

1 Personality traits change after an opportunity to mate

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11 **ABSTRACT**

12 There is growing evidence that personality traits can change throughout the life course in humans
13 and nonhuman animals. However, the proximate and ultimate causes of personality trait change
14 are largely unknown, especially in adults. In a controlled, longitudinal experiment, we tested
15 whether a key life event for adults – mating – can cause personality traits to change in female
16 threespine sticklebacks. We confirmed that there are consistent individual differences in activity,
17 sociability and risk taking, and then compared these personality traits among three groups of
18 females: 1) control females; 2) females that physically mated; 3) females that socially
19 experienced courtship but did not mate. Both the physical experience of mating and the social
20 experience of courtship caused females to become less willing to take risks and less social. To
21 understand the proximate mechanisms underlying these changes, we measured levels of
22 excreted steroids. Both the physical experience of mating and the social experience of courtship
23 caused levels of dihydroxyprogesterone ($17\alpha,20\beta$ -P) to increase, and females with higher
24 $17\alpha,20\beta$ -P were less willing to take risks and less social. These results provide experimental
25 evidence that personality traits and their underlying neuroendocrine correlates are influenced
26 by formative social and life-history experiences well into adulthood.

27

28 Key words: personality, mating, hormones, sticklebacks

29

30 INTRODUCTION

31 An outstanding question in both the human and animal personality literature concerns the
32 stability of individual differences throughout the life course. By definition, personality traits are
33 relatively consistent across situations and/or over time [1,2], but they are not immutable, even
34 in adults. For example, studies in humans have found significant mean-level change in all trait
35 domains at some point during the life course [3,4]; people become more conscientious, warmer
36 and calmer after the age of 30 [3]. Personality traits might change over ontogeny due to intrinsic
37 maturation [4] and/or because juveniles and adults experience different environments, including
38 different social roles that might favor different behavioral strategies. Alternatively, or in addition,
39 personality traits might change following a particular experience because the experience exposes
40 the animal to different selection pressures, and/or represents an important life history decision
41 that influences residual reproductive value. For example, important events such as
42 metamorphosis [5,6], migration, dispersal, sexual maturation [7,8], reproduction, parenting, etc.
43 can expose individuals to different environments and selective pressures, thereby driving
44 changes in personality traits.

45 Our understanding of the adaptive significance of personality trait change throughout the
46 life course is limited because the causes of personality trait change are challenging to study. For
47 one, self-selection can be a problem because some behavioral types of individuals might be more
48 likely to experience a particular life-history event than others [9,4]. Second, even if all individuals
49 experience the particular event, they might do so at different times or at different ages; therefore
50 differences between those that did versus did not experience the event could reflect the
51 confounding effects of time, age, season or maturation [10,11]. Moreover, it can be difficult to
52 pinpoint the exact causes of personality trait change following a key life-history event because
53 life-history events often comprise a series of sub-events leading up to them, making it difficult to
54 isolate the effects of becoming a parent, for example, from the effects of courtship, mating, and
55 reproduction, all of which need to occur before parenting can begin.

56 To circumvent these problems, here, we directly measured the impact of a specific life
57 event - mating - on personality trait development in adult female threespine sticklebacks

58 (*Gasterosteus aculeatus*) in a controlled, randomized and longitudinal experiment. Among life-
59 history events, the experience of mating and reproducing for the first time is likely to be one of
60 the most important life events for any organism. For example, courtship and/or sexual
61 experience often influences subsequent female mate preference [12,13]; females generally
62 become more selective with mating experience [13]. Therefore, we might expect them to
63 become more cautious, i.e. less bold and aggressive, after mating. On the other hand, we might
64 expect females to become more bold after mating because they have less to lose, i.e. their
65 residual reproductive value is lower. In general, recent theory on the adaptive evolution of
66 personality traits predicts that a female's recent mating and courtship experience will influence
67 her willingness to take risks in the future [14,15].

68 Here, we examine the influence of mating for the first time on personality trait
69 development in female sticklebacks. Sticklebacks are famous for their natural intraspecific
70 variation in behavior [16,17], and a previous study found that the experience of reproduction and
71 parenting influenced the development of risk taking behavior in male sticklebacks [18]. In
72 contrast to males, female sticklebacks do not provide parental care. Instead, female sticklebacks
73 become gravid and lay eggs in males' nests, where they are fertilized externally [17,19].
74 Sticklebacks from most freshwater populations die at the end of their first and only breeding
75 season [17,19].

76 We repeatedly measured personality traits on individual females and compared three
77 groups of females: 1) females that did not have an opportunity to mate (control); 2) females that
78 physically mated; 3) females that had an opportunity to mate and experienced courtship socially
79 but did not mate (courtship control). Personality traits were repeatedly measured in all groups
80 of females both before and after females had an opportunity to mate. This experimental design
81 allowed us to determine if the physical act of mating and reproducing is required to cause
82 personality traits to change, or if the social experience of courtship is sufficient. In order to track
83 the potential proximate mechanisms underlying changes in personality traits as a function of
84 mating, we used a noninvasive method to measure levels of steroids excreted in the water both
85 before and after a mating opportunity [20]. Given the dramatic neuroendocrine changes
86 associated with reproduction [21,22], we predicted that females that mated would experience

87 greater steroid fluctuations compared to females that had not mated, and that those hormonal
88 fluctuations would be related to behavior. We focused on cortisol because of its hypothesized
89 link to personality variation [23] and on steroids involved in reproduction because it was the life
90 history event of interest.

91

92 **METHODS**

93 Threespine sticklebacks were collected from Putah Creek, California, U.S.A.. Neither males nor
94 females showed signs of reproductive maturity therefore we assume that females were virgins
95 at the time of the experiment. Females were housed in all-female groups in 'home' tanks (35.5 L
96 × 33 W × 25 H cm, 10 fish/tank) with a gravel bottom, plastic plants, and an opaque shelter and
97 stayed in these home tanks for the duration of the experiment, except when individuals were
98 transferred to separate 'observation' tanks (60.75 L × 30 W × 20 H cm, set up the exact same as
99 the home tanks) for behavior trials. Fish were maintained at 20°C on a summer photoperiod (16:
100 8 h light: dark cycle). The fish were daily fed a mixed diet consisting of frozen bloodworm, brine
101 shrimp, and Mysis shrimp ad lib each day.

102

103 **Experimental design**

104 Individual females were randomly assigned to either the control group or to have a mating
105 opportunity. Females given a mating opportunity were paired with a control female (matched for
106 size) who was always measured at the same time as her partner. This design allowed us to control
107 for variation among females in time to become gravid and to reproduce, as well as for self-
108 selection, i.e. if some behavioral types of females are less choosy or more attractive than others.
109 Females in the control group (n = 37) were not exposed to a male or given an opportunity to
110 mate, but like females in the other conditions, they were socially housed, therefore differences
111 between control females and females given a mating opportunity do not reflected differences in
112 the opportunity for social interactions per se. Moreover, many females (n = 12) in the control
113 group also became gravid over the course of the experiment and released their eggs in their

114 home tank. We tested for the effects of releasing eggs on behavior by comparing the behavior of
115 control females before vs after releasing eggs, and there was no effect (activity: $F_{(1,220)} = 2.74$, p-
116 val = 0.10; social behavior: $F_{(1,220)} = 1.57$, p-val = 0.19; risk-taking behavior: $F_{(1,220)} = 0.05$, p-val =
117 0.82; $17\alpha,20\beta$ -P: $F_{(1,12)} = 0.001$, p-val = 0.99). Therefore, behavioral differences between females
118 in the control group and females given a mating opportunity do not reflect differences in
119 gravidity, or the effects of releasing eggs. Some of the females given a mating opportunity (n =
120 23) mated, while others (n = 22) did not and served as “courtship controls”, because like the
121 mated females, they had the social experience of being courted, but unlike the mated females
122 they did not physically mate. We did not detect any latent differences between females that
123 mated and courtship control females that would lead to nonrandom representation of behavioral
124 types between the mated and courtship control groups, e.g. mated and courtship control females
125 did not differ in size ($t_{43.95} = 0.16$, $P = 0.87$) or behavior (see Results). Both courtship control and
126 mated females had multiple opportunities to mate (mated females: range = 1 – 8 opportunities,
127 mean \pm SE = 2.9 ± 0.29 , courtship control females: range = 1 – 7, mean \pm SE = 3.4 ± 0.31).

128 The behavior of females was measured in the behavioral assays on six occasions, thrice in
129 the “Before” trials and thrice in the “After” trials, with 24 h between trials. Females given a
130 mating opportunity were placed in a tank with a male who had built a nest (60.75 L \times 30 W \times 20
131 H cm). Females started the After behavioral assays 24 hours after the mated female reproduced
132 or after the courtship control female released her eggs in her home tank (presumably to avoid
133 the costs of becoming egg bound [24]). All females were measured for length and weight on the
134 last day of the After trials.

135

136 **Behavioral assays**

137 *Activity:* The focal fish was placed in a shelter at one end of the tank. After one minute,
138 the observer gently removed the cork of the shelter, and recorded the number of areas (four 15
139 cm squares) crossed for three minutes.

140 *Social behavior:* 30 minutes after the activity assay, three females from the same
141 population were placed into a flask at the opposite side of the refuge and we recorded the
142 number of times the focal fish contacted the flask for 5 minutes.

143 *Risk taking behavior:* 30 minutes after the social behavior assay, a model great egret
144 (*Casmerodius albus*) head was placed over the observation tank. Then, we added live
145 bloodworms directly under the egret. When the focal fish approached the worms within one
146 body length, we released the egret twice in quick succession, and then fixed the egret so that it
147 remained above the water. Following this simulated attack, we recorded time foraging under risk
148 for five minutes.

149

150 **Measuring excreted steroids**

151 After the third trial of both the Before and After trials, we placed the focal fish in a 500 ml long-
152 necked glass flask filled with 100 ml of water. We then placed the flask in a covered bucket (to
153 minimize stress) for 30 minutes. Then, we transferred 50 ml of the water into a 50 ml sterile
154 polypropylene conical tube.

155 Steroids were extracted from the water samples by pulling water through C18 Sep-Pak
156 cartridges (Waters Ltd.) that had been primed with 5 mL methanol followed by 5 mL distilled
157 water. After the sample had dripped through at a rate of approximately 2 mL/min, the cartridge
158 was washed with 5 mL of distilled water, and the steroids were eluted from the columns into
159 13*100 mm borosilicate vials via 5 ml of diethyl ether. The ether was dried by evaporation
160 overnight. The dried hormones were then frozen at -80°C.

161 Samples were analyzed via mass spectrometry with the 5500 QTRAP LC/MS/MS system
162 (AB Sciex, Foster City, CA). In order to control for differences in body size, hormone release rates
163 were calculated as the amount of released hormone per gram of body weight per hour (ng/g/hr).
164 We focus here on 17 α ,20 β -P (17 α ,20 β -dihydroxy-4-pregnen-3-one, hereafter referred to as
165 17 α ,20 β -P, n = 19 individuals with one measure Before and one measure After).

166

167 **Statistical analyses**

168 *Repeatability of behavior and hormones*

169 To confirm that there were consistent individual differences in behavior, we estimated
170 repeatability during the Before trials. Repeatability for the three treatment groups was estimated
171 separately to confirm that all groups showed similar patterns prior to the mating opportunity. To
172 test whether mating influences rank-order stability, we estimated the repeatability of behavior
173 and hormone titres across the six Before and After trials for the treatment groups separately.

174 Repeatability was estimated as the ratio of between-individual variance to total variance
175 with linear mixed-effects models (with individual identity as a random factor) in R v.3.4.4
176 (<http://www.r-project.org>) [25].

177

178 *How do personality traits and hormones change following mating?*

179 To detect mean-level personality trait change after mating, we used linear mixed-effects models
180 (LMMs) with the lmer function in the R package lme4 v.1.1-17 [26]. Models included the following
181 fixed effects: treatment (three levels: control, courtship control, and mated), Before/After (two
182 levels: before vs after mating), trial nested within Before/After, the number of days between the
183 first and sixth trial (days in the experiment), the number of mating attempts, the interaction
184 between treatment x Before/After, and individual as a random effect.

185 We used LMMs to investigate changes in hormonal release rate according to the same
186 explanatory variables cited above. However, we split the all data set by the period (Before/After)
187 as we did not have enough statistical power to test for the interaction between treatment and
188 period. We used LM to investigate a potential link between hormones and personality traits
189 (average behavior across the three before or after trials).

190 More details about the methods (behaviors recorded, hormones measured and their
191 relevance, detailed protocols and technics, and statistics) are in electronic supplementary
192 material.

193

194 **RESULTS**

195 **Repeatability of behavior**

196 During the Before trials, individual differences in behavior were repeatable in all
197 treatment groups (electronic supplementary material, Table S1), confirming these behaviors can
198 be considered personality traits. Among-individual variation was consistently higher than within-
199 individual variation.

200 Individual differences in behavior were also repeatable between the Before and After
201 trials (Table 1) indicating some element of stability of individual behavioral types throughout the
202 experiment. However, the repeatability of social behavior and risk taking behavior before and
203 after the mating opportunity was significantly lower in both the mated and courtship control
204 treatment groups compared to the control group (Table 1). This pattern appears to reflect greater
205 among-individual variation in the control group, and higher within-individual variation in the
206 mated and courtship control groups (Table 1). Greater within-individual variation in the mated
207 and courtship control groups is visually evident in the behavioral reaction norms (electronic
208 supplementary material, Fig. S1), especially between trials 3 and 4, i.e. the interval during which
209 females in these groups experienced courtship and/or mating. The repeatability of activity did
210 not differ among the three treatment groups (Table 1).

211

212 **Effects of a mating opportunity on behavior**

213 We did not detect any differences among the treatment groups in activity during the
214 Before ($F_{(2,243)} = 2.90$, p-val = 0.10) or After trials ($F_{(2,243)} = 0.48$, p-val = 0.62), and no difference in
215 activity between the Before and After trials ($F_{(2,489)} = 2.29$, p-val = 0.13) (Fig. 1A).

216 Females in both the mated and courtship control groups were less social (fewer contacts
217 with conspecifics) after they were given a mating opportunity ($t_{131.97} = -4.09$, $P < 0.001$; $t_{123.21} = -$
218 4.07 , $P < 0.001$, respectively), but the social behavior of females in the control group did not

219 change across the experiment ($t_{217.44} = 0.34$, $P = 0.73$, Fig. 1B). The mated and courtship control
220 females did not differ in social behavior ($t_{263.19} = -1.54$, $P = 0.12$). Females in the three treatment
221 groups did not differ in social behavior during the Before trials ($F_{(2,243)} = 1.93$, $p\text{-val} = 0.15$).

222 Time foraging under risk was lower in both the mated and courtship control groups after
223 they were given a mating opportunity ($t_{131.81} = -3.19$, $P < 0.001$; $t_{129.63} = -4.52$, $P < 0.001$,
224 respectively), but the time that control females spent foraging under risk did not vary across the
225 experiment ($t_{219.67} = -0.09$, $P = 0.93$, Fig. 1C). The mated and courtship control groups did not
226 differ ($t_{265.57} = -1.4$, $P = 0.13$). Females in the three treatment groups did not differ in risk taking
227 behavior during the Before trials ($F_{(2,243)} = 0.13$, $p\text{-val} = 0.88$).

228 Non-significant results about the other explanatory variables are in the electronic
229 supplementary material.

230

231 **17 α ,20 β -P was higher after a mating opportunity and was negatively correlated with social** 232 **behavior and risk taking behavior**

233 The experience of courtship caused 17 α ,20 β -P to increase: 17 α ,20 β -P did not differ
234 among the three treatment groups during the Before trials ($F_{(2,16)} = 1.69$, $p\text{-val} = 0.22$), but
235 17 α ,20 β -P was significantly higher during the After trials in both the mated and courtship control
236 groups compared to the control group ($F_{(2,16)} = 3.49$, $p\text{-val} = 0.04$, electronic supplementary
237 material Fig. S2).

238 We did not detect a relationship between behavior and 17 α ,20 β -P during the Before trials
239 (number of contacts: $F_{(1,17)} = 0.42$, $p\text{-val} = 0.52$; willingness to forage under risk: $F_{(1,17)} = 0.24$, $p\text{-val} = 0.63$). However, during the After trials, there was a negative relationship between the level
240 of 17 α ,20 β -P and both the number of contacts ($F_{(1,17)} = 5.94$, $p\text{-val} = 0.02$, Fig. 2) and the
241 willingness to forage under risk ($F_{(1,17)} = 8.02$, $p\text{-val} = 0.01$, Fig. 2). Visual inspection of the data
242 suggests that this pattern was particularly strong among females that had an opportunity to mate
243 (Fig. 2). We did not detect a relationship between activity and 17 α ,20 β -P (respectively, $F_{(1,17)} =$
244 0.21 , $p\text{-val} = 0.64$).

246 Non-significant results about other steroids are in the electronic supplementary material.

247

248 **DISCUSSION**

249 This study addresses important questions about personality change throughout the
250 lifespan by analyzing the stability and change of personality traits in a controlled, randomized
251 and longitudinal experiment. Specifically, we analyzed how repeatability, within and among
252 individual variation in personality, and mean level changes in personality traits depend on a key
253 life event: mating for the first time. We provide evidence that adult females became less social
254 and less willing to take risks after a mating opportunity.

255 This conclusion is bolstered by the study's strong experimental design. We confirmed that
256 there are consistent individual differences in behavior by repeatedly measuring the same
257 individuals in a battery of behavioral assays. The repeated measures design revealed that
258 individuals given a mating opportunity retained their new behavioral type for the duration of the
259 experiment. Moreover, it allowed us to compare within- and among-individual variance
260 components, revealing greater within-individual variation in individuals given a mating
261 opportunity compared to the control group. This is strong evidence that the mean-level
262 differences between treatment groups reflects within-individual change, i.e. individuals changed
263 their behavior after a mating opportunity. In addition, we confirmed that self-selection was not
264 a problem: at the beginning of the experiment, females in the three treatment groups did not
265 differ in behavior, but they diverged following the mating opportunity.

266 Interestingly, regardless of whether they physically mated or if they just had the social
267 experience of courtship, females became less social and less willing to take risks after a mating
268 opportunity. We do not know why some females given a mating opportunity mated and others
269 did not. It is possible, for example, that mated females experienced less aggression from males
270 during the mating opportunity, that mated females were more attractive to males, that mated
271 females were less choosy, or less interested in mating generally. However, prior to entering the
272 experiment, we did not detect any differences in behavior or body size or reproductive state
273 (gravidity) between mated and courtship control females (electronic supplementary material),
274 both types of females were given numerous opportunities opportunities to mate. There was not

275 a systematic difference between the males that were offered to females that did versus did not
276 mate, and we ensured that all females were gravid and ready to spawn when given a mating
277 opportunity. Mate choice in sticklebacks is mutual [27]; therefore, we suspect that some females
278 did not mate simply because they were not offered the right match. Despite the fact that mated
279 vs courted females might have differed in attractiveness, choosiness or the way they interacted
280 with males, both types of females became less social and less willing to take risks and experienced
281 an increase in progesterone. These results strongly suggest that there is something about the
282 experience of having an opportunity to mate with males that changes females' personality, i.e.
283 the social experience is sufficient to cause personality traits to change. That mating and
284 experiencing courtship do not differ in their impact on female personality might stem from the
285 fact that mating in this system is similarly costly to experiencing courtship. The similar effects on
286 personality may be from the similar physiological impacts of the behaviors involved in each case;
287 a different outcome might be expected when the act of mating for females is more costly than
288 engaging in courtship only. If that is the case, then the impact of a mating opportunity on
289 personality in this study may be a conservative example of the impact of mating when
290 considering systems in which the females then go on to perform parental care.

291 The similarity between courtship control and mated females in this experiment suggest
292 that social experience with potential mates – not just sexual experience – can influence
293 personality traits in females. This result is consistent with what we know about the importance
294 of social experience for behavior in both humans and nonhuman animals. For example, for young
295 adults, people's openness and their interaction with their social environment influences their
296 chances of meeting a partner [28,29]. The nonhuman animal literature is rife with examples
297 showing that previous courtship experience with male signals alters female mating decisions
298 [13,30]: females are often more choosy about their mates after social experience with an
299 attractive male and less choosy after social experience with an unattractive male, presumably
300 because females change their preference functions as they update their estimate of the
301 distribution of mate quality [31]. Indeed, there is evidence that female sticklebacks modify their
302 mate preference in response to their estimate of the quality and availability of mates [32,33].
303 Therefore, it is possible that females used the mating opportunity in this experiment to update

304 their assessment of mate availability, which went on to influence their social and risk taking
305 behavior.

306 Females excreted more $17\alpha,20\beta$ -P after they were given a mating opportunity, regardless
307 of whether they mated, and individual variation in behavior was related to individual variation in
308 $17\alpha,20\beta$ -P. $17\alpha,20\beta$ -P promotes the secretion of ovarian fluid in sticklebacks [34] and it is likely
309 that it is the maturation inducing hormone in stickleback [24]. In other fishes, a sharp peak of
310 $17\alpha,20\beta$ -P occurs prior to spontaneous or induced ovulation [35,36]. Studies in goldfish and other
311 fishes have shown that exposure to a potential mate can trigger ovulation, presumably via
312 pheromones [37], and there is some evidence for chemical communication between males and
313 females during courtship in stickleback [38]. Therefore, the higher levels of $17\alpha,20\beta$ -P in females
314 given a mating opportunity in this experiment could reflect their recent experience with a
315 potential mate. Alternatively, because $17\alpha,20\beta$ -P can act as a pheromone used during
316 communication among females [39], higher levels of $17\alpha,20\beta$ -P in both the mated and courtship
317 control groups might reflect $17\alpha,20\beta$ -P that was released by females that mated while they were
318 co-housed with courtship control females. Interestingly, contrary to our prediction based on the
319 coping styles literature [23], cortisol did not appear to be involved in mediating the effects of a
320 mating opportunity on personality.

321 Regardless of the proximate physiological mechanisms involved, the finding that risk
322 taking behavior and social behavior decreased following a mating opportunity is consistent with
323 theory which posits that life-history tradeoffs - specifically between investment in current and
324 future reproduction - can generate behavioral types [14]. Specifically, individuals with a greater
325 expectation of future reproduction are expected to be shyer and less aggressive than individuals
326 with a lower expectation of future reproduction [14]. In the context of this experiment, females
327 that had an opportunity to mate may have interpreted this experience as information that
328 potential mates are abundant, therefore these females may have a higher expectation for future
329 reproduction, and thus became less social and less willing to take risks in order to protect their
330 assets [15].

331 It is now a truism that early life experience is important for behavioral development in
332 humans and nonhuman animals [4,40], but whether and why personality traits continue to
333 change through adulthood is less understood. Experimental studies that manipulate and control
334 particular life events in nonhuman animals have the potential to make important contributions
335 in this area. Moreover, this topic deserves more attention in the animal personality literature
336 because it has a number of ecological and evolutionary implications that have yet to be explored.
337 For example, personality change in young wild individuals may have strong consequence for
338 dispersal and/or the establishment of social groups, with potential consequences for social
339 interactions among individuals within the group. More generally, these results highlight the
340 importance of phenotypic plasticity over ontogeny for the generation and maintenance of
341 personality variation within natural populations; changes in the timing of important life history
342 events or other experiences could have consequences for the distribution of personality variation
343 within natural populations.

344

345 Ethics. All applicable international, national, and/or institutional guidelines for the care
346 and use of animals were followed. All procedures performed in this study involving animals were
347 in accordance with the ethical standards of the University of Illinois, Urbana Champaign (IACUC
348 protocol #18080).

349 Data accessibility. Data available from the Dryad Digital Repository at: Digital Repository
350 at: <https://doi.org/10.5061/dryad.wstqjq2h3> [41].

351 Authors' contributions. C.M. contributed to study design, carried out the experiment and
352 the laboratory work, analyzed the data, and co-wrote the manuscript; A.M.B. contributed to
353 study design and co-wrote the manuscript.

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Figures

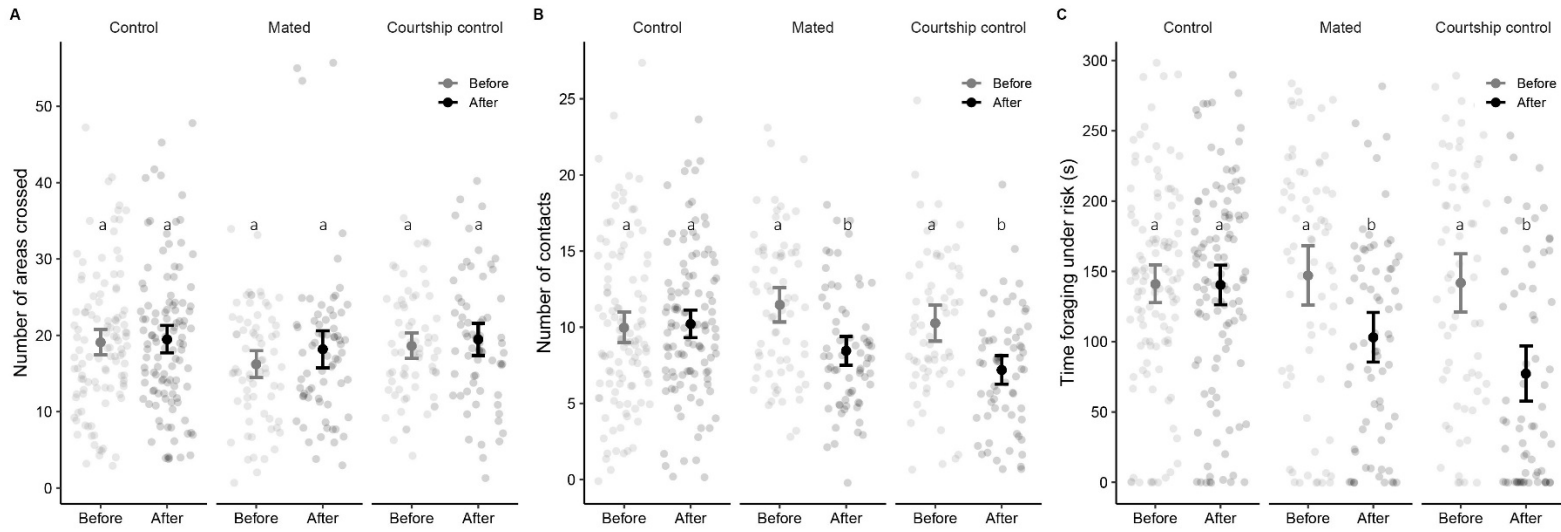


Figure 1. Mean-level change in behavior as a function of courtship and mating. Bars represent 95% confidence intervals. Different letters within each figure indicate means that are significantly different (p-val < 0.05).

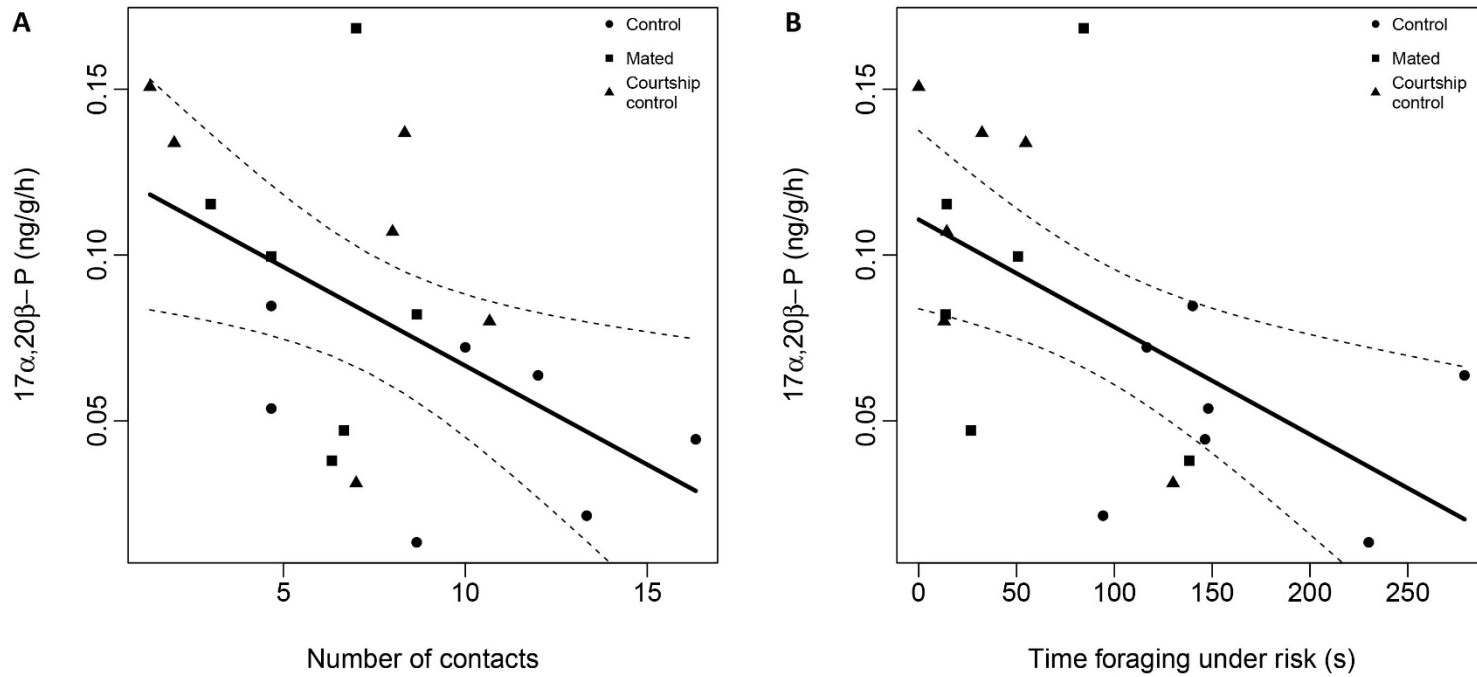


Figure 2. Relationship between progesterone and A) the social behavior (number of contacts), and B) the risk taking behavior (time foraging under risk) during the “After” trials. Each circle represents the average time an individual spent foraging under risk during the three “After” trials. The dashed line represents the 95% confidence interval.

Table

Treatment groups	Activity: number of areas crossed			Social behavior: number of contacts			Risk taking behavior: time foraging under risk		
	Among	Within	R	Among	Within	R	Among	Within	R
Control (n=37)	54.6	31.17	0.64 (0.48, 0.74)	15.46	10.58	0.59 (0.43, 0.71)	4332	1051	0.81 (0.71, 0.87)
Mated (n=22)	34.81	44.89	0.44 (0.22, 0.59)	7.11	14.27	0.33 (0.12, 0.51)	3158	3935	0.45 (0.22, 0.61)
Courtship control (n=23)	32.47	27.35	0.53 (0.32, 0.69)	6.54	14.78	0.31 (0.12, 0.49)	2775	5059	0.35 (0.14, 0.53)

Table 1. Repeatability (R) and variance components (among- and within-individual) of behavioral traits across the before and after trials.

Supplemental material

Figures

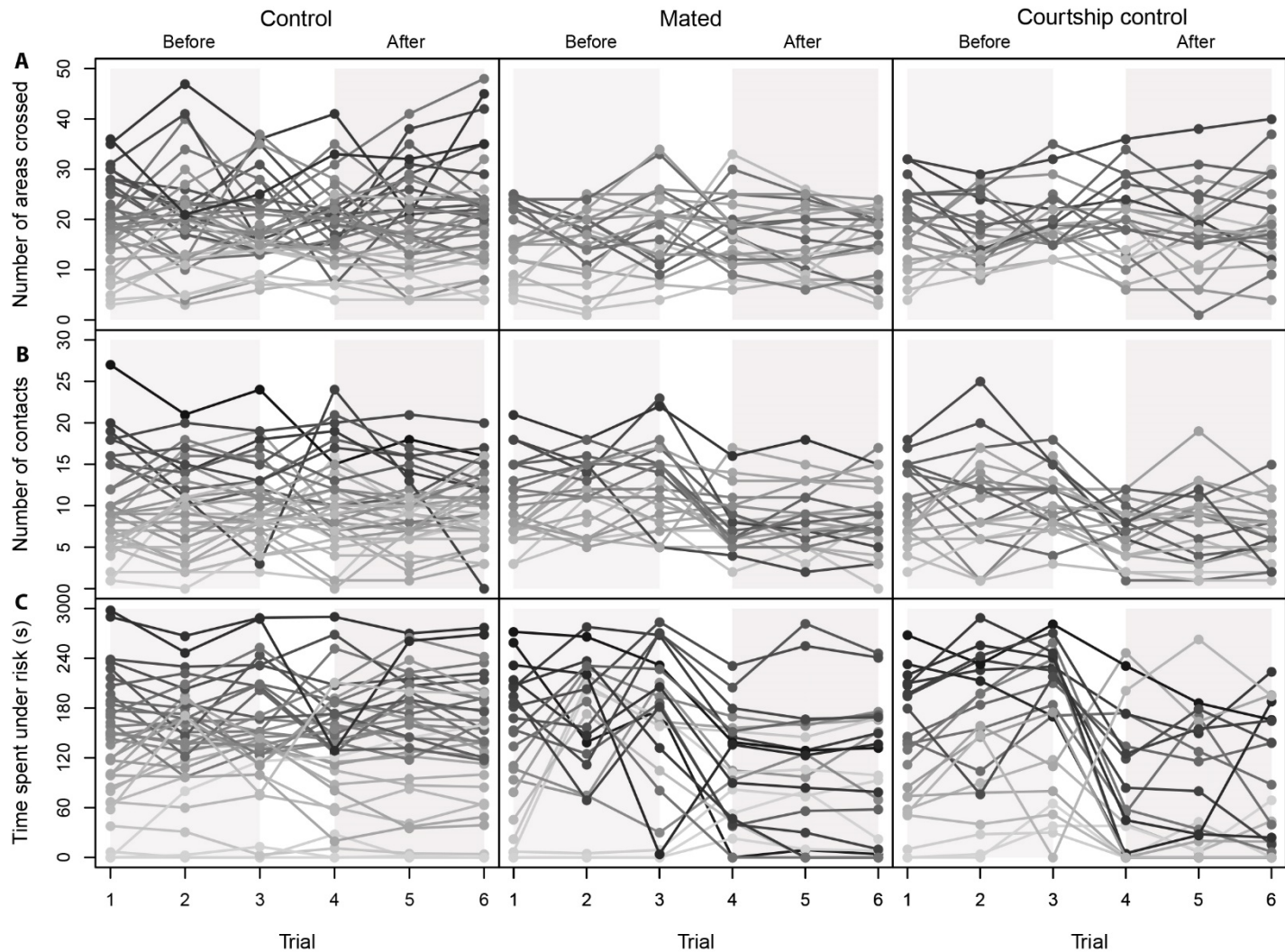


Figure S1. Behavioral reaction norms showing individual differences in behavior the three treatment groups. Top to bottom shows: A) number of areas crossed during the activity assay, B) number of contacts during the social behavior assay and C) time spent foraging under risk during the risk taking behavior assay. Each line represents the behavior of a different individual female across all six trials in shades of grey. Trials 1-3 represent behaviors measured during the “Before” trials, trials 4-6 represent behaviors measured during the “After” trials.

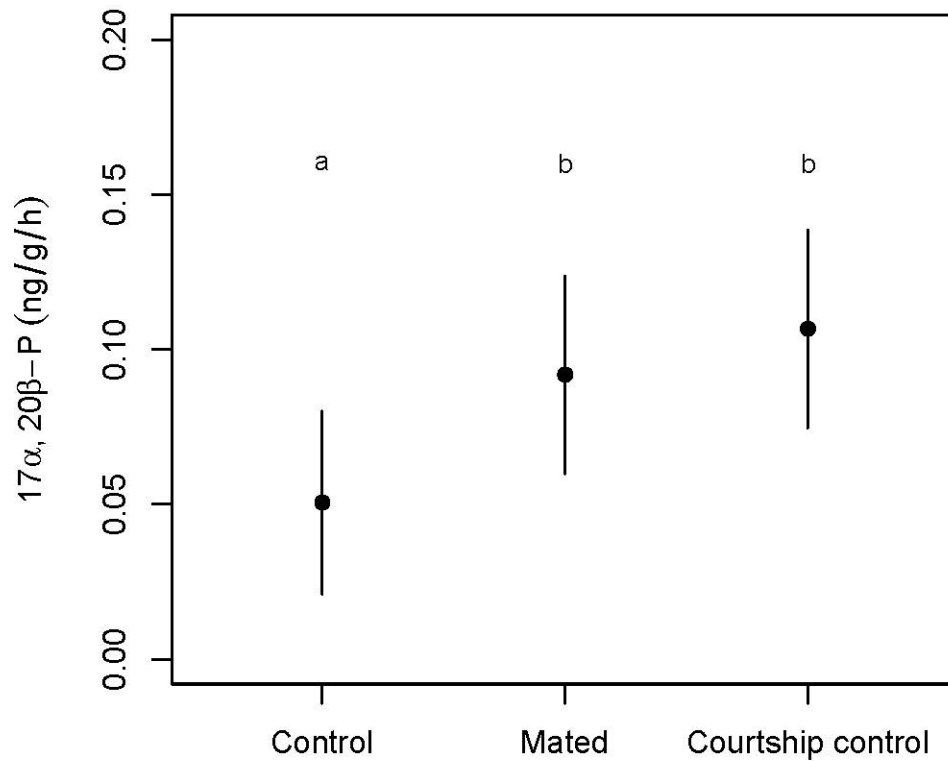


Figure S2. Differences in average excreted progesterone among treatment groups. Shown are the “After” progesterone levels. Bars represent the 95% confidence interval. Different letters indicate means that are significantly different (p-val < 0.05).

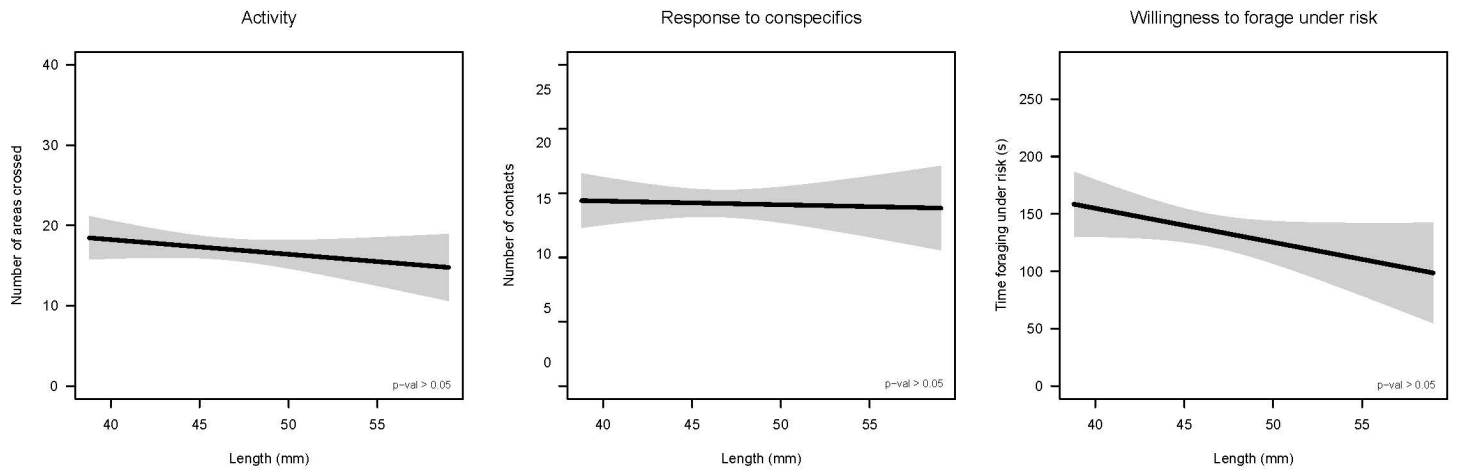


Figure S3. There was no relationship between body size (standard length) and behavior (A: activity, B: social behavior, C: risk taking behavior). The graph shows the predicted linear regression between length and each behavior, and the associated confidence interval (95%). Shown from left to right are the number of areas crossed during the activity assay, the number of contacts during the social behavior assay, and the time foraging under risk during the risk taking assay.

Tables

	Mating opportunity	Control
Number of areas crossed		
Among	26.17	44.72
Within	24.88	35.66
R	0.463 (0.28, 0.62)	0.55 (0.34, 0.69)
Number of contacts		
Among	13.47	15.32
Within	9.52	7.70
R	0.58 (0.40, 0.72)	0.66 (0.48, 0.76)
Time foraging under risk		
Among	4435.90	4425.90
Within	2858.50	757.10
R	0.59 (0.43, 0.81)	0.85 (0.75, 0.91)

Table S1. Repeatability (R) and variance component (among- and within-individual) of behavioral traits during the “Before” trials. For both control females and females in the mating opportunity treatment we estimated the repeatability of activity (number of crossed areas), their social behavior (number of contacts), and their risk taking behavior (time foraging under risk) across the three “Before” trials. Models included individual as a random effect and adjusted models included trial as a co-variate. Numbers in brackets indicate 95% credibility intervals (82 individuals with 3 repetitions). Repeatability, among- and between-individual variation did not differ between the two groups prior to the experience of courtship and reproduction.

Social behavior			
	Number of areas crossed	Number of orients	Time spent with conspecifics
Social behavior			
Number of contacts	1	0.38	0.36
Number of orients		1	-0.42
Time spent with conspecifics			1

Risk taking behavior			
	Latency to forage under risk	Number of pecks	Time spent foraging under risk
Risk taking behavior			
Latency to forage under risk	1	-0.67	0.52
Number of pecks		1	0.70
Time spent foraging under risk			1

Table S2. Matrix of the Spearman's correlation coefficients among behaviors for the social behavior and the risk taking behavior assays; behaviors were averaged across the six trials (n=82 individuals).