Effects of Social Conditions During Adolescence on Courtship and Aggressive Behavior are not Abolished by Adult Social Experience

ABSTRACT: Social experience during adolescence has long-lasting consequences for adult social behavior in many species. In zebra finches, individuals reared in pairs during adolescence start to court females faster, sing more courtship motifs to females and are more aggressive compared with group-reared males. We investigated whether such differences are stable during adulthood or can be abolished by novel social experience after adolescence by giving all birds extensive experience with group life during adulthood. Courtship and aggressiveness increased in all males, but pair-reared males still had a higher motif rate and were more aggressive than group-reared males. Males no longer differed in courtship latency. In addition to the stable treatment differences, individual differences in behavior remained stable over time. Our results show that differences in behavior acquired during adolescence are preserved into adulthood, although adults still change their social behavior. Adolescence can thus be seen as a sensitive period during which social conditions have a lasting effect on adult behavior. © 2014 Wiley Periodicals, Inc. Dev Psychobiol

Keywords: social behavior; phenotypic plasticity; behavioral flexibility; behavioral stability; sensitive period; imprinting; individual differences; zebra finch; Taeniopygia guttata

INTRODUCTION

Morphological, physiological and behavioral traits are the result of a complex interaction of genetic and environmental factors during development, the genotype providing stable information on factors relevant over evolutionary time spans, and environmental factors informing about current conditions or predicting future ones (Haldane, 1946; Comstock & Moll, 1963; West-Eberhard, 2003). Phenotypic changes in response to environmental stimuli are beneficial for the organism because they adjust traits to the current or future environment (Bradshaw, 1965; Greene, 1989; Levitan, 1989; Montgomerie, Lyon, & Holder, 2001; Charmantier et al., 2008). Therefore, organisms should ideally remain plastic throughout their whole life. However, maintaining plasticity is thought to be costly (Auld, Agrawal, & Relyea, 2010; DeWitt, Sih, & Wilson, et al., 1998; Snell-Rood, 2013), and costs may be a reason why plasticity often decreases substantially during ontogeny (Gabriel, Lutberg, Sih, & Tollrian, 2005; Sultan, 2007), and why behavioral and neural plasticity in response to external stimulation is often restricted to certain stages in early development, so called “sensitive periods” (Bateson, 1979; Knudsen, 2004; Lorenz, 1935).

Lorenz (1935) coined the term “imprinting” for this type of learning, to point to the stability of behaviors...
established in the course of sensitive periods and it has been shown later that song learning, which had been named an “imprinting like process” in the early learning literature, shared almost every feature with the originally described process of sexual and filial imprinting (Bischof, 1997; ten Cate, Vos, & Mann, 1993). Although there was a lot of debate concerning the question of how stable these changes actually are (from “irreversible” to “persistent”) there is no doubt that acquisition of behavioral or neural traits during sensitive periods is more stable than that outside of such periods (Bischof, 2007; Suomi, 1981; Knudsen, 2004). It is however important to emphasize that sensitive periods are not regulated by age or time per se but by developmental processes that follow each other in an ordered fashion and can thus be advanced or delayed experimentally (Immelmann & Suomi, 1981; Michel & Tyler, 2005). Also, the concepts of imprinting does not imply that individuals are completely inflexible. If it is not possible to express the imprinted behavior because the environmental conditions are not adequate, animals are generally able to modify their behavior. However, if they are subsequently again free to choose, the imprinted behavior is preferred even after a long period during which they were forced to alter their behavior (Immelmann, 1972). In song learning, it has also been shown that the effects of early song learning dominate the adult song of a songbird, but that smaller changes are still possible (Jones, ten Cate, & Slater, 1996).

Studies on birds in the context of social learning suggest that individuals may go through several sensitive periods during development, each of them with a specific relevance for the acquisition of social behavior (Bischof, 1997). Earlier studies mainly concentrated on sensitive period learning during very early stages of life (Immelmann & Suomi, 1981; Lorenz, 1935), but more recent experiments in the context of sexual imprinting and song learning demonstrate that adolescence is also a sensitive phase for the acquisition of adult social behavior. The best evidence is provided by studies on zebra finches (Taeniopygia guttata) which show that social conditions during adolescence strongly influence both the establishment of the adult sexual preference (Bischof, 1994; Kruit and Meeuwissen, 1991; Oetting, Proeve, & Bischof, 1995) and the adult song (Bischof, 1997; Jones et al., 1996).

Recent studies show that social conditions during adolescence also affect adult male zebra finches’ courtship activity, aggressiveness, and grouping behavior (Ruploh, Bischof, & von Engelhardt, 2013, 2014). Adult males reared in heterosexual pairs during adolescence [defined here as the transitional period between childhood and adulthood (Sachser, Hennessy, & Kaiser, 2011; Sisk & Foster, 2004; Spear, 2000)] start to court females faster, sing more courtship motifs to females and are more aggressive towards competitors for mates compared with adult males who spent adolescence in small mixed-sex groups of conspecifics. These group differences persisted 4 months after the initial recordings, although the birds were housed in visual isolation to other birds in between. This suggests that differences in social stimulation during adolescence affect social behavior permanently (Ruploh et al., 2013). Because males were housed individually between tests, such stable differences could be due to a lack of opportunity of pair-reared males to experience social interactions, such as solicitation and rejection by females and aggressive interactions with other males competing for mates (Ruploh et al., 2013). In the current study, we therefore asked whether the social behavior of pair-reared males would converge with that of group-reared males if they were able to catch up on social group experience after adolescence. If, on the other hand, differences in adult courtship and aggressive behavior are maintained during adulthood this would suggest a specific effect of social conditions within a sensitive period during adolescence that cannot be replaced by similar social experience during adulthood.

To investigate this question, we used the pair-grouped and group-reared birds that had already been behaviorally characterized in the previous experiments mentioned above (Ruploh et al., 2013). In the course of the present experiment, these males were offered extensive opportunity to interact socially with both males and females by exposing them to various social group conditions. We then performed the same behavioral tests as in the previous study to measure the males courtship and aggressive behavior. Since the same males were tested for courtship and aggressiveness before and after adult group life experience, we were also able to analyze whether the individual differences in behavior persisted over time.

METHODS

Ethical Standards

All experimental procedures applied in this study are not regulated by the German animal protection law and do not require special approval. Animal facilities were approved (dated 18 April 2002) for keeping and breeding zebra finches for research purposes by the local government authority responsible for health, veterinary and food monitoring (Gesundheits-, Veterinär- und Lebensmittelüberwachungsamt).
Subjects

The 27 male zebra finches that were subjects of this study had already been subject to a number of social behavior tests. For detailed information about subjects and housing conditions see (Ruploh et al., 2013, 2014). Briefly, experimental males hatched in one of five outdoor aviaries at the University of Bielefeld and were produced by 20 different breeding pairs in 22 different broods. Shortly after nutritional independence, on day 40 ± 2 from hatching, the experimental birds were moved to other aviaries with differing social composition. Males were either kept in heterosexual pairs or in small mixed-sex groups of three males and three females until adulthood (day 110 ± 2). These ages were chosen to ensure that individuals experienced the different social conditions during adolescence (for more details regarding adolescence in zebra finches see discussion). Experimental groups were visually but not acoustically isolated from each other. Siblings were never housed together and birds within one group did not differ in age by more than 4 days. After day 110 ± 2, all males were caged individually (cage size: .3 m × .4 m × .4 m), with auditory but no visual contact with other birds (Fig. 1). For practical reasons, the study was conducted in two batches. The experimental treatment was identical, but males from batch 1 were kept in outdoor aviaries (6 m × 2 m × 3 m) (social treatment starting between August and mid October 2010), while males from batch 2 were housed indoors in cages (.3 m × .8 m × .4 m; pair-reared birds) or in small aviaries (1 m × 2 m × 2 m, group-reared birds) (social treatment starting between mid November 2010 and mid December 2011). Therefore, batches experienced different ambient temperatures and photoperiods. In total, we had 14 pair-reared males (eight from batch 1 and six from batch 2) and used the same number of age-matched group-reared males, selecting one at random when several similar-aged individuals were available. One group-reared male of batch 2 unfortunately died shortly after the adult group experience, reducing the final sample size to 13 for this experimental group. Prior to the present experiment, male courtship activity and aggressiveness had been measured twice, first, when they were about 135 days old and then again at an age of about 255 days (Ruploh et al., 2013). In between, the males were housed again individually with auditory, but no visual contact to other birds. Birds thus underwent no novel social experience (except during the tests) between the first and the second recording. After these two test phases, experimental males were individually exposed to an unfamiliar group of six male and six female conspecifics for 48 hr (Ruploh et al., 2014), had the opportunity to breed in mixed-sex flocks [batch 1 (male age 530 ± 49 days): two aviaries housing four randomly assigned males from each treatment with eight unfamiliar females, eight nest boxes available in each aviary; batch 2 (male age 385 ± 33 days): two aviaries housing three randomly assigned males from each treatment with six females, six nest boxes available in each aviary] for a period of about 4 months and were finally housed as a single flock (all experimental males) in a large aviary (2.4 m × 3.0 m × 3.0 m) for approximately 2.5 weeks (Fig. 1). The test procedures described below are identical with those used in the previous

FIGURE 1 Timeline of subjects’ social and experimental experience (means ± SE). The scale of the continuous sections reflects the true relative durations of experimental periods, dotted sections are not in scale and indicate periods of individual housing. For details see text.
study (Ruploh et al., 2013) for testing male courtship activity and aggressiveness.

For acclimatization, all experimental males were caged individually one week before the first test was conducted. At this time, the birds were 826 ± 44 (mean ± S.D.) days old. Throughout the experiments, a commercial zebra finch diet (Elles, Mischfutter für Exoten, L. Stroetmann Saat, 48163 Münster, Germany) and water were provided ad libitum. This diet was supplemented twice weekly with egg food (Céde N.-V., 9940 Evergem, Belgium) and germinated seeds and once weekly with fresh greens.

**Courtship Song**

An unfamiliar female was placed in a cage which was then attached to the front of the male’s home cage. Directed song was quantified by recording the latency to the first courtship song and by counting the number of directed motifs sung within 10 min. A latency of 600 s was assigned to males that did not sing at all. Tests took place between 9:00 and 11:00 am in the room where the males were housed between tests so that there was constant background noise due to the presence of other conspecifics. Two different stimulus females were used, each equally often for males from both social rearing conditions.

**Aggression Towards Other Males**

One male from each social background and an unfamiliar female were placed in a cage (0.3 m × 0.8 m × 0.4 m) that was equipped with four perches (two in the upper half and two in the lower half of the cage). We counted the number of times males chased each other. Chasing rates between males may differ not only because of their intrinsic motivation to attack, but also because they respond differently to the appearance or behavior of their opponent. Males were observed alternately in 12 five-minute intervals, resulting in a total sample time of 1 hr for each male and a total observation time of 2 hr. A chase was defined as a flight at the other male followed by his immediate displacement, and a chase was considered to be finished when the chased bird landed on a perch or the floor. Tests took place between 9:00 am and 11:00 am. Again, other zebra finches were present and could be heard in the background during testing. For individual identification, one of 26 leg bands with different color combinations was randomly assigned to each male. Each pair of males was tested with a new unfamiliar female.

Since the number of available males differed between the two experimental conditions (14 males reared in pairs, but only 13 group-reared males) we could only test 13 pairs in the aggression test, thus reducing the total sample size to 26 for this test.

**Data Analysis**

Behavioral measures were transformed to obtain normally distributed residuals and equal variances between experimental groups, thus allowing the use of parametric statistics. The latency to court, the total number of produced directed song motifs and the sum of chasings across all 12 observation periods were log transformed. Before data transformation a value of one was added to each measure to be able to transform zeros, since some birds did not sing or chase at all.

We tested whether experimental males still differed in their social behavior after adult group life experience by calculating an ANOVA with “treatment” and “batch” as fixed factors. An interaction effect between treatment and batch and an effect of batch were never detected (p > .2). Thus differences in housing (such as temperature and photoperiod) between batches did not affect our results and we removed batch from all models. For the treatment effect, we calculated the one-sided significance, since the direction of the difference could be clearly predicted from our previous study, i.e. pair-reared males should show a lower latency to court, a higher motif rate and more chasing than group-reared males.

To analyze the stability of male behavior before and after group-living conditions during adulthood, we combined the current data set with the last measures of courtship activity and aggressiveness before all males experienced group life (i.e., at an age of about 255 days, Ruploh et al., 2013). We than calculated a linear mixed-effects model (LMM) with “treatment”- “batch”, “session” (before vs. after adult group-life), and their interactions as fixed factors. Interactions between fixed factors and the main effect of batch were not significant for any recorded variable and thus removed from all models. The consistency of individual differences in behavior was assessed by calculating the significance of a random effect of bird ID from the respective final models. The variation explained by differences among individuals was calculated according to Nakagawa and Schielzeth (2010) as the percentage of residual variance of the final models (i.e. after taking significant fixed effects of treatment and session into account).

To estimate the within-treatment change in social behavior from prior to post group-living during adulthood, a LMM with “session” as fixed factor was calculated for each treatment separately.

All analyses were performed in SPSSv21 (Armonk, NY) and the significance level $\alpha$ was set at $p < .05$.

**RESULTS**

**Courtship Song**

Male zebra finches that were reared in heterosexual pairs or in mixed-sex groups during adolescence no longer differed in their latency to court an unfamiliar female after experiencing group life during adulthood ($F_{1,25} = .37, p = .27$, Fig. 2A, right). One would expect to see an increase in courtship latency of pair-reared males if they had become more similar to group-reared males due to the social experience during adulthood. Instead, they decreased their courtship latencies ($F_{1,13} = 12.00, p = .004$, Fig. 2A, left). However, group-reared males also decreased their courtship latencies ($F_{1,12} = 24.87, p < .001$, Fig. 2A, left) so that they started to court as fast as pair-reared males. Individual
differences in courtship latency were stable (random effect of ID: 0.20 \pm 0.10, Wald Z = 2.03, p = .04) and explained 44% of the residual variance, after taking treatment effects and the overall reduction of courtship latencies across sessions into account.

Male zebra finches that were reared with a single female during adolescence sang at a significantly higher rate than group-reared males ($F_{1,25} = 4.34, p = .02$, Fig. 2B, right), even after they experienced group life as adults. Over time, motif rate increased significantly in pair-reared males ($F_{1,13} = 16.32, p = .001$, Fig. 2B, left) and in group-reared males ($F_{1,12} = 12.70, p = .004$, Fig. 2B, left). Individual differences in courtship rates were not stable over time (random effect of ID: 0.05 \pm 0.03, Wald Z = 1.34, p = .18) and explained 28% of the residual variance, after taking treatment differences and the overall increase in courtship rate across sessions into account.

Aggression Towards Other Males

Males reared in pairs were still more aggressive in a mate competition context than group-reared males, although they had experienced group life during adulthood ($F_{1,24} = 3.36, p = .04$, Fig. 2C, right). Pair-reared males were significantly more aggressive than during the previous tests ($F_{1,12} = 6.23, p = .03$, Fig. 2C, left), whereas males reared in groups showed only a tendency towards increased aggressiveness ($F_{1,12} = 3.24, p = .10$, Fig. 2C, left). Individual differences in aggressiveness were stable over time (random effect of ID: 0.34 \pm 0.17, Wald Z = 1.9, p = .05) and explained 43% of the residual variance, after taking treatment differences and the overall increase in aggressiveness across sessions into account.

DISCUSSION

Previous experiments (Ruploh et al., 2013, 2014) demonstrated that the social environment experienced during adolescence affects the adult social behavior of male zebra finches. The differences in courtship activity and aggressiveness between males from different rearing conditions remained stable for several months. Both pair- and group-reared birds might not have changed their behavior since they were housed individually between the behavioral tests and therefore had no social experience during adult life.

We therefore investigated here whether the social behavior of pair-reared males would converge with that of group-reared males if they were able to catch up on social group experience after adolescence. Our present study shows that the effects of adolescent experience can still be seen after males from both adolescent social
rearing conditions can make social group experience during adulthood, favoring the view that adolescence is a sensitive period during which adult social behavior is shaped permanently.

Influences of social conditions during early and adolescent development on adult behavior, morphology, physiology and gene expression have been described frequently (e.g., birds: Holveck, Geberzahn, & Riebel, 2011; Mariette, Cathaud, Chambon, & Vignal, 2013; Riebel, Naguib, & Gil, 2009; White, Gros-Louis, King, Papakhian, & West, 2007; fish: Arnold & Taborsky, 2010; Chapman, Ward, & Krause, 2008; Taborsky, Arnold, Junker, & Tschopp, 2012; Taborsky, Tschirren, Meunier, & Aubin-Horth, 2013; mammals: Branchi, 2009; Delville, Melloni, & Ferris, 1998; Ferris, Messenger, & Sullivan, 2005; Sachser, Hennessy, & Kaiser, 2011; Sachser, Kaiser, & Hennessy, 2013). While there is no doubt that such influences exist, there is still a debate about the long-term persistence of the observed effects of developmental social conditions.

Permanent influences of social experience during adolescence on male zebra finches social behavior are well known from studies on avian song learning and sexual imprinting (Bischof, 1997, 2007), two important model systems for the investigation of the neural, hormonal and genomic mechanisms of early learning (Bischof, Geißler, & Rollenhagen 2002; Spencer, Buchanan, Goldsmith, & Catchpole, 2003; Thompson et al., 2013; Wade, Lampen, Qi, & Tang, 2013). In mammals, the social behavioral development of guinea pigs has been described to be particularly sensitive to social stimuli during adolescence (Sachser et al., 2011, 2013), with long-lasting influences on adult social behavior that suggest impressive similarities between the influence of the social environment during adolescence in zebra finches and guinea pigs. Other species, however, such as the brown-headed cowbird *Molothrus ater*, also remain sensitive to social conditions during adulthood, and their social behavior can be repeatedly adjusted to changing environmental conditions (Gersick, Snyder-Mackler, & White, 2012; White, Gersick, Freed-Brown, & Snyder-Mackler, 2010). The notion of a persistent influence of adolescence on adult social behavior thus cannot be generalized, but has to be examined separately for every species.

The stable effect, seen here, of the social environment during adolescence on adult male zebra finches’ behavior does not imply that courtship and aggressive behavior are completely inflexible in the adult birds. This study and our previous data on the same birds clearly show that individuals are able to change their behavior over time, and depending upon the context. The present data reveals that males from both experimental groups increased song motif rate and aggressiveness towards competitors for mates (though in group-reared males there was only a statistical trend for aggressiveness) over time. Since our experiment was not designed to investigate the causes of such an increase in courtship activity and mate competitiveness, there is not only one explanation for this result. The increase might be attributable to male age and the accompanied decline in residual reproductive value, resulting in increased reproductive effort (Copeland & Fedorka, 2012; Hayes, Booksmythe, Jennions, & Backwell, 2013; Karl, Heuskin & Fischer, 2013; Velando, Drummond, & Torres, 2006; Williams, 1966). It may also be due to short-term effects like sexual deprivation due to the periods of same-sex and individual housing (Proeve, 1987) preceding the tests. The resulting increase in sexual motivation may also explain why males no longer differed in the latency to court, since they started to court females so rapidly (after about 10 s rather than about 100 s as previously) that any remaining treatment differences may have been obscured.

In an earlier experiment (Ruploh et al., 2014) with the same birds, both pair- and group-reared males showed context-dependent and short-term phenotypic flexibility of courtship activity and aggressiveness: When males from both social backgrounds were placed into a group of conspecifics over a period of 48 hr, the number of courtship song motifs of pair-reared males did not differ from those of group-reared males and was as low as the motif rate of group-reared males in the present study. Also, courtship rate of all males strongly decreased over 48 hr. Similarly, pair-reared males reduced their level of aggressiveness to that of group-reared males within 48 hr, although on average they tended to be more aggressive at the beginning of the experiment (Ruploh et al., 2014). When pair-reared males encountered the social setting of the present experiment, they again showed significantly higher rates of courtship and aggressive behavior compared with group-reared males, demonstrating that males from both treatments were still different. These observations indicate that individuals may primarily differ in how they initially respond to a novel social situation and it will be interesting to investigate the long-term consequences of these initial differences in more detail.

Context-dependent flexibility during adulthood has also been described for sexual preferences of male zebra finches. Males that were sexually imprinted on Bengalese finches (*Lonchura striata*) preferred these birds as sexual partners when adult if they could choose between a Bengalese finch and a zebra finch (Immelmann, 1969a). A male zebra finch imprinted on a Bengalese finch will pair and breed with a zebra finch.
female if there is no access to a female Bengalese finch. However, if it can afterwards choose between a zebra finch and a Bengalese finch female, it will again prefer the foster species (Immelmann, 1972). We therefore suggest that in a similar way adolescent social conditions may have influenced the adult preference for a certain level of courtship activity and aggressiveness in a given context, even though males can still adjust their behavior to different situations.

Why did the average courtship rate and aggressiveness of pair-reared males not converge with that of group-reared males in spite of their group experience during adulthood? One explanation might be that not only the group-reared birds, but also the pair-reared birds received positive social feedback during adult group housing and therefore maintained their behavioral strategies. Indeed, data from the adult breeding groups, which will be presented in a separate paper, show that almost all males of both groups attracted a mate, obtained a nest and reared offspring until independence. However, pair-reared males are less integrated in a group and lose more weight when housed for two days with unfamiliar conspecifics (Ruploh et al., 2014). Pair-reared males thus receive at least initially a negative social feedback, although they seem to be in the long term similarly successful. It is therefore currently unclear to what extent social feedback during adulthood may contribute to the maintenance of differences in adult male social behavior.

What might be the mechanisms underlying the adult stability of behavioral differences? Especially for imprinting and song learning there is quite a lot of literature concerning the physiological basis of sensitive periods (Bischof et al., 2002; Spencer et al., 2003; Thompson et al., 2013; Wade et al., 2013). Ontogenetic cortical plasticity in mammals as well as the organization of neural circuits within the auditory system of owls follow the same principles and may be based on similar physiological events (Bischof, 2007; Knudsen, 2004). A variety of mechanisms, including neurogenesis, increase and reduction in dendritic spines, synapse reorganization, myelination and levels of neurotransmitter or receptors may cause or contribute to limit plasticity to certain periods in life, and, perhaps paradoxically, neuroendocrine plasticity, including neurogenesis, can even be required to maintain traits stable during adulthood (Bischof, 2007; Knudsen, 2004; Nordeen & Nordeen, 2004; Pytte et al., 2012). Finally, also the genomic mechanisms of learning and sensitive phases are increasingly being studied in birds (Clayton, 2013; Drnevich et al., 2013; London, Dong, Replogle, & Clayton, 2009; Scharff & Adam, 2013). From our present experiments we are not able to draw any conclusions regarding the physiological basis for the obvious stability of the acquired behavioral differences. It might, however, be interesting to investigate whether the rules that form neuronal circuits and shape simple as well as complex behaviors are also applicable to the development of more complex social behavior.

What are the benefits of periods of enhanced sensitivity to environmental influences early in life? Adjustment of behavior to environmental conditions requires collecting and storing environmental information. Ideally, this has to be done before the respective behavior is needed for an animal’s survival and reproduction. Enhanced sensitivity in early development is thus ecologically worthwhile. However, the ability to incorporate new environmental information into behavioral outputs is also necessary during adulthood. It is therefore, at the first glance, difficult to understand why the sensitivity to environmental conditions often declines with age, as the present study and many others suggest (Crawford, Harwert, Smith, & von Noorden, 1996; Immelmann, 1979; Marler & Peters, 1987; Wiesel & Hubel, 1965). An explanation may be that plasticity also incurs costs, for example for the maintenance of sensory and regulatory systems that detect and process environmental conditions, or costs arising from the production of a more flexible and necessarily redundant neural network (Auld et al., 2010; DeWitt et al., 1998; Lieshoff, Proeve & Bischof, 2000; Snell-Rood, 2013). This makes it reasonable to assume that adult plasticity may be reduced if the costs are not outweighed by benefits. Adult plasticity may not have evolved in very short-lived species, such as the zebra finch (Zann, 1996), since the benefits of plasticity are low if there is little chance that individuals encounter a change in their environment during their lifetime. In addition, canalization of a previously flexible trait might not only reduce the costs of plasticity but may also be beneficial by allowing more rapid decision-making. Between-species differences in life expectancy and/or the variability of the environment may therefore contribute to the naturally occurring variation in adult behavioral plasticity.

Interestingly, zebra finch song also shows only very limited plasticity during adulthood unlike in many other bird species that continue to learn or produce new song types (Immelmann, 1969b; Jones et al., 2006; Kroodsma, 1978; Beecher & Brenowitz, 2005). Concerning socially relevant behavior, they may thus be closed-ended learners in general.

While the sensitive period for the shaping of adult courtship activity and aggressiveness would certainly include adolescence, the current data does not allow us to determine whether it is restricted to this time span.
In humans and mammals, adolescence is usually defined as the transition from childhood to adulthood, a period characterized by large changes in the social environment and behavior that is accompanied by neural and hormonal reorganization (Spear, 2000; Sisk & Foster, 2004; Sachser et al., 2011). Zebra finches leave their nests with about 20 days, become nutritionally independent around day 35–40 and sexually mature between 70 and 90 days. Within this time span, the social environment of the young bird changes dramatically, with interactions shifting from parents and siblings towards peers and unrelated adults. This period is also characterized by neural, hormonal and behavioral changes and can be directly compared to adolescence in mammals (Bischof, 2007; Brown & Spencer, 2013; Proeve, 1987) Since all males were housed individually between the end of adolescence (day 110 ± 2) and the beginning of adult group-housing (day 481 ± 108) we cannot exclude the possibility that the birds are still sensitive to a change in social conditions within this time span. We also do not know whether social conditions before the experimental treatment started (day 45) may have effects similar to those during adolescence since all males were kept in groups during that time. It is, however, obvious that the adolescent social environment can either override earlier influences or has an influence on behavior in addition to such earlier effects since it strongly affected adult behavior. Further analyses provide additional support for the idea that adult social experience was not able to override the influence of conditions earlier in life: Social rearing conditions during adolescence did not explain all stable individual differences in behavior. We found consistent individual differences in male courtship latencies and aggressiveness, even after taking into account effects of the adolescent social background and temporal changes. These individual differences must be attributable to genetic or to additional early environmental factors or to a combination of both. Birds may have a different genetic background, may differ in pre- or post-natal maternal, paternal or sibling effects, and the birds may have experienced different avian environments before the experimental treatment started. To disentangle all these different influences is a task for further studies.

NOTES

We thank Ursula Kodytek, Brigitta Otte, Ursula Rennemann, Kristina Ruhe, Jana Derbogen, Uwe Dettmer, Werner Jamin, and Michael Meyerhoff for taking care of the animals. We thank Suzanne von Engelhardt for language polishing.

REFERENCES

Persistent Effects of Adolescent Social Experience


