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Female preference for male body size in brown trout, *Salmo trutta*: is big still fashionable?

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The study of female preference for male traits is of primary importance for understanding the role of sexual selection in the evolution of natural populations. Female preference is usually investigated in controlled conditions to facilitate the manipulation of variables. However, such results are rarely confirmed in wild populations where many variables act together. Inferring the role of female preference in the outcome of reproduction thus requires field studies and a specific approach to behavioural data. We observed, over 2 years, the courtship behaviours of male and female brown trout in six populations distributed along a French watershed. We focused on behavioural items linked to female preference for male body size. We built a behavioural model describing the relationships between behaviour and female preference and estimated the parameters of the model using a Bayesian modelling approach. We found a significant preference for body size ratio: females tended to prefer males at least 1.45 times their own size. This preference varied between populations and was influenced by female size. Operational sex ratio had only a weak influence on female preference. Our model explained 44% of the observed variation in behaviour. Finally, because observed body size ratio at mating was generally greater than 1, we conclude that female preference plays a major role in the outcome of reproduction in wild populations of brown trout. These results are compared with existing knowledge and theory and their possible consequences at the population level are discussed.

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Sexual selection theory is fundamentally based on the concept of anisogamy, which refers to the huge difference in size and numbers between gametes produced by the two sexes (Andersson 1994). Because males produce large numbers of gametes, but also because their reproductive success is not certain (Kokko et al. 2006), they are expected to favour quantity over quality in their reproductive effort. This trait implies that they will usually try to mate as many times as possible with the more fecund females within the limits of sperm depletion and competition. The outcome of this paradigm is that intrasexual male competition is generally intense (Clutton-Brock & Parker 1992). For females, which produce fewer gametes but invest much more energy in each of them, and for whom reproductive success is usually not an obstacle, one can expect that they will focus on mate quality, and thus they should show more selective behaviour: this is so because males with higher fitness may increase the fitness of offspring ('good genes' hypothesis, Williams 1966) and may also provide direct benefits, for instance through parental care. The fitness of males should be related to several cues, on which female preference will rely. This leads to the existence of secondary sexual traits, and studies of species with these traits have largely provided support for sexual selection theory. Even in species that lack an obvious sexual dimorphism, the process is the same: females have to select males on some traits, to improve the fitness of their progeny.

This is potentially the case in several species of salmonids for which sexual dimorphism is not striking, to the point where it becomes difficult to tell a male from a female outside the breeding season (i.e. when females are not mature). While for semelparous species, colour patterns (Craig & Foote 2001), jawbone shape (Tchernavin 1938) or adipose fin size (Järvi 1990) seem to be under strong sexual selection, this is rarely the case for facultative anadromous and iteroparous species. In these species, some traits have been investigated (Petersson et al. 1999), but body size appears to be the main trait under female preference (Foote & Larkin 1988; Foote 1989; Blanchfield & Ridgway 1999; De Gaudemar et al. 2000; Fleming & Reynolds 2004). Body size can either reflect good survival or fast growth, which could both be indicators of fitness under the 'good genes' hypothesis (Petersson & Järvi 2007), or not (Jacob et al. 2007), but it can also be a good indicator of paternal capacity to defend the redd during spawning (Cote & Hunte 1989). The consequences of this situation are numerous, because body size, and thus growth, is heritable and under selection for many other reasons (Theriault et al. 2007). Body size therefore represents

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the primary component of female preference for males, and it is expected that females will select the bigger males for spawning. This may lead to a runaway process (Fisher 1930), provided there is no important cost associated with such a choice. One can also expect assortative mating (Jennions & Petrie 1997) if body size is a phenotype with local adapted optima corresponding to various ecological constraints (Endler & Houde 1995).

The demonstration of female preference for some trait, inheritance of these traits for males and, potentially, inheritance of female preference have been the major focus of numerous experimental studies, especially in fishes (Houde 1988; Foote 1989; Endler & Houde 1995; Brooks & Endler 2001). While male secondary sexual traits appear to be heritable, it is far more difficult to understand and demonstrate the transmission of complex female preference (Brooks & Endler 2001; Haesler & Seehausen 2005). Yet, proving experimental by the existence of such mechanisms does not tell us how important they are in natural environments and whether they really influence the course of evolution (Qvarnström et al. 2006). In the wild, studies usually focus on an observed male–female pair at mating instead of the real choice of females. Mating patterns are the combined result of female and male preferences and intrasexual and intersexual competition. While such information in the wild is nowadays potentially accessible via genetic analyses, female preference may be harder to observe. To disentangle the different components involved in mate choice, one must investigate whether female preference is really expressed in natural populations, and whether this preference has an impact on the outcome of reproduction.

We studied female preference in wild populations of brown trout in the River Nive, France, based on video recordings of numerous courtship behaviours. In this species, the female digs several nests where she deposits her eggs while males compete to fertilize them. Because dominance rank is strongly correlated with male size, the bigger male is expected to gain access to fertilization, and the female preference is generally overlooked. To investigate the existence and role of this preference, we focused on the time sequence prior to spawning, because spawning itself is a trade-off between male preference, male competition and female preference, and, as pointed out by Postma et al. (2006), the final pairing may provide little information on female preference. Therefore we built a behavioural model which took into account several different behavioural items indicating female preference. We also took care to remove any behaviour provoked by male aggression to ensure that the data reflected only pure female preference. The parameters of the behavioural model were estimated using a Bayesian inference approach. Our objectives were to test for (1) the existence and importance of female preference with respect to male body size in the wild, (2) spatial variation in preference and (3) several explanatory scenarios of variation in preference. In particular, we looked at the effect of the operational sex ratio (OSR, the ratio of males to females) on female preference: females are expected to become choosier when the OSR increases (Schroder 1981; Fleming 1996; Beall & De Gaudemar 1999) provided the cost of choosiness is not too high. We also investigated the role of female size in female preference: female size can be correlated with both age and growth opportunities (depending on habitat). First-time spawners may behave differently from experienced spawners (Kodric-Brown & Nicoletto 2001), and females living in harsh habitats may also select locally adapted phenotypes.

METHODS

Study Site

The Nive is a coastal foothill river of the Pyrénées Moutains located in southwestern France (43°N, 2°W). The river is 90 km long and drains a watershed of 990 km^2. It is roughly distributed in three main streams that correspond to three parallel valleys: the Béhérobie and Arnéguy merge in Saint-Jean Pied de Port to form the main stem or Grande Nive. The Aldudes river is the main tributary on the left bank of the Grande Nive. Our sampling sites were located on the Aldudes (three sites: Ithurrihandi, Village, Baïgorry), which is a fragmented tributary, and on the main stem (three sites: Soussignaté and Saint-Jean before the confluence with the Arnéguy, and Bastan located near the main stem on a left-bank tributary), where fish can freely migrate (Fig. 1). Mean annual discharges in the main stem and the Aldudes are similar (about 8 m^3/s). On the Aldudes, the Ithurrihandi site is completely isolated by a 10 m natural fall. On the main river, the Saint-Jean site is a protected reserve (no fishing allowed).

Data Sampling

Sampling covered the spawning period (November–March) for 2 years (2001–2002 and 2006–2007). Each site was visited at least twice a week by two observers, resulting in approximately 500 visits in the field over the 2 years of study. Observation methods were standardized between all observers. At each visit, newly dug redds were counted. When an active redd was located, we used a D-90 Sony digital video camera to record activity on and around the redd. The camera was positioned on the bank, 2–8 m from the redd, using a x10 zoom and a polarizing filter to remove light reflections. For each redd, the observer noted with an audio digital recorder the dominant male (as the one being near the female and chasing other fish more frequently), the active female, the number and sizes of all individuals including peripheral males. A marked scale was usually placed near the redd, to measure approximate fish sizes (total length). These sizes were later confirmed or corrected from the video records. Based on visual estimation of size and general colour patterns, it was usually possible to identify each male around the redd, but the reliability of this identification could not be tested. We observed the behaviour of the active female, such as chases of males, departures from the redd and digging activity. We also recorded interactions between males, and males harassing or chasing the female. Some complementary observations were also realized at night using white spotlights, but were not included in the analysed data. Temperature was noted at each observation (Pocket thermometer Checktemp-1, Hanna Instruments, Leighton Buzzard, U.K.), and a continuous record of temperatures was obtained on the Bastan site during the whole spawning period (Minilog T datalogger, VEMCO, Halifax, Nova Scotia, Canada).

Behavioural Model

To build a simple behavioural model to analyse data, we made several assumptions. First, we assumed that once a redd had been established, the female could readily select positively or negatively a male according to her preference. Second, we assumed all interactions occurred between one male and the female: we removed the sequences where more than one male interacted, because it was difficult to know to which male the female was reacting. Third, we assumed that for a given female, all observations were independent (i.e. no effect of the male identity or the order of interactions). Finally, we tried to remove all observations where there was a suspicion of male interference with female choice, such as a male harassing or chasing females, to ensure as much as possible that only observations reflecting free female choice would be considered. After a preliminary analysis of the video data, we decided to remove video sequences shorter than 15 min, because these sequences were not usually related to courtship behaviour. Actual spawning sequences were not taken into account in the

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