Juvenile social experience affects pairing success at adulthood: congruence with the loser effect?

Mylene M. Mariette, Charlène Cathaud, Rémi Chambon and Clémentine Vignal

Social interactions with adults are often critical for the development of mating behaviours. However, the potential role of other primary social partners such as juvenile counterparts is rarely considered. Most interestingly, it is not known whether interactions with juvenile females improve males’ courtship and whether, similar to the winner and loser effects in a fighting context—outcome of these interactions shapes males’ behaviour in future encounters. We investigated the combined effects of male quality and juvenile social experience on pairing success at adulthood in zebra finches (Taeniopygia guttata). We manipulated brood size to alter male quality and then placed males in either same- or mixed-sex juvenile dyads until adulthood. We found that males from reduced broods obtained more copulations and males from mixed-sex dyads had more complete courtships. Furthermore, independent of their quality, males that failed to pair with juvenile females, but not juvenile males, had a lower pairing success at adulthood. Our study shows that negative social experience with peers during adolescence may be a potent determinant of pairing success that can override the effects of early environmental conditions on male attractiveness and thereby supports the occurrence of an analogous process to the loser effect in a mating context.

1. Introduction

Social context encountered during ontogeny may have a profound influence on individual sexual development and consequently on the strength and direction of sexual selection [1]. Quite a substantial part of the courtship behaviour [2,3], mate choice preferences [4,5] and social skills [6] possibly involved in mate acquisition are indeed learnt, and therefore modulated by environmental and social conditions. For example, there is strong evidence that learning from a tutor often plays a major role in song acquisition (reviewed in [3,7]). Likewise, mating preferences for the right species (imprinting: [8]), the opposite sex [9], a specific phenotype [10] or high-quality mates [11–13] have all been found to be shaped by experience, either during ontogeny or at adulthood. Social environments that provide more opportunities for learning may therefore allow individuals to improve courtship performance [14] or mate choice [13] and consequently become more reproductively competitive [15]. For example, beside the tutor role of males, interactions with females during courtship development may allow juvenile males to fine-tune their display to females’ preferences, or to learn to interpret females’ behaviour. Indeed, in brown-headed cowbirds (Molothrus ater ater), adult females guide juvenile males’ song practicing by performing a specific visual display on hearing their preferred songs [16].

While the effect of early social interactions between young and adults on courtship (and especially song) development has been well studied, much less is known on the potential role of peers. Yet, many social interactions also take place between broodmates or unrelated juveniles and may affect individuals’ social behaviour at adulthood. For example, in starlings, Sturnus vulgaris, subadults preferentially copy songs from each other rather than from adults [17],
whereas in zebra finches, the presence of male siblings interferes with accurate learning of the father’s song [18] while that of a female sibling might have a positive effect [19].

Besides courtship quality, social interactions may also affect males’ courting intensity, persistence or propensity. In particular, even though courtship rate is at least partly limited by an individual’s intrinsic quality or condition [20], males have been found to moderate their courtship intensity according to the responsiveness of the female being courted [21–23]. In addition, in Drosophila spp., rejection by heterospecific females decreases males’ propensity to court this type of females in future encounters compared with males that have been accepted by heterospecific females [24]. Beyond mate phenotype learning, these findings suggest that males may decrease courting effort when past mate rejection predicts that their chances of success are low [25] and imply that the outcome of previous interactions influences males’ behaviour in future encounters.

This hypothesis has interestingly received strong empirical support in a fighting context, in many social and territorial species. Indeed, previous winners are more likely to escalate fights and win against new opponents, and previous losers to avoid or lose future fights, an effect that persists for a few hours to three weeks after the initial fight (reviewed in [26,27]). These ‘winner and loser effects’ may be adaptive if previous aggressive interaction outcome allows individuals to optimize their fighting strategy to the current social context, thereby avoiding unprofitable costly fights without missing ‘easy win’ opportunities (self-assessment hypothesis) [27]. Alternatively, new opponents, if they are able to detect whether an individual won or lost its previous contest and use this information to gauge its fighting abilities, may also adjust their behaviour accordingly (social cue hypothesis) [27]. Whether a similar mechanism also occurs in a mating context, whereby previous pairing success and failure would influence a male subsequent courting effort and pairing probability, is currently unknown. Yet, similar benefits to considering previous mating experience are likely, either for males to assess their relative attractiveness and adjust their courting strategy accordingly [28], or for females to assess male quality based on other females’ decision (i.e. mate-copying strategy [29]). Likewise, there is evidence that the hormonal mechanisms underlying the winner effect [30] might also occur in a mating context [31]. Lastly, just as in a fighting context where the loser effect is stronger than the winner effect [26], we may expect an experience of failure to influence future behaviour more strongly than a successful mating, especially if males by default display at their maximum rate (given their condition [20]).

Social interactions, and the role they play in development, are likely to be especially important in group-living species. The zebra finch (Taeniopygia guttata) is a socially monogamous, colonial and highly social passerine that forages and moves in groups [32]. After nutritional independence, juveniles mostly associate with individuals of the same age, with whom some may form affiliative bonds [32]. Zebra finches’ partners spend most of their time together throughout the day and year [32,33]. They pair for life, although repairing commonly occurs because of relatively high mortality rates [32]. When no opposite-sex partner is available, adults may form same-sex pair-bonds of similar strength to mixed-sex pairs [34]. Recent experiments in captivity suggest that male courtship intensity towards an unfamiliar female may be influenced by social context or experience. Namely, juvenile males developing in groups rather than in pairs have a lower courtship rate as adults (and may be less preferred by females [35]); and adult males appear to adjust their courtship rate depending on previous social feedback from other males in single-sex groups [36] or directly in response to female sexual responsiveness during courtship [22]. Courtship rate is also condition-dependent in this species. In particular, experimentally altering early environmental conditions via brood size or diet manipulations has repeatedly been found to affect nestling growth [37,38] and several aspects of male ‘overall quality’ at adulthood, including morphology, metabolic rate, courtship performance and attractiveness (i.e. females’ preference for these males) [37–40].

Here, we investigated the effect of exposure to female counterparts and of experiencing pairing failure or success at the end of the juvenile stage, on males’ pairing success at adulthood. In order to disentangle the effect of these social factors from that of male true quality or condition (hereafter ‘intrinsic quality’ as opposed to signalled quality), we manipulated brood sizes, a procedure known to alter male phenotype at adulthood in this species [37–40]. Then, after reaching nutritional independence, males from experimental broods were placed in either same- or mixed-sex dyads during the whole juvenile stage, where we estimated their initial propensity to pair as subadults and final pairing status upon reaching sexual maturity. During this social treatment, all juvenile males could interact and pair with a juvenile companion but only those in the mixed-sex group were exposed to juvenile females’ social feedback. We then tested male courtship rate, mating and pairing success with unfamiliar females at adulthood and expected males from the mixed-sex group (i.e. experienced with females) and males from reduced broods (i.e. high intrinsic quality) to do better. In addition, if an equivalent process to the loser effect occurs in a mating context, we expected males that recently failed to pair with their juvenile female companion to be less likely to pair with new females at adulthood.

2. Material and methods
(a) Overview and general procedures
Experimental males were followed from hatching to about two months past sexual maturity, and received successively (i) a brood manipulation treatment to alter early food intake from hatching to nutritional independence (at approx. 40 days old), (ii) a social manipulation treatment throughout the juvenile stage from after nutritional independence to sexual maturity (at approx. 90 days old), (iii) a pairing test immediately after the social treatment and (iv) a courtship and mating test two months later (see electronic supplementary material, figure S1). The purpose of the latter was not to test how long the effect of social experience lasts. Rather, it assessed whether the brood manipulation was successful in altering male intrinsic quality as perceived by females and whether the social treatment had any long-term effects on male courtship performance and mating success, while limiting the possible influence of recent social experience on males’ motivation to court females.

When they find an appropriate partner, zebra finches typically pair within one to three days (M. M. Mariette 2011, unpublished data). Courtship and copulation mostly occur on the day of pair formation (and before nesting), whereas partners continue to frequently express affiliative behaviours (clumping and
and allopreening) and males to sing undirected songs throughout the duration of the pair-bond [32]. For this species, it is therefore usual to measure male courtship rate and mating success (i.e. copulation) during short five-minute-encounters with females [36,41,42], and pairing status (including for same-sex pairs) from the presence of affiliative and the quasi-absence of aggressive behaviours between partners on any day post-pair-bond formation [9,34,42]. Like adults, juveniles share affiliative behaviours with peers that become increasingly exclusive to a preferred social partner with age [32], and it is hence possible to assess juvenile pairing status in the same way as for adults. Here, we established males’ pairing status, during both the social treatment and the pairing test at adulthood, based on 30 minutes of video recording where we noted the number and duration of affiliative behaviours (i.e. clumping (sitting next to each other, with their flanks in physical contact), allopreening, sharing a nest), and the number of aggressive behaviours (i.e. pecking, bill fencing, bill clapping, displacing, chasing; all described in Zann [32]). All these behaviours were then combined into a global ‘interaction score’ that was used as a criterion for pairing status, using the same threshold for all juvenile and adult interactions (see §2). In addition, from the same videos, we recorded the number of undirected song bouts, and, as a measure of social attraction, the number of male approaches towards the other individual (i.e. lands close to or hops towards other individual and stays within 10 cm of it for at least 2 s). To obtain the number of occurrences of each above-mentioned behaviour per observation, a ‘behaviour’ was counted each time it was interrupted by a pause or another behaviour.

(b) Brood manipulation

In a large indoor aviary (6.5×5.5×3.5 m; temperature: 20–30°C, daylight: 07.30–20.30), 28 adult domestic zebra finch pairs with wild-type plumage were allowed to breed freely under constant daylight: 07.30–20.30), 28 adult domestic zebra finch pairs with wild-type plumage were allowed to breed freely under constant conditions, and produced 45 broods in total (spread over three breeding peaks from April to August 2011). Clutch size, brood size and laying and hatching dates were recorded for all nests. Two to three days after hatching, broods of similar age were partially cross-fostered and brood size increased or decreased by zero, one or two chicks. However, owing to unusually low hatching success (mean = 59%) because of egg damage caused by parents’ rings, most broods were small (mean = 2.75 ± 1.03) and we could only establish ‘control’- and ‘reduced’-sized broods. In control broods, the number of nestlings raised (mean ± s.d.: 3.65 ± 0.93) was within 25% of the original clutch size, whereas reduced broods (2.4 ± 0.82 nestlings) were one- to two-thirds smaller than the original clutch size. The 34 experimental males came from 25 broods (i.e. 20 males from 14 reduced and 14 males from 11 control broods), and the 22 juvenile female companions from 16 broods (i.e. seven reduced and nine control).

(c) Social treatment

During the 50-day social treatment, each juvenile male encountered successively either two male or two female juvenile companions, each for 25 days, as follows. After reaching nutritional independence and the end of the sensory period of song learning [32], juveniles were caught in the aviary (mean ± s.d. age: 54 ± 7 days; median: 52 days). Males were transferred to a cage (40×45×50 cm) with either another juvenile male (same-sex treatment, n = 17) or a juvenile female (mixed-sex treatment, n = 17) of similar age and from another experimental brood (either ‘reduced’ or ‘control’). An unfamiliar adult pair was placed in a cage next to each juvenile dyad to expose them to normal adult social behaviour. After 25 days, each male was moved to a new cage, with a new juvenile companion (of the same sex as the first) and new adult neighbours. They remained in this second dyad for another 25 days, before being transferred to an individual cage. The day before splitting each dyad, birds were filmed for 45 minutes using a video camera (Sony super steady shot HDR-SR11) to record behavioural interactions and pairing status, as explained above. The first ten and last five minutes of video were discarded (i.e. 30 minutes analysed) to eliminate possible disturbance effects. Social interactions at the end of the first dyad provided a proxy for males’ intrinsic propensity to pair (as a subadult), and those at the end of the second dyad indicated whether males had succeeded or failed to pair upon reaching sexual maturity. In addition, the number of male approaches estimated male social attraction throughout the social treatment.

(d) Pairing success: four-day test

To alleviate the effect of variations in females’ mate preferences, during the pairing test, each experimental male encountered successively two unfamiliar adult females from the stock, as follows. One to three days after the second dyad was split (age = 105 days), an unfamiliar adult female was introduced into the male’s cage and they were left to freely interact. The female was then removed from the male’s cage in the evening of the fourth day, and the procedure was repeated on the next day (day five) with a second adult female for another four days. On days four and eight, birds were filmed for 45 minutes to record male behaviour and pairing status with the first and second females, respectively (n = 66 videos for 34 males; two videos were lost before analysis; as above, 30 minutes were analysed).

(e) Mating success: five-minute test

After the above pairing test, males were maintained in individual cages where they nonetheless had visual, chemical and acoustic contacts with neighbours, for about 75 days (± 22 s.d.; the duration of this period had no effect on male subsequent success). Then, courtship rate and mating success of all experimental males (except one male from the same-sex group that died before the test) were assessed in a standard no-choice five-minute test [36,38,41,42] where female mate preferences are highly repeatable [42] and not confounded by female social preferences or sampling behaviour [43]. Every week, a batch of four males (two from each social treatment group) were tested in a room adjacent to a holding room. Each male was placed in a separate cage, so that it could hear but not see other birds, and allowed to acclimatize for two days. Then, for four consecutive mornings (starting at 10.30), the four males were observed successively. Each male was therefore tested four times (except for the first four males, which were tested only three times), with a different unfamiliar stock female each time, so it encountered four (randomly chosen) females in total, at 24 h intervals. As soon as the female was introduced into the male cage, a five-minute observation (hereafter a ‘trial’) began, during which a single experienced observer watched from behind a curtain to quantify the time the male spent interacting with the female (‘activity duration’), the number of male approaches, bill wiping (ritualized wiping on perch) and directed song bouts, and the presence of male head-feather fluffing, mounting attempts and successful copulations. Head-feather fluffing was recorded only in the last 68 trials (n = 34 trials for each social treatment group) after the absence of this typical behaviour for some males was noted by the observer, blind to experimental treatments. The female was removed at the end of the five-minute trial. Interactions were non-aggressive: bill fencing commonly occurred, especially with uninterested females, but no chasing or pecking was ever observed. Female copulation solicitation behaviour occurred too rarely (i.e. in only 11% of trials) to be analysed statistically so female acceptance was only assessed by mounting behaviour and copulation (which never occurs without female consent [41]). Among the 16 females (of 22) used in more than three trials, 93% were mounted by at least

![Image](http://rspb.royalsocietypublishing.org/Downloaded from http://rspb.royalsocietypublishing.org/ on January 22, 2018)
one male, and 80% accepted copulation at least once. Deleting trials with females that never copulated did not change any result unless otherwise indicated.

(f) Statistical analyses

To establish males’ pairing status during the social treatment and the pairing test, an interaction score was calculated from social behaviours for all videos together, so that interactions with both juvenile companions and both adult females were directly comparable. Beforehand, clumping and nest sharing were pooled into a single ‘clumping’ variable because 21 cages (i.e. 16%) mistakenly did not have nests; the absence of nests had no effect on any of the behaviours considered ($\chi^2$ tests: all $p > 0.48$). Aggressive behaviours were also pooled into an aggression index, where different behaviours were weighted according to their level of aggressiveness as: $\text{index} = n$. pecks + $2g$. bill fences + $n$. bill claps + $n$. displacements + 5 × $n$. chases. We used this weighted aggression index rather than entering each aggressive behaviour singly into the computation of the interaction score to avoid variables with many nil values and the overemphasizing of aggressive relative to affiliative behaviours. Affiliative behaviours and the aggression index were then entered into a principal component analysis (PCA) to obtain the interaction score. The PCA retained one component with eigenvalue larger that one, explaining 49% of the variance and with the following weight: number and duration of clumping: 0.83 and 0.59, respectively; duration of allogrooming: 0.83; occurrence of reciprocal allogrooming: 0.75 and aggression index: −0.41. PCA score approximately followed a bimodal distribution, with the nadir at about −0.5, and values below that threshold corresponding to a quasi-absence of affiliative behaviours, with varying level of aggression. Only individuals with a PCA score above the −0.5 threshold were then considered as having successfully paired. For robustness, because ‘socially tolerant’ birds might conceivably accept very short clumping from non-mate in cages, we repeated all analyses with a higher threshold (PCA score = −0.30), corresponding for paired individuals to more than three minute clumping (i.e. 10% of the time) or some allogrooming, and we also used PCA score as a continuous variable and present results on raw behaviours.

All statistical analyses were carried out in R (v. 2.14.1, R Foundation for Statistical computing). We used generalized linear-mixed models (GLMMs; function lmer from the lme4 package) with a Poisson distribution for count/duration response variables or a binomial distribution, with the nadir at about $2g$ meters and their confidence interval, as well as z-scores and the corresponding p-values.

3. Results

(a) Brood manipulation effect on morphology

Male nestlings were lighter before fledging (mean age: 16.7 days) in control than in reduced broods (mean mass ± s.d.: 11.12 ± 1.40 g and 12.43 ± 1.42 g; $t$-test: $n = 41$ nestling males surviving to adulthood (including 33 males used in the social treatment), $t_{38} = 3.2$, $p = 0.003$). Males’ weight before fledging strongly predicted their weight at adulthood ($R = 0.70$, $p < 0.001$, $n = 41$). However, the brood manipulation effect was no longer significant at adulthood (control: 16.18 ± 2.69 g reduced: 17.33 ± 2.31 g; $t$-test: $n = 41$, $t_{38} = 1.5$, $p = 0.149$). As found previously [37], the brood manipulation therefore affected nesting growth, which later had to be compensated for to reach similar weight at adulthood.

(b) Social interactions within juvenile dyads

The brood manipulation of either the male or its companion had no effect on pairing, within either the first or second dyads (all $p > 0.47$). At the end of the social treatment (mean age = 103 days: adult), two-thirds of males were paired in both groups (67% and 71% paired in mixed- and same-sex groups), whereas at the end of the first dyad (mean age = 78 days: subadult), all males were paired in the same-sex group and only half (53%) in the mixed-sex group. Importantly, pairing status in the second dyad was not affected by males’ initial propensity to pair as a subadult in the first dyad (in the mixed-sex group: $p = 0.15$; not testable in same-sex group). Lastly, contrary to those in the same-sex group, males that remained unpaired by the end of the social treatment in the mixed-sex group were not less socially motivated than paired males, because they
approached both their first and second female companions more (both \( p < 0.001 \)). Statistics are detailed in the electronic supplementary material, S2.

Overall, by randomly ascribing juvenile companions to males and taking advantage of differential affinity between individuals that was not dependent on male intrinsic quality or social attraction, our treatment was successful in producing four types of experimental males that either succeeded or failed to pair with a male or female upon reaching sexual maturity at the end of the social treatment.

(c) Social interactions and pair-bond: four-day test

Forty-five per cent of males had paired with the adult female after four days.

The brood manipulation had no effect on any of the behaviours considered in the pairing test (see electronic supplementary material, table S3a).

Contrary to our prediction, more males from the same-sex group clumped and allopreened the adult female than males from the mixed-sex group (GLMMs, respectively: \( z = -2.07, p = 0.038 \) and \( z = -2.15, p = 0.032 \)), although there was no effect of the social treatment on the duration of these behaviours among the males that expressed them (see electronic supplementary material, table S3a). As a result, males from the same-sex group paired with the adult females in 56% of trials against 47% for males from the mixed-sex group, 3 but that difference was not significant (see electronic supplementary material, table S3a). These patterns did not appear to be related to differences in males’ social motivation because their was no difference between mixed- and same-sex males in the number of times they approached the adult females, and males from the mixed-sex group sang more (undirected songs) than those from the same-sex group (see electronic supplementary material, table S3a).

In addition, males that had been paired as subadults with a female (i.e. juv1-paired in the mixed-sex group) then allopreened adult females for longer in the pairing test (GLMM: \( z = 3.12, p = 0.002 \)).

Moreover, in agreement with the loser effect hypothesis transposed to a mating context, males that had remained unpaired by the end of the juvenile stage (i.e. juv2-unpaired) were then less likely to approach, clump, allopreen (GLMMs: \( 0.001 < p < 0.040 \)) and pair (\( z = 2.21, p = 0.027 \)) with adult females than juv2-paired males (see electronic supplementary material, table S3a). Each of these effects was because of males that failed to pair with the juvenile female rather than those that did not pair with the juvenile male (see electronic supplementary material, table S3b; GLMMs with three-level predictor variable: approach: \( z = -2.09, p = 0.037 \); others: figure 1). Likewise, the social interaction score with adult females (PCA score) was lower for the former than the latter (see electronic supplementary material, table S3b and figure 1).

These patterns did not appear to simply correspond to individual consistency in social behaviour and pairing success as no such consistency was observed between the end of the social treatment and the pairing test except for males that failed to pair with the juvenile female (see slopes in figure 2 and electronic supplementary material, table S4b). By contrast, individual consistency during the pairing test was similar in all four groups (figure 2 and electronic supplementary material, table S4b).

In summary, a male’s recent experience of failing to pair with a female during the late juvenile stage had a strong impact on its subsequent pairing success, whereas no effects of the brood manipulation or of the training benefits gained from interacting with female peers were detected.

(d) Mating success: five-minute test

Copulation success was relatively high for this type of test [41], with copulation occurring in 29% of trials.

As expected, the brood manipulation affected male mating success at adulthood, with males from experimentally reduced broods being more likely to mount and copulate with the females than males from control broods (see electronic supplementary material, table S5 and figure 3a-c). Males from reduced broods tended to sing more than controls (GLMM: \( z = 2.12, p = 0.034 \)), and they approached the female more often (\( z = 2.20, p = 0.028 \)), were more likely to raise their head feathers (figure 3a) and started courting the female sooner than control males (\( z = -2.16, p = 0.031 \); electronic supplementary material, table S6).

In addition, there was no effect of the social treatment (i.e. sex of juvenile companions) on mating success or singing rate but it did affect more subtle elements of male courtship. Namely, males from the mixed-sex group did more bill wiping (GLMM: \( z = 3.00, p = 0.003 \)) and were more likely to raise their head feathers than same-sex males (see electronic supplementary material, table S5 and figure 3a).

Moreover, in the mixed-sex group, juv1-unpaired males were unexpectedly more likely to mount (\( 14/30 = 47\% \) of trials; GLMM: \( z = -3.12, p = 0.002 \)) and obtain copulations (\( 9/30 = 30\% \); GLMM: \( z = -2.29, p = 0.022 \)) with adult females than juv1-paired males (\( 4/36 = 11\% \) and \( 2/36 = 6\% \), respectively).

Lastly, juv2-pairing status no longer had any effect on male success, with juv2-unpaired males having a similar copulation success and courtship behaviour to formerly paired males (see electronic supplementary material, table S5), including when a three-level predictor was used.

4. Discussion

As predicted, we found that early nutritional stress imposed by the brood manipulation affected male morphology at fledging as well as courtship and mating success at adulthood, and that interacting with juvenile females during development improved some subtle elements of male courtship display. The latter, however, did not translate into a higher mating or pairing success at adulthood. Instead, males from the mixed-sex group tended to actually be less successful at pairing with adult females than those from the same-sex group. This was because, while males’ success towards females was not related to previous interactions with juvenile males, males that failed to pair with their last female companion were then less likely to pair with new adult females. These males were neither from larger broods (i.e. no lower intrinsic quality) nor were they less socially attracted to females before that experience nor less likely to pair as a subadult (first dyad). Taken together, our results therefore suggest that, as for the loser effect, previous negative experience can be a strong determinant of male pairing success that may in some cases override the effect of male intrinsic quality.
Males that failed to pair with a female, but not a male, at the end of the juvenile stage, were more likely to again fail pairing with new adult females during the pairing test. Several lines of evidence suggest that it was specifically this social experience during the social treatment that caused the observed effect rather than some pre-existing traits of these juv2-unpaired males from the mixed-sex group. Indeed, these males did not appear to be particularly ‘socially impaired’ before that experience: they actually approached both their juveniles companions more than juv2-paired males (but later approached adult females less), and many were paired with their first juvenile companion. Also, these were not specifically poor-quality males: the outcome of social interactions during the social treatment was random relative to the brood manipulation (which nonetheless successfully affected male morphology and mating success), and these males did not have a lower courtship rate nor mating success in the mating test (once the effect of their negative social experience was presumably gone, several weeks later). Lastly, the tendency for these males to repeatedly fail pairing is unlikely to simply reflect an individual’s overall consistency in mate acquisition capacity, because they were the only group to show such consistency during and after the social treatment. Experiments directly manipulating the social feedback received by males [23], but also their pairing status, would nonetheless be valuable to confirm our findings.

By demonstrating that previous experience of failure affects male behaviour and the outcome of future interactions, our results suggest that a process equivalent to the loser effect, extensively studied in a fighting context, may occur in a mating context. However, as for experiments in a fighting context, we cannot determine whether this effect is adaptive or merely a by-product of physiological response to previous interactions [27]. In addition, it is not known whether males directly adjusted their approaching and
courtship persistence to previous social feedback (self-assessment hypothesis) or whether new females detected that juv2-unpaired males were previously unsuccessful and discriminated against them (social cue hypothesis) [27]. Interestingly, both these hypotheses, formulated for the winner and loser effect in a fighting context, have independently received considerable attention in a mating context. Specifically, as evidence for context-specific mate preference and mating success accumulates [44,45], there is growing acceptance that males may need to assess their relative attractiveness at any place and time to optimize mating strategy (e.g. stop courting unwilling females and move to a different group: [28,46]). A recent theoretical model suggests that previous performance may be useful in that assessment [47]. Likewise, regarding the social-cue hypothesis, there is extensive evidence that, when difference in male quality is small, females eavesdrop on males’ previous mating interactions and copy the choice of other females [29], as a form of public information use. If failing to pair, such as losing a fight, leave some detectable cues on males [27,30], this might provide a means for mate choice copying without females witnessing the choice of others. Interestingly, if this is true and unsuccessful males keep failing to pair with subsequent females, this would largely increase reproductive skew by exacerbating inter-individual differences in mating success.

The same-sex group provided an interesting counterpoint to the mixed-sex group because it also had paired and unpaired individuals since, as reported before in adults [34], some juvenile males paired with their male companion (albeit with moderate interaction scores). In particular, the deprivation of affiliative behaviours during the juvenile

Figure 2. Interaction scores (first PCA component-loading affiliative behaviours positively and aggression index negatively) in same- (a,c) and mixed-sex (b,d) treatment groups for experimental males with their second juvenile companion and the two females encountered during the four-day test. Scores higher than −0.5 (horizontal line) correspond to paired individuals and those lower to unpaired individuals. Data points corresponding to the same individual are in the same colour and connected by a line. (Online version in colour.)
stage could not explain the subsequent low pairing success of unpaired males from the mixed-sex group, because their same-sex group counterparts, which were also deprived of such interactions, were not affected. Furthermore, the absence of a loser-effect equivalent in the same-sex group makes sense if the social feedback from juvenile males is not a reliable estimate of a male’s chance of success towards females and males therefore do not adjust their courtship persistence to past experience with males. Alternatively, unpaired males in the same-sex group may not bear the ‘loser cue’ for females to discriminate against them if they did not experience a strong rejection from their male companion but instead were merely less socially motivated individuals (who, in contrast to their mixed-sex counterparts, approached their first juvenile companion less).

Likewise, failure to pair during the first juvenile dyad was not related to pairing success at adulthood, possibly because individuals were younger at that stage or because, as for the winner and loser effect, the most recent experience has a stronger effect than previous ones on future interactions [26].

Notably, we found no evidence suggesting an equivalent process to the winner effect, because previously paired males were no more likely to be successful again with new females. Such an effect might have been masked by the stress caused by the separation from the previous mate. However, considering that partners are constantly together, being separated for more than 12 h would usually only occur when one partner is dead. We expect re-pairing to occur rapidly after the loss of a partner, because breeding can start at any time in this opportunistic species. Accordingly, in captivity, if held without any auditory and visual contact with their partner, then there is almost immediate re-pairing if another individual is available [48].

Male past experience was the main determinant of male pairing success in the four-day test, whereas mating success in the five-minute test several weeks later was mostly determined by male early nutritional stress. This suggests that the effect of previous experience may disappear with time (as expected for the loser effect [26]), revealing an effect of early nutritional stress that was initially masked by that of previous experience. In addition, it is possible that the effect of brood manipulation was not present in the four-day pairing test, because males were able to mitigate its effect when allowed to interact with the female for several days.

Overall, our results demonstrate that a male’s previous experience with females upon reaching sexual maturity has a strong influence on its subsequent pairing success, independently of its intrinsic quality and social attraction, and thereby provide evidence towards the occurrence of a loser effect equivalent in a mating context. Given the growing interest in the effect of social factors on individual mating success, bridging this field to the extensive theoretical and empirical work carried out on the winner and loser effect in the fighting context is likely to be extremely valuable.

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