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SHORT COMMUNICATION

Mating patterns of first-generation hybrids of the roach, *Rutilus rutilus* (L.), and the silver bream, *Blicca bjoerkna* (L.)

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Abstract Mating patterns among first-generation hybrids of the roach, *Rutilus rutilus*, and the silver bream, *Blicca bjoerkna*, between hybrids or with parent-species males, have been investigated under experimental reproduction conditions. The results reveal that the level of sexual activity of these hybrids is high. Hybrid females mated simultaneously and successively with all types of male, resulting in fertilised eggs. Individual participation of roach males in mating was never observed, however.

Keywords Mating · Hybrid reproduction · Mixed reproduction · Hybrids · Cyprinids

Introduction

Roach, *Rutilus rutilus* (L.), and silver bream, *Blicca bjoerkna* (L.), are two cyprinid fish species of phytophilous breeders (Diamond 1985; Fahy 1988; Mills 1991; Juradjda et al. 2004). In Europe, these species usually live in sympatry in the same type of river (Huet 1949; Philippart 1989). Natural hybrids of these two species have been observed in European waters by several authors (Wheeler 1969; Penczak 1978; Swinney and Coles 1982), but they are not frequent. In natural environments, hybridisation and introgression in freshwater fishes are probably facilitated by temporal overlap of spawning activity (considering that males can be ready to release milt over several weeks), similar preferences for spawning grounds, for example aquatic vegetation, and competition for spawning habitats as a result of anthropomorphic activity, for example river modification and the introduction of exotic species. The presence of these hybrids is a valid reason to study all aspects of their biology.

As for more frequent hybrids in natural environments, the reproductive behaviour of rare hybrids, for example roach and silver bream hybrids, is unknown. Investigating the reproductive behaviour and potential sexual partners of the hybrids would increase knowledge about these poorly studied individuals and about their potential ecological impact. The spawning behaviour of the parent species has already been studied and described as polyandrous in both roach (Diamond 1985; Fahy 1988; Kozlouskiz 1991; Wedekind 1996) and silver bream (Poncin et al. 2004).

This paper is the first to report the sexual activity of the first-generation hybrids (F1) resulting from reciprocal crossbreeding of the roach and silver bream. The objective of the study was to increase understanding of the mating patterns of these hybrids in a controlled environment and to evaluate individual participation of hybrid males and parent species males in matings with hybrid females.

Materials and methods

Production of the spawners

Roach and silver bream specimens were captured in fish ladders at the Lixhe dam (Meuse Belgian River, 50°45′N; 5°40′E) during the reproductive migration in spring 2003. They were morphologically identified on the basis of descriptions by Regan (1911), Spillman (1961), Wheeler

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Table 1 Crossbreeding and characteristics of F0 spawners used to obtain the F1 generation (fork length, weight, age and soft rays of the anal fin)

F1 crossbreedings	Characteristics of F0 spawners				
Male × female	Fish	Fork length (mm)	Weight (g)	Age (years)	Soft rays of anal fin (number)
$R_m \times R_f$	R_f	196	115	5	11
$B_m \times R_f$	B_m	230	228	5	20
$R_m \times B_f$	R_m	250	251	5	11
$B_m \times B_f$	B_f	216	226	5	20

R, *Rutilus rutilus*; B, *Blicca bjoerkna*; f, female; m, male

(1969), and Maitland (1972). Eggs from the females of each fish species were divided into two groups, one of which was mixed with sperm from the male of the other species (first-generation hybrids) and the other with the sperm of the conspecific male (intraspecific crossbreeding). These crossbreedings, designed to obtain fish spawners, and the characteristics of the fish used are indicated in Table 1. By this method it was possible to obtain reciprocal crossbreeding hybrids such as silver bream male × roach female ($B_m \times R_f$ or BR) and roach male × silver bream female ($R_m \times B_f$ or RB). Parent fish species (roach and silver bream) were produced starting from intraspecific crossbreedings. The hybrid and parent species used were reared in captivity (at 20°C) at the Tihange aquaculture station in Belgium. At 24 months of age all individuals were sexually mature.

Experimental procedure

Selected females were gravid and males produced milt. The experimental procedure and the biological characteristics of the hybrids and parent species used in this study were divided into two sets of conditions for experiments conducted in duplicate (8 April and 14 April 2005 for the first and the second replicates, respectively), as presented in Table 2. Under the first conditions (hybrid reproduction) a female F1 hybrid was placed to reproduce with three corresponding hybrid males. Under the second conditions (mixed reproduction) a female hybrid was placed with a corresponding hybrid male, a parent species male roach, and a parent species male silver bream. By sue of these procedures participation of fish in mating was individually analysed. Mating was defined as sexual contact between fish of the opposite sex then expulsion of gametes. Two hybrid types were used in these experiments:

1. the F1 BR hybrids, and
2. the F1 RB hybrids.

Experiments were conducted in a 0.92 × 0.40 × 0.40-m experimental nylon basket installed in a 6.00 × 1.00 ×

Table 2 Experiments and biological characteristics of the hybrids and parent species used

Reproduction conditions		Experiments in duplicate (first–second replicates)					
		Sex	Fork length (mm)	Weight (g)	N°	Soft rays of anal fin (number)	Breeding tubercles
Hybrid reproduction							
1	3♂RB × 1♀RB	F	145–157	44–52		15–15	Absent
		M	145–140	40–37	D1	15–15	Absent
		M	130–155	25–53	D2	15–15	Absent
		M	120–157	21–45	D3	15–15	Absent
2	3♂BR × 1♀BR	F	155–152	60–55		15–15	Absent
		M	142–140	35–32	A1	15–15	Absent
		M	135–147	36–39	A2	15–15	Absent
		M	123–135	26–36	A3	15–15	Absent
Mixed reproduction							
3	1♂RB, 1♂R, 1♂B × 1♀RB						
	RB	F	135–154	37–53		15–15	Absent
	RB	M	130–140	25–38	D4	15–15	Absent
	R	M	145–162	46–52	C2	11–11	Present
	B	M	130–135	31–35	B2	20–20	Absent
4	1♂BR, 1♂R, 1♂B × 1♀BR						
	BR	F	135–150	37–55		15–15	Absent
	BR	M	120–143	26–40	A4	15–15	Absent
	R	M	150–152	48–49	C1	11–11	Present
	B	M	145–145	45–51	B1	20–20	Absent

RB, first-generation F1 hybrid, *R. rutilus* male × *B. bjoerkna* female; BR, F1 hybrid, *B. bjoerkna* male × R. rutilus female; R, *R. rutilus*; B, *B. bjoerkna,*; ♂, male (M); ♀, female (F); N°, classification of males (A, F1 BR hybrid male; B, male *B. bjoerkna*; C, male *R. rutilus*; D, male F1 RB hybrid, *Arabic numeral* number of males); range, values of the first and second replications

0.67-m tank (closed-loop). It was equipped with a bullor for oxygenation and a 0.16 × 0.16-m synthetic spawning substrate simulating vegetation. Fish were maintained at a temperature of 20 ± 0.1°C, 8.1 ± 0.6 mg L^{-1} dissolved oxygen, pH 7.9 ± 0.3, and the photoperiod was set at 16 h of light and 8 h of darkness. These correspond to the spawning conditions of these species in natural environments (Herzig and Winkler 1986; Spivak 1987; Tarkan 2006). Fish were placed in the experimental nylon basket the day before behaviour was recorded.

Behaviour was recorded with a video camera immersed from 8 to 18 h, corresponding to the beginning and end of spawning activity. Mating success, expressed as the percentage of ''eyed'' embryos 1 day after spawning, was evaluated from samples of 100 eggs (two replicates per experiment) under a microscope and was analysed by use of Fisher's exact probability *FEP*-test, with probability values of <0.05 regarded as significant.

Results

Mating pattern

Mating patterns of first-generation hybrids between roach and silver bream are summarised in Tables 3 and 4. Females of both hybrids were able to reproduce successfully with all hybrid and parent species males. Participation of all experimental males in mating occurred both simultaneously (three males at the same time) and successively (only one or two males involved).

For both types of female hybrid the number of matings per hour in the presence of all males (two parent species and their hybrid) was a factor of two lower for the female RB hybrid than for the female BR hybrid (mean frequencies 0.6 and 1.2 times per hour, respectively). Individual participation of roach males in mating was never observed, in contrast with silver bream males which were observed mating with the female RB hybrid. Under the mixed reproduction conditions BR male and RB male hybrids engaged in 0.7 and 1.2 matings per hour. These values were higher than those for the hybrid reproduction conditions (0.4 and 0.3 matings).

With regard to simultaneous involvement of two males in hybrid reproduction, the highest mean mating frequency was 0.4 and 0.3 times per hour for the male BR and RB hybrids, respectively. Under mixed reproduction conditions mean mating frequency was lowest for the female BR hybrid, a factor of 7.5 less than for the female RB hybrid (0.4 and 3.0 times per hour, respectively), and was exclusively with the male silver bream and the BR or RB hybrid male.

For both hybrid female species under hybrid reproduction conditions, the most frequently observed mating was by a female hybrid and the three corresponding male hybrids. Mean mating frequency with these males was five times greater for the female BR hybrid than for the female RB hybrid (22.5 and 4.5 times per hour, respectively). Under the mixed reproduction conditions, on the other hand, two major mating combinations were observed most frequently:

1. the female BR hybrid with its corresponding hybrid male associated with the silver bream and roach males (mean frequency 1.2 times per hour); and

Table 3 Mating participation by males (number per hour) with first-generation hybrid female, *B. bjoerkna* male × *R. rutilus* female (BR) in reproduction between hybrids and mixed reproduction from 8 to 18 h

Classification of males	Mating of F1 female BR hybrid (number per hour)					
	3♂BR × 1♀BR			1♂BR, 1♂R, 1♂B × 1♀BR		
	Replicates		Mean ± SD	Replicates		Mean ± SD
	First	Second		First	Second	
A1	0.1	0.5	0.3 ± 0.3	–	–	–
A2	0.2	0.3	0.3 ± 0.1	–	–	–
A3	0.6	0.2	0.4 ± 0.3	–	–	–
A4	–	–	–	0.9	0.5	0.7 ± 0.3
B1	–	–	–	0.0	0.0	0.0
C1	–	–	–	0.0	0.0	0.0
A1 + A2	0.6	0.2	0.4 ± 0.3	–	–	–
A1 + A3	0.4	0.0	0.2 ± 0.3	–	–	–
A2 + A3	0.2	0.3	0.3 ± 0.1	–	–	–
A4 + B1	–	–	–	0.2	0.5	0.4 ± 0.2
A1 + A2 + A3	29.9	15.1	22.5 ± 10.5	–	–	–
A4 + B1 + C1	–	–	–	0.7	1.7	1.2 ± 0.7

A, male F1 BR hybrid; B, male *B. bjoerkna*; C, male *R. rutilus*; Arabic numerals indicate umber of males participating in the matings; SD, standard deviation

Table 4 Mating participation of males (number per hour) with first-generation hybrid female, *R. rutilus* male × *B. bjoerkna* female (RB) in reproduction between hybrids and mixed reproduction from 8 to 18 h

Classification of males	Matings in F1 female RB hybrid (number per hour)					
	3♂RB × 1♀RB			1♂RB, 1♂R, 1♂B × 1♀RB		
	Replicates		Mean ± SD	Replicates		Mean ± SD
	First	Second		First	Second	
D1	0.2	0.4	0.3 ± 0.1	–	–	–
D2	0.1	0.0	0.05 ± 0.07	–	–	–
D3	0.1	0.0	0.05 ± 0.07	–	–	–
D4	–	–	–	1.5	0.8	1.2 ± 0.5
B2	–	–	–	0.5	0.2	0.4 ± 0.2
C2	–	–	–	0.0	0.0	0.0
D1 + D2	0.2	0.2	0.2 ± 0.0	–	–	–
D1 + D3	0.0	0.1	0.05 ± 0.07	–	–	–
D2 + D3	0.4	0.1	0.3 ± 0.2	–	–	–
D4 + C2	–	–	–	0.2	0.2	0.2 ± 0.0
D4 + B2	–	–	–	2.4	3.6	3.0 ± 0.8
D1 + D2 + D3	2.8	6.1	4.5 ± 2.3	–	–	–
D4 + B2 + C2	–	–	–	0.8	0.3	0.6 ± 0.4

B, male *B. bjoerkna*; C, male *R. rutilus*; D, male F1 hybrid, RB; Arabic numerals indicate umber of males participating in the matings; SD, standard deviation

2. the female RB hybrid with its corresponding hybrid male associated with the male silver bream (3.0 times per hour).

For both types of female hybrid the second highest mating frequency observed was the female hybrid with its corresponding hybrid male—mean frequencies of 0.7 and 1.2 times per hour for female BR and RB hybrids, respectively.

Mating success

Mating success assessed 1 day after spawning (Fig. 1) revealed that for the female BR hybrid the percentage of eyed embryos was not significantly different (Fisher's exact probability *FEP*-test, $p = 0.34$) for hybrid reproduction and mixed reproduction conditions (mean values 20.0 and 22.9%, respectively). For the female RB hybrid the difference between these two reproduction conditions was significant (16.8 and 29.3%, respectively; *FEP*-test, $P < 0.0001$). For both types of female hybrid the difference was not significant under the same reproduction conditions (*FEP*-test, $P = 0.269$ and 0.052 for hybrid reproduction and mixed reproduction conditions, respectively).

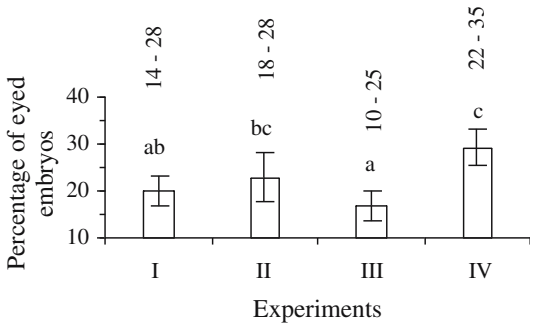

Fig. 1 Percentage of eyed embryos in eggs 1 day after spawning. *RB* first-generation F1 hybrid, *R. rutilus* male × *B. bjoerkna* female, *BR* F1 hybrid, *B. bjoerkna* male × *R. rutilus* female, *R R. rutilus*, *B B. bjoerkna*, ♂ male, ♀ female, *mean values* are means from four observations from duplicate experiments, *vertical bars* are standard deviations of four observations, *ranges* extreme values, values across common bars with different letters differ significantly (Fischer's exact test, $P < 0.05$), *I* 3♂BR × 1♀BR, $n = 400$, *II* 1♂BR, 1♂R, 1♂B × 1♀BR $n = 387$, *III* 3♂RB × 1♀RB $n = 379$ and *IV* 1♂RB, 1♂R, 1♂B × 1♀RB, $n = 400$, *n* total numbers of eggs observed

Discussion

As seems to be true for most hybrids, the sexual activity of hybrids of the roach and silver bream had never been investigated. Our experiments revealed that hybrid females have the biological capacity to reproduce with hybrid males and also with males of the parent species. Our experimental procedure revealed the total absence of ethologic barriers, which would explain a mechanism of prezygotic reproductive isolation. The absence of aggressiveness and territoriality during reproduction experiments under hybrid conditions, as in mixed reproduction, seemed normal, more particularly because the biological materials used came from interspecific and intraspecific crossbreedings of two species of cyprinid fish in which no aggressiveness has been observed by several authors (Diamond 1985; Mills 1991; Poncin et al. 1996; Poncin et al. 2004). According to some laboratory studies conducted on model

species, for example sticklebacks (*Gasterosteus aculeatus* L.), some behaviour, for example aggressiveness, may be an hereditary characteristic (Cheverud 1988; Bakker 1994). Wedekind (1996), however, observed a male roach defending part of the spawning ground only during their short spawning period under natural conditions. Under experimental conditions Kortet et al. (2004) also observed aggressive behaviour by roach males, for example butting and chasing other males, during the spawning period.

As a result of this study we have increased knowledge of the spawning behaviour of F1 hybrids between roach and silver bream and demonstrated that the level of sexual activity of these hybrids is high. As a result, parent species males, especially roach, were unable to mate individually with the female hybrid. The female hybrids successfully spawned with one or more males without an active intersexual and intrasexual selection between hybrid and parent species, resulting in fertilised eggs. This confirms the success of mating under our experimental conditions; we can, consequently, conclude that these hybrids (male and female) are fertile. This was reinforced by the second-generation F2 and the backcross generations produced in our crossbreeding experiments (Nzau Matondo et al. 2007). In comparison with conspecific breeding, fertilisation rates were inferior (Yakovlev et al. 2000; Urbányi et al. 2006). Combination of the genomes of these two species by introgression appears possible, however, with a consequence at the ecological level—the genetic risk of natural stock contamination by post-F1-generation hybrids. Such hybrids do not frequently encounter natural conditions, probably because of the low probability of capturing them and because identifying them as a hybrid requires experience.

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