

## Research



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# Personality traits change after an opportunity to mate

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

## 1. Introduction

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

Our understanding of the adaptive significance of personality trait change throughout the life course is limited because the causes of personality trait change are challenging to study. For one, self-selection can be a problem because some behavioural types of individuals might be more likely to experience a particular life-history event than others [4,9]. Second, even if all individuals experience a particular event, they might do so at different times or different ages; therefore, differences between those that did versus did not experience the event could reflect the confounding effects of time, age, season or maturation [10,11]. Moreover, it can be difficult to pinpoint the exact causes of personality trait change following a key

life-history event because life-history events often comprise a series of sub-events leading up to them, making it difficult to isolate the effects of becoming a parent, for example, from the effects of courtship, mating and reproduction, all of which need to occur before parenting can begin.

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

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

We repeatedly measured personality traits on individual females and compared three groups of females: (i) females that did not have an opportunity to mate (control); (ii) females that had physically mated, and (iii) females that had had an opportunity to mate and experienced courtship socially but did not mate (courtship control). Personality traits were repeatedly measured in all groups of females both before and after females had an opportunity to mate. This experimental design allowed us to determine if the physical act of mating and reproducing is required to cause personality traits to change, or if the social experience of courtship is sufficient. In order to track the potential proximate mechanisms underlying changes in personality traits as a function of mating, we used a noninvasive method to measure levels of steroids excreted in the water both before and after a mating opportunity [20]. Given the dramatic neuroendocrine changes associated with reproduction [21,22], we predicted that females which mated would experience greater steroid fluctuations compared to females that had not mated and that those hormonal fluctuations would be related to behaviour. We focused on cortisol because of its hypothesized link to personality variation [23] and on steroids involved in reproduction because it was the life-history event of interest.

## 2. Methods

Threespine sticklebacks were collected from Putah Creek, California, USA. Neither males nor females showed signs of reproductive maturity; therefore, we assume that females were virgins at the

time of the experiment. Females were housed in all-female groups in 'home' tanks (35.5 L × 33 W × 25 H cm, 10 fish tank<sup>-1</sup>) with a gravel bottom, plastic plants, and an opaque shelter and stayed in these home tanks for the duration of the experiment, except when individuals were transferred to separate 'observation' tanks (60.75 L × 30 W × 20 H cm, set-up exactly the same as the home tanks) for behaviour trials. Fish were maintained at 20°C on a summer photoperiod (16:8 h light:dark cycle). The fish were daily fed a mixed diet consisting of frozen bloodworm, brine shrimp and Mysis shrimp ad libitum each day. Individuals were handled as little as possible, and non-invasive measurements were used to determine hormone levels to maximize animal welfare. The experiments were approved by the Institutional Animal Care and Use Committee at the University of Illinois Urbana-Champaign (IACUC protocol no. 18080).

### (a) Experimental design

Individual females were randomly assigned to either the control group or to have a mating opportunity. Females given a mating opportunity were paired with a control female (matched for size) who was always measured at the same time as her partner. This design allowed us to control for variation among females in time to become gravid and to reproduce, as well as for self-selection, i.e. if some behavioural types of females are less choosy or more attractive than others. Females in the control group ( $n = 37$ ) were not exposed to a male or given an opportunity to mate, but like females in the other conditions, they were socially housed, and therefore, differences between control females and females given a mating opportunity do not reflect differences in the opportunity for social interactions *per se*. Moreover, many females ( $n = 12$ ) in the control group also became gravid over the course of the experiment and released their eggs in their home tank. We tested for the effects of releasing eggs on behaviour by comparing the behaviour of control females before versus after releasing eggs, and there was no effect (activity:  $F_{1,220} = 2.74$ ,  $p$ -value = 0.10; social behaviour:  $F_{1,220} = 1.57$ ,  $p$ -value = 0.19; risk-taking behaviour:  $F_{1,220} = 0.05$ ,  $p$ -value = 0.82;  $17\alpha,20\beta$ -P:  $F_{1,12} = 0.001$ ,  $p$ -value = 0.99). Therefore, behavioural differences between females in the control group and females given a mating opportunity do not reflect differences in gravidity or the effects of releasing eggs. Some of the females given a mating opportunity ( $n = 23$ ) mated, while others ( $n = 22$ ) did not and served as 'courtship controls', because like the mated females, they had had the social experience of being courted, but unlike the mated females, they did not physically mate. We did not detect any latent differences between females that had mated and courtship control females that would lead to the non-random representation of behavioural types between the mated and courtship control groups, e.g. mated and courtship control females did not differ in size ( $t_{43,95} = 0.16$ ,  $p = 0.87$ ) or behaviour (see Results). Both courtship control and mated females had multiple opportunities to mate (mated females: range = 1–8 opportunities, mean  $\pm$  s.e. =  $2.9 \pm 0.29$ , courtship control females: range = 1–7, mean  $\pm$  s.e. =  $3.4 \pm 0.31$ ).

The behaviour of females was measured in the behavioural assays on six occasions, thrice in the 'Before' trials and thrice in the 'After' trials, with 24 h between trials. Females given a mating opportunity were placed in a tank with a male who had built a nest (60.75 L × 30 W × 20 H cm). Females started the After behavioural trials 24 h after the mated female reproduced or after the courtship control female released her eggs in her home tank (presumably to avoid the costs of becoming egg bound [24]). All females were measured for length and weight on the last day of the After trials.

### (b) Behavioural assays

#### (i) Activity

The focal fish was placed in a shelter at one end of the tank. After 1 min, the observer gently removed the cork of the shelter, and

**Table 1.** Repeatability (*R*) and variance components (among- and within-individual) of behavioural traits across the Before and After trials.

treatment groups	activity: number of areas crossed			social behaviour: number of contacts			risk-taking behaviour: time foraging under risk		
	among	within	<i>R</i>	among	within	<i>R</i>	among	within	<i>R</i>
control ( <i>n</i> = 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 ( <i>n</i> = 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 ( <i>n</i> = 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)

recorded the number of areas (four 15 cm squares) crossed for 3 min.

### (ii) Social behaviour

About 30 min after the activity assay, three females from the same population were placed into a flask at the opposite side of the refuge and we recorded the number of times the focal fish contacted the flask for 5 min.

### (iii) Risk-taking behaviour

About 30 min after the social behaviour assay, a model great egret (*Casmerodius albus*) head was placed over the observation tank. Then we added live bloodworms directly under the egret. When the focal fish approached the worms within one body length, we released the egret twice in quick succession, and then fixed the egret so that it remained above the water. Following this simulated attack, we recorded time foraging under risk for 5 min.

### (c) Measuring excreted steroids

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

Steroids were extracted from the water samples by pulling water through C18 Sep-Pak cartridges (Waters Ltd.) that had been primed with 5 ml methanol followed by 5 ml distilled water. After the sample had dripped through at a rate of approximately 2 ml min<sup>-1</sup>, the cartridge was washed with 5 ml of distilled water, and the steroids were eluted from the columns into 13 × 100 mm borosilicate vials via 5 ml of diethyl ether. The ether was dried by evaporation overnight. The dried hormones were then frozen at -80°C.

Samples were analysed via mass spectrometry with the 5500 QTRAP LC/MS/MS system (AB Sciex, Foster City, CA). In order to control for differences in body size, hormone release rates were calculated as the amount of released hormone per gram of body weight per hour (ng g<sup>-1</sup> h<sup>-1</sup>). We focus here on 17 $\alpha$ ,20 $\beta$ -P (17 $\alpha$ ,20 $\beta$ -dihydroxy-4-pregnen-3-one, hereafter referred to as 17 $\alpha$ ,20 $\beta$ -P, *n* = 19 individuals with one measure Before and one measure After).

### (d) Statistical analyses

#### (i) Repeatability of behaviour and hormones

To confirm that there were consistent individual differences in behaviour, we estimated repeatability during the Before trials. Repeatability for the three treatment groups was estimated separately to confirm that all groups showed similar patterns prior to the mating opportunity. To test whether mating influences rank-order stability, we estimated the repeatability of behaviour

and hormone titres across the six Before and After trials for the treatment groups separately.

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

#### (ii) How do personality traits and hormones change following mating?

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

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

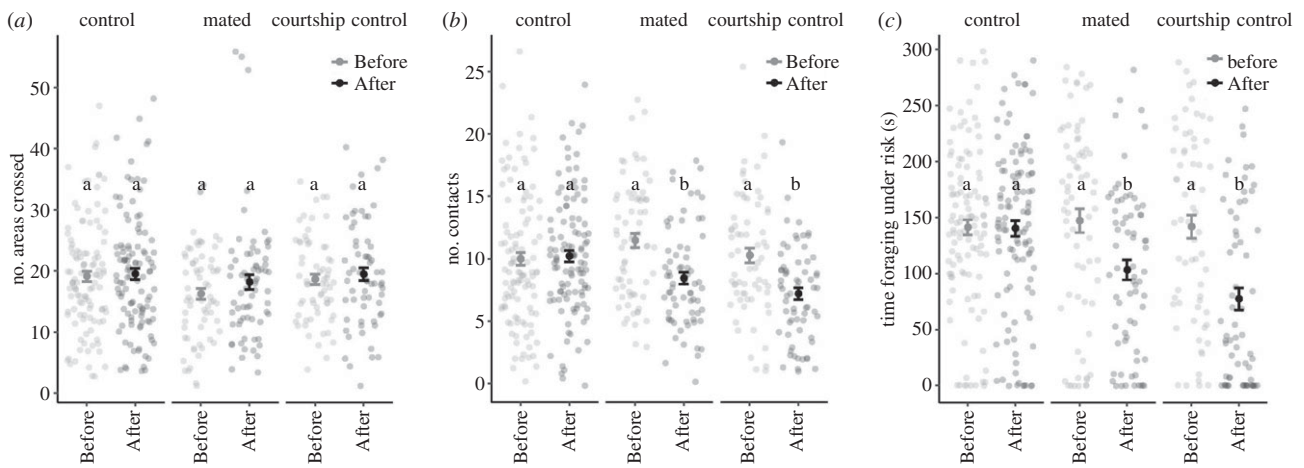
More details about the methods (behaviours recorded, hormones measured and their relevance, detailed protocols and technics, and statistics) are in the electronic supplementary material.

## 3. Results

### (a) Repeatability of behaviour

During the Before trials, individual differences in behaviour were repeatable in all treatment groups (electronic supplementary material, table S1), confirming these behaviours can be considered personality traits. Among-individual variation was consistently higher than within-individual variation.

Individual differences in behaviour were also repeatable between the Before and After trials (table 1) indicating some element of stability of individual behavioural types throughout the experiment. However, the repeatability of social behaviour and risk-taking behaviour before and after the mating opportunity was significantly lower in both the mated and courtship control treatment groups compared to the control group (table 1). This pattern appears to reflect greater among-individual variation in the control group and higher within-individual variation in the mated and courtship control groups (table 1). Greater within-individual variation in the mated and courtship control groups is



**Figure 1.** Mean-level change in behaviour as a function of courtship and mating. Bars represent standard errors. Different letters within each figure indicate means that are significantly different ( $p$ -value  $< 0.05$ ).

visually evident in the behavioural reaction norms (electronic supplementary material, figure S1), especially between trials 3 and 4, i.e. the interval during which females in these groups experienced courtship and/or mating. The repeatability of activity did not differ among the three treatment groups (table 1).

### (b) Effects of a mating opportunity on behaviour

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

Females in both the mated and courtship control groups were less social (fewer contacts with conspecifics) after they were given a mating opportunity ( $t_{131.97} = -4.09$ ,  $p < 0.001$ ;  $t_{123.21} = -4.07$ ,  $P < 0.001$ , respectively), but the social behaviour of females in the control group did not change across the experiment ( $t_{217.44} = 0.34$ ,  $p = 0.73$ ; figure 1b). The mated and courtship control females did not differ in social behaviour ( $t_{263.19} = -1.54$ ,  $p = 0.12$ ). Females in the three treatment groups did not differ in social behaviour during the Before trials ( $F_{2,243} = 1.93$ ,  $p$ -value = 0.15).

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

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

### (c) $17\alpha,20\beta$ -P was higher after a mating opportunity and was negatively correlated with social behaviour and risk-taking behaviour

The experience of courtship caused  $17\alpha,20\beta$ -P to increase:  $17\alpha,20\beta$ -P did not differ among the three treatment groups during the Before trials ( $F_{2,16} = 1.69$ ,  $p$ -value = 0.22), but

$17\alpha,20\beta$ -P was significantly higher during the After trials in both the mated and courtship control groups compared to the control group ( $F_{2,16} = 3.49$ ,  $p$ -value = 0.04; electronic supplementary material, figure S2).

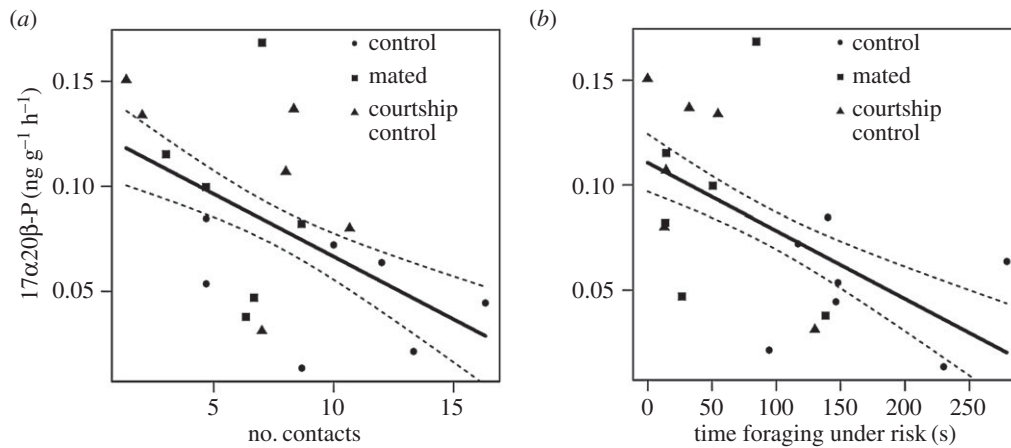
We did not detect a relationship between behaviour and  $17\alpha,20\beta$ -P during the Before trials (number of contacts:  $F_{1,17} = 0.42$ ,  $p$ -value = 0.52; willingness to forage under risk:  $F_{1,17} = 0.24$ ,  $p$ -value = 0.63). However, during the After trials, there was a negative relationship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

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

## 4. Discussion

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

This conclusion is bolstered by the study's strong experimental design. We confirmed that there are consistent individual differences in behaviour by repeatedly measuring the same individuals in a battery of behavioural assays. The repeated measures design revealed that individuals given a mating opportunity retained their new behavioural type for the duration of the experiment. Moreover, it allowed us to compare within- and among-individual variance components, revealing greater within-individual variation in individuals given a mating opportunity compared to the control group. This is strong evidence that the mean-level differences between treatment groups reflect within-individual change, i.e. individuals changed their behaviour after a mating opportunity. In addition, we confirmed that self-selection was not a problem:



**Figure 2.** Relationship between progesterone and (a) the social behaviour (number of contacts) and (b) the risk-taking behaviour (time foraging under risk) during the 'After' trials. Each symbol represents the mean number of contacts and the average time an individual spent foraging under risk during the three 'After' trials. The dashed line represents the 95% confidence interval.

at the beginning of the experiment, females in the three treatment groups did not differ in behaviour, but they diverged following the mating opportunity.

Interestingly, regardless of whether they physically mated or if they just had the social experience of courtship, females became less social and less willing to take risks after a mating opportunity. We do not know why some females given a mating opportunity mated and others did not. It is possible, for example, that mated females experienced less aggression from males during the mating opportunity, that mated females were more attractive to males, that mated females were less choosy, or less interested in mating generally. However, prior to entering the experiment, we did not detect any differences in behaviour or body size or reproductive state (gravidity) between mated and courtship control females (electronic supplementary material), both types of females were given numerous opportunities to mate. There was not a systematic difference between the males that were offered to females that did versus did not mate, and we ensured that all females were gravid and ready to spawn when given a mating opportunity. Mate choice in sticklebacks is mutual [27]; therefore, we suspect that some females did not mate simply because they were not offered the right match. Despite the fact that mated versus courted females might have differed in attractiveness, choosiness or the way they interacted with males, both types of females became less social and less willing to take risks and experienced an increase in progesterone. These results strongly suggest that there is something about the experience of having an opportunity to mate with males that changes females' personality, i.e. the social experience is sufficient to cause personality traits to change. That mating and experiencing courtship do not differ in their impact on female personality might stem from the fact that mating in this system is similarly costly to experiencing courtship. The similar effects on personality may be from the similar physiological impacts of the behaviours involved in each case; a different outcome might be expected when the act of mating for females is more costly than engaging in courtship only. If that is the case, then the impact of a mating opportunity on personality in this study may be a conservative example of the impact of mating when considering systems in which the females then go on to perform parental care.

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

Females excreted more  $17\alpha,20\beta\text{-P}$  after they were given a mating opportunity, regardless of whether they mated, and individual variation in behaviour was related to individual variation in  $17\alpha,20\beta\text{-P}$ .  $17\alpha,20\beta\text{-P}$  promotes the secretion of ovarian fluid in sticklebacks [34], and it is likely that it is the maturation inducing hormone in sticklebacks [24]. In other fishes, a sharp peak of  $17\alpha,20\beta\text{-P}$  occurs prior to spontaneous or induced ovulation [35,36]. Studies in goldfish and other fishes have shown that exposure to a potential mate can trigger ovulation, presumably via pheromones [37], and there is some evidence for chemical communication between males and females during courtship in stickleback [38]. Therefore, the higher levels of  $17\alpha,20\beta\text{-P}$  in females given a mating opportunity in this experiment could reflect their recent experience with a potential mate. Alternatively, because  $17\alpha,20\beta\text{-P}$  can act as a pheromone used during communication among females [39], higher levels of  $17\alpha,20\beta\text{-P}$  in both the mated and courtship control groups might reflect  $17\alpha,20\beta\text{-P}$  that was released by females that mated, while they were co-housed with courtship control females.

Interestingly, contrary to our prediction based on the coping styles literature [23], cortisol did not appear to be involved in mediating the effects of a mating opportunity on personality.

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

It is now a truism that early life experience is important for behavioural development in humans and nonhuman animals [4,40], but whether and why personality traits continue to change through adulthood is less understood. Experimental studies that manipulate and control particular life events in nonhuman animals have the potential to make important contributions in this area. Moreover, this topic deserves more attention in the animal personality literature because it has a number of ecological and evolutionary implications that have yet to be explored. For example, personality change in young wild individuals may have a strong consequence for dispersal and/or the establishment of social

groups, with potential consequences for social interactions among individuals within the group. More generally, these results highlight the importance of phenotypic plasticity over ontogeny for the generation and maintenance of personality variation within natural populations; changes in the timing of important life-history events or other experiences could have consequences for the distribution of personality variation within natural populations.

**Ethics.** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in this study involving animals were in accordance with the ethical standards of the University of Illinois, Urbana-Champaign (IACUC protocol no. 18080).

**Data accessibility.** Data is available from the Dryad Digital Repository: <https://dx.doi.org/10.5061/dryad.wstqjq2h3> [41].

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

**Competing interests.** We declare we have no competing interests.

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