

1 **With our powers combined: integrating behavioral and**  
2 **genetic data to estimate mating success and sexual**  
3 **selection.**

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5 **Zoé Gauthey, Cédric Tentelier, Olivier Lepais, Arturo Elosegi, Laura Royer, Stéphane**  
6 **Glise and Jacques Labonne.**

7 *Z. Gauthey, O. Lepais, C. Tentelier, L. Royer, S. Glise and J. Labonne , UNIV PAU & PAYS*  
8 *ADOUR, INRA, UMR 1224, Ecologie Comportementale et Biologie des Populations de*  
9 *Poissons, Aquapôle, quartier Ibarron, 64310 Saint-Pée sur Nivelle, France.*

10 *A. Elosegi, Faculty of Science and Technology, University of the Basque Country UPV/EHU,*  
11 *48080 Bilbao, Spain.*

12 Corresponding author: C. Tentelier. ORCID ID: [orcid.org/0000-0003-2178-4900](https://orcid.org/0000-0003-2178-4900)

13

## 14 **Abstract**

15 The analysis of sexual selection classically relies on the regression of individual phenotypes  
16 against the marginal sums of a males  $\times$  females matrix of pairwise reproductive success,  
17 assessed by genetic parentage analysis. When the matrix is binarized, the marginal sums give  
18 the individual mating success. Because such analysis treats male and female  
19 mating/reproductive success independently, it ignores that the success of a male  $\times$  female  
20 sexual interaction can be attributable to the phenotype of both individuals. Also, because it is  
21 based on genetic data only, it is oblivious to costly yet unproductive matings, which may be  
22 documented by behavioral observations. To solve these problems, we propose a statistical  
23 model which combines matrices of offspring numbers and behavioral observations. It models  
24 reproduction on each mating occasion of a mating season as three stochastic and  
25 interdependent pairwise processes, each potentially affected by the phenotype of both  
26 individuals and by random individual effect: encounter (Bernoulli), concomitant gamete  
27 emission (Bernoulli), and offspring production (Poisson). Applied to data from a mating  
28 experiment on brown trout, the model yielded different results from the classical regression  
29 analysis, with only a limited effect of male body size on the probability of gamete release and  
30 a negative effect of female body size on the probability of encounter and gamete release.  
31 Because the general structure of the model can be adapted to other partitioning of the  
32 reproductive process, it can be used for a variety of biological systems where behavioral and  
33 genetic data are available.

## 34 **Keywords**

35 Bateman gradient; fish; mate choice

36

## 37 **Introduction**

38 Sexual reproduction involves two different individuals which both invest energy in gamete  
39 encounter and possibly in offspring survival. The reproductive output of a given mating is  
40 therefore attributable to both partners. In a given population, the distribution of the  
41 reproductive success  $RS_{i,j,k}$  gained by a pair of individuals  $i$  and  $j$  on a mating occasion  $k$  can  
42 be summarized by a 3-dimension array of number of offspring produced between all possible  
43 pairs of males and females for each mating occasion. Then, summing such array over all the  
44 mating occasions leads to the so-called *parental table* classically used in studies of sexual  
45 selection (Arnold and Duvall 1994). An estimate of such matrix is typically generated by  
46 parentage analysis based on genetic markers (Bateman 1948, Garant et al. 2001, Avise et al.  
47 2002, Jones and Ardren 2003, Jones et al. 2004, Serbezov et al. 2010) possibly complemented  
48 by direct observations of mating behavior (Pemberton et al. 1992, Coltman et al. 1999, Collet  
49 et al. 2014).

50 Classical methods in sexual selection use these parental tables to study adaptive value of traits  
51 in populations by measuring different indices of sexual selection in males and females such as  
52 opportunity for selection, selection gradients and selection differentials (Bateman 1948, Wade  
53 1979, Wade and Arnold 1980, Crow 1989). To do so, they further reduce the matrix to its  
54 margins, individual reproductive success being the sum of offspring on the individual's row or  
55 column, and mating success being the number of positive cells on the individual's row or  
56 column, *i.e.* the number of different individuals with which at least one offspring was  
57 produced. Sexual selection is predicted to operate provided there is variance in reproductive  
58 success and in mating success, and a strong link between these two. Likewise, a phenotypic  
59 trait is considered to be sexually selected when it covaries with mating success.

60 This approach has two important caveats. First, the definition of mating as the occurrence of  
61 common offspring does not account for multiple - possibly unfertile - matings, which are part  
62 of the cost of reproduction. Second, the lack of consideration for the fundamental dependency  
63 between the mating and reproductive success of an individual and the mating and  
64 reproductive success of its mates biases the estimation of selection acting on individual traits.

65 An illustration of the first caveat is the wealth of definitions for individual mating success  
66 during one reproductive period (Bateman 1948, Arnold and Duvall 1994, Parker and Tang-  
67 Martinez 2005, Uller and Olsson 2008, Jones 2009, Gowaty et al. 2012, Fritzsche and  
68 Booksmythe 2013). Mating success can either be viewed as the number of copulations, the  
69 number of different individuals with which the focal individual has copulated, the number of  
70 copulations that yield progeny or the number of individuals with which progeny is produced.

71 While the two latter definitions inform precisely on the fitness benefits, the first and second  
72 definitions also integrate potential costs, be it time, energy, predation risk, or disease  
73 transmission. Because benefits and costs are both essential to understand the evolution of  
74 sexual selection, it should be of interest to study both points of view in a single framework to  
75 estimate sexual selection indices. It is noteworthy that the definition of mating success is to a  
76 great extent constrained by methodological possibilities. Standard methodological approaches  
77 using parental tables obtained from genetic assignments can only target the fourth definition  
78 and generally produce biased estimates of it (Collet et al. 2014). These approaches deduce  
79 individual mating success by counting the number of non-zero elements on the individual line  
80 of the parental table. In this case, a zero value for a given pair can be the outcome of either  
81 pre-copulatory, post-copulatory or sampling processes: no copulation, copulation but no  
82 gamete fertilization, gamete fertilization but offspring dying before sampling, offspring alive  
83 but failing to be sampled. Similarly, a non-zero value can also carry more information than  
84 just the total reproductive success between a pair of individuals, since it can be the outcome of

85 a variable number of matings, which is of importance to measure reproductive investment. In  
86 this perspective, matrices of copulation success as obtained by direct observations of mating  
87 behavior obviously contain data that are complementary to parentage assignment methods  
88 (Collet et al. 2014). We therefore need statistical models integrating both behavioral and  
89 genetic data to provide estimates of the various definitions of mating success, by  
90 disentangling pre-copulatory and post-copulatory components as already suggested by several  
91 authors (Arnold and Wade 1984, Pischedda and Rice 2012, Pélissié et al. 2014).

92 The second caveat is less evoked in the literature although intuitively simple: in sexual  
93 reproduction, reproductive success between two individuals should be attributable to both.  
94 Yet, one usually analyzes reproductive success as an individual characteristic, with no regard  
95 for the effect of the sexual partner. Classical studies only focus on the marginal sums of the  
96 parental table, and therefore cannot control for sexual partner trait or mating success variation.  
97 Selection indices are estimated by regressing the margins of the parental table against the  
98 vector of values of phenotypic traits, independently for males and females. A direct  
99 consequence is that we might detect a significant correlation between a trait and mating  
100 success or reproductive success for a sex, and interpret it as evidence of direct selection,  
101 whereas indirect selection could for instance be at work by mean of non-random association  
102 between sexual partners' traits. We therefore need an approach in which the mating and  
103 reproductive success of a pair of individuals accounts for the phenotype of both individuals,  
104 instead of using twice the same data to draw seemingly independent conclusions.

105 To solve both matters, we propose a model that combines genetic data (parental table) and  
106 behavioral data (encounter and mating matrix) to 1) describe the different components of  
107 reproductive success (here encounter rate, rate of gamete release, number of offspring  
108 produced) for each mating occasion within the reproductive season, and 2) infer the joint

109 effects of both male and female phenotype on each component of the reproductive success.  
110 The conditional structure linking the successive components of pairwise reproductive success  
111 is the key to extract information from both behavioral and genetic data: presence of offspring  
112 from a pair of parents implies encounter and gamete release, even if these are absent from  
113 behavioral data, whereas observation of gamete release despite the absence of common  
114 offspring allows distinguishing between zero-value due pre-copulatory and post-copulatory  
115 mechanisms. We illustrate the model using a reproduction experiment data for *Salmo trutta* as  
116 a case study, with body size as an example of phenotypic covariate as it is known to be  
117 involved in sexual selection in salmonids (Jacob et al. 2007, Labonne et al. 2009) and could  
118 therefore have an effect on each of these components of sexual selection. More precisely,  
119 larger males were expected to have a higher probability of encounter and mating with females  
120 because they could oust smaller males from nesting sites. In cases of multiple mating (several  
121 males ejaculate over a female's eggs), they were also expected to sire more offspring than  
122 smaller males because their closer proximity with females during spawning gives them an  
123 advantage in sperm competition. Larger females may be expected to have a higher probability  
124 of encounter because they may attract more males than smaller females. However, larger  
125 females may not have a higher probability of mating. Because body size is highly correlated  
126 with the number of eggs, larger females were expected to produce more offspring.

## 127 **Methods**

### 128 **Reproduction experiment**

129 The experiment was conducted in semi-natural channel beside Lapitxuri stream, a tributary to  
130 the Nivelle River in south-western France (+43° 16' 59", -1° 28' 54") (De Gaudemar and Beall  
131 1999), from November 2012 to the end of March 2013 (brown trout spawning season under  
132 this latitude). The experimental setup is the one used in the “constant environment” treatment

133 in Gauthey et al. (2016). Three linear and communicating sections of the channel were used  
134 during the experiment, each measuring 10 meter long and 2.80 meters wide. The central  
135 section was fit out for spawning, with the appropriate gravel size (1 to 4 cm diameter), water  
136 depth (20 cm) and current speed ( $0.11 \text{ m.s}^{-1}$ ). In the two extreme sections, a more complex  
137 environment was installed with bigger substrate size, visual obstacles (woods, bricks) and  
138 pools that provided hiding and resting areas. The parent pool consisted in 52 brown trout  
139 adults (19 males and 33 females) captured in two rivers: River Bastan ( $+43^{\circ} 16' 2.51''$ ,  $-1^{\circ} 22'$   
140  $32.46''$ ) and River Urumea ( $+43^{\circ} 14' 31.81''$ ,  $-1^{\circ} 55' 28.98''$ ). Upon electrofishing, each trout  
141 was anesthetized ( $30 \text{ mg.l}^{-1}$  benzocaine), sexed, measured for fork length, weighed, and  
142 photographed to allow individual identification on subsequent video recordings. On waking,  
143 fish were released in the three section of the semi-natural river, where they were free to move  
144 until the end of the experiment.

#### 145 **Behavioral data**

146 The fish were observed for at least 15 min in the morning and in the evening from the bank, in  
147 order to detect behaviors associated to spawning activity. When reproductive behaviors  
148 indicating that a female and one/or several male(s) were close to spawning (digging female,  
149 chases between males), subaquatic and aerial digital camera videos were placed in the river or  
150 on the bank in order to record the spawning act (Aymes et al. 2010, Tentelier et al. 2011).

151 For each observed mating occasion (one female lays her eggs and at least one male releases  
152 sperm), up to 3 hours of videos were analyzed, 1h30 before gamete release and 1h30  
153 thereafter in order to identify individuals involved in the encounter process and in the gamete  
154 release process. To do so, a zone of one meter around the female's nest construction was  
155 defined. Individual recognition was performed by comparing pictures took before the  
156 experiment to the image on the video. As black and red spot density and position vary

157 consistently between individuals and do not change during the reproduction period, they were  
158 accurate tools for individual discrimination. Such discrimination was however difficult when  
159 fish were too far from the camera, in which case they were labelled as “unknown” (about 30%  
160 of observations). Individuals were considered present when they entered the zone. They were  
161 considered absent when they were outside the zone. A female and a male were considered to  
162 have encountered each other on a given mating occasion if they were both present on the zone  
163 at least once during the three-hour period. The total number of encounters observed during the  
164 experiment was stored in a males  $\times$  females matrix. The simultaneous gamete release of both  
165 male and female was also stored in a males  $\times$  females matrix. The term “observed mate” will  
166 be hereafter used to refer to individuals that have actually been seen copulating together. The  
167 behavioral survey ended when no reproductive behavior had been detected for one week.

#### 168 **Genetic data**

169 At emergence (800 degree.days: about two months after the last spawning event), juveniles  
170 stemming from the reproduction in the experimental channel were collected by either  
171 electrofishing or trapping at the downstream end of the experimental reach. They were  
172 anesthetized and killed under a lethal dose of 2-phenoxyethanol and placed individually in a  
173 tube of absolute ethanol (90°) upon molecular analysis. A small piece of pelvic fin was also  
174 taken on adults and stored in 90% ethanol upon molecular analysis. DNA extraction, PCR  
175 amplification and genotyping at eight microsatellite loci provided data for parentage analysis  
176 run on Cervus software (Kalinowski et al. 2007), as described in Gauthey et al. (2015). The  
177 parentage analysis resulted in the parental table, a males  $\times$  females matrix figuring the number  
178 of offspring assigned to each pair.

#### 179 **Classical selection analysis**



180 Behavioral and genetic data were analyzed using classical methods. We computed the  
181 opportunity for selection, as the ratio of variance in the number of offspring genetically  
182 assigned on its squared mean. Likewise, opportunity for sexual selection was computed as the  
183 ratio of variance in the number of genetic mates on its squared mean. The term “genetic mate”  
184 is hereafter used to refer to mates deduced from genetic assignment analysis. Bateman’s  
185 gradient ( $\beta_{ss}$ ) was measured using a simple linear regression between the number of offspring  
186 assigned and number of genetic mates. To quantify selection on individual phenotype, body  
187 size was regressed against the number of encounters and the number of observed mates on  
188 videos, and on the number of offspring and number of genetic mates.

## 189 **Statistical model**

190 The general philosophy of the model was to consider reproduction between pairs of  
191 individuals as a series of  $K$  mating occasions, defined as events on which at least one male x  
192 female pair mated, *i.e.* encountered, emitted gametes simultaneously and produced offspring.  
193 So, each mating occasion consisted of three successive processes: encounter (a binomial  
194 variable indicating if male  $i$  met female  $j$  on mating occasion  $k$ ), gamete release (a binomial  
195 variable indicating if male  $i$  and female  $j$  both emitted their gametes on mating occasion  $k$ ),  
196 and the number of offspring produced (a discrete quantitative non negative variable  
197 describing the number of offspring produced by male  $i$  and female  $j$  on mating occasion  $k$ ).  
198 Any pair could be involved in each process of any mating occasion so the three processes  
199 could be modelled as arrays, the dimensions of which were males, females and mating  
200 occasions. The effect of male and female body size, as well as random individual effects on  
201 each process conditional of the preceding one was then assessed with Bayesian inference.

202 Although behavioral data stored in matrices of encounter and gamete release were only  
203 available for the  $K_{obs}$  mating occasions that were video recorded, genetic data on the number

204 of offspring produced pool all  $K$  mating occasions, because offspring were sampled at the end  
205 of the spawning season, as it is often the case. Hence, a first challenge to the model was to  
206 unfold the parental table (matrix of pairwise reproductive success)  $N_{i,j}$  in  $K$  sub matrices, with  
207  $K$  the total number of mating occasions that occurred in the mating season. We simply  
208 assumed that  $N_{i,j} = \sum_{k=1}^K N_{i,j,k}$ . However, behavioral data are generally incomplete: here the  
209 total number of mating occasions  $K$  ( $K_{obs} \leq K$ ) as well as the probability  $p_o$  to observe  
210 encounter between a male  $i$  and a female  $j$  at each of the  $K_{obs}$  known mating occasions must  
211 be estimated. For the probability of observation, the occurrence of an observed encounter  
212  $OE_{i,j,k}$  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  
213 variables sampled in Bernoulli distributions of mean  $p_e$  and  $p_o$ , respectively the probability  
214 that the encounter happened and the probability that it was observed. A zero  $O_{i,j,k}$  meant we  
215 had no direct behavioral data, so encounter rate and rate of gamete release could not be  
216 directly estimated. In such case, we simply simulated the expected behavioral data using the  
217 posterior densities from estimated parameters for the  $K_{obs}$  mating occasions where behavioral  
218 data were known. The total number of mating occasions,  $K$ , could be estimated directly in the  
219 model because the posterior distribution revealed the best combination of behavioral and  
220 genetic data conditional on the value of  $K$ . When behavioral data were re-simulated from their  
221 posterior distribution, the value of  $K$  could therefore be jointly estimated.

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

$$224 \quad \text{logit}(E_{i,j,k}) = e_1 \times BS_i + f_1 \times BS_j + a_{1,i} + b_{1,j}$$

$$225 \quad \text{logit}(G_{i,j,k}) = e_2 \times BS_i + f_2 \times BS_j + a_{2,i} + b_{2,j}$$

$$226 \quad \log(N_{i,j,k}) = e_3 \times BS_i + f_3 \times BS_j + a_{3,i} + b_{3,j}$$

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

231 Statistical inference was conducted in the Bayesian framework under JAGS 4.1.0 (Plummer  
232 2003). Two independent MCMC samples of 10000 draws with a thinning of 100 were used,  
233 with 5000 draws as a burning period, and another 5000 draws to obtain posterior estimates.  
234 Chain convergence was checked using the Gelman-Rubin test (Gelman and Rubin 1992). In  
235 each chain, we used non informative Gaussian and independent prior distributions (mean = 0,  
236 variance = 1000) for hyperparameters:  $e_1, e_2, e_3, f_1, f_2, f_3$ , Beta prior distribution  $B(1,1)$  for  $p_0$ ,  
237 Gamma distribution  $\Gamma(0.001, 0.001)$  for the precision of each Gaussian distribution in which  
238 random effects ( $a_1, a_2, a_3, b_1, b_2, b_3$ ) were drawn, and a uniform distribution [15,150] for  $K$ .  
239 The full model code and data are available in Supplementary material Appendix 1.

240

## 241 **Results**

### 242 **Behavioral and genetic data**

243 Three individuals were removed from the data set because of escape from the experimental  
244 channel (2 males and 1 female). This event happened during the two first weeks of the  
245 experiment when reproductive period just started and these individuals were not observed as  
246 sexually active on the videos. These three individuals were therefore discarded from the  
247 different analyses.

248 In total, 22 spawning acts were video recorded ( $K_{obs}$  mating occasions) during the  
249 reproductive season. Within these  $K_{obs}$  occasions, 14 females out of 32 and 12 males out of 17  
250 were observed, totalizing 75 pairwise encounters. Thirteen females and 7 males were  
251 observed releasing their gametes, totalizing 22 pairwise copulations (no multiple mating -  
252 where several male emit their gametes simultaneously - was observed). For five mating  
253 occasions, some individuals (1, 1, 2, 2 and 4 individuals respectively) which did not release  
254 their gametes were too far from the camera to be unambiguously identified. These individuals  
255 were therefore not taken into account for the encounter observations. Stripping at recapture  
256 showed that almost all individuals (especially females) had released their gametes by the end  
257 of the experiment (only two females did not lay their eggs), and some redds were detected in  
258 places where we did not place our cameras, indicating that a significant proportion of  
259 spawning events was not observed.

260 A total of 555 juveniles and 49 parents were genotyped. Among those individuals, 551  
261 juveniles were assigned to 41 pairs of parents (10 males and 22 females) at a confidence level  
262 of 95%. Number of offspring varied from 0 to 201 in males (mean  $\pm$  sd= 32  $\pm$  64) and  
263 between 0 and 86 for females (mean  $\pm$  sd= 17  $\pm$  24). Only 12 pairs were both seen releasing  
264 gametes and assigned offspring, so joint gamete release was assessed for 29 pairs by genetic  
265 data only. At the individual level, the number of gamete releases observed on video was  
266 correlated to the number of mates inferred from the genetic analysis (Pearson's  $r = 0.66$ ,  $p <$   
267  $0.0001$ ). From the genetic data, the opportunity for selection was 4.49 for males and 2.34 for  
268 females. The opportunity for sexual selection was 2.69 for males and 0.81 for females.  
269 Bateman's gradient was 17.06 for males ( $t = 4.229$  on 15 degrees of freedom,  $p = 0.0008$ ) and  
270 13.70 for females ( $t = 4.175$  on 30 degrees of freedom,  $p = 0.0002$ ).

271 Using the behavioral data only, we found that male body size did not affect number of  
272 females encountered ( $t = 1.195$  on 15 df,  $p = 0.251$ , Fig. 1.a), but it affected positively the  
273 number of mates (slope = 0.03,  $t = 3.268$  on 15 df,  $p = 0.005$ , Fig. 1.b). Female body size  
274 affected neither the number of males encountered ( $t = 0.072$  on 30 df,  $p = 0.943$ , Fig. 1.a) nor  
275 the number of mates ( $t = -0.304$  on 30 df,  $p = 0.763$ , Fig. 1.b). Using the genetic data only, we  
276 found that male body size had a positive effect on number of mates ( $t = 3.851$  on 15 df,  $p =$   
277  $0.002$ , Fig. 1.b) and number of offspring ( $t = 0.2604$  on 15 df,  $p = 0.003$ , Fig. 1.c), whereas  
278 female body size affected neither the number of mates ( $t = 0.659$  on 30 df,  $p = 0.515$ , Fig. 1.b)  
279 nor the number of offspring ( $t = 0.1782$  on 30 df,  $p = 0.845$ , Fig. 1.c).

280

## 281 **Model output**

282 The posterior of all parameters for the model are provided in Supplementary material  
283 Appendix 2. Although only 22 pairwise gamete releases were recorded on video and 41  
284 families were detected by genetic analysis, the posterior distribution of  $K$ , the number of  
285 mating occasions, had a median of 117 [1<sup>st</sup> quartile = 103; 3<sup>rd</sup> quartile = 132]. The posterior  
286 distribution of the probability of observing an encounter between two individuals in a given  
287 mating occasion,  $p_o$ , had a median of 0.66 [0.63 ; 0.76]. Based on the joint posterior  
288 probabilities of all parameters (effects of male and female body size, and individual random  
289 effects), the model predicted an average ( $\pm$  standard deviation) of 47 ( $\pm$  25) encounters per  
290 male, 25 ( $\pm$  27) encounters per female, 9.8 ( $\pm$  8.4) gamete releases per male, 5.2 ( $\pm$  8.2)  
291 gamete releases per female, 32 ( $\pm$  36) offspring per male and 17 ( $\pm$  33) offspring per female.

292 Male body size had no effect on the probability of encounter or on the number of offspring  
293 produced at each mating occasion, and had a very slight positive effect on the probability of

294 gamete release (Fig. 2). The posterior distribution of the parameter associated to the effect of  
295 male body size on gamete release ( $e_2$ ) had a median of  $7.7428 \cdot 10^{-3}$ , which corresponds to an  
296 odd of encounter multiplied by only 1.007 for each additional millimeter. Given that male  
297 body size ranged from 165 to 342 mm, this would predict, other things equal, a 3.7 odds ratio  
298 between the longest male and the shortest one. Female body size had a negative effect on both  
299 the probability of encounter and the probability of gamete release but did not affect the  
300 number of offspring produced (Fig. 2). The median of the posterior distributions on  $f_1$  and  $f_2$   
301 were -0.02386 and -0.02126, resulting in odds of encounter and gamete release being  
302 multiplied by 0.976 and 0.979, respectively, for each millimeter. Given that female body size  
303 ranged from 177 to 270 mm, the odds ratio between the longest and the shortest female would  
304 be 0.11 for encounter and 0.14 for gamete release.

305 Random effects were more variable for females than for males for the probability of  
306 encounter and the probability of gamete release, while male random effects were more  
307 variable than female's for the number of offspring (Fig. 3). Moreover, random effects on  
308 probability of encounter, probability of gamete release and number of offspring were  
309 positively correlated for both sexes (Fig. 3). Because random effects for the probability of  
310 encounter and gamete release act on the logit scale and random effects for the number of  
311 offspring act on its logarithm, they should be interpreted such that individuals having a  
312 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  
313 than the average individual, respectively.

314 Joint posterior probability distributions were used to predict the number of encounters, gamete  
315 releases and offspring for each individual and these predictions were plotted against the  
316 number of encounters and gamete releases observed on videos and number of offspring  
317 genetically assigned (Fig. 4). In most cases, numbers predicted by the model exceeded the

318 number of observations, but the number of offspring predicted by the model could be smaller  
319 than the number of offspring actually assigned, especially for females.

320

## 321 **Discussion**

322 In this study, we used two approaches to estimate the effect of a phenotypic trait (here body  
323 size as an example in brown trout) on different components of sexual selection. Both  
324 approaches lay on behavioral observation of encounter and mating, and genetic assignation of  
325 offspring. On the one hand, we applied classical analyses on data pulled out from the marginal  
326 sums of each male  $\times$  female matrix: number of encounters and gamete releases observed on  
327 videos, and number of offspring and mates inferred from genetic assignation. There we found  
328 that body size, in males only, would correlate positively with mating success and offspring  
329 number, but not with encounter rate. On the other hand, we developed a statistical framework  
330 combining all these data, thereby enabling information to circulate through the successive  
331 processes of encounter, gamete release and offspring production. This new approach  
332 accounted for the three-dimensional structure of the data: males, females and mating  
333 occasions. This allowed a qualified definition of mating success and disentangling the joint  
334 effects of male and female phenotypes on the different components of reproductive success.  
335 There we found that body size, in females only, would correlate negatively with encounter  
336 rate and mating success, but not with offspring number.

### 337 **What is mating success?**

338 The multiple definitions of mating success have been shaped by a dichotomy of approaches,  
339 which our model aimed at overcoming. On the one hand, because the classical approach based  
340 on the genetic parental table is oblivious to both ineffective mating acts and multiple

341 inseminations between the same pair of individuals, it has constrained the definition of mating  
342 success to the number of individuals with which the focal individual produces offspring that  
343 are alive at sampling (Arnold and Duvall 1994). On the other hand, the not less classical  
344 approach based on the sole observation of copulatory behavior, unable to access the  
345 reproductive output, focused the definition of mating success on the number of copulations or  
346 number of copulatory partners. By combining behavioral and genetic data in a common  
347 framework, our analysis embraced multiple aspects of mating success. The combination of  
348 genetic data and behavioral observations to account for mating acts the offspring of which  
349 were not sampled was also adopted for instance by Collet et al. (2014) and Péliissié et al.  
350 (2014) but their approach relied on complete knowledge of copulation events in the mating  
351 group to disentangle the contribution of pre-copulatory and post-copulatory components of  
352 reproductive success. Our approach consisted in merging the behavioral and genetic datasets,  
353 both incomplete – a common situation in ecology and evolution –, and took advantage of the  
354 conditional structure of the successive components of mating success: encounter,  
355 simultaneous gamete release and offspring production.

356 At the scale of the reproductive group, our behavioral observations showed 75 male × female  
357 encounters and 22 pairwise gamete releases, whereas the parental table based on genetic  
358 assignation indicated that 41 broods were produced. Given that only 12 pairs both were  
359 observed copulating and had their offspring sampled, a rough estimate of the probability that a  
360 pair was observed mating would be  $12/41 = 0.29$ , and a rough estimate of the probability of a  
361 pair having its offspring sampled would be  $12/22 = 0.54$ . This would mean that  
362  $12/(0.29*0.54) = 76$  matings had occurred, 10 of which were video recorded only, 29 of  
363 which were detected genetically only, 12 of which were detected both on video and by the  
364 genetic analysis, and 25 were missed by both methods. In our model, the parameter  $K$ , called  
365 the number of mating occasions, was estimated to be 117, meaning that each pair had 117



366 occasions to mate. This concept of mating occasion, defined as an event on which any male x  
367 female pair *may* encounter, emit gametes and produce offspring, was much broader than  
368 mating, defined as an event on which a male x female pair *does* encounter, emit gamete and  
369 produce offspring. By splitting individual mating success in a number of mating occasions  
370 (trials), our modelling approach considered mating success as the result of a Bernoulli  
371 process, with inferences made on the probability of success. Moreover, this success of joint  
372 gamete release was conditioned on the success of encounter on each occasion, and  
373 conditioned in turn the number of offspring produced. This conditional structure is in line  
374 with the concepts of “sexual networks” and “sexual niche” (McDonald et al. 2013, Ziv et al.  
375 2016), which acknowledge that an individual interacts with (competes with, courts, chooses  
376 among) only a subset of the population. Hence, sexual selection should be measured among  
377 individuals that actually interact.

378 Individual variance in mating success is the fuel for sexual selection, and the opportunity for  
379 sexual selection is computed as the variance in number of mates on the squared mean of  
380 number of mates. Based on classical treatment of genetic data, opportunity for sexual  
381 selection was higher for males (2.69) than for females (0.81) as usually expected (Bateman  
382 1948). However, our model indicated that both the probability of encounter and the  
383 probability of gamete release on a mating occasion was more variable among females than  
384 among males, since the effect of body size (Fig. 2) and the individual random effects (Fig. 3)  
385 on these probabilities were larger for females than for males. This counter-intuitive result  
386 may be due to the model detecting a higher mates number (gamete releases) than the sole  
387 genetic approach. Moreover, for both sexes random effects on the probability of encounter,  
388 the probability of gamete release and the number of offspring produced were positively  
389 correlated. This suggests that some individuals performed consistently better than others for  
390 the three processes, *i.e.* had a higher probability of encounter, a higher probability of gamete

391 release once a partner was encountered, and a higher number of offspring produced once  
392 mated, unconditional on body size.

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

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

406 Applying classical linear regressions to our data indicated that larger males tended to have  
407 more encounters, and had significantly more gamete releases, more genetic mates and more  
408 offspring, while female body size affected none of the behavioral or genetic indicators of  
409 reproductive success. However, our model accounting for the size of both males and females  
410 as well as individual random effects on each reproductive process indicated that larger  
411 females had a lower probability of encounter with males and a lower probability of gamete  
412 release, whereas male size affected neither encounter, gamete release nor number of offspring.  
413 Hence the output of the two analyses differed a lot.

414 The difference between the linear regression approach and ours is due to three features of our  
415 model which lack in the classical approach: 1) conditioning of each process (encounter,  
416 gamete release and offspring production) on the preceding one, 2) simultaneous estimation of  
417 the effect of male and female phenotype, and 3) random individual effects. The conditional  
418 structure of the model allowed to infer the effect of individual phenotype on each process  
419 independently, whereas regression made on all individuals may confound them. For instance,  
420 our analysis indicated that larger males tended to have a higher probability of releasing  
421 gametes with the females they encountered, but once mated they did not tend to sire more  
422 offspring. According to the regression analysis, though, the number of offspring was  
423 positively related to body size, but this relationship was indirect and mediated by the positive  
424 relation between number of mates and number of offspring (Bateman gradient). Although  
425 reproductive success may be split into multiplicative components on each of which individual  
426 phenotype can be regressed, such analysis requires as many regressions as components (e.g.  
427 Arnold and Wade 1984, Tontelier et al. 2016), whereas our model encompasses them all.

428 By considering the mating occasion as the statistical unit, we assumed that the realization of  
429 each process was potentially attributable to both sexual partners, thereby decomposing the  
430 variance between both male and female body size effects. The consequences on the results are  
431 rather strong, since for instance, we detected that female body size was then negatively  
432 impacting both encounter and mating processes. Additionally, the use of random effects on  
433 process further avoided to falsely attribute variance to body size. The classical approach –  
434 which implies a pseudo-replication effect since the data are used twice, once for males, once  
435 for females - could see no effect of female body size.

436 Now as to why female body size, for instance, had a negative effect on encounter and gamete  
437 release probability, and no positive effect on offspring number, we must turn to the behavioral

438 knowledge of the species. In particular, assortative or disassortative encounter and mating, be  
439 it the result of mate choice, intrasexual competition or chance, is possible in brown trout  
440 (Petersson et al. 1999, Labonne et al. 2009): bigger females tend to be aggressively  
441 monopolized by bigger males, thereby limiting their access to a higher number of potential  
442 mates. Unfortunately our dataset is too small to properly infer the effect of interaction  
443 between male and female phenotype on the different components of reproductive success  
444 (Moshgani and Dooren 2011), though it is very easy to implement in the model.

#### 445 **Further applications of the model**

446 The experimental design and the quantity of data we used to illustrate our model indubitably  
447 constrained the analysis we carried out, and one can wonder how the model can be transposed  
448 to other systems, with other types of data on either the components of reproductive success or  
449 traits affecting them. For instance, because we sampled all offspring at the end of the  
450 experiment, the genetic data did not inform much on the number of offspring produced at  
451 each mating occasion. However, in other systems where clutches are well separated in time or  
452 space, even within a reproductive season, the parental table of genetic data would also be  
453 three-dimensional (male  $\times$  female  $\times$  occasion) and inferences on each component of  
454 reproductive success would probably be more accurate. Also, depending on the system  
455 studied, reproductive success may be further decomposed, and inference might be done on  
456 individual or environmental features affecting the additional components. For example, one  
457 may disentangle copulation from gamete fertilization by combining behavioral data and  
458 single-molecule PCR and genotyping of zygotes just after copulation. Here, an additional  
459 three-dimension matrix containing gamete fertilization of each male-female pair at each  
460 occasion would be built, and fertilization success would be included in the model, conditioned  
461 by copulation success, and conditioning the number of offspring. This would disentangle

462 fertilization success from zygote survival, something we were not able to do in our case study  
463 on brown trout.

464 Regarding traits affecting components of reproductive success, we illustrated our approach  
465 with body size only, a trait which is known to affect intrasexual competition and intersexual  
466 preference in brown trout and other salmonids (Foote and Larkin 1988, Foote 1989, de  
467 Gaudemar 1998, Blanchfield and Ridgway 1999, Fleming and Reynolds 2004, Labonne et al.  
468 2009). Other traits could have been used, like color, which is known to play a role in brown  
469 trout reproductive success (Jacquin et al. submitted, Wedekind et al. 2008). In particular,  
470 dynamic traits could be included in our framework, since the statistical unit in our analysis is  
471 the mating occasion. Indeed, an individual could be allowed to bear a different trait value on  
472 each mating occasion, such as mating experience (Saleem et al. 2014), the outcome of  
473 previous intrasexual contests (Hsu et al. 2006), energy stores (Gauthey et al. 2015). For  
474 example, sperm depletion may lead to reduced number of offspring sired by a male on late  
475 mating occasions without affecting probability of copulation (Damiens and Boivin 2006).  
476 Finally, each mating occasion may be characterized by a given environment which could  
477 affect each component of reproductive success, either directly or in interaction with individual  
478 phenotype. For instance, water turbidity may relax sexual selection on fish coloration  
479 (Seehausen et al. 1997, Candolin et al. 2007). Likewise, individual location and wind or water  
480 current on each day of the reproductive season may have an interactive effect on pairwise  
481 reproductive success through the probability of encounter between gametes (Dow and Ashley  
482 1998, Kregting et al. 2014).

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

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

489

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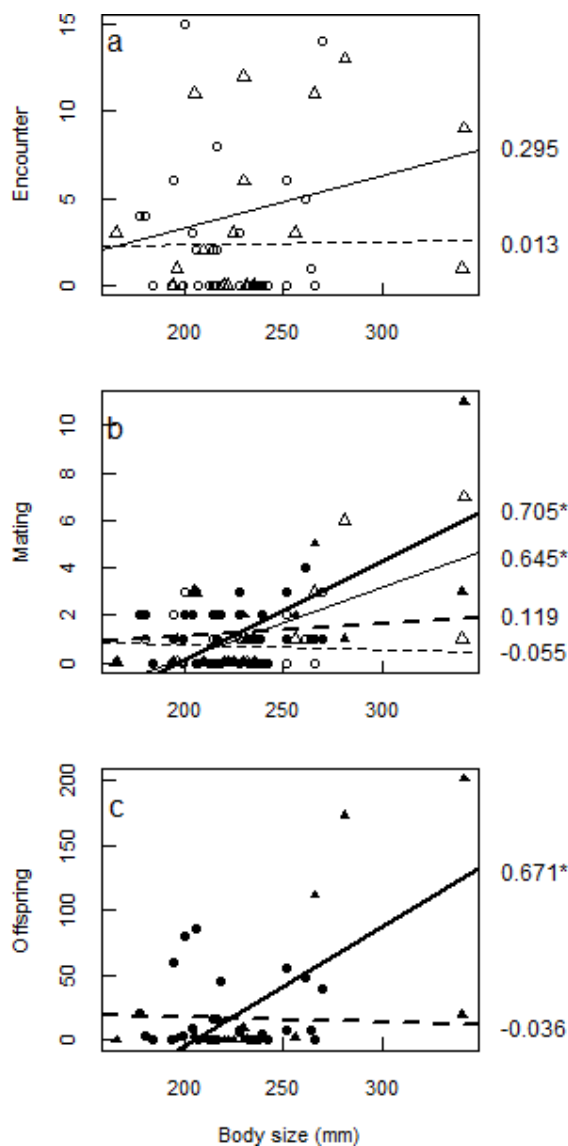
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- 608

609 **Figures and figure legends**

610

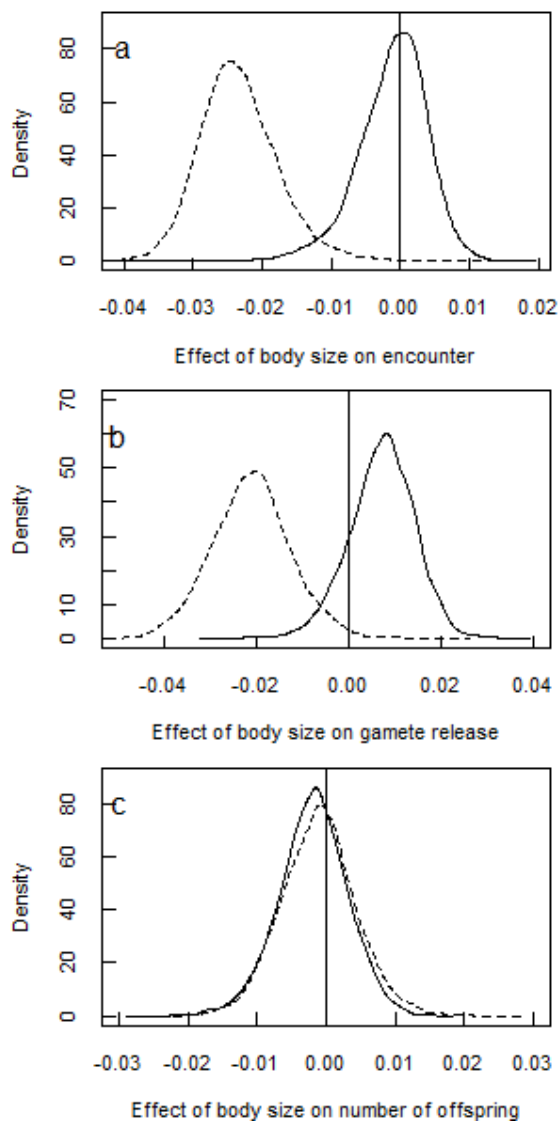


611

612 **Figure 1.** Linear regressions of brown trout body size against a) the number of individuals of  
613 the opposite sex which were encountered, b) the number of mates and c) the number of  
614 offspring assigned. Circles and dashed lines are for females, and triangles and solid lines are  
615 for males. Empty and filled symbols correspond to behavioural and genetic data, respectively.  
616 For b) mating success was measured as the number of individuals of the opposite sex with

617 which the focal individual was observed emitting gametes (empty symbols) and as the number  
618 of individuals with which it shared offspring (filled symbol). Values on the right margin  
619 indicate the Pearson's correlation coefficient of the corresponding regression line, with  
620 asterisk indicating  $p < 0.05$ .

621



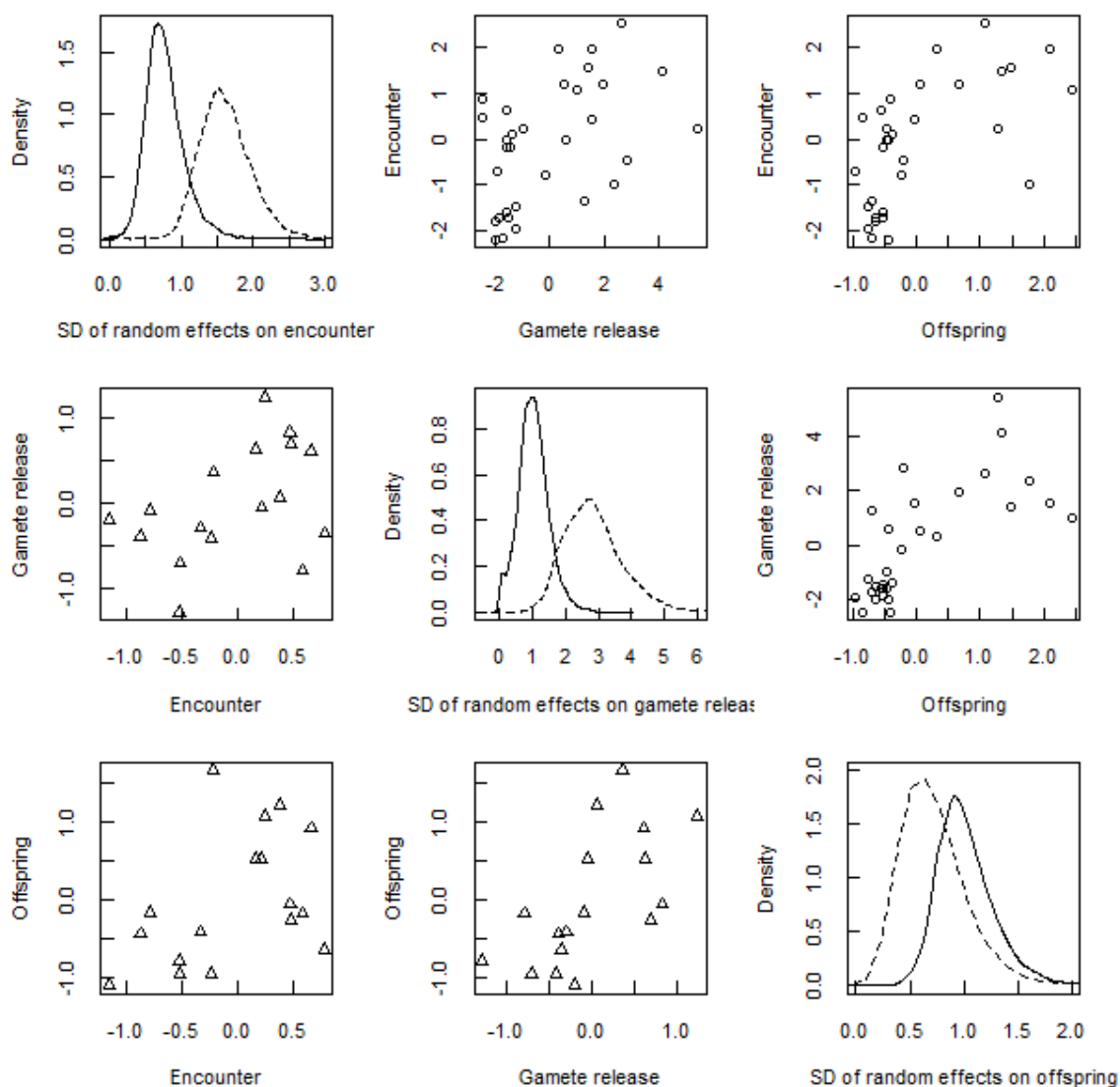
622

623 **Figure 2.** Posterior probability distributions of model parameters associated to the effect of  
624 brown trout body size on a) the probability of encounter, b) the probability of gamete release  
625 and c) the number of offspring produced on each mating occasion. Dashed and solid lines are  
626 for females and males, respectively

627

628

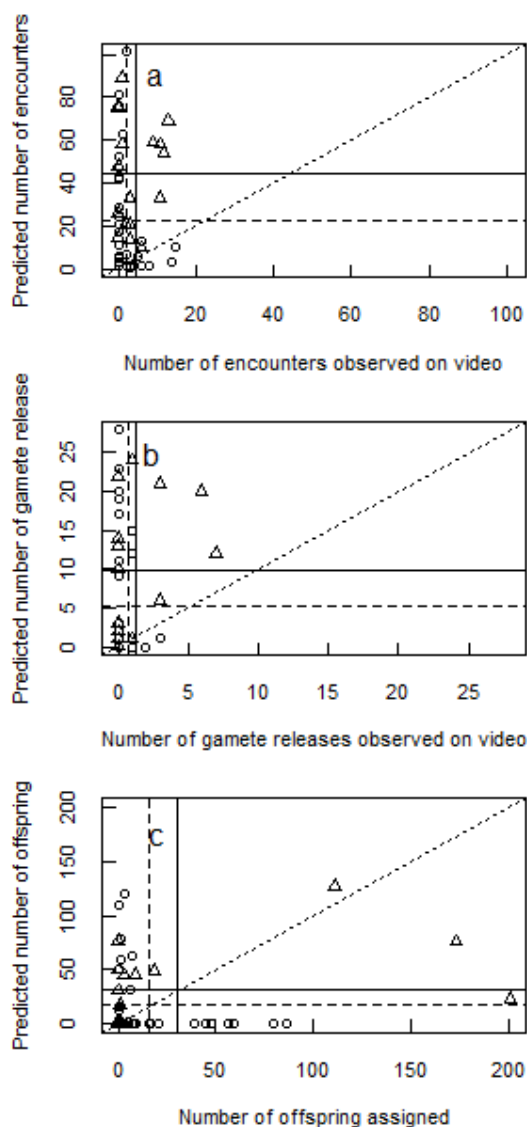
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630

631 **Figure 3.** Random individual effects on the probability of encounter, the probability of  
632 gamete release and the number of offspring produced by brown trout on each mating  
633 occasion. The diagonal indicates the posterior probability distribution of the standard  
634 deviation of the Gaussian distribution in which random effects for the three components of  
635 reproductive success were drawn (dashed and solid lines are for females and males,  
636 respectively). Plots above the diagonal show the pairwise relations between random  
637 individual effects on each process, for females (one circle per female). Plots below the  
638 diagonal show the same thing for males (one triangle per male).





639

640 **Figure 4.** Predictions based on the joint posterior distributions of model parameters, against  
641 values observed in the raw data for a) the number of encounters, b) the number of gamete  
642 releases and the number of offspring assigned to individual brown trout. Circles and triangles  
643 are for females and males respectively. Dashed and solid lines indicate, for females and males  
644 respectively, the mean of each variable. The dotted line has intercept zero and slope one,  
645 which would correspond to a perfect fit between observed and predicted values.

646

647 **Reference to supplementary material**

648 Supplementary material (Appendix oik.XXXXXX at [www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)).

649 Appendix 1-2.

650

651 **Supplementary material Appendix 1.** JAGS code (including data) for the model inferring  
652 the effect of brown trout body size on consecutive processes of reproductive success.

653 Gauthey, Z. et al. 2017. With our powers combined: integrating behavioral and genetic data to  
654 estimate mating success and sexual selection. – *Oikos* 000: 000-000

655

656 ## Supplementary File 1: model code and data.

657 ## Gauthey, Z. et al. 2017. With our powers combined:  
658 integrating behavioral and genetic data to estimate mating  
659 success and sexual selection. *Oikos* 000: 000-000

660 ##### JAGGS 4.0 CODE

661

662 model {

663     # likelihood

664

665     ##### ENCOUNTER PROCESS

666

667     for (i in 1:I) {

668         for (j in 1:J) {

```
669           # inference of male and female body size on
670 encounter probability

671           # includes random effects

672           logit(pe[i,j])<- e[1]*TM[i]+f[1]*TF[j]+a[1,i] +
673 b[1,j]

674           for (k in 1:Kobs) {

675               # actual meeting process, pe=encounter
676 probability

677               E[i,j,k] ~dbern(pe[i,j])

678               # noise process , po= detection probability

679               O[i,j,k]~dbern(po)

680           }

681       }

682   }

683

684   # data fit for observed encounters

685   for (i in 1:I) {

686       for (j in 1:J) {
```

```
687         for (k in 1:Kobs) {
688             # observed encounters are products of
689 actual meeting and detection
690             OEinter[i,j,k]<-O[i,j,k]*E[i,j,k]
691         }
692         # decomposing the observed encounter matrix
693         OES[i,j]<-sum(OEinter[i,j,])
694         OE[i,j]~dnorm(OES[i,j],100)
695     }
696 }
697
698 # data generation for non-observed encounters
699 for (k in (Kobs+1):Kmax) {
700     for (j in 1:J) {
701         for (i in 1:I) {
702             E[i,j,k] ~ dbern(pe[i,j])
703         }
704     }
```

```
705     }
706
707     ##### GAMETE RELEASE PROCESS
708
709     # observed gamete releases
710     for (i in 1:I) {
711         for (j in 1:J) {
712             for (k in 1:Kobs) {
713                 # can release gametes only if encounter
714 happened
715
716                 G[i,j,k] <- E[i,j,k] * GE[i,j,k]
717
718                 # probability to release gametes
719
720                 GE[i,j,k] ~ dbern(pg[i,j,k])
721
722                 # inference of male and female body size on
723 gamete release probability
724
725                 # includes random effects
726
727                 logit(pg[i,j,k]) <-
728 e[2] * TM[i] + f[2] * TF[j] + a[2,i] + b[2,j]
```

```
723         }

724     # decomposing the observed mating matrix

725     Gsum[i,j] <- sum(G[i,j,])

726     Gcumul[i,j] ~ dnorm(Gsum[i,j], 100)

727     }

728 }

729

730 #non-observed releases

731 for (i in 1:I) {

732     for (j in 1:J) {

733         for (k in (Kobs+1):Kmax) {

734             # can release gametes only if encounter

735 happened

736             G[i,j,k] <- E[i,j,k] * GE[i,j,k]

737             # probability to release gametes

738             GE[i,j,k] ~ dbern(pg[i,j,k])

739             # inference of male and female body size on

740 gamete release probability
```

```
741             # includes random effects
742
743             logit (pg [i, j, k] ) <-
744 e [2] *TM [i] +f [2] *TF [j] +a [2, i] + b [2, j]
745         }
746     }
747 }
748
749     ##### OFFSPRING NUMBER PROCESS
750
751     # offspring number for observed gamete releases
752     for (i in 1:I) {
753         for (j in 1:J) {
754             for (k in 1:Kobs) {
755                 # can release gametes only if encounter AND
756 gamete release happened
757                 SRreal [i, j, k] <-
758 E [i, j, k] *G [i, j, k] *Nreal [i, j, k]
759
760                 # Number of offspring produced
```



```
760           Nreal[i,j,k]~dpois(pn[i,j,k])

761           # inference of male and female body size on
762 number of offspring produced

763           # includes random effects

764           log(pn[i,j,k])<-
765 e[3]*TM[i]+f[3]*TF[j]+a[3,i] + b[3,j]

766
767         }

768
769     }

770 }

771 # offspring number for non-observed gamete releases

772 for (i in 1:I) {

773     for (j in 1:J) {

774         for (k in (Kobs+1):Kmax) {

775             # remove data that are generated above the
776 estimate of actual total mating occasions number (RN)

777             counter[i,j,k]<-step(RN-k)
```

```
778             # can release gametes only if encounter AND
779 gamete release happened

780             SRreal[i,j,k] <-             counter[i,j,k] *
781 E[i,j,k] * G[i,j,k] * Nreal[i,j,k]

782             # Number of offspring produced

783             Nreal[i,j,k] ~ dpois(pn[i,j,k])

784             # inference of male and female body size on
785 number of offspring produced

786             # includes random effects

787             log(pn[i,j,k]) <-
788 e[3] * TM[i] + f[3] * TF[j] + a[3,i] + b[3,j]

789         }

790     }

791 }

792

793     # decomposing the parental table for offspring number

794     for (i in 1:I) {

795         for (j in 1:J) {

796             SR[i,j] ~ dnorm(mu[i,j], 1000)
```

```
797             mu[i,j] <- sum(SRreal[i,j,1:Kmax])
798         }
799     }
800     # estimating the real number of mating occasions
801     (somewhere between Kobs and Kmax)
802     RN~dpois(MRN)
803
804     # Calculating male margins for encounter matrix, mating
805     matrix, and offspring number parental table
806     for (i in 1:I) {
807         Emale[i] <- sum(E[i,,])
808         Gmale[i] <- sum(G[i,,])
809         Rmale[i] <- sum(SRreal[i,,])
810
811     }
812
813     # Calculating female margins for encounter matrix, mating
814     matrix, and offspring number parental table
```

815

816       for (j in 1:J) {

817               Efemale[j] <- sum(E[,j,])

818               Gfemale[j] <- sum(G[,j,])

819               Rfemale[j] <- sum(SRreal[,j,])

820       }

821

822       # random effects for males on encounter, gamete release,  
823 and offspring number production processes.

824       for(i in 1:I) {

825               a[1,i] ~ dnorm(0, taum1)

826               a[2,i] ~ dnorm(0, taum2)

827               a[3,i] ~ dnorm(0, taum3)

828       }

829

830       # random effects for females on encounter, gamete release,  
831 and offspring number production processes.

832       for(i in 1:J) {

```
833         b[1,i]~dnorm(0,tauf1)
834         b[2,i]~dnorm(0,tauf2)
835         b[3,i]~dnorm(0,tauf3)
836     }
837
838
839 # priors
840     # we know from independent data that detection probability
841 is not close from 0 nor from 1
842     # so we use an informative prior
843     po~dbeta(50,30)
844     # we know from literature that middle size brown trout do
845 not spawn a large number of time on average
846     # we also know         that at least 22 mating occasions were
847 observed.
848     # so we use an informative prior
849     MRN~dunif(23,150)
```

```
850     # non-informative prior for male and female body size
851     effects on encounter,gamete release, and offspring number
852     production processes.
```

```
853     for(i in 1:3) {
854         e[i]~dnorm(0,0.001)
855         f[i]~dnorm(0,0.001)
856     }
```

```
857     # non-informative prior for male and female random effects
858     on encounter,gamete release, and offspring number production
859     processes.
```

```
860     taum1~dgamma(0.001,0.001)
861     taum2~dgamma(0.001,0.001)
862     taum3~dgamma(0.001,0.001)
863     tauf1~dgamma(0.001,0.001)
864     tauf2~dgamma(0.001,0.001)
865     tauf3~dgamma(0.001,0.001)
866 }
```

```
867
```

```
868
```

869

870 ##### DATA

871

872 # female size

873 TF<-

874 c(228,218,214,232,236,199,238,216,237,204,228,242,252,266,216,

875 215,261,184,207,252,193,239,264,214,235,194,270,206,177,180,20

876 0,212)

877 # male size

878 TM<-

879 c(230,225,342,230,341,235,165,194,196,266,209,205,281,222,231,

880 220,253)

881 # estimated offspring number from parental table

882 # males are in rows and females in columns, ordered as in body

883 size vectors

884 SR<-

885 structure(c(0,0,14,0,17,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,

886 0,0,0,0,0,0,0,0,

887 0,

888 0,

889 2,0,1,0,0,0,2,0,0,8,0,0,7,1,0,0,33,0,0,27,0,0,0,0,0,0,39,0,0,2

890 ,79,0,

891 0,6,3,0,0,

892 0,

893 3,0,0,0,0,0,0,0,0,0,0,7,0,0,0,0,0,9,0,0,0,0,0,0,0,0,0,0,0,0,0,0,

894 0,

895 0,

896 0,

897 0,

898 0,

899 0,

900 0,

901 0,0,0,0,0,0,0,0,0,0,0,1,0,

902 0,

903 0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,4,7,0,0,59,0,40,0,0,

904 0,0,

905 0,

906 0,

907 0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,1,0,

908 0,



909 0,44,15,0,0,3,0,0,0,0,0,0,0,0,0,0,17,0,5,0,0,28,0,1,0,0,1,0,0,40,1

910 8,0,1,0,

911 0,

912 0,

913 1,0,

914 0,

915 0,

916 0,

917 0,1,0,

918 0),.Dim=c(17L,32L))

919 # observed encounters in the experiment. Matrix structured as

920 for offspring numbers

921 OE<-

922 structure(c(0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,2,0,0,0,0,1,0,0,0,0,0,

923 2,0,0,0,0,0,0,

924 0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,1,0,

925 0,

926 0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,3,0,0,0,3,

927 0,

928 0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,1,0,1,0,0,0,0,0,0,0,0,0,1,3,0,1,1,3,

929 0,

930 0,0,0,0,0,0,0,0,1,0,

931 0,

932 0,

933 0,

934 0,0,1,0,1,

935 0,

936 0,

937 0,

938 0,1,0,0,0,

939 0,

940 0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,1,0,1,0,0,0,0,0,0,0,1,0,0,2,2,0,0,0,3,

941 0,

942 0,

943 0,

944 0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,1,0,1,0,0,0,1,0,0,0,0,0,1,2,0,1,1,2,

945 0,

946 0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,2,0,1,0,0,0,1,0,0,0,0,0,0,0,3,1,2,0,2,

947 0,

948 0,

949 0,

```
950 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
951 0,
```

```
952 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
953 0,
```

```
954 0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1,
```

```
955 0),.Dim=c(17L,32L))
```

```
956 # observed gamete releases in the experiment. Same matrix
```

```
957 structure as others
```

```
958 Gcumul<-
```

```
959 structure(c(0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
960 0,0,0,0,0,0,0,0,
```

```
961 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
962 0,
```

```
963 0,0,0,0,0,0,0,0,0,0,2,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,3,0,0,0,1,
```

```
964 0,
```

```
965 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
966 0,
```

```
967 0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
968 0,
```

```
969 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,
```

```
970 0,
```

971 0,

972 0,

973 0,

974 0,

975 0,

976 0,

977 0,1,0,0,2,0,0,0,0,0,

978 0,

979 0,

980 0,

981 0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,1,

982 0,

983 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,2,0,1,0,0,0,0,0,0,0,0,0,0,0,2,0,1,

984 0,

985 0,

986 0,

987 0,

988 0,

989 0,

990 0,

```
991  0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,0,
992  0),.Dim=c(17L,32L))

993  # male number

994  I<-17

995  #female number

996  J<-32

997  # number of observed mating occasions

998  Kobs<-22

999  # maximum expected number of mating occasions

1000 Kmax<-150
```

**Supplementary material Appendix 2.**

**Table A2.** Posterior distributions for the hyperparameters of the model inferring the effect of brown trout body size on consecutive processes of reproductive success.

Hyperparameter	Meaning	Prior distribution	Posterior median [2.5% quantile ; 97.5% quantile]
$e_1$	Effect of male size on encounter	Normal (0, 0.001)	-0.0009 [-0.015 ; 0.008]
$e_2$	Effect of male size on gamete release	Normal (0, 0.001)	0.009 [-0.005 ; 0.02]
$e_2$	Effect of male size on number of offspring	Normal (0, 0.001)	-0.001 [-0.011 ; 0.007]
$f_1$	Effect of female size on encounter	Normal (0, 0.001)	-2.399E-02 [-3.450E-02 ; -8.921E-03]
$f_2$	Effect of female size on gamete release	Normal (0, 0.001)	-2.041E-02 [-3.402E-02 ; -5.834E-03]
$f_2$	Effect of female size on number of offspring	Normal (0, 0.001)	-1.155E-03 [-1.124E-02 ; 8.798E-03]
$\alpha_1$	Precision of male random effect on encounter	Gamma (0.001, 0.001)	1.61 [0.45 ; 7.53]
$\alpha_2$	Precision of male random effect on gamete release	Gamma (0.001, 0.001)	1.57 [0.29 ; 348.1]
$\alpha_3$	Precision of male random effect on number of offspring	Gamma (0.001, 0.001)	1.27 [0.42 ; 3.29]

$\beta_1$	Precision of female random effect on encounter	Gamma (0.001, 0.001)	34.8 [14.9 ; 79.7]
$\beta_2$	Precision of female random effect on gamete release	Gamma (0.001, 0.001)	0.22 [0.07 ; 0.69]
$\beta_3$	Precision of female random effect on number of offspring	Gamma (0.001, 0.001)	0.89 [0.42 ; 1.88]
$p_o$	Probability of observing a mating event	Beta (1,1)	0.66 [0.56 ; 0.75]
$K$	Total number of mating events	Uniform (15, 150)	116 [82 ; 147]

Gauthey, Z. et al. 2017. With our powers combined: integrating behavioral and genetic data to estimate mating success and sexual selection. –

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