length is included as a covariate (ANCOVA: $F_{3,97}=11.48$, $P<0.001$). However, the ventilation rate of the least preferred species *A. cygnea* is about twice as high as the ventilation rates of the artificial mussels as well as the live *U. pictorum* and *A. anatina* that were used in these choice experiments. Thus, there may be a maximum ventilation rate that bitterling prefer, and *A. cygnea* may exceed this maximum. This does not explain the fact that among-species preference for *U. pictorum* over *A. anatina* is opposite to the rank order of ventilation rates of these species. Bitterling may therefore use a second cue to select among species whose ventilation rates overlap.

Our results suggest that ventilation rate is an important factor determining oviposition preference. We found no support for any visual or olfactory cues but they cannot be ruled out as secondary cues. This study also highlights how the use of one proximate cue may be adaptive for offspring survival across host species and may explain the flexible host preferences exhibited by bitterling between mussel genera (Mills and Reynolds 2002). These results may be used to determine offspring survival among host species in different environmental conditions. Thus the effects of the environment on host cues, such as reduced ventilation rates (Reynolds and Guillaume 1998), can be translated through knowledge of host selection into changes in bitterling offspring survival. This is especially important for species such as the European bitterling, which are endangered across much of their range.

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References

- Candolin U, Reynolds JD (2001) Sexual signaling in the European bitterling: females learn the truth by direct inspection of the resource. *Behav Ecol* 12:407–411
- Davenport J, Woolmington AD (1982) A new method of monitoring ventilatory activity in mussels and its use in a study of the ventilatory patterns of *Mytilus edulis*. *J Exp Mar Biol Ecol* 62:55–67
- Dorn NJ, Cronin G, Lodge DM (2001) Feeding preferences and performance of an aquatic lepidopteran on macrophytes: plant hosts as food and habitat. *Oecologia* 128:406–415
- Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, N.J.

- Heschl A (1989) Integration of “innate” and “learned” components within the IRME for mussel recognition in the European bitterling *Rhodeus amarus* (Bloch). *Ethology* 81:193–208
- La Barbara M, Vogel S (1976) An inexpensive thermistor flowmeter for aquatic biology. *Limnol Oceanogr* 21:750–756
- Lessells CM, Boag PT (1987) Unrepeatable repeatabilities: a common mistake. *Auk* 104:116–121
- Majerus MEN, Geoghegan IE, Majerus TMO (2000) Adaptive preferential selection of young coccinellid hosts by the parasitoid wasp *Dinocampus coccinellae* (Hymenoptera: Braconidae). *Eur J Entomol* 97:161–164
- Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos* 79:417–428
- Mayhew PJ (2001) Herbivore host choice and optimal bad motherhood. *Trends Ecol Evol* 16:165–167
- Meyhofer E (1985) Comparative pumping rates in suspension-feeding bivalves. *Mar Biol* 85:137–142
- Mills SC, Reynolds JD (2002) Host species preferences by bitterling (*Rhodeus sericeus*) spawning in freshwater mussels and consequences for offspring survival. *Anim Behav* (in press)
- Montgomery JC, Baker CF, Carton AG (1997) The lateral line can mediate rheotaxis in fish. *Nature* 389:960–963
- Montgomery J, Carton G, Voigt R, Baker C, Diebel C (2000) Sensory processing of water currents by fishes. *Philos Trans R Soc Lond Ser B* 355:1325–1327
- Reynolds JD, Guillaume HP (1998) Effects of phosphate on the reproductive symbiosis between bitterling and freshwater mussels: implications for conservation. *J Appl Ecol* 35:575–581
- Reynolds JD, Debusse VJ, Aldridge DC (1997) Host specialisation in an unusual symbiosis: European bitterlings spawning in freshwater mussels. *Oikos* 78:539–545
- Sadeghi H, Gilbert F (1999) Individual variation in oviposition preference, and its interaction with larval performance in an insect predator. *Oecologia* 118:405–411
- Scheirs J, De Bruyn L, Verhagen R (2000) Optimization of adult performance determines host choice in a grass miner. *Proc R Soc Lond Ser B* 267:2065–2069
- Smith C, Reynolds JD, Sutherland WJ, Jurajda P (2000) Adaptive host choice and avoidance of superparasitism in the spawning decisions of bitterling (*Rhodeus sericeus*). *Behav Ecol Sociobiol* 48:29–35
- Smith C, Rippon K, Douglas A, Jurajda P (2001) A proximate cue for oviposition site choice in the bitterling (*Rhodeus sericeus*). *Freshw Biol* 46:903–911
- Tankersley RA, Dimock RV (1993a) The effect of larval brooding on the respiratory physiology of the freshwater Unionid mussel *Pyganodon cataracta*. *Am Midl Nat* 130:146–163
- Tankersley RA, Dimock RV (1993b) Endoscopic visualization of the functional morphology of the ctenidia of the Unionid mussel *Pyganodon cataracta*. *Can J Zool* 71:811–819
- Vogel S (1981) *Life in moving fluids. The physical biology of flow*, 1st edn. Willard Grant, Boston
- Zar JH (1984) *Biostatistical analysis*, 2nd edn. Prentice-Hall, Englewood Cliffs