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Two examples of fixed behavioural patterns in salmonines: female false spawning and male digging

Received: November 18, 2005 / Accepted: April 14, 2006 / Published online: June 7, 2006

Abstract Data collected from underwater video recordings in the wild and in a semi-natural channel were used to study two examples of relatively unknown behaviour in the Salmoninae subfamily – false spawning in females and digging in *Oncorhynchus* males. Observations suggest that false spawning should be regarded as an incomplete fixed behavioural pattern (FBP) and that male digging represents two special types of FBP (displacement FBP) with threatening and courting functions as ultimate causes.

Key words Spawning behaviour · Salmon and trout · Underwater video · Incomplete stimuli · Displacement reactions

Introduction

Salmonines spawn in or on gravel beds in rivers or lake shores where the eggs incubate under the protection of the gravel environment (Groot 1996). During spawning, salmonines share common behavioural patterns (reviewed by Esteve 2005b). Females excavate a series of nests in the gravel where they subsequently lay their eggs. Males divide their time between competing with other male rivals and courting nesting females. During nest building females test nest depth and condition for suitability by “probing” with their anal fins. When the nest is finished, females signal eminent oviposition by lying on it with their mouths agape and their bodies trembling. At this time the dominant male and other males, join the female and both sexes emit their gametes. After ovipositing, females immediately cover the eggs with gravel by gentle beating of their tails (“covering digging”). All the spawning behaviour previously described is stereotypical across species (Esteve 2005a) and is apparently innate (does not require learning) making these activ-

ities typical “fixed behavioural patterns” (FBPs) – invariant sequences of actions that can be elicited over and over when presented with the right external stimulus (Lorenz 1932, 1935, 1940; Tinbergen 1939, 1942, 1948; Fabricius 1950). Several experiments have demonstrated this by recognizing some of the key stimuli necessary for salmonines to perform some of this behaviour. For example, Fabricius and Gustafson (1954) showed that the sight of gravel alone was able to induce “exploring” (females search for areas to place their nests by swimming in circles with their lower jaw touching the gravel) and “digging” (females excavate, with rapid thrusts of their tails, the nests in which they lay their eggs) in arctic charr. In this study, a mature female was introduced into an aquarium after placing a glass plate over a section of gravel. The female performed normal exploring and digging behaviour over the glass, even though she had no physical contact with the gravel or a male courting her. Hartman (1970) identified “egg release” as a strong stimulus for “covering digging” behaviour. In this study, a rainbow trout female chased away from her nest immediately after spawning was observed digging twice about 2 m from her nest within 10 s. Tautz and Groot (1975), identified nest depth and structure as important stimuli inducing “oviposition.” These authors artificially built a depression simulating the shape of a nest in an enclosed channel. When a mature and unspawned female was directed to the area the number of digging bouts the female completed before ovipositing on that nest was substantially less than the average required to build a new nest (75 compared with 255). I used a fish dummy imitating an ovipositing female to investigate the necessary stimuli for inducing male sperm release (Fig. 1). The dummy was made to vibrate by using a rod with a line attached to its tail. Forty-nine sperm emissions from five different sockeye males were recorded as a result of this stimulus. This experimental design demonstrated that visual and vibratory stimuli elicit male sperm release (Fig. 2; Esteve 2005a). These results validate the observations of others who also used dummies to investigate salmonines spawning behaviour (Newcombe and Hartman 1980; Satou et al. 1987, 1991, 1994; Takeuchi et al. 1987; Foote et al. 2004). The entire Salmoninae spawning process can be

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understood as a long chain of inter-related FBPs that run in increased intensity leading to gamete release (Tautz and Groot 1975; Satou et al. 1987; 1994; de Gaudemar and Beall 1999; Berejikian et al. 2000).

Despite the long history of research on salmonine reproduction there are two types of behaviour for which the underlying cause and function remain relatively unknown – false spawning in females and male digging in the *Oncorhynchus* genus. The consistency and predictability of both types of behaviour classifies them as FBPs (Esteve 2005a). During false spawning, females perform behaviour identical with the spawning act (gaping and trembling) but do not



Fig. 1. A dummy imitating an ovipositing female



Fig. 2. A sockeye male releases sperm to a dummy

Fig. 3. The same pair of Atlantic salmon during false (left, previously published in Esteve 2005b) and real (right) spawning



release eggs (Jones and Ball 1954; Schroder 1981; Fig. 3). False spawning is common among all the salmonines and was first thought to occur because the female found the nest was not suitable for oviposition at the very last minute (Jones and Ball 1954). There are, however, no studies supporting or refuting this hypothesis. It has been suggested that false spawning is a form of female choice by which females trick undesirable males; females mimic the spawning act to fool their mates into sperm release, and then, by delaying spawning, allow other, more desirable, mates the opportunity to participate (Petersson and Järvi 2001). It is also possible that false spawning increases the final number of males with which the female mates (Schroder 1981). *Oncorhynchus* males dig during the spawning process (Heard 1972; Schroder 1981; Fig. 4). Male salmon digging, instead of being a nest building behaviour, has, however, been regarded as an aggressive display and authors have linked it with male–male rivalry (Chebanov 1980; Healey and Prince 1998; Quinn 1999). Only McCart (1969) described male digging as a displacement reaction. Displacement reactions occur when a conflict prevents a motivated animal from expressing an FBP. As a result, the animal performs an irrelevant action, usually belonging to a different drive from the original behaviour (Tinbergen 1952a; Hinde 1953; Eibl-Eibesfeldt and Kramer 1958). Pioneering work by Tinbergen and Van Iersel (1947) with sticklebacks discovered two different types of displacement reaction – fighting displacements and sexual displacements. According to the authors, a fighting displacement occurs when there is conflict between the attacking and escaping impulses. In contrast, a sexual displacement occurs when there is a strong sexual motivation but lack of external stimuli required for the release of the consummatory act. Although Quinn (2005) suggested there may be more than one form and function of male digging no author has attempted to describe them or verify whether the displacement reactions described by Tinbergen and Van Iersel (1947) are at play in *Oncorhynchus* males.

In this paper, data from underwater video recordings are used to discuss the proximate and ultimate causes of false spawning in salmonine females and digging in the *Oncorhynchus* males. First, the causes of false spawning are examined using observations of 18 instances of false spawning performed by ten different females. The occurrence of digging, change of mate, and the increase in the final num-



Fig. 4. Sockeye salmon's male digging behaviour

ber of mates between false and a real spawning were recorded. If females perform a false spawning because of nest incompleteness (proximate cause) we should expect they will dig their nests after the false spawning. If females were mimicking spawning just to fool their mates (ultimate cause) we should expect they would change their mate in the real spawning. Also, if females were mimicking spawning to attract more males (ultimate cause) we should see an increase in the final number of mates during real spawning. Second, the work by Tinbergen and Van Iersel (1947) with sticklebacks together with underwater video observations of sockeye (*Oncorhynchus nerka*), chum (*Oncorhynchus keta*), and pink salmon (*Oncorhynchus gorbuscha*) are used to propose male digging as two special types of FBP – displacement FBPs.

Materials and methods

Remote underwater video

Hi-8 mm and mini DV video cameras mounted in acrylic underwater housings were used to record the behaviour of salmonines in the wild and in semi-natural spawning channels (Esteve 2005a). The camera was placed approximately 1.0–0.3 m from a developing redd. The video signal was transmitted via a cable to a mini DV digital video cassette recorder (Sony GV-D900E). Recordings of the live picture were initiated from the riverbank by use of a remote commander (Sony RM 95) that enabled manual zooming and focussing. All the cameras used were provided with angular lenses ($0.5\times$) and their shutter speed was 25 frames s^{-1} . Atlantic salmon (*Salmo salar*) were recorded in the Nansa River (Spain) during December 1997. *Oncorhynchus* species were recorded during 2000 to 2004 in the following rivers across Canada and USA: (a) Big Beef Creek, WA: coho and chum salmon; (b) Cedar River, WA: sockeye salmon; (c) Chehalis River, BC: coho salmon; (d) Skykomish River, WA: pink salmon; (e) Steep Creek, AK: chinook salmon (*Oncorhynchus tshawytscha*); and, finally, (f) Weaver Creek, BC: sockeye, chum and pink salmon.

False spawning

Underwater video recordings were used to examine the history of 18 instances of false spawning by ten different females (one Atlantic salmon, three sockeyes, one chum, three cohos, one pink, and one chinook). A false spawning was counted every time a female was seen trembling and gaping but without releasing eggs. The criteria for distinguishing between real and false spawning was the presence or absence of covering digging (after a real spawning *Salmo* and *Oncorhynchus* females always perform covering digging, Esteve 2005b). In all instances, females spawned some minutes after the false spawning (0.5–16 min, $N = 18$). The occurrence of “digging” in the time period between false and actual spawning was recorded. Any time the female changed her original mate after a false spawning was also recorded. Similarly, any time there was an increase in the final number of males in the real spawning was recorded. To avoid counting the same female more than once (pooling fallacy; Martin and Bateson 1993) the probability of digging and changing mates and of increasing the final number of mates after a false spawning was averaged for each of the ten females (Table 1). With regard to proximate causes, the following hypothesis was examined:

- H_{01} : The occurrence of digging is independent of having performed a false spawning ($P = 0.5$).

Similarly, to investigate ultimate causes two hypotheses were examined:

- H_{02} : The occurrence of mate change is independent of false spawning ($P = 0.5$).
- H_{03} : The final number of mates is independent of false spawning ($P = 0.5$).

A binomial distribution test was employed (Siegel and Castellan 1988).

Male digging

Underwater video data for pink, sockeye, and chum salmon were examined to classify male salmon digging on the basis of two types of displacement reaction described by Tinbergen and Van Iersel (1947) – fighting displacement and sexual displacement. Ten 1-h underwater videotapes from each of the species were randomly chosen (from a long-term sample of video recordings; Esteve 2005a) to count both types of displacement (Tables 2, 3, 4, 5). The underwater tapes selected contained recordings of the behaviour of seven sockeyes, seven chum, and six pink males. Fighting displacement digging was counted every time a male was seen to dig in the presence of another male during a rivalry dispute. Sexual displacement digging was counted every time a male was seen to dig close to the female without the presence of other males. The probability of performing each type of displacement per hour of spawning activity was averaged for each of the males observed.

Table 1. False spawning history from ten different females. The occurrence of digging, change of mate, and increase in the number of mates between false and real spawning is indicated. The probability (0–1) for digging, changing mate, and increasing the final number of mates is averaged for each female

	Species	<i>n</i> Fs	Digging	Average	Change of mate	Average	Increase	Average
Female 1	Atl. Salmon	1	Yes	1	No	0	Yes	1
Female 2	Sockeye	3	Yes	1	No	0	Yes	0.67
			Yes		No			
Female 3	Sockeye	1	Yes	1	No	0	No	0
Female 4	Sockeye	2	Yes	0.5	No	0	No	0
			No				No	
Female 5	Chum	1	Yes	1	No	0	No	0
			Yes				Yes	
Female 6	Coho	5	Yes	1	No	0	No	0.2
			Yes				No	
			Yes				No	
			Yes				No	
Female 7	Coho	1	Yes	1	No	0	Yes	1
Female 8	Coho	1	No	0	No	0	Yes	1
Female 9	Pink	2	No	0	No	0	Yes	1
			No				Yes	
Female 10	Chinook	1	Yes	1	No	0	Yes	1
Total				0.75		0		0.59

n Fs is the number of times false spawning occurred

Table 2. Numbers of the two types of male displacement digging in 10 h of spawning activity of seven sockeye males. The average number of occurrences of digging per male per hour is included

One-hour tape	Male	Fighting displacement (Fd)	Average Fd/male/h	Sexual displacement (Sd)	Average Sd/male/h
1	Sock 1	2	2	0	0
2	Sock 1	2			
3	Sock 2	3	4	0	0
4	Sock 2	5			
5	Sock 3	9	9	2	2
6	Sock 4	1	1	0	0
7	Sock 4	1		0	
8	Sock 5	15	15	2	2
9	Sock 6	2	2	6	6
10	Sock 7	0	0	9	9
Range		0–15		0–9	
Total		40	4.71	19	2.71

Table 3. Numbers of the two types of male displacement digging in 10 h of spawning activity of seven chum males. The average number of occurrences of digging per male per hour is included

One-hour tape	Male	Fighting displacement (Fd)	Average Fd/male/h	Sexual displacement (Sd)	Average Sd/male/h
1	Chum 1	1	1	0	0
2	Chum 1	1		0	
3	Chum 2	4	4	7	7
4	Chum 3	1	1	0	0
5	Chum 3	1		0	
6	Chum 4	0	0	0	0
7	Chum 5	11	5.5	0	0
8	Chum 5	0		0	
9	Chum 6	2	2	1	1
10	Chum 7	1	1	0	0
Range		0–11		0–7	
Total		22	2.07	8	1.14

Table 4. Numbers of the two types of male displacement digging in 10 h of spawning activity of six pink salmon males. The average number of occurrences of digging per male per hour is included

One-h tape	Male	Fighting displacement (Fd)	Average Fd/male/h	Sexual displacement (Sd)	Average Sd/male/h
1	Pink 1	1	0.5	0	0
2	Pink 1	0		0	
3	Pink 2	1	1	0	0
4	Pink 3	3	3	0	0
5	Pink 4	0	0	0	0
6	Pink 5	0	0	0	0
7	Pink 6	0	0.5	0	0
8	Pink 6	1		0	
9	Pink 6	0		0	
10	Pink 6	1		0	
Range		0–3		0	
Total		7	0.83	0	0

Table 5. Numbers of the two types of male displacement digging in 10 h of spawning activity for each species. The average number of occurrences of displacement digging per male per hour of observation and the range of performing each type of displacement are included

Species	Males observed	Fighting displacement (Fd)	Average Fd/male/h	Sexual displacement (Sd)	Average Sd/male/h
Sockeyes	7	40	4.71 (0–15)	19	2.71 (0–9)
Chums	7	22	2.07 (0–5.5)	8	1.14 (0–7)
Pinks	6	7	0.83 (0–3)	0	0
Total	20	69	2.54	27	1.28

Results and discussion

Although the reproductive behaviour of salmonines varies substantially within and between species (Wilson 1997), there are no apparent major differences between performance of the two FBPs examined in this study. False spawning is performed during the latter stages of nest building and invariably follows a similar pattern across species – females mimic the spawning by gaping and trembling in a probing position (Figs. 3 (left) and 5). Male digging, on the other hand, can be consistently divided into two types that differ depending on the contextual situation of the males and on its performance (discussed below). There are certainly differences (related to population density and levels of male–male competition) in the rate by which different species, or even populations, perform both kinds of digging; these differences do not, however, affect its proximate and ultimate causes.

False spawning

For the ten females observed, the probability of digging after having performed a false spawning was 0.75 (Table 1) and the H_{01} hypothesis was rejected ($P < 0.05$) suggesting that false spawning is a consequence of nest incompleteness. As Tautz and Groot (1975) demonstrated, nest depth is a strong stimulus for females to spawn. Other observations also reinforce this idea. According to Tinbergen (1952a), FBPs may be seen in numerous degrees of intensity, from full intensity down to an almost imperceptible indication. On many occasions I have seen the same female performing

**Fig. 5.** False spawning of coho salmon female (previously published in Esteve 2005b)

false spawning of different, increasing, intensity before ovipositing. This includes “probing” (females lay on their nests with their bodies arched and their anal fin pressed into the gravel) while partially “gaping” that lasts 1–2 s to a total spawning mimic including “trembling” and fully “gaping” over 5 s. Real spawning, the same as other FBPs will not occur until the stimuli received has reached a threshold level (Tinbergen 1948; Fabricius 1950). Thus, false spawning is probably an incomplete FBP that occurs at different intensities when the stimuli received by females from the nest are not sufficient to reach the threshold level necessary for egg release. Other than nest readiness, the stimulus needed by females for ovipositing is provided by the male. Insufficient male stimulus may explain situations where

females did not dig their nest. During real spawning both male and female have to remain in parallel with their vents close together. At this time the pair is known to exchange visual and vibratory signals, which coordinate oviposition and sperm release (Satou et al. 1991, 1994). Incorrect positioning of the male may, occasionally, explain the occurrence of false spawning (Fig. 6). FBPs are elicited by a heterogeneous combination of stimuli (several sign stimuli act together) (Tinbergen 1948). With this in mind, a combination of both factors (nest depth and male position) is probably responsible for false spawning behaviour in the salmonines.

Irrespective of the cause of false spawning behaviour, my results did not elucidate a hypothesis for its function. Of the ten females observed, the probability of changing their mate after a false spawning was 0 and the H_{02} hypothesis was therefore rejected ($P < 0.001$). Females do not change their mates after a false spawning. Of the same ten females, the probability of increasing the final number of mates after a false spawning was 0.59 and the H_{03} hypothesis was not rejected ($P = 0.20$). Although false spawning seems to be independent of the final number of mates, given the high probability found (0.59) and the low sample size of this study, these results may change as further observations are reported. Intentionally or not, on many occasions females fool the males into sperm release (personal observations). Although such erroneous emission of sperm does not prevent males from fertilizing the female's eggs in the real spawning event, it probably alerts other males. This observation agrees with those of Schroder (1981), who states that females performing false spawning provide cues to males in the vicinity about imminent spawning. By increasing the

number of mates, females can increase the genetic diversity of their offspring and/or the quality of the participating males (Pettersson and Järvi 2001).

Male digging

Surprisingly, in the salmonine literature, only McCart (1969) has addressed male salmon digging as a displacement reaction. This may be interpreted as a lack of communication between early ethologists and later salmon researchers. Male digging in salmon follows the exact rationality of two of the displacement reactions explained by Tinbergen and Van Iersel (1947) in sticklebacks. Although sticklebacks differ from salmonines in their mating system (males build a nest and attract females) both types of displacement can be applied to salmonine males. The incompatibility of the attacking–escaping impulses or the lack of female stimuli for inducing male sperm release can be present in any species in which courtship and male–male competition are present. Reports describing these two types of displacement reaction for a variety of species support this idea (Hinde 1953; Eibl-Eibesfeldt and Kramer 1958). Fighting displacement digging in salmonines is basically a “one male–one male” interaction that normally occurs when a territorial male encounters a similar or bigger male. Fighting displacement digging often occurs around the boundary of the area in where females excavate their nests (redd) and is always associated with male rivalry. Compared with females' nest digging, fighting displacement digging is performed with fewer tail beats and no extension of pectoral fins. Also, males maintain a fast swimming speed while digging. In

Fig. 6. Video frame sequence of false spawning by an Atlantic salmon female. Observe how the male failed to remain parallel to the female (frames are separated by 1 s; from left to right)



contrast, sexual displacement digging is a “one male–one female” interaction that occurs in situations where a very motivated male does not receive the female’s stimuli for sperm release (gaping, probing, and vibrating). Sexual displacement digging is more similar to female nest building digging – intense and concentrated in a specific location. They are usually performed within a redd boundary without the presence of other males. The intensity and location of sexual displacement digging do not rule out the possibility of their contribution to nest building. According to my results, fighting displacement digging is more common than sexual displacement digging, although the differences are not significant (Table 5; Wilcoxon signed rank test, $S = 37.5$ $P = 0.0761$). These differences will, nevertheless, vary, presumably depending upon the level of male–male competition. Also, although more observations are required, both types of displacement digging seem to be more common in sockeye and less so in pink salmon with chum salmon at an intermediate level. The reason for this trend is unknown and most probably has a phylogenetic basis (Esteve 2005a).

If fighting displacement digging is the result of simultaneous activation of incompatible behaviour, we can predict females should also perform them (as they can also experience an attack–escape conflict). I have observed displacement digging by sockeye, chum, and pink salmon females. In each species I always observed a similar pattern; a female on her nest was attacked by another, she then retaliated by chasing the other. On her way back to her nest she performed displacement digging. Digging, in this case, may be the result of an escaping impulse (because the female after the attack is no longer on her territory) conflicting with an attacking one. Alternatively female displacement digging can be induced when male fights prevent females from working on their nests (S.L. Schroder, personal communication).

Male digging in *Oncorhynchus* sp. can be characterized as a typical FBP – they are innate, highly stereotypical, and can be elicited repeatedly by some stimuli. One means of demonstrating this is to induce them artificially by use of the appropriate stimuli. I accomplished this by using a 900 W light illuminating an active redd occupied by a single pair of sockeye salmon spawning during dark hours in the Cedar River, WA. When the light was directed straight into the redd both fish escaped. When the light was pointed into an adjacent area and only partially illuminated the redd, however, the escape urge was increased only to a level to make it conflict with the urge to stay in the redd. By use of this method ten instances of male displacement digging and five instances of female displacement digging were counted in a 50-min period (Esteve 2005a).

Irrespective of what induces male displacement digging, its adaptive value is not known. Tinbergen (1952b), however, proposed that displacement reactions initiated by the fighting drive often have a threat function and that those initiated by the mating drive may have the power to release sexual responses in the partner. Also, as stated by Wilson (1975), displacement reactions are derived from pre-existing motor patterns that have been “emancipated” in evolution from the old functional context. In this regard,

salmon male digging may have gradually adopted courtship and fighting functions as ultimate causes.

Conclusions and recommendations for further research

Female false spawning and male digging are two special cases of FBPs. False spawning is an incomplete FBP induced when females do not receive enough stimuli (from their nest or their mate) for oviposition. This low-intensity FBP has probably been preserved during the course of evolution because it has the adaptive value of increasing the final number of males. The relatively small number of individuals observed in this study makes it necessary to confirm this with further observations, however. Male digging in the *Oncorhynchus* genus represents two types of displacement FBP. The first, fighting displacement, occurs because there is a conflict between two opposite FBPs of similar intensity and possibly has the function of threatening other males and courting females. The second, sexual displacement, occurs when an FBP cannot be released (sperm release) because the opposite sex fails to give the necessary stimuli (gaping and trembling). Although the function of sexual displacement digging may be to court females, we cannot rule out the possibility of its contributing to nest building. The fact that male digging is only present in members of the *Oncorhynchus* genus and absent in other genera within the Salmoninae subfamily (Esteve 2005b) is intriguing and invites further research into the understanding of the evolution of this trait.

Acknowledgements I thank Carmen Grisolia, Pep Gener, Felipe Melero, Victor Ewert, Martin Lopez, Gordy George, Victor Esteve, Alex da Silva, Caro Minte-Vera, Mane de Sousa, and Mafalda Esteve for helping me to record the fish underwater. This manuscript has benefited from comments by Jesus Jurado Molina, Steve Schroder, Barry Berejikian, Cheryl Murphy, and three anonymous reviewers. The field work was partially funded by a research assistantship from the University of Washington, Centre of Streamside Studies. The manuscript was planned during a two-year visit to the University of Washington under Tom Quinn’s guidance and is part of a Ph.D. thesis directed by Adolfo de Sostoa at the University of Barcelona.

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