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With our powers combined: integrating behavioral and genetic data to estimate mating success and sexual selection

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Abstract

The analysis of sexual selection classically relies on the regression of individual phenotypes against the marginal sums of a males × females matrix of pairwise reproductive success, assessed by genetic parentage analysis. When the matrix is binarized, the marginal sums give the individual mating success. Because such analysis treats male and female mating/reproductive success independently, it ignores that the success of a male × female sexual interaction can be attributable to the phenotype of both individuals. Also, because it is based on genetic data only, it is oblivious to unproductive matings, which may be documented by behavioral observations. To solve these problems, we propose a statistical approach which combines matrices of offspring numbers and behavioral observations. It models reproduction on each mating occasion of a mating season as three stochastic and interdependent pairwise processes, each potentially affected by the phenotype of both individuals and by random individual effect: visit of a female by a male, concomitant gamete emission, and offspring production. Applied to data from a mating experiment on brown trout, the model yielded different results from the classical regression analysis, with only a negative effect of female body size on the probability of visit and gamete release, while the classical approach based on regression found a positive effect of male size on the number of both visits and offspring, and no effect of female size. Because the general structure of the model can be adapted to other partitioning schemes of the reproductive process, it can be used for a variety of biological systems where behavioral and genetic data are available.

Keywords

Introduction

Sexual reproduction involves two different individuals which both invest energy in gamete encounter and possibly in offspring survival. The reproductive output of a given mating event is therefore attributable to both partners. In a population, the distribution of the reproductive success $RS_{i,j,k}$ gained by a pair of individuals i and j on a mating occasion k can be summarized by a 3-dimension array of number of offspring produced between all possible pairs of males and females for each mating occasion. Here, and throughout this article, "pair" refers to two individuals engaged in a mating interaction, and is applicable to all mating systems, not only to monogamous ones involving stable pairs. Then, summing such array over all mating occasions leads to the so-called "parental table" classically used in studies of sexual selection (Arnold and Duvall 1994). An estimate of such matrix is typically generated by parentage analysis based on genetic markers (e.g. Garant et al. 2001, Jones and Ardren 2003, Jones et al. 2004) possibly complemented by direct observations of mating behavior (Pemberton et al. 1992, Coltman et al. 1999, Collet et al. 2014).

Classical methods in sexual selection use these parental tables to infer the adaptive value of traits in populations by calculating different indices of sexual selection in males and females such as measures of inequality in mating success or reproductive success, selection gradients and selection differentials (Bateman 1948, Wade 1979, Wade and Arnold 1980, Crow 1989). To compute all these indices, they further reduce the matrix to its margins, individual reproductive success being the sum of offspring on the individual's row or column, and mating success being the number of positive cells on the individual's row or column, i.e. the number of different individuals with which at least one offspring was produced. Sexual selection is predicted to operate when mating success affects reproductive success. The opportunity for selection, computed as the variance of individual reproductive success divided by the squared mean of individual reproductive success, quantifies the rate at which absolute fitness will increase in the population relative to the standing variance in absolute fitness, assuming that all variance in fitness is due to additive genetic effects (i.e., the heritability of fitness is one) (Jones 2009). The opportunity for sexual selection, computed for each sex as the variance of individual mating success divided by the squared mean of individual mating success, is the part of the opportunity for selection that is due to differences in mating success between individuals. The link between mating success and reproductive success is often quantified as the Bateman's gradient (Arnold 1994), computed as the slope of reproductive success on mating success (= the selection gradient of the mating success). When there is opportunity for sexual selection, a phenotypic trait is considered to be sexually selected if it covaries with mating success.

This approach has some pitfalls and shortcomings, and although widely used, its output may often be misinterpreted (Kokko et al. 1999, Klug et al. 2010, Jennions et al. 2012). In this paper, we will address two important caveats. First, the definition of mating as the occurrence of shared offspring does not account for multiple - possibly

infertile – mating events, which are part of the cost of reproduction (Arnqvist and Nilsson 2000). Second, the lack of consideration for the fundamental dependency between the mating and reproductive success of an individual and the mating and reproductive success of its mates biases the estimation of selection acting on individual traits.

An illustration of the first caveat is the wealth of definitions for individual mating success during one reproductive period (Bateman 1948, Arnold and Duvall 1994, Parker and Tang-Martinez 2005, Uller and Olsson 2008, Jones 2009, Gowaty et al. 2012, Fritzsche and Booksmythe 2013). Mating success can either be viewed as 1) the number of copulations, 2) the number of different individuals with which the focal individual has copulated, 3) the number of copulations that yield progeny or 4) the number of individuals with which progeny is produced. While the two latter definitions inform precisely on the fitness benefits, the first and second definitions also integrate potential costs, be it time (Charnov 1976), energy (Franklin et al. 2012), predation risk (Magnhagen 1991), or disease transmission (Poiani and Wilks 2000). Because both benefits and costs associated with phenotypic traits are essential to understand their evolution under sexual selection, it would be of interest merging both points of view in a single framework to estimate sexual selection indices. It is noteworthy that the definition of mating success is to a great extent constrained by methodological possibilities. Standard methodological approaches using parental tables obtained from genetic assignations can only target the number of individuals with which progeny of the focal individual is produced and generally result in biased estimates (Collet et al. 2014). These approaches deduce individual mating success by counting the number of non-zero elements on the individual line of the parental table. In this case, a zero value for a given pair can be the outcome of either pre-copulatory, post-copulatory or sampling processes: no copulation, copulation but no gamete fertilization, gamete fertilization but offspring dying before sampling, offspring alive but failing to be sampled. Hence, a pair may have mated but because of post-copulatory processes, their mating may go unnoticed in the parental table. In other words, mating success based on parental table certainly underestimates the actual number of matings, in the sense of copulations. Similarly, a non-zero value can also carry more information than just the total reproductive success between a pair of individuals, since it can be the outcome of a variable number of matings, which is of importance to measure reproductive investment. In this perspective, matrices of copulation success as obtained by direct observations of mating behavior obviously contain data that are complementary to parentage assignation methods (Collet et al. 2014). We therefore need statistical models integrating both behavioral and genetic data to provide estimates of the various definitions of mating success, by disentangling pre-copulatory and post-copulatory components as already suggested by several authors (Arnold and Wade 1984a, Pischedda and Rice 2012, Pélissié et al. 2014).

The second caveat is less evoked in the literature although intuitively simple: in sexual reproduction, reproductive success between two individuals should be attributable to both. Yet, one usually analyzes reproductive success as an individual character-

istic, with no regard for the effect of the sexual partner. Classical studies only focus on the marginal sums of the parental table, and therefore cannot control for sexual partner trait or mating success variation (Arnold and Wade 1984a, b). Selection indices are estimated by regressing the margins of the parental table against the vector of values of phenotypic traits, independently for males and females. A direct consequence is that one might detect a significant correlation between a trait and mating success or reproductive success for a sex, and interpret it as evidence of direct selection, whereas indirect selection could for instance be at work by mean of non-random association between sexual partners' traits. We therefore need an approach in which the mating and reproductive success of a pair of individuals accounts for the phenotype of both individuals, instead of using twice the same data to draw seemingly independent conclusions.

To solve both matters, we propose an approach that combines genetic data (parental table) and behavioral data (visit matrix and mating matrix) to 1) describe the different components of reproductive success (here visit rate, rate of gamete release, number of offspring produced) for each mating occasion within the reproductive season, and 2) infer the joint effects of both male and female phenotype on each component of the reproductive success. The conditional structure linking the successive components of pairwise reproductive success is the key to extract information from both behavioral and genetic data: presence of offspring from a pair of parents implies the male having visited the female and released his gametes concomitantly with hers, even if these are absent from behavioral data, whereas observation of gamete release despite the absence of common offspring allows distinguishing between zero-value due pre-copulatory and post-copulatory mechanisms. We illustrate the model using a reproduction experiment data for *Salmo trutta* as a case study, with body size as an example of phenotypic covariate as it is known to be involved in sexual selection in salmonids (Jacob et al. 2007, Labonne et al. 2009) and could therefore have an effect on each of these components of sexual selection. Brown trout mating system is polygynandrous (Labonne et al. 2013). While each female digs her nest on a spawning ground for tens of minutes to hours, one to ten males court her and chase each other to acquire proximity with her. When the nest is completed, the female lays her eggs and one or several males release their sperm on it. Females can lay up to five clutches, not necessarily fertilized by the same males, so polygyny is sequential while polyandry can be both simultaneous and sequential. Given this system, larger males were expected to have a higher probability of visit and mating with females because they could oust smaller males from nesting sites (Jacob et al. 2007). In cases of multiple mating (several males ejaculate over a female's eggs), they were also expected to sire more offspring than smaller males because their closer proximity with females during spawning gives them an advantage in sperm competition. Larger females may be expected to have a higher probability of being visited because they may attract more males than smaller females (Serbezov et al. 2010). Because body size is highly correlated with the number of eggs laid by brown trout females (Jonsson and Jonsson 1999), larger females were expected to produce more offspring.

Methods

Reproduction experiment

The data used in this study were taken from the "constant environment" treatment in Gauthey et al. (2016) and are presented in Supplementary File 1. The experiment was conducted in a semi-natural channel beside Lapitxuri stream, a tributary to the Nivelle River in south-western France (+43°16'59", -1°28'54") (De Gaudemar and Beall 1999). Behavioral observations and offspring sampling were performed from November 2012 to the end of March 2013, which corresponds to brown trout spawning season under this latitude. Three successive linear and communicating sections of the channel were used during the experiment, each measuring 10 meter long and 2.80 meters wide. The central section was fit out for spawning, with the appropriate gravel size (1 to 4 cm diameter), water depth (20 cm) and current speed (0.11 m.s^{-1}). In the two extreme sections, a more complex environment was installed with bigger substrate size, visual obstacles (wood, bricks) and pools that provided hiding and resting areas. Adult trout (19 males and 33 females) were captured in two Pyrenean rivers: River Bastan (France, +43°16'2.51", -1°22'32.46") and River Urumea (Spain, +43°14'31.81", -1° 55'28.98"). The adult sex ratio was female-biased in order to get a high number of spawning acts for a given number of fish. Upon electrofishing, each trout was anesthetized (30 mg.L^{-1} benzocaine), sexed by gentle abdominal pressure upon which males released some sperm, measured for fork length, weighed, and photographed to allow individual identification on subsequent video recordings. On waking, fish were released in the semi-natural river, where they were free to move until the end of the experiment. Electrofishing seemed to cause no serious damage to the adult fish, as all of them were still alive at the end of the experiment, and most of them were seen interacting on the videos or had their offspring sampled, which proved their contribution to spawning.

Behavioral data

The fish were observed for at least 15 min in the morning and in the evening from the bank, in order to detect behaviors associated to spawning activity. When reproductive behaviors indicating that a female and one/or several male(s) were close to spawning (digging female, chases between males), subaquatic (Bullet camera VB21 EH-W, sensor 1/3" Sony 960H Ex-view HAD CCD) and aerial videocameras (Sony Handycam DCR-SR90) were placed in the river or on the bank to record the spawning act (Aymes et al. 2010 https://www.youtube.com/user/Aymesetal2010/, Tentelier et al. 2011). Aerial cameras were hidden behind fences, less than 4 m away from where activity was detected. Since underwater cameras were placed in the channel less than 1 m from where activity was detected, the fish escaped but usually resumed activity after a few minutes. Graduated iron bars were placed on the substrate to estimate the size of acting individuals, and help for individual recognition.

Previous observations indicate that most interactions between individuals involved in a mating occasion occurred within one meter around the nest, and within the hour before egg laying, although some interactions could occur afterwards (Tentelier et al. 2011, 2016b). For each observed mating occasion (one female lays her eggs and at least one male releases sperm), up to three hours of videos were analyzed, 1h30 before gamete release and 1h30 thereafter in order to identify individuals involved in the visit process and in the gamete release process. To do so, a zone of one meter around the female's nest construction was defined. Individual recognition was performed by the same observers comparing pictures taken before the experiment to the image on the video. As body size, and black and red spot density and position vary consistently between individuals and do not change during the reproduction period, they were accurate tools for individual discrimination. Indeed, the conjunction of typical male or female behavior (nest digging, courting, egg or sperm release), body size and spot patterns left little room for ambiguousness in the recognition of individuals which were active in front of the camera (Gauthey et al. 2016). Such discrimination was however difficult when fish were too far from the camera, in which case they were labelled as "unknown" and their presence was not assigned to any known individual, and was ignored from the analysis. Individuals were considered present when they entered the 1 m-wide zone around the female's nest. They were considered absent when they were outside this zone. A male was considered to have visited a female on a given mating occasion if they were both present on the 1 m wide zone at least once during the three-hour period. The total number of visits observed during the experiment was stored in a males × females matrix. The simultaneous gamete release of both male and female was also stored in a males × females matrix. The behavioral survey ended when no reproductive behavior had been detected for one week.

Genetic data

At the end of the behavioral survey (February 15th 2013), adult fish were electrofished, and under anesthesia (30 mg.L^{-1} benzocaine), a small piece of pelvic fin was sampled and stored in 90% ethanol for molecular analysis. The abdomen of females was gently palpated to check whether they still carried eggs, and all individuals were released in the river where they had been captured in the first place. At emergence (800 degree. days: about two months after the last spawning event), juveniles stemming from the reproduction in the experimental channel were collected by either electrofishing or trapping at the downstream end of the experimental reach. They were anesthetized and killed under a lethal dose of 2-phenoxyethanol and placed individually in a tube of absolute ethanol (90%) upon molecular analysis. DNA extraction, PCR amplification and genotyping at eight microsatellite loci provided data for parentage analysis run on Cervus software (Kalinowski et al. 2007), as described in Gauthey et al. (2015). The parentage analysis resulted in the parental table, a males × females matrix figuring the number of offspring assigned to each pair.

Classical selection analysis

Behavioral and genetic data were analyzed using classical methods. We computed the opportunity for selection, as the ratio of variance in the number of offspring genetically assigned on its squared mean. Likewise, opportunity for sexual selection was computed as the ratio of variance in the number of genetic mates on its squared mean. The term "genetic mate" is hereafter used to refer to mates deduced from genetic assignation analysis. Bateman's gradient (β_{ss}) was measured using a simple linear regression between the number of offspring assigned and number of genetic mates. To quantify selection on individual phenotype, body size was regressed against the number of visits and the number of observed mates on videos, and on the number of offspring and number of genetic mates.

Statistical model

The general philosophy of the model was to consider reproduction between pairs of individuals as a series of K mating occasions, defined as events on which at least one male × female pair mated, i.e. the male visited the female, they emitted gametes simultaneously and produced offspring. So, each mating occasion consisted of three successive processes: visit (a Bernoulli variable indicating if male i visited female j on mating occasion k), gamete release (a Bernoulli variable indicating if male i and female j both emitted their gametes on mating occasion k), and the number of offspring produced (a Poisson variable, including zeros, describing the number of offspring produced by male i and female j on mating occasion k). Any pair could be involved in each process of any mating occasion so the three processes could be modelled as arrays, the dimensions of which were males, females and mating occasions. The effect of male and female body size, as well as random individual effects on each process conditional of the preceding one was then assessed with Bayesian inference.

Although behavioral data stored in matrices of visit and gamete release were only available for the K_{obs} mating occasions that were video recorded, genetic data on the number of offspring produced pool all K mating occasions, because offspring were sampled at the end of the spawning season. Hence, a first challenge to the model was to unfold the parental table (matrix of pairwise reproductive success) $N_{i,j}$ in K sub matrices, with K the total number of mating occasions that occurred in the mating season. We simply assumed that $N_{i,j} = \sum_{k=1}^{K} N_{i,j,k}$. However, behavioral data are generally incomplete: here the total number of mating occasions K ($K_{obs} \leq K$) as well as the probability p_o to observe a male i visiting a female j at each of the K_{obs} known mating occasions must be estimated. For the probability of observation, the occurrence of an observed visit $OE_{i,j,k}$ was modeled as $OE_{i,j,k} = E_{i,j,k} \times O_{i,j,k}$, where $E_{i,j,k}$ and $O_{i,j,k}$ were both binomial variables sampled in Bernoulli distributions of mean p_e and p_o, respectively the probability that the visit happened and the probability that it was observed. A zero $O_{i,j,k}$ meant we had no direct behavioral data, so visit rate and rate of gamete release

could not be directly estimated. In such case, we simply simulated the expected behavioral data using the posterior densities from estimated parameters for the K_{obs} mating occasions where behavioral data were known. The total number of mating occasions, K, could be estimated directly in the model because the posterior distribution revealed the best combination of behavioral and genetic data conditional on the value of K. When behavioral data were re-simulated from their posterior distribution, the value of K could therefore be jointly estimated.

We tested the additive effects of male and female body size (BS_i and BS_j) on visit rate ($E_{i,j,k}$), rate of gamete release ($G_{i,j,k}$) and offspring number ($N_{i,j,k}$) as following:

$$\text{logit}(E_{i,j,k}) = e_1 \times BS_i + f_1 \times BS_j + a_{1,i} + b_{1,j}$$
$$\text{logit}(G_{i,j,k}) = e_2 \times BS_i + f_2 \times BS_j + a_{2,i} + b_{2,j}$$
$$\log(N_{i,j,k}) = e_3 \times BS_i + f_3 \times BS_j + a_{3,i} + b_{3,j}$$

where $a_{.,i}$ and $b_{.,j}$ were male and female random effects, which were included to account for the fact that each individual could be involved in several mating occasions during the season. e_1, e_2, e_3 are the male body size effects on visit rate, rate of gamete release, and offspring number respectively, and f_1, f_2 and f_3 are the female body size effects likewise.

Statistical inference was conducted in the Bayesian framework under JAGS 4.1.0 (Plummer 2003). Two independent MCMC samples of 10000 draws with a thinning of 100 were used, with 5000 draws as a burning period, and another 5000 draws to obtain posterior estimates. Chain convergence was checked using the Gelman-Rubin potential scale reduction ($\sqrt{R}$), based on the within-chain and between-chains variances (Gelman and Rubin 1992). A value of $\sqrt{R}$ substantially above 1 indicates that the chain has not converged for the considered parameter. In each chain, we used non informative Gaussian and independent prior distributions (mean = 0, variance = 1000) for hyperparameters: e_1, e_2, e_3, f_1, f_2, f_3, informative Beta prior distribution $B(50,30)$ for p_o as we know from independent data using this setup that the detection probability is high, non informative Gamma distribution $G(0.001, 0.001)$ for the precision of each Gaussian distribution in which random effects (a_1, a_2, a_3, b_1, b_2, b_3) were drawn, and an informative uniform distribution [23,150] for K as we know that at least 22 mating occasions were actually observed and brown trout female of the size used in this study do not spawn more than 4 or 5 times per season. All parameters and their prior distributions are given in Table 1. The full model code is available in Supplementary File 2.

Results

Behavioral and genetic data analyzed independently

Three individuals (2 males and 1 female) were removed from the data set because they escaped from the experimental channel. This event happened during the two first

Table 1. Symbol, meaning, prior distribution, and 2.5%, 50% and 97.5% quantiles of posterior distribution for each hyperparameter used in the JAGS model for the analysis of sexual selection in brown trout. For prior distributions, parametrization is: Normal (m=mean, t=precision), Gamma (a=shape, b=rate), Beta (a=number of trials, b=number of successes) and Uniform (a=minimum, b=maximum). √R is Gelman and Rubin (1992) potential scale reduction which, when substantially higher than 1, indicates that the chain has not converged for the considered parameter.

Parameter	Meaning	Prior distribution	Posterior median [2.5% quantile; 97.5% quantile]	√R
e_1	Effect of male size on visit	Normal (0, 0.001)	-0.0009 [-0.015 ; 0.008]	1.01
e_2	Effect of male size on gamete release	Normal (0, 0.001)	0.009 [-0.005 ; 0.02]	1.01
e_2	Effect of male size on number of offspring	Normal (0, 0.001)	-0.001 [-0.011 ; 0.007]	1.02
f_1	Effect of female size on visit	Normal (0, 0.001)	-2.399E-02 [-3.450E-02 ; -8.921E-03]	1.01
f_2	Effect of female size on gamete release	Normal (0, 0.001)	-2.041E-02 [-3.402E-02 ; -5.834E-03]	1.04
f_2	Effect of female size on number of offspring	Normal (0, 0.001)	-1.155E-03 [-1.124E-02 ; 8.798E-03]	1.00
a_1	Precision of male random effect on visit	Gamma (0.001, 0.001)	1.61 [0.45 ; 7.53]	1.29
a_2	Precision of male random effect on gamete release	Gamma (0.001, 0.001)	1.57 [0.29 ; 348.1]	1.07
a_3	Precision of male random effect on number of offspring	Gamma (0.001, 0.001)	1.27 [0.42 ; 3.29]	1.10
b_1	Precision of female random effect on visit	Gamma (0.001, 0.001)	34.8 [14.9 ; 79.7]	1.11
b_2	Precision of female random effect on gamete release	Gamma (0.001, 0.001)	0.22 [0.07 ; 0.69]	1.50
b_3	Precision of female random effect on number of offspring	Gamma (0.001, 0.001)	0.89 [0.42 ; 1.88]	1.44
p_o	Probability of observing a mating event	Beta (50,30)	0.66 [0.56 ; 0.75]	1.01
K	Total number of mating events	Uniform (23, 150)	116 [82 ; 147]	1.00

weeks of the experiment when reproductive period just started and these individuals were not observed as sexually active on the videos. These three individuals were therefore discarded from the different analyses.

In total, 22 spawning acts were video recorded (K_{obs} mating occasions) during the reproductive season. Within these K_{obs} occasions, 14 females out of 32 and 12 males out of 17 were observed, totalizing 75 pairwise visits. Thirteen females and 7 males were observed releasing their gametes, totalizing 22 pairwise copulations. No multiple mating (where several males emit their gametes simultaneously) was observed. For five mating occasions, some individuals which did not release their gametes were too far from the camera to be unambiguously identified (1, 1, 2, 2 and 4 unidentified individuals for each occasion, respectively). These individuals were therefore not taken into account for the observations of visits. Abdominal palpation at recapture showed that almost all individuals (especially females) had released their gametes by the end of the experiment (only two females did not lay their eggs), and some nests were detected in places where we did not place our cameras, indicating that a significant proportion of spawning events was not observed.

A total of 555 juveniles and 49 parents were genotyped. Among those individuals, 551 juveniles were assigned to 41 pairs of parents (10 males and 22 females) at a confidence level of 95%. Number of offspring varied from 0 to 201 in males (mean ± sd= 32 ± 64) and between 0 and 86 for females (17 ± 24). Only 12 pairs were both seen releasing gametes and assigned offspring, so joint gamete release was assessed for 29 pairs by genetic data only. At the individual level, the number of gamete releases observed on video was correlated to the number of mates inferred from the genetic analysis (Pearson's r = 0.66, p < 0.0001). From the genetic data, the opportunity for selection was 4.49 for males and 2.34 for females. The opportunity for sexual selection was 2.69 for males and 0.81 for females. Bateman's gradient was 17.06 for males (t = 4.229 on 15 degrees of freedom, p = 0.0008) and 13.70 for females (t = 4.175 on 30 degrees of freedom, p = 0.0002).

The summary of the regressions of body size on components of reproductive success are given in Table 2. Using the behavioral data only, male body size seemed not to affect the number of females visited (Fig. 1a), but to affect positively the number of mates (Fig. 1c). Female body size affected neither the number of visiting males (Fig. 1b) nor the number of mates (Fig. 1d). Using the genetic data only, male body size was shown to have a positive effect on number of mates (Fig. 1c) and number of offspring (Fig. 1e), whereas female body size affected neither (Fig. 1d, f).

Behavioral and genetic data combined in the same model

The posterior of all parameters for the model are provided in Table 1, and predictions of numbers of visits, gamete releases and offspring based on these posterior are in Supplementary File 1. Gelman-Rubin potential scale reduction was close to one for all hyperparameters but was higher for the precision of the Normal distribution from which
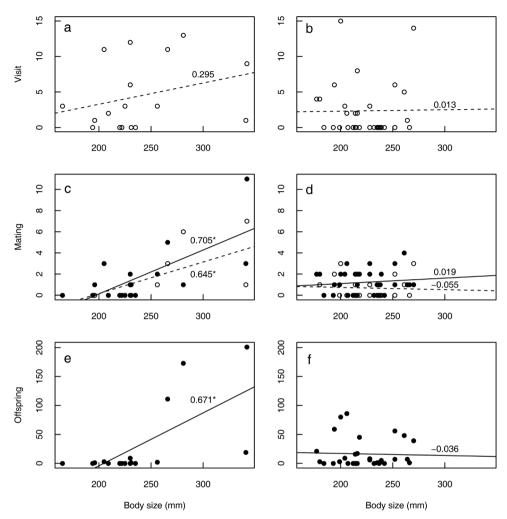
Figure 1. Linear regressions of brown trout body size against components of reproductive success for males (**a, c, e**) and females (**b, d, f**): the number of individuals of the opposite sex which were visited (**a, b**), the number of mates (**c, d**) and the number of offspring assigned (**e, f**). Open symbols and dashed lines are for behavioral data, and filled symbols and solid lines are for genetic data. For c and d, mating success was measured as the number of individuals of the opposite sex with which the focal individual was observed emitting gametes (open symbols, dashed line) and as the number of individuals with which it shared offspring (filled symbols, solid line). Values close to regression lines indicate the Pearson's correlation coefficient of the corresponding regression line, with asterisk indicating $p < 0.05$.

random effects were drawn, indicating that the Markov chains may have not converged for these hyperparameters. Although only 22 pairwise gamete releases were recorded on video and 41 families were detected by genetic analysis, the posterior distribution of K, the number of mating occasions, had a median of 117 [1st quartile = 103; 3rd quartile = 132]. The posterior distribution of the probability of observing a male visiting a

Table 2. Summary for the linear regressions of male and female brown trout body size on the number visits to or from individuals of the opposite sex observed on video recordings, number of gamete releases observed on video recordings, number of mates inferred from genetic assignation of offspring, and number of offspring genetically assigned.

Males		Estimate	Standard error	t value	p
Visits	Intercept	-2.718	6.077	-0.447	0.661
	Body size	0.030	0.025	1.195	0.251
Gamete releases	Intercept	-5.804	2.213	-2.623	0.019
	Body size	0.029	0.009	3.268	0.005
Genetic mates	Intercept	-8.170	2.612	-3.127	0.007
	Body size	0.041	0.011	3.851	0.002
Offspring	Intercept	-187.096	63.152	-2.963	0.010
	Body size	0.914	0.260	3.511	0.003
Females					
Visits	Intercept	1.895	6.260	0.303	0.764
	Body size	0.002	0.028	0.072	0.943
Gamete releases	Intercept	1.156	1.551	0.746	0.462
	Body size	-0.002	0.007	-0.304	0.763
Genetic mates	Intercept	0.068	1.756	0.039	0.969
	Body size	0.005	0.008	0.659	0.515
Offspring	Intercept	24.096	39.949	0.603	0.551
	Body size	-0.035	0.178	-0.198	0.845

female in a given mating occasion, p_o, had a median of 0.66 [0.63 ; 0.76]. Based on the joint posterior probabilities of all parameters (effects of male and female body size, and individual random effects), the model predicted 47 ± 25 (mean ± SD) visits per male, 25 ± 27 visits per female, 9.8 ± 8.4 gamete releases per male, 5.2 ± 8.2 gamete releases per female, 32 ± 36 offspring per male and 17 ± 33 offspring per female.

Male body size had no effect on the probability of visit or on the number of offspring produced at each mating occasion, and had a slight non-significant tendency to increase the probability of gamete release (Fig. 2). Female body size had a negative effect on both the probability of being visited and the probability of gamete release but did not affect the number of offspring produced (Fig. 2). The median of the posterior distributions on f_1 and f_2 were -0.02386 and -0.02126, resulting in odds of visit and gamete release being multiplied by 0.976 and 0.979, respectively, for each millimeter.
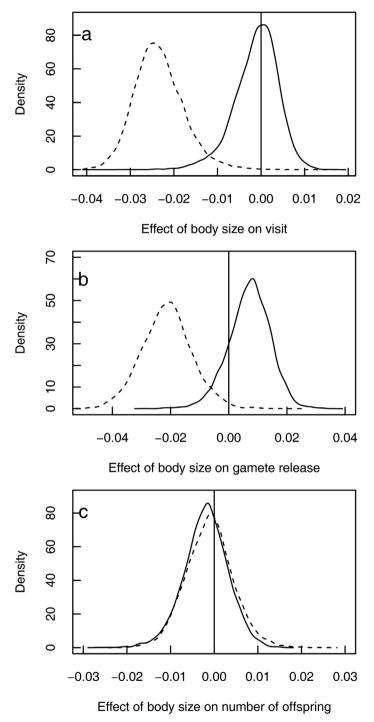
Figure 2. Posterior probability distributions of model parameters associated to the effect of brown trout body size on **a** the probability of visit **b** the probability of gamete release and **c** the number of offspring produced on each mating occasion. Dashed and solid lines are for females and males, respectively
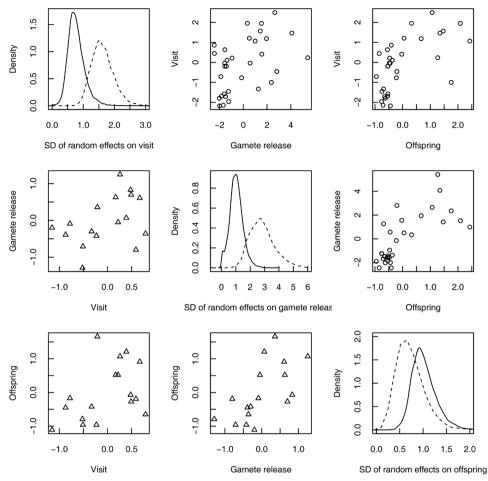
Figure 3. Random individual effects on the probability of visit, the probability of gamete release and the number of offspring produced by brown trout on each mating occasion. The diagonal indicates the posterior probability distribution of the standard deviation of the Gaussian distribution in which random effects for the three components of reproductive success were drawn (dashed and solid lines are for females and males, respectively). Plots above the diagonal show the pairwise relations between random individual effects on each process, for females (one circle per female). Plots below the diagonal show the same thing for males (one triangle per male).

Given that female body size ranged from 177 to 270 mm, the odds ratio between the longest and the shortest female would be 0.11 for visit and 0.14 for gamete release.

Random effects were more variable for females than for males for the probability of visit and the probability of gamete release, while male random effects were more variable than female's for the number of offspring (Fig. 3). Moreover, random effects on probability of visit, probability of gamete release and number of offspring were positively correlated for both sexes (Fig. 3). Because random effects for the probability of visit and gamete release act on the logit scale and random effects for the number of
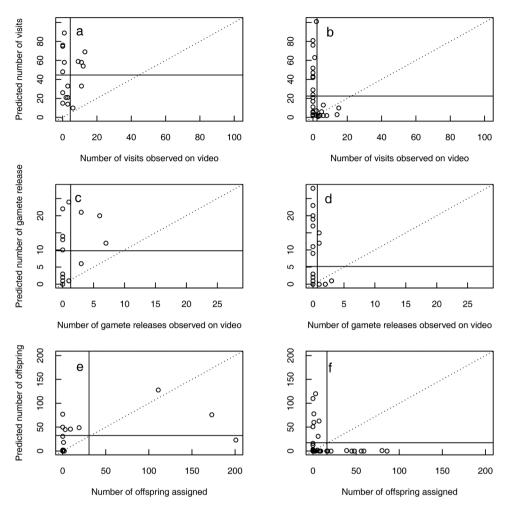
Figure 4. Predictions based on the joint posterior distributions of model parameters, against values observed in the raw data for the number of visits (**a, b**), the number of gamete releases (**c, d**) and the number of offspring (**e, f**) for brown trout males (**a, c, e**) and females (**b, d, f**). For each panel, solid lines indicate the mean of each variable, and the dashed line has intercept zero and slope one, which would correspond to a perfect correspondence between observed and predicted values.

offspring act on its logarithm, they should be interpreted such that individuals having a random effect of 0.5, 1, 2 or 4 have 1.6, 2.7, 7.4 or 54.6 times higher odds or more offspring than the average individual, respectively.

Joint posterior probability distributions were used to predict the number of visits, gamete releases and offspring for each individual and these predictions were plotted against the number of visits and gamete releases observed on videos and number of offspring genetically assigned (Fig. 4). In most cases, numbers predicted by the model exceeded the number of observations, but the number of offspring predicted by the model could be smaller than the number of offspring actually assigned, especially for females.

Discussion

In this study, we combined behavioral observations with genetic assignation of off-spring to estimate the effect of a phenotypic trait (here body size as an example in brown trout) on different components of sexual selection. On the one hand, we applied classical analyses on data pulled out from the marginal sums of each male × female matrix: number of visits and gamete releases observed on videos, and number of offspring and mates inferred from genetic assignation. There we found that body size, in males only, would correlate positively with mating success and offspring number, but not with visit rate. Because of the strong skew in mating data, and in particular the wealth of zeros, the classical regression approach probably suffers bias due to high leverage of a few successful individuals. On the other hand, we developed a statistical framework combining all these data, thereby enabling information to circulate through the successive processes of visit, gamete release and offspring production. This approach accounted for the three-dimensional structure of the data: males, females and mating occasions. This allowed a qualified definition of mating success, a more rigorous modelling of the many zeros in the dataset, and disentangling the joint effects of male and female phenotypes on the different components of reproductive success. There we found that body size, in females only, would correlate negatively with visit rate and mating success, but not with offspring number.

What is mating success?

The multiple definitions of mating success have been shaped by a dichotomy of approaches, which our model aimed at overcoming. On the one hand, because the classical approach based on the genetic parental table is oblivious to both ineffective mating acts and multiple inseminations between the same pair of individuals, it has constrained the definition of mating success to the number of individuals with which the focal individual produces offspring that are alive at sampling (Arnold and Duvall 1994). On the other hand, the more ethological approach based on the sole observation of copulatory behavior, unable to access the reproductive output, focused the definition of mating success on the number of copulations or number of copulatory partners (Fiske et al. 1998, Kutsukake and Nunn 2006, Thompson et al. 2011). By combining behavioral and genetic data in a common framework, our analysis embraced multiple aspects of mating success over the course of the experiment. Combining genetic data and behavioral observations in order to account for mating acts the offspring of which were not sampled was also adopted for instance by Collet et al. (2014) and Pélissié et al. (2014) but their approach relied on complete knowledge of copulation events in the mating group to disentangle the contribution of pre-copulatory and post-copulatory components of reproductive success. Our approach consisted in merging the behavioral and genetic datasets, both incomplete – a common situation in ecology and evolution –, and taking advantage of the conditional

structure of the successive components of mating success: visit, simultaneous gamete release and offspring production.

At the scale of the reproductive group, our behavioral observations showed 75 male × female visits and 22 pairwise gamete releases, whereas the parental table based on genetic assignation indicated that 41 broods were produced. Given that only 12 pairs both were observed copulating and had their offspring sampled, a rough estimate of the probability that a pair was observed mating would be 12/41 = 0.29, and a rough estimate of the probability of a pair having its offspring sampled would be 12/22 = 0.54. This would mean that 12/(0.29*0.54) = 76 mating events had occurred, 10 of which were video recorded only, 29 of which were detected genetically only, 12 of which were detected both on video and by the genetic analysis, and 25 were missed by both methods. In our model, the parameter K, called the number of mating occasions, was estimated to be 117, meaning that each pair had 117 occasions to mate. This concept of mating occasion, defined as an event on which any male × female pair *may* visit, emit gametes and produce offspring, was much broader than mating, defined as an event on which a male *does* visit a female, emit gamete with her and produce offspring with her. By splitting individual mating success in a number of mating occasions (trials), our modelling approach considered mating success as the result of a Bernoulli process, with inferences made on the probability of success. Moreover, this success of joint gamete release was conditioned on the success of visit on each occasion, and conditioned in turn the number of offspring produced. This conditional structure is in line with the concepts of "sexual networks" and "sexual niche" (McDonald et al. 2013, Ziv et al. 2016), which acknowledge that an individual interacts with (competes with, courts, chooses among) only a subset of the population. Hence, sexual selection should be measured among individuals that actually interact.

At the individual scale, the number of visits and gamete releases predicted by the model were higher than those observed in the raw data. This was expected, because it was one aim of the model to combine behavioral and genetic data to distinguish unobserved mating events from genuine non-mating. The model output indicates that males and females had approximately ten times as many visits and gamete releases as observed. On average, the number of offspring estimated by the model was the same as the number observed. However, they were not correlated at the individual level. A possible explanation for this lack of fit may be the failure of the Markov chains to converge towards stable estimates for the hyperparameters controlling the precision of the Normal distribution in which random effects were drawn (a_1, a_2, a_3, b_1, b_2, b_3). This was probably due to the sparsity of the data matrices, in which most rows and columns only had one or very few non-zero elements, meaning that we lack within-individual replication to estimate random effects properly. In polygynandrous systems such as brown trout's, this only could be solved by a stronger sampling effort. In other systems where individuals interact with very few mates, random effects are probably not worth modelling. Individual variance in mating success is the fuel for sexual selection, and the opportunity for sexual selection is computed as the variance in number of mates

on the squared mean of number of mates. Based on classical treatment of genetic data, opportunity for sexual selection was higher for males (2.69) than for females (0.81) as usually expected (Bateman 1948). However, our model indicated that both the probability of visit and the probability of gamete release on a mating occasion was more variable among females than among males, since the effect of body size and the individual random effects on theses probabilities were larger for females than for males. This counter-intuitive result may be due to the model predicting a higher mate number (gamete releases) than the sole genetic approach. Moreover, for both sexes random effects on the probability of visit, the probability of gamete release and the number of offspring produced were positively correlated. This suggests that some individuals performed consistently better than others for the three processes, i.e. had a higher probability of visit, a higher probability of gamete release once a partner was visited, and a higher number of offspring produced once mated, irrespective of body size. However, as discussed above, the Gelman-Rubin potential for scale reduction and the sparsity of the data matrices, with many rows or columns containing only one non-zero value suggest that the random effects were not well estimated.

Combined effects of male and female phenotype on the components of reproductive success

Sexual selection on phenotypic traits is classically quantified for each sex separately, by regressing the number of mates against phenotypic trait in a separate model for each sex (Andersson 1994). Here, the statistical unit is the individual, and individual mating success and reproductive success are assumed independent among individuals. However, mating and reproduction are essentially matters of pair, hence both male and female traits contribute to pairwise mating success and reproductive success on a given occasion. Our approach was therefore to consider the mating occasion as the statistical unit, and infer the effect of traits (here, body size) borne by individuals involved in that occasion on its outcome. This approach departs from selection theory, to which regression models fit well (Price 1970, Lande and Arnold 1983, Moorad and Wade 2013), but allows insight on the mechanisms by which traits affect reproductive success.

Applying classical linear regressions to our data indicated that larger males tended to have more visits, and had significantly more gamete releases, more genetic mates and more offspring, while female body size affected none of the behavioral or genetic indicators of reproductive success. However, our model accounting for the size of both males and females as well as individual random effects on each reproductive process indicated that larger females had a lower probability of being visited by males and a lower probability of gamete release, whereas male size affected neither visit, gamete release nor number of offspring. Hence the output of the two analyses differed greatly.

The difference between the linear regression approach and ours is due to three features of our model which lack in the classical approach: 1) conditioning of each process (visit, gamete release and offspring production) on the preceding one, 2) si-

multaneous estimation of the effect of male and female phenotype, and 3) random individual effects. First, the conditional structure of the model allowed to infer the effect of individual phenotype on each process independently, whereas regression made on all individuals may confound them. For instance, our analysis indicated that larger males tended to have a higher probability of releasing gametes with the females they visited, but once mated they did not tend to sire more offspring. According to the regression analysis, though, the number of offspring by males was positively related to their body size, but this relationship was indirect and mediated by the positive relation between number of mates and number of offspring a male could gain (Bateman gradient). Although reproductive success may be split into multiplicative components on each of which individual phenotype can be regressed, such analysis requires as many regressions as components (e.g. Arnold and Wade 1984a, Tentelier et al. 2016a), whereas our model encompasses them all. The second feature of our approach was to consider the mating occasion as the statistical unit, thereby assuming that the realization of each process was potentially attributable to both sexual partners, thereby decomposing the variance between both male and female body size effects. The consequences on the results are rather strong, since for instance, we detected that female body size was then negatively impacting both visit and mating processes. The third feature of our approach was the use of random effects on each process, which should have allowed a better decomposition of variance and avoided to falsely attribute variance to body size. The classical approach – which implies a pseudo-replication effect since the data are used twice, once for males, once for females - could see no effect of female body size. However, the modelling of individual random effects, although justified *a priori* in the polygynandrous system studied here, is probably the main weakness of our case study because the data matrices were to sparse to reach convergence on these parameters.

Now as to why female body size, for instance, had a negative effect on visit and gamete release probability, and no positive effect on offspring number, we must turn to the behavioral knowledge of the species. In particular, assortative or disassortative visit and mating, be it the result of mate choice, intrasexual competition or chance, is possible in brown trout (Petersson et al. 1999, Labonne et al. 2009): bigger females tend to be aggressively monopolized by bigger males, thereby limiting their access to a higher number of potential mates. Unfortunately our dataset is too small to properly infer the effect of interaction between male and female phenotype on the different components of reproductive success (Moshgani and Dooren 2011), though it is very easy to implement in the model (on our dataset, model including interaction did not converge at all).

Further applications of the approach

The experimental design and the quantity of data we used to illustrate our model indubitably constrained the analysis we carried out, and one can wonder how the approach can be transposed to other systems, with other types of data on either the components

of reproductive success or traits affecting them. In fact, we hope the approach presented in this study will encourage empiricists interested in sexual selection to collect data of different nature on different stages of the reproduction process, and combine them in *ad hoc* models, capitalizing on ours. For instance, because we sampled all offspring at the end of the experiment, the genetic data did not inform much on the number of offspring produced at each mating occasion. However, in other systems where clutches are well separated in time or space, even within a reproductive season, the parental table of genetic data would also be three-dimensional (male × female × occasion) and inferences on each component of reproductive success would probably be more accurate. Also, depending on the system studied, reproductive success may be further decomposed, and inference might be done on individual or environmental features affecting the additional components. For example, one may disentangle copulation from gamete fertilization by combining behavioral data and single-molecule PCR and genotyping of zygotes just after copulation. Here, an additional three-dimension matrix containing gamete fertilization of each male-female pair at each occasion would be built, and fertilization success would be included in the model, conditioned by copulation success, and conditioning the number of offspring. This would disentangle fertilization success from zygote survival, something we were not able to do in our case study on brown trout, and which would be useful in polygynandrous or promiscuous systems.

Regarding traits affecting components of reproductive success, we illustrated our approach with body size only, a trait which is known to affect intrasexual competition and intersexual preference in brown trout and other salmonids (Labonne et al. 2013). Other traits could have been used, like color, which is known to play a role in brown trout reproductive success (Jacquin et al. in press , Wedekind et al. 2008). In particular, dynamic traits could be included in our framework, since the statistical unit in our analysis is the mating occasion. Indeed, an individual could be allowed to bear a different trait value on each mating occasion, such as mating experience (Saleem et al. 2014), the outcome of previous intrasexual contests (Hsu et al. 2006), or energy stores (Gauthey et al. 2015). For example, sperm depletion may lead to reduced number of offspring sired by a male on late mating occasions without affecting probability of copulation (Damiens and Boivin 2006). Finally, each mating occasion may be characterized by a given environment which could affect each component of reproductive success, either directly or in interaction with individual phenotype. For instance, water turbidity may relax sexual selection on fish coloration (Seehausen et al. 1997, Candolin et al. 2007). Likewise, individual location and wind or water current on each day of the reproductive season may have an interactive effect on pairwise reproductive success through the probability of encounter between gametes (Dow and Ashley 1998, Kregting et al. 2014). This dynamic approach, based on mating occasion being the statistical unit, is also applicable to strictly monogamous species, in which the male and the female of a pair can meet each other successively in different environments and bearing different phenotypes.

Beyond the analysis of experimental data, the parameters estimated in a model such as the one presented here can readily be included in individual based models of sexual interaction, which implement mating as a stochastic process the success of

which may be influenced by the phenotype of both individuals involved (Piou and Prévost 2012, Courtiol et al. 2016). Hence, we hope our approach will facilitate the interaction between experimental and theoretical work on sexual selection.

AUTHOR CONTRIBUTION

ZG, CT and JL designed the experiment, collected and analyzed the data, and wrote the manuscript, OL analyzed the genetic data, AE designed the experiment and revised the manuscript, LR analyzed the behavioral data, SG ran the experimental facility. ZG: 25%, CT: 20%, OL: 10%, AE: 5%, LR: 10%, SG: 5%, JL: 25%.

Authors	Contribution	ACI
ZG	0.25	2
CT	0.2	1.5
OL	0.1	0.67
AE	0.05	0.32
LR	0.1	0.67
SG	0.05	0.32
JL	0.25	2

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References

Andersson M (1994) Sexual selection. Princeton University Press, 624 pp.

Arnold SJ (1994) Bateman's principles and the measurement of sexual selection in plants and animals. American Naturalist 144: 126–149. https://doi.org/10.1086/285656

Arnold SJ, Wade MJ (1984a) On the measurement of natural and sexual selection: Applications. Evolution 38: 720–734. https://doi.org/10.1111/j.1558-5646.1984.tb00345.x

Arnold SJ, Wade MJ (1984b) On the measurement of natural and sexual selection: Theory. Evolution 38: 709–719. https://doi.org/10.1111/j.1558-5646.1984.tb00344.x

Arnold SJ, Duvall D (1994) Animal mating systems: a synthesis based on selection theory. American Naturalist 143: 317–348. https://doi.org/10.1086/285606

Arnqvist G, Nilsson T (2000) The evolution of polyandry: multiple mating and female fitness in insects. Animal Behaviour 60: 145–164. https://doi.org/10.1006/anbe.2000.1446

Aymes JC, Larrieu M, Tentelier C, Labonne J (2010) Occurrence and variation of egg cannibalism in brown trout *Salmo trutta*. Naturwissenschaften 97: 435–439. https://doi.org/10.1007/s00114-010-0656-0

Bateman AJ (1948) Intra-sexual selection in Drosophila. Heredity 2: 349–368. https://doi.org/10.1038/hdy.1948.21

Candolin U, Salesto T, Evers M (2007) Changed environmental conditions weaken sexual selection in sticklebacks. Journal of Evolutionary Biology 20: 233–239. https://doi.org/10.1111/j.1420-9101.2006.01207.x

Charnov EL (1976) Optimal foraging, the marginal value theorem. Theoretical Population Biology 9(2): 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Collet JM, Dean RF, Worley K, Richardson DS, Pizzar T (2014) The measure and significance of Bateman's principles. Proceedings of the Royal Society B 281: 20132973. https://doi.org/10.1098/rspb.2013.2973

Coltman DW, Bancroft DR, Robertson A, Smith JA, Clutton-brock TH, Pemberton JM (1999) Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. Molecular Ecology 8: 1199–1209. https://doi.org/10.1046/j.1365-294x.1999.00683.x

Courtiol A, Etienne L, Feron R, Godelle B (2016) The evolution of mutual mate choice under direct benefits. American Naturalist 188: 521–538. https://doi.org/10.1086/688658

Crow JF (1989) Some possibilities for measuring selection intensities in man. Human Biology 61: 763–775.

Damiens D, Boivin G (2006) Why do sperm-depleted parasitoid males continue to mate? Behavioral Ecology17: 138–143. https://doi.org/10.1093/beheco/arj009

De Gaudemar B, Beall E (1999) Reproductive behavioural sequences of single pairs of Atlantic salmon in an experimental stream. Animal Behaviour 57: 1207–1217. https://doi.org/10.1006/anbe.1999.1104

Dow BD, Ashley MV (1998) Factors influencing male mating success in bur oak, Quercus macrocarpa. New For. 15: 161–180. https://doi.org/10.1023/A:1006557904751

Fiske P, Rintamäki PT, Karvonen E (1998) Mating success in lekking males: a meta-analysis. Behavioral Ecology 9: 328–338. https://doi.org/10.1093/beheco/9.4.328

Franklin AM, Squires ZE, Stuart-Fox D (2012) The energetic cost of mating in a promiscuous cephalopod. Biology Letters 8: 754–756. https://doi.org/10.1098/rsbl.2012.0556

Fritzsche K, Booksmythe I (2013) The measurement of sexual selection on females and males. Current Zoology 59: 558–563. https://doi.org/10.1093/czoolo/59.4.558

Garant D, Dodson JJ, Bernatchez L (2001) A genetic evaluation of mating system and determinants of individual reproductive success in Atlantic salmon (Salmo salar L.). Journal of Heredity 92: 137–145. https://doi.org/10.1093/jhered/92.2.137

Gauthey Z, Freychet M, Manicki A, Herman A, Lepais O, Panserat S, Elosegi A, Tentelier C, Labonne J (2015) The concentration of plasma metabolites varies throughout reproduction and affects offspring number in wild brown trout (*Salmo trutta*). Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 184: 90–96. https://doi.org/10.1016/j.cbpa.2015.01.025

Gauthey Z, Panserat S, Elosegi A, Herman A, Tentelier C, Labonne J (2016) Experimental evidence of population differences in reproductive investment conditional on environmental stochasticity. Science of The Total Environment 541: 143–148. https://doi.org/10.1016/j.scitotenv.2015.09.069

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Statistical Science 7: 457–472. https://doi.org/10.1214/ss/1177011136

Gowaty PA, Yong-Kyu Kim Y-K, Anderson WW (2012) No evidence of sexual selection in a repetition of Bateman's classic study of Drosophila melanogaster. PNAS 109: 11740–11745. https://doi.org/10.1073/pnas.1207851109

Hsu Y, Earley RL, Wolf LL (2006) Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. Biological Reviews 81: 33–74. https://doi.org/10.1017/S146479310500686X

Jacob A, acob A, Nusslé S, Britschgi A, Evanno G, Müller R, Wedekind C (2007) Male dominance linked to size and age, but not to "good genes" in brown trout (*Salmo trutta*). BMC Evolutionary Biology 7: 207. https://doi.org/10.1186/1471-2148-7-207

Jacquin L et al. (in press) Melanin in a changing world: coloration of brown trout predicts their reproductive success in variable environments.

Jennions MD, Jennions MD, Kokko H, Klug H (2012) The opportunity to be misled in studies of sexual selection. Journal of Evolutionary Biology 25: 591–598. https://doi.org/10.1111/j.1420-9101.2011.02451.x

Jones AG (2009) On the opportunity for sexual selection, the Bateman gradient and the maximum intensity of sexual selection. Evolution 63: 1673–1684. https://doi.org/10.1111/j.1558-5646.2009.00664.x

Jones AG, Ardren WR (2003) Methods of parentage analysis in natural populations. Molecular Ecology 12: 2511–2523. https://doi.org/10.1046/j.1365-294X.2003.01928.x

Jones AG, Arguello JR, Arnold SJ (2004) Molecular parentage analysis in experimental newt populations: the response of mating system measures to variation in the operational sex ratio. American Naturalist 164: 444–456. https://doi.org/10.1086/423826

Jonsson N, Jonsson B (1999) Trade-off between egg mass and egg number in brown trout. Journal of Fish Biology 55: 767–783. https://doi.org/10.1111/j.1095-8649.1999.tb00716.x

Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16: 1099–1106. https://doi.org/10.1111/j.1365-294X.2007.03089.x

Klug H, Heuschele J, Jennions MD, Kokko H (2010) The mismeasurement of sexual selection. Journal of Evolutionary Biology 23: 447–462. https://doi.org/10.1111/j.1420-9101.2009.01921.x

Kokko H, Mackenzie A, Reynolds JD, Lindström J, Sutherland WJ (1999) Measures of inequality are not equal. American Naturalist 154: 358–382. https://doi.org/10.1086/303235

Kregting LT, Thomas FI, Bass AL, Yund PO (2014) Relative effects of gamete compatibility and hydrodynamics on fertilization in the green sea urchin *Strongylocentrotus droebachiensis*. Biological Bulletin 227: 33–39. https://doi.org/10.1086/BBLv227n1p33

Kutsukake N, Nunn CL (2006) Comparative tests of reproductive skew in male primates: the roles of demographic factors and incomplete control. Behavioral Ecology and Sociobiology 60: 695–706. https://doi.org/10.1007/s00265-006-0213-1

Labonne J, Augery M, Parade M, Brinkert S, Prevost E, Héland M, Beall E (2009) Female preference for male body size in brown trout, *Salmo trutta*: is big still fashionable? Animal Behaviour 77: 129–137. https://doi.org/10.1016/j.anbehav.2008.09.018

Labonne J, Régnier T, Tentelier C (2013) Reproductive system in brown trout: ongoing evolution? In: Polakof S, Moon TW (Eds) Trout: from Physiology to Conservation. Nova Science Publishers, 351–371.

Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. Evolution 37: 1210–1226. https://doi.org/10.1111/j.1558-5646.1983.tb00236.x

Magnhagen C (1991) Predation risk as a cost of reproduction. Trends in Ecology & Evolution 6: 183–186. https://doi.org/10.1016/0169-5347(91)90210-O

McDonald GC, James R, Krause J, Pizzari T (2013) Sexual networks: measuring sexual selection in structured, polyandrous populations. Philosophical Transactions of the Royal Society of London B: Biological Sciences 368(1613): 20120356. https://doi.org/10.1098/rstb.2012.0356

Moorad JA, Wade MJ (2013) Selection Gradients, the Opportunity for Selection, the Coefficient of Determination. American Naturalist 181: 291–300. https://doi.org/10.1086/669158

Moshgani M, Dooren TJMV (2011) Maternal and paternal contributions to egg size and egg number variation in the blackfin pearl killifish Austrolebias nigripinnis. Evolutionary Ecology 25: 1179–1195. https://doi.org/10.1007/s10682-011-9469-7

Parker PG, Tang-Martinez Z (2005) Bateman Gradients in Field and Laboratory Studies: A Cautionary Tale. Integrative and Comparative Biology 45: 895–902. https://doi.org/10.1093/icb/45.5.895

Pélissié B, Jarne P, Sarda V, David P (2014) Disentangling precopulatory and postcopulatory sexual selection in polyandrous species. Evolution 68: 1320–1331. https://doi.org/10.1111/evo.12353

Pemberton JM, Albon SD, Guinness FE, Clutton-Brock TH, Dover GA (1992) Behavioral estimates of male mating success tested by DNA fingerprinting in a polygynous mammal. Behavioral Ecology 3: 66–75. https://doi.org/10.1093/beheco/3.1.66

Petersson E, Järvi T, Olsén H, Mayer I I, Hedenskog M (1999) Male-male competition and female choice in brown trout. Animal Behaviour 57: 777–783. https://doi.org/10.1006/anbe.1998.1043

Piou C, Prévost E (2012) A demo-genetic individual-based model for Atlantic salmon populations: Model structure, parameterization and sensitivity. Ecological Modelling 231: 37–52. https://doi.org/10.1016/j.ecolmodel.2012.01.025

Pischedda A, Rice WR (2012) Partitioning sexual selection into its mating success and fertilization success components. PNAS 109: 2049–2053. https://doi.org/10.1073/pnas.1110841109

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd international workshop on distributed statistical computing Vol. 124, 8 pp.

Poiani A, Wilks C (2000) Sexually Transmitted Diseases: A Possible Cost of Promiscuity in Birds? The Auk 117: 1061–1065. https://doi.org/10.1642/0004-8038(2000)117[1061:STDAPC]2.0.CO;2

Price GR (1970) Selection and covariance. Nature 227: 520–521. https://doi.org/10.1038/227520a0

Saleem S, Ruggles PH, Abbott WK, Carney GE (2014) Sexual Experience Enhances Drosophila melanogaster Male Mating Behavior and Success. PLOS ONE 9: e96639. https://doi.org/10.1371/journal.pone.0096639

Seehausen O, Van Alphen JJ, Witte F (1997) Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science 277: 1808–1811. https://doi.org/10.1126/science.277.5333.1808

Serbezov D, Bernatchez L, Olsen EM, Vøllestad LA (2010) Mating patterns and determinants of individual reproductive success in brown trout (*Salmo trutta*) revealed by parentage analysis of an entire stream living population. Molecular Ecology 19: 3193–3205. https://doi.org/10.1111/j.1365-294X.2010.04744.x

Tentelier C, Larrieu M, Aymes JC, Labonne J (2011) Male antagonistic behaviour after spawning suggests paternal care in brown trout, *Salmo trutta*. Ecology of Freshwater Fish 20: 580–587. https://doi.org/10.1111/j.1600-0633.2011.00507.x

Tentelier C, Lepais O, Larranaga N, Manicki A, Lange F, Rives J (2016a) Sexual selection leads to a tenfold difference in reproductive success of alternative reproductive tactics in male Atlantic salmon. The Science of Nature 103: 47. https://doi.org/10.1007/s00114-016-1372-1

Tentelier C, Aymes JC, Spitz B, Rives J. (2016b) Using proximity loggers to describe the sexual network of a freshwater fish. Environmental Biology of Fishes 99: 621–631. https://doi.org/10.1007/s10641-016-0504-y

Thompson DJ, Hassall C, Lowe CD, Watts PC (2011) Field estimates of reproductive success in a model insect: behavioural surrogates are poor predictors of fitness. Ecology Letters 14: 905–913. https://doi.org/10.1111/j.1461-0248.2011.01655.x

Uller T, Olsson M (2008) Multiple paternity in reptiles: patterns and processes. Molecular Ecology 17: 2566–2580. https://doi.org/10.1111/j.1365-294X.2008.03772.x

Wade MJ (1979) Sexual selection and variance in reproductive success. American Naturalist 114: 742–747. https://doi.org/10.1086/283520

Wade MJ, Arnold SJ (1980) The intensity of sexual selection in relation to male sexual behaviour, female choice, sperm precedence. Animal Behaviour 28: 446–461. https://doi.org/10.1016/S0003-3472(80)80052-2

Wedekind C, Jacob A, Evanno G, Nusslé S, Müller R (2008) Viability of brown trout embryos positively linked to melanin-based but negatively to carotenoid-based colours of their fathers. Proceedings of the Royal Society of London B: Biological Sciences 275: 1737–1744. https://doi.org/10.1098/rspb.2008.0072

Ziv EB, Ilany A, Demartsev V, Barocas A, Geffen E, Koren L (2016) Individual, social, sexual niche traits affect copulation success in a polygynandrous mating system. Behavioral Ecology and Sociobiology 70: 901–912. https://doi.org/10.1007/s00265-016-2112-4

Supplementary material 1

Data and model outputs

Authors: Zoé Gauthey, Cédric Tentelier, Olivier Lepais, Arturo Elosegi, Laura Royer, Stéphane Glise, Jacques Labonne

Data type: Body size, behavioural and genetic data, and model output.

Explanation note: The first page of this spreadsheet shows, for each individual, its body size, the number of visits and gamete releases observed on video, the number of offspring genetically assigned as well as the model output for visits, gamete releases and number of offspring: individual random effect, mean, median and standard deviation of model prediction. The second, third and fourth pages show the male x female matrices for visits, gamete releases and number of offspring, respectively.

Link: https://doi.org/10.3897/rethinkingecology.2.14956.suppl1

Supplementary material 2

JAGS code for the model

Authors: Zoé Gauthey, Cédric Tentelier, Olivier Lepais, Arturo Elosegi, Laura Royer, Stéphane Glise, Jacques Labonne

Data type: Programming code.

Explanation note: This file contains the commented code for running the model in JAGS 4.0 (can also be opened in a text editor). It contains the data (vectors of body size, matrices of observed visits, gamete releases and offspring). Initial values of parameters for simulations are not included but are available upon request.

Link: https://doi.org/10.3897/rethinkingecology.2.14956.suppl2