

Interspecific barriers between salmonids when hybridisation is due to sneak mating

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Male sneaking behaviour can lead to interspecific hybridisation if sneakers attempt to fertilise ova in heterospecific mating, contributing to break down of interspecific barriers. In south European rivers, sneaking Atlantic salmon males fertilise an important proportion of ova from adult females in heterospecific crosses, up to 65%. In a south French flow-

controlled stream, we found that they were able to naturally fertilise brown trout ova in absence of brown trout males. Aggressiveness of brown trout males towards sneaking salmon males and low survival of hybrids issued from salmon sneakers are found to be interspecific barriers.

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Introduction

Alternative male mating strategies and tactics are described for very different animal taxa. Some examples can be found in mammals (Gemmell *et al.*, 2001), birds (Pitcher and Stutchbury, 2000), crustaceans (Shuster and Sassaman, 1997), anurans (Lucas and Howard, 1995), insects (Thomkins and Simmons, 2000) and all the range of poikylotherms (for a good revision see *Journal of Heredity* **92** (2), 2001). Males can adopt different behaviour patterns with differential reproductive success. Fish species are not an exception. Salmonids (Gross, 1985, 1996), Blennioids (Neat, 2001), Poecilids (Pilastro and Bisazza, 1999) and other fish taxa exhibit very diverse male mating behaviour that vary from actively courting of the female to furtively release sperm when a female is courted by other males (sneaking). Small young Atlantic salmon males (called *mature parr*) which mature in the river before migrating to the sea exhibit a typical sneaking behaviour with a high fertilisation success in the wild (Martinez *et al.*, 2000). At the southern edge of their geographical distribution, almost all Atlantic salmon males mature before seaward migration because freshwater maturation is enhanced by higher temperatures (Rowe and Thorpe, 1990; Prévost *et al.*, 1992). The rapid growth of juveniles in rivers leads to parr maturity in the first or second year of life, both in North America (Letcher and Terrick, 1998) and Europe (Utrilla and Lobon-Cervia, 1999). Up to 80% of the male parr may mature in some rivers (Héland and Dumas, 1994; Nicieza and Braña, 1995). As a consequence, the contribution of sneaking males to the gene pool of southern wild populations is

very important; they increase population size (Myers, 1984; L'Abée-Lund 1989), which maintains genetic variability (Garcia-Vazquez *et al.*, 2001).

Atlantic salmon (*Salmo salar* L.) and brown trout (*S. trutta* L.) are sympatric species in western Europe, from Norway to northern Spain. Hybrids of Atlantic salmon and brown trout are found in the wild over the range of distribution of both species. In surveys of European rivers, hybridisation rates ranged from 0.1 to 13% (Verspoor, 1988; Jansson *et al.*, 1991). The maternal species has been determined in a few cases. In hybrids from European rivers the mother was Atlantic salmon in some cases (Youngson *et al.*, 1992, 1993; Garcia-Vazquez *et al.*, 2001) and brown trout in others (Hartley, 1996; Jansson and Ost, 1997). American wild hybrids were reported to be the product of a cross between female brown trout and male Atlantic salmon (McGowan and Davidson, 1992a; Gephard *et al.*, 2000).

It is thought that alternative male mating behaviour can promote interspecific hybridisation, and break down interspecific barriers. Alternative male behaviour patterns such as sneaking, takeover and interception lead to cross-mating between *Mnais* damselfly species (Nomakuchi and Higashi, 1996). Natural hybridisation among distant members of *Bufo* toad species may be due to alternative mating tactics of males (Gergus *et al.*, 1999). For fish species, although there is a considerable number of studies on alternative male mating strategies, this point has been rarely addressed. Between species male parasitic spawning has been described in *Axoclinus* triplefin blenny fish (Neat, 2001). Hybrids issued from brown trout mother were sampled in river areas where sneaker Atlantic salmon males are present (Elo *et al.*, 1995; Jansson and Ost, 1997; Gephard *et al.*, 2000). This suggests that the sneaking behaviour of small Atlantic salmon males is responsible for interspecific hybridisation between Atlantic salmon and brown trout. However, clear experimental

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evidence for such interspecific crosses being due to sneaking Atlantic salmon does not currently exist.

In this work we investigated the role of mature parr in the hybridisation between Atlantic salmon and brown trout at the southernmost latitude of the distribution of Atlantic salmon in western Europe (43°N). In rivers flowing into the Bay of Biscay from northern Spain and southern France, where most Atlantic salmon parr mature in freshwater, hybrids issued from sneaking Atlantic salmon are likely to occur. However, all juvenile and adult hybrids found in the wild were offspring of Atlantic salmon females in this area (Beall *et al*, 1997; Garcia-Vazquez *et al*, 2001), contrarily to what would be expected if sneaker salmon contributed to interspecific hybridisation. We investigated possible interspecific barriers in a controlled stream, where mature individuals of both species in different situations were released.

Materials and methods

Experimental procedures

Experiments were conducted in a controlled-flow channel diverted from the Lapitxuri stream, a tributary of the River Nivelles (see Beall and de Gaudemar, 1999, for a description of the site and experimental installations). Wild mature individuals of both species, caught by trapping or electrofishing in the Nivelles, were measured and weighed, and scales sampled for age determination. Adipose fins were clipped for DNA analyses; and simultaneously placed in separate, 30 m² sections of the channel where they could spawn without any human interference. All the animal manipulation was made in large circular tanks (2 m diameter) full of well oxygenated river water, under effect of anaesthetics 2-P-E at the standard doses. Animal suffering and stress was avoided in each step of the experimental manipulation, keeping animals anaesthetised and handling them carefully. The experiments did not result in animal mortality in any case. To avoid detracting of many breeders from the wild population, we limited our experimental design by reducing the number of replicates. Scale and fin tissue sampling is not aggressive for salmon in any way and do not represent any risk for their survival. Behavior is not affected by this tissue sampling.

Table 1 presents the experimental design. To homogenise as much as possible the experimental situations, all Atlantic salmon adults (AS) were grilse (anadromous individuals returning to the river after 1 year in the sea). Much smaller mature Atlantic salmon males (*Atlantic salmon parr*, ASP) were 1 or 2-year-old. Brown trout (BT) males and females were of different ages (and subsequently of different sizes), depending on the experimental situation. We designed three control conspecific situations with only brown trout (A, B and C) involving a total number of 16 females and 22 males. Interspecific situations with sneaking salmon males without possibility of mate choice (allospecific males) were D, E and F, F including also a larger anadromous salmon male. Interspecific situations with possibility of mate choice (both sneaker allospecific and conspecific males) were G and H.

To compare the survival of hybrids issued from brown trout mother with that of hybrids issued from the reciprocal cross, we prepared two experimental situations

involving one AS female and one BT male: I and J. Two conspecific situations with Atlantic salmon females and sneaker mature parr were also prepared (K and L).

Spawning activity was directly observed and recorded with an Ikegami low light surveillance camera.

Survival estimate

At the end of each experiment, ie, when no more spawning activity was observed, fish were removed and the females were gently stripped by pressing on the abdominal cavity to express any remaining eggs (to determine egg retention). Egg retention was deduced from the estimated fecundity of each female. The number of ova or absolute fecundity F is given by the relation $F = 1689.9 W^{1.1046}$, where W is female weight in kg; $r^2 = 0.83$, $n = 85$; Beall and de Gaudemar, 1999) to estimate the number of eggs deposited. Survival of progeny of each section (egg survival to the fry stage) was estimated by the ratio of the number of fry recovered after emergence to the estimated total number of eggs deposited in that section.

Fertilisation of ova in all sections was confirmed by carefully open the redds (nests) and checking the presence of living eggs some weeks after spawning. Eyed eggs were sampled from redds in the experimental channel and alcohol-preserved for genetic analysis. The rest of the offspring remained in the channel to determine fry survival in each experimental situation. Fry were captured either by trapping during the first dispersal after yolk sac absorption and emergence, with modified fyke nets placed at the end of each section, or by electrofishing. In the D and F situations survival was very low and all the emerging individuals were ethanol-preserved for genetic analyses.

Genetic analysis

Two diagnostic loci were employed for species identification: the 5S rRNA genes and the restriction pattern of the histone genes. A portion of the adipose fin was used for extracting DNA. Total DNA extraction was carried out according to Taggart *et al* (1992). PCR analysis of the 5S rDNA was carried out following Pendas *et al* (1995) and restriction analysis of the histone genes followed Perez *et al* (1999).

For identification of offspring of small sneaking males when a large salmon male is present (situation F), we have carried out paternity analysis employing VNTR loci (Martinez *et al*, 2000).

Results

Table 2 presents the results of the experiments carried out in the Lapitxuri channel. Hybrids issued from Atlantic salmon sneaker males were obtained only in absence of conspecific males (situations D, E and F). By direct observation, as well as analysing the videotapes recorded, we found that the behaviour of mature salmon parr was always sneaking in all the three situations. Salmon parr remained hidden behind stones waiting for the moment of oviposition for rapidly approaching the female and releasing sperm. As expected, all the offspring recovered in these three sections of the experimental channel presented genotypes corresponding to hybrids, for both 5S rRNA and histone gene markers analysed: one gene variant of *S. salar* and one gene variant of *S. trutta*. In the situation F the large salmon male did

Table 1 Experimental situations prepared in the controlled stream

Situation	Type	Females	Males
(a) Brown trout females			
A	Control BT	5 BT (28.5–221 g, 13.3–26.4 cm)	6 BT (27.8–117.6 g, 13.4–21.8 cm)
B	Control BT	5 BT (93–690 g, 20.9–40 cm)	10 BT (30.8–612.2 g, 14.2–39.8 cm)
C	Control BT	7 BT (123.1–724.6 g, 22.3–43.4 cm)	6 BT (39.1–1119.5 g, 15.3–49.5 cm)
D	Heterospecific – no choice	5 BT (180–430 g, 24–35 cm)	6 ASP (5–17 g, 6.5–9.8 cm)
E	Heterospecific – no choice	5 BT (44.2–166.4 g, 15.4–24 cm)	6 ASP (9–32.9 g, 8.9–13.7 cm)
F	Heterospecific – no choice	5 BT (90–280 g, 20–28.5 cm)	1 AS (2190 g, 66.3 cm) + 6 ASP (5–15 g, 7–11.5 cm)
G	Heterospecific – choice	5 BT (67–236 g, 17.7–27 cm)	6 ASP (7.5–23.9 g, 8.4–13.5 cm) + 6 BT (19.3–108.5 g, 12.1–21.5 cm)
H	Heterospecific – choice	5 BT (46.8–255 g, 15.7–27.4 cm)	6 ASP (23.8–40.8 g, 12.8–15.8 cm) + 6 BT (29.2–112.2 g, 13.4–23.3 cm)
(b) Atlantic salmon females			
I	Heterospecific – no choice	1 AS (2330 g, 64.5 cm)	1 BT (1845 g, 56.8 cm)
J	Heterospecific – no choice	1 AS (2380 g, 62.9 cm)	1 BT (424 g, 34.3 cm)
K	Control AS	1 AS (2325 g, 64.9 cm)	6 ASP (5–35 g, 7–13.5 cm)
L	Control AS	1 AS (2370 g, 65.2 cm)	6 ASP (5–10 g, 7–10.5 cm)

BT = brown trout; AS = Atlantic salmon (anadromous); ASP = Atlantic salmon (mature parr). In parentheses, weight (g) and length (cm) of the individuals employed as parentals.

Table 2 Results of hybridisation experiments in the Lapitxuri controlled flow channel

Situation	Type	Interspecific courtship	Aggressive behaviour	Fry survival %	Number of offsprings typed
(a) Brown trout female					
A	Control BT	–	–	59.7	–
B	Control BT	–	–	74.7	–
C	Control BT	–	–	10.7	–
D	Heterospecific – no choice	Sneaking	No	1.3	18 H
E	Heterospecific – no choice	Sneaking	No	0	11 H
F	Heterospecific – no choice	Sneaking	No	1.96	9 H
G	Heterospecific – choice	No	BT males to ASP	40.2	100 BT
H	Heterospecific – choice	No	BT males to ASP	70.6	100 BT
(b) Atlantic salmon female					
I	Heterospecific – no choice	Yes	No	26.6	100 H
J	Heterospecific – no choice	Yes	No	33.3	79 H
K	Control AS	–	–	16.1	–
L	Control AS	–	–	15.5	–

BT = Brown trout; ASP = Atlantic salmon parr; AS = Atlantic salmon; H = hybrid.

not participate in reproduction. Paternity analyses demonstrated that the nine survivor hybrids were offspring of two or three mature parr, not of the adult male.

In presence of brown trout males (situations G and H), sneaker Atlantic salmon parr were not able to fertilise brown trout ova. Analyses of video records and direct observation of the reproductive behaviour showed that the aggressiveness of brown trout males towards sneaking Atlantic salmon prevented any success of ova fertilisation by sneakers. All the offspring recovered was genetically pure *S. trutta*.

Egg survival until fry stage was very variable among situations. In conspecific crosses it ranged from 10.7 (C) to 74.7 (B). Survival of hybrids was extremely low (0–1.95%, situations D–F), significantly different from fry

survival of pure brown trout in the same experimental conditions (Contingency Chi-square 180.02 with $P < 0.001$).

Hybrids of Atlantic salmon females and brown trout males (Table 2, situations I and J) were obtained by a typical courtship behaviour between the trout male and the salmon female. The directly observed and video recorded courtship pattern included, as in the case of anadromous salmon males with salmon females (de Gaudemar and Beall, 1999), repeated sequences of male quivering, crossover and swimming around the female followed by female digging into the substrate to prepare the nest. Direct observation and video records evidenced that male trouts did not adopt sneaking behaviour in any case. As expected, all the offspring recovered in the two

channel sections was genetically hybrid of *S. salar* and *S. trutta*. Mean survival at fry emergence was 29.1%. Moved into farm conditions they were able to reach their third year of age.

When salmon females reproduced with sneaker conspecific males (situations K and L), fry survival average was 15.8%, significantly higher than fry survival of hybrids issued from sneaker salmon (Chi-square 170.17 with $P < 0.001$).

Discussion

We demonstrate that interspecific hybrids can be obtained by sneaking behaviour of Atlantic salmon parr. However, their survival was extremely low in the experimental stream (0–1.95%), much lower than the survival of pure brown trout. Could the poor survival we found for hybrids obtained from brown trout females be attributed to the fact that they were offspring of mature male parr, not of adult salmon? Artificial breeding experiments have shown that sperm of mature parr and anadromous salmon do not differ in their capacity to fertilise eggs successfully and to produce viable offspring in conspecific crosses (Thorpe and Morgan, 1980). Our results obtained in the Lapitxuri stream clearly show that the survival of pure Atlantic salmon offspring of mature male parr is much higher than the survival of interspecific hybrids offspring of this type of males, therefore the poor survival of the hybrids is derived from the cross interspecificity. It is a interspecific barrier and not to a poor survival of mature male parr offspring *per se*.

The survival of hybrids naturally produced with Atlantic salmon sperm and brown trout ova was much lower than the survival of hybrids obtained by fertilisation of Atlantic salmon ova under the same experimental conditions (around 30%). There are no clear results about the relative viability of the reciprocal hybrids of Atlantic salmon and brown trout in breeding experiments carried out in farm conditions. Some showed higher survival of hybrids produced from trout eggs (Refstie and Gjedrem, 1975) whereas other reported a greater success with hybrids produced using salmon eggs (Piggins, 1970; McGowan and Davidson, 1992b). Results from these experiments probably depend on the particular strains used in the cross and on gamete quality at the time of fertilisation (Chevassus, 1979).

Our experiments at the Lapitxuri stream unequivocally demonstrate that sneaking behaviour leads to hybridisation between Atlantic salmon and brown trout. Hybrids were obtained from brown trout females and sneaking mature male parr. This confirms by first time that alternative male mating behaviour allows interspecific hybridisation in salmonids, as suggested by Elo *et al* (1995), Jansson and Ost (1997) and Gephard *et al* (2000) from field observations, and by Olsén *et al* (2000) from the potency of heterospecific stimuli in endocrine responses in male parr. Similar results were obtained in other taxa: insects (Nomakuchi and Higashi, 1996), anuran (Gergus *et al*, 1999) and also other fish (Neat, 2001). Following this rationale, the species in which males adopt sneaking mating strategies will more probably provide the male in interspecific crosses with the species in which males present only one mating strategy than the reverse. Are hybrids issued from *S. salar* sneaker males and *S. trutta*

females more frequent than the reciprocal hybrids in south European rivers?

The answer is certainly not. Previous results on hybrid surveys in south European rivers revealed that none of the many hybrids found in wild could be the product of a cross of a brown trout female and an Atlantic salmon male. Analysis of mitochondrial DNA demonstrated that they were always offspring of Atlantic salmon females (Beall *et al*, 1997; Garcia-Vazquez *et al*, 2001). Therefore the contribution of Atlantic salmon mature male parr to interspecific hybridisation, if existing in southern Europe, was very low or negligible. However, they should exist because mature parr are very abundant in these rivers (Héland and Dumas, 1994; Nicieza and Braña, 1995; Utrilla and Lobon-Cervia, 1999). The existence of this type of hybrids in the wild has been proved unambiguously in North American rivers (Gephard *et al*, 2000). Our results show that, although in a very small proportion (around 1%), these hybrids can survive until dispersion from nest. But we have found another interspecific barrier: the aggressiveness of brown trout males towards sneaking male parr. This pre-mating barrier works obviously only in presence of brown trout males. It is difficult to overcome by male parr in south European rivers because brown trout populations are very abundant (Reyes-Gavilan *et al*, 1996). Therefore there are always brown trout males around mature females to eventually attack sneaking Atlantic salmon mature males and consequently there are few chances to produce hybrids. It is logical to suppose that hybrids derived from sneaker Atlantic salmon parr exist, although in a so low rate that their detection is very difficult in random surveys, even if thousands of individuals are sampled.

In conclusion, we have found that interspecific *S. salar* × *S. trutta* hybrids are produced by sneaking behaviour of Atlantic salmon males. Although sneaking behaviour leads to a breakdown of pre-mating interspecific barriers, other pre- and post-mating interspecific barriers existing between these two species (aggressiveness of trout males, low survival of hybrids) counteract the effect of such breakdown and most probably avoid significant increases of hybridisation rate in south European rivers.

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