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Mate preference does not influence reproductive motivation and parental cooperation in female zebra finches

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Abstract

In socially monogamous species, low availability of sexually active unpaired individuals in the local population may constrain mate choice, resulting in mating with sub-optimal partners. Here we experimentally investigate whether female reproductive behaviour is different when paired with a preferred or a non-preferred male in the zebra finch (*Taeniopygia guttata*). First, we assessed female mating preferences using a four-way choice apparatus, then females were caged together with either their preferred or least-preferred male. Female reproductive motivation, assessed by the propensity of laying eggs within two weeks from pairing and clutch mass, did not differ between the two experimental groups. Females responded to mate removal by either increasing their care, so as to compensate for the lost care of their mate, or by significantly reducing incubation. This bimodal response was not explained by mate preference, nevertheless, we found that females with lower baseline (i.e., pre-manipulation) incubation effort were more likely to cease incubation during mate removal. Taken together, we found no evidence that female reproductive behaviour varies along with mate preference.

1. Introduction

In socially monogamous species, including more than 90% of bird species (Lack, 1968), the availability of sexually active unpaired individuals in the local population may constrain mate choice. Some individuals, therefore, may be forced to mate with sub-optimal partners, and such individuals may consequently have different reproductive behaviours as opposed to those mated with a preferred partner. Parental investment, for instance, has often been reported to vary with mate quality as postulated by the differential allocation (Burley, 1986, 1988; Sheldon, 2000) and the reproductive compensation hypotheses (Gowaty, 2003, 2008; Gowaty et al., 2007; or 'positive differential allocation' and 'negative differential allocation', following Ratikainen & Kokko, 2010). These hypotheses have contrasting predictions with regards to when to expect female reproductive and parental effort to increase with varying male attractiveness. Positive differential allocation predicts increasing male attractiveness should result in increasing female reproductive effort, as the cost of increased female effort is offset by higher offspring quality. Negative differential allocation, however, predicts females should respond to decreasing, rather than increasing, male attractiveness with higher reproductive effort to compensate for likely offspring viability deficits due to mating with low-quality males. Moreover, a recent study suggests that having a non-preferred mate can be stressful for the female, and such females may delay the onset of reproduction (Griffith et al., 2011).

Biparental care of the young can be considered partly as cooperation between two, usually unrelated individuals (Harrison et al., 2009), and partly as a reproductive behaviour with inevitable sexual conflict (Lessells, 2006). Biparental systems, therefore, provided rich sources for theoretical analyses of conflict and cooperation (Maynard Smith, 1977; Barta et al., 2002; McNamara et al., 2003; McNamara & Weissing, 2010). Experimental studies followed up these theoretical advances when parental effort of one of the parents was manipulated and the response of its partner was observed (e.g., Wright & Cuthill, 1989; Clutton-Brock, 1991; Liker, 1995; Griggio et al., 2005; Kosztolányi et al., 2009; Lendvai et al., 2009). A recent meta-analysis showed that the most common response in these studies was partial compensation, so that the parental effort of the non-manipulated parent did not fully compensate for the loss of care provisioning by the mate (Harrison et al., 2009). Nevertheless, besides partial compensation, no compensation,

full compensation or overcompensation by the mate of the manipulated parents also frequently occurred (Harrison et al., 2009). Here we conjectured that, similarly to differential allocation in parental investment, the large variation between and within studies of parental cooperation may be explained by mate preference. To address this hypothesis, we manipulated mate preference and mate parental contribution simultaneously, and analysed female compensation based on mate preference.

Our experiment stands out from previous empirical studies by combining two well-established approaches to test predictions of the differential allocation hypotheses in parental cooperation context. Therefore, we use methods that have not been combined in one experiment previously. First, instead of general (or artificial) preference for male traits, we carry out a rigorous, interactive mate preference test, and pairs are established based on the actual preference of the female for a given male. Second, besides parental effort, we focus on parental cooperation for the loss of incubation effort by the male by monitoring female compensation during temporary male removal. During male removal, acoustic, visual and olfactory interactions (Caspers & Krause, 2011; Krause et al., 2012) between pair members are sustained because our intention is to create an experimental situation in which males are present, but do not contribute to parenting ('mate restriction' henceforth). This concept is based on theoretical and empirical studies suggesting that an individual should compensate differently when its mate disappears as opposed to when it is present but does not contribute to parental care (cf., Whittingham et al., 1994; McNamara et al., 2003; Lendvai et al., 2009).

We use the socially monogamous zebra finch (*Taeniopygia guttata*), to investigate the proposition that mate preference influences parental behaviour. This small songbird with biparental care of eggs and young is very suitable to address our research questions; the species is well-established within experimental studies of sexual selection, sexual conflict and parental care (e.g., Swaddle & Cuthill, 1994; Royle et al., 2002; Forstmeier & Birkhead, 2004; Bolund et al., 2009; Pariser et al., 2010). We had two specific objectives with this experiment. First, to test whether female zebra finches paired with their preferred males are more likely to initiate breeding and invest more in egg-production than those paired with their least-preferred males ('reproductive motivation' henceforth); and second, to test compensatory responses of females to temporary mate restriction, based on their mate preference.

2. Material and methods

2.1. *Study population and keeping conditions*

The experiment was carried out involving 61 female and 116 male zebra finches that were collected from 12 different breeders (from Hungary and Romania) to ensure a low level of inbreeding and large genetic variation. Our intention was to create large variation with regards to plumage morphology, so that in addition to wild-type birds, black cheek, white, fawn, pied, Florida fancy, dominant silver and penguin mutations were included in the study population. Age and breeding experience also varied, although all birds participating in the study were sexually mature at the onset of the experiment. Zebra finches were ringed with a numbered aluminium ring for individual identification (AC Hughes, Hampton Hill, UK), so that neither the males nor the females were colour ringed to avoid artificially influencing mating preferences (Burley, 1988; Pariser et al., 2010). Birds were individually caged prior to the experiment (size of each cage was 42 × 30 × 44 cm) in four indoor aviaries (two male-only rooms, and two mixed rooms of females and pairs) at Göd Biological Station of Eötvös University, 22 km north of Budapest (47°40′N, 19°07′E). The sizes of the indoor aviaries were 3.4 × 3.4 × 2.4 m (male rooms), and 5.1 × 3.4 × 2.4 m (female and pair rooms). Within rooms, cages were only visually separated from one another. Each female cage was provided with a plastic nest box (13 × 10 × 9 cm; Versele-Laga, Astene, Belgium), and for pairing and reproduction (i.e., following mating preference test) the male was moved to the cage of the female.

Room temperature was kept between 18–21°C during the experiment. The windows were blinded and we used a 14:10 h light:dark regime throughout the experiment (lights on at 6 a.m.) using compact fluorescent light sources connected to a timer to facilitate the birds' reproductive activity.

Fresh drinking and bathing water as well as seeds (Exota bird food, Deli Nature, Schoten, Belgium) and protein-rich soft bird food (home-made out of wheat germ, wheat bran, grits, cob-meal, sesame seed, shredded coconut, sunflower seed, honey, vanilla, yeast, desiccated milk, carrot, cheese, chicken's egg (minced with shell) and green leaves) was provided twice weekly ad libitum. The soft bird food also contained vitamin and mineral supply (Nekton E and Nekton S, Pforzheim, Germany). Sepia and commercially available cat litter was provided in each cage as a calcium source and for the birds to fret their beaks.

2.2. General experimental design

The experiment was carried out between 1 June 2009 and 15 February 2010, and it consisted of two major stages. First we carried out a mate preference test for each female, and females then were allocated randomly to two groups: mated with either their (i) most or (ii) least preferred male. Second, reproduction of pairs was monitored daily, and if the pair started to incubate, we recorded normal parental behaviour during incubation and the females' compensation during temporary mate restriction.

2.3. Mate preference test

We used a four-way choice apparatus following the design of Swaddle & Cuthill (1994; Figure 1), in which a male can be presented in each of the four stimulus compartments. Following Waas & Wordsworth (1999) and our own experiences with regards to different behaviour of the same subjects in interactive and non-interactive choice tests, the males and females were separated by a wire mesh so that they could interact. In addition to the background room illumination, a 40 W light bulb and a fluorescent tube (Aqua Relle Hg, TL-D 18 W, Philips, Eindhoven, The Netherlands) emitting in the UV wavelength range, were mounted above each stimulus compartment to ensure that artificial light conditions and the lack of UV light components did not compromise the colour perception and thus the mating preferences of our subjects (Bennett et al., 1996).

Females were familiarised with the choice apparatus in groups of five for 8 h (no males were presented in stimulus compartments), and were then individually tested on two consecutive days, as follows. On day 1, the female was first left alone for 1 h (between 8 a.m. and 9 a.m., local time), after which the four randomly chosen males were presented to the female: one male in each stimulus compartment (Figure 1). After a four-hour test (between 9 a.m. and 1 p.m.), the males in opposite stimulus compartments were swapped (together with their home cages), and following a 15-min relaxation period, the female was again tested for four hours (between 1:15 p.m. and 5:15 p.m.). On day 2, the same female with the same four males was tested again for 8 h following the above schedule, but this time the males were rotated 90° (clockwise or counter-clockwise, randomly) at the start of the test day compared to day 1, so that by the end of day 2 each male was presented in each stimulus compartment in the apparatus. After the last 4-h test session of the female ended on day 2, the four males offered to the next
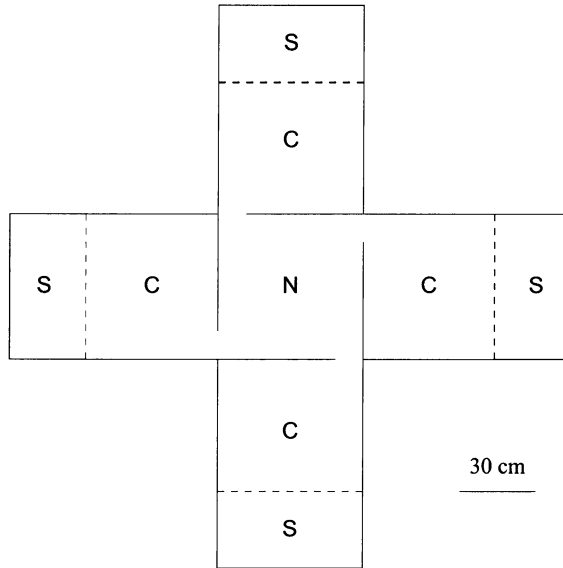
Figure 1. Plan view of the four-way mate choice apparatus. The middle, neutral chamber (N) opens in four choice chambers (C), and a stimulus compartment (S) is attached to each of the choice chambers in which males in their home cages are presented.

female were familiarised with the choice apparatus by placing them in the stimulus compartments for one hour without any female present (between 5:30 p.m. and 6:30 p.m.).

Female movement during mate preference test was monitored by a specially designed automatic infrared motion detector system that is described and validated elsewhere (Pogány et al., 2014). Duration and number of visits of the female to each male was calculated from the output of the detector system for the two test days, separately. A male was considered to be preferred if the female spent most of her choice time in front of that male, relative to the other three males. Therefore, for each male a preference score was calculated for test day 1 and test day 2 (separately) as follows: time spent in front of male/total time spent in front of all males; the male with the highest preference score was considered as preferred. Those females were selected for further tests, which consistently followed their preferred male between test day 1 and test day 2 ($N = 39$ of 61 females). Most of the females which showed no consistent preference in their first mate preference test ($N = 18$ of 22 females) were once more tested with a different set of four males to increase sample size. 10 of these 18 females were consistent in their second

mate preference test, and together with these, a total of 49 females were included in further tests (80.3% of all females tested). Each male was involved in the mate preference test of 1–5 different females (mean ± SD number of mate test per male: 3.15 ± 0.11 trials).

The four males were randomly allocated to the female (i.e., regardless of colour morph, age, size or any other characteristics), although we took care to avoid testing the female with males from the same breeder she derived from, as these birds might have had previous experience with each other or could be related. We controlled for possible confounding effects by randomizing female order, male order and the initial stimulus compartment of males. Side effects were also controlled by swapping males and presenting each male in each of the stimulus compartments (see above).

2.4. Reproductive motivation of females

Of the 49 females that showed consistent preference towards a male between different tests, 27 and 22 were allocated to their preferred and least-preferred mate (based on the combined data of test day 1 and test day 2), respectively. Different sample sizes in groups reflect random allocation of each female to either of the two groups. To create pairs, the selected male was placed into the cage of the female, and nest material (hay) was provided. The nest box of each pair was examined daily for 14 days, and we recorded the start of egg-laying, the number of eggs laid and whether the female started incubating or not. A female was considered as reproducing if she laid any eggs and started to incubate within 14 days from the start of pair formation. Clutch mass (total egg mass in the clutch) was measured on day 8 of incubation.

2.5. Parental cooperation experiment

29 females that laid eggs and started incubation entered the parental cooperation test (14 females with their preferred and 15 females with their least-preferred male). The remaining females involved those that did not lay eggs ($N = 12$ females) or laid eggs but did not start incubation ($N = 8$ females); these females were separated from their males, and were excluded from further analysis.

Parental cooperation was estimated by recording incubation behaviour on three consecutive days: days 8–10 from the start of incubation (pre-manipulation, male removal and post-manipulation, henceforth). Male and female pre-manipulation incubation effort was recorded on day 8 by setting

up a camera attached to a four-channel digital video recorder (HDR-04RP, Hunt Electronic, New Taipei City, Taiwan) to record the entire cage for ca. 6 h (mean ± SE: 359.20 ± 0.71 min, between 9 a.m. and 3 p.m.). Male and female zebra finches share incubation and offspring provisioning, albeit not equally; females spent approximately 1.5 times as much time on incubation as males (see Results and Figure 2). Following recording pre-manipulation incubation (day 9 of incubation, male removal), the male was captured and placed into an adjacent empty cage attached to that of the female, and female incubation during male temporary removal was recorded for ca. 6 h (353.88 ± 4.88 min), after which the male was immediately replaced into the cage of the female. On the next day (day 10 of incubation, post-manipulation), incubation behaviour of the pair was again recorded for ca. 6 h (359.20 ± 0.70 min). Zebra finches incubate for 12–14 days before eggs start hatching, hence our recording of incubation behaviour and manipulations were carried out in the second half of the incubation period. From each video recording, time inside the nest by the female (and by the male, separately, in case of recordings from day 8 and 10 of incubation) was coded and used as an estimate of parental effort. We considered entering the nest and leaving the nest when the entire body of the parent disappeared in the nest box or re-appeared, respectively.

2.6. Statistical analyses

Statistical analyses were carried out using R 3.0.2 (R Core Team, 2013). If the analysis and our data required, the appropriate transformation was applied to normalise distribution. Minimal adequate models were obtained using the Akaike's information criterion (AIC). For significant explanatory variables in final models, we provide mean (for categorical explanatory variables) or B (i.e., slope of line, for covariates) ± SE.

Reproductive motivation of females was analysed in two ways. First, start of incubation (binary response variable) was analysed using binomial Generalized Linear Models (GLM) with mate preference (factor with two levels: preferred vs. least-preferred) as fixed effects. Second, we analysed clutch mass (response) in females that started to incubate using GLMs with mate preference as fixed effect.

In initial models of both measures of reproductive motivation we tested for the possible confounding effects of female body condition (residuals from body mass regressed on tarsus length) and seasonal changes (Julian

date until pair formation). We kept the latter covariates in the models and provide statistics only if they had significant effects.

We analysed parental cooperation in two ways. First, female pre-manipulation incubation was calculated as the proportion of total observation time the female spent inside the nest on day 8 of incubation. Female (arcsine transformed) pre-manipulation incubation (response) was analysed in GLMs with mate preference as fixed factor. We provide an additional model including male pre-manipulation incubation as a covariate, because female and male pre-manipulation incubations were negatively correlated (Pearson's $r = -0.79$, df $= 27$, $p < 0.0001$; Figure 2).

Second, female compensation was calculated as the change in proportion of total observation time spent incubating from day 8 of incubation (pre-manipulation) to day 9 of incubation (mate restriction). Approximately a third of the females reacted with extremely low incubation to mate restriction (see Results), whereas the remaining two-third of females increased incubation during manipulation. Therefore, we analysed compensation responses on two levels; compensation category (binary response variable, defined by the sign of female compensation) was analysed using binomial GLMs with mate preference (fixed factor) and female pre-manipulation incubation (covariate) as explanatory variables. In addition, in the subset of females that positively compensated for the loss of male effort, the effect of mate preference (fixed factor) was investigated on (arcsine) female compensation in GLMs with female pre-manipulation incubation (covariate) as explanatory variables.

In initial models of parental cooperation, we tested for the possible confounding effects of female body condition, seasonal changes, clutch size and residual clutch mass (from linear regression of clutch mass on clutch size).

3. Results

3.1. Female reproductive motivation

59% of ($N = 49$) females started incubation in our experiment. Start of incubation between females mated to their preferred and least-preferred males was not different (GLM, mate preference: $\chi^2 = 1.35$, df $= 1$, $p = 0.245$).

Females laid 4.48 ± 0.15 (mean $\pm$ SE) eggs, and clutch mass was 4.37 ± 0.21 g. Clutch mass was not different between experimental groups ($F_{1,26} = 0.06$, $p = 0.814$), although it tended to decrease with advancing season ($B = -0.005 \pm 0.003$, $F_{1,26} = 3.16$, $p = 0.087$).

3.2. Parental cooperation

Baseline (pre-manipulation) female incubation was higher than male incubation (females: $68.54 \pm 3.09\%$ vs. males: $43.20 \pm 3.26\%$; $t_{56} = 5.646$, $p < 0.0001$; Figure 2). Pre-manipulation incubation of females paired with their preferred or least-preferred male was not different (GLM, $F_{1,26} = 0.002$, $p = 0.964$; Figure 2), and decreased with advancing season ($B = -0.001 \pm 0.0005$, $F_{1,26} = 8.24$, $p = 0.008$). Controlling for male pre-manipulation incubation in the models lead to similar results in terms of both of these variables (mate preference: $F_{1,25} = 1.77$, $p = 0.196$; season: $B = -0.001 \pm 0.0003$, $F_{1,25} = 5.41$, $p = 0.028$; male pre-manipulation incubation: $B = -0.76 \pm 0.12$, $F_{1,25} = 50.07$, $p < 0.001$; Figure 2).
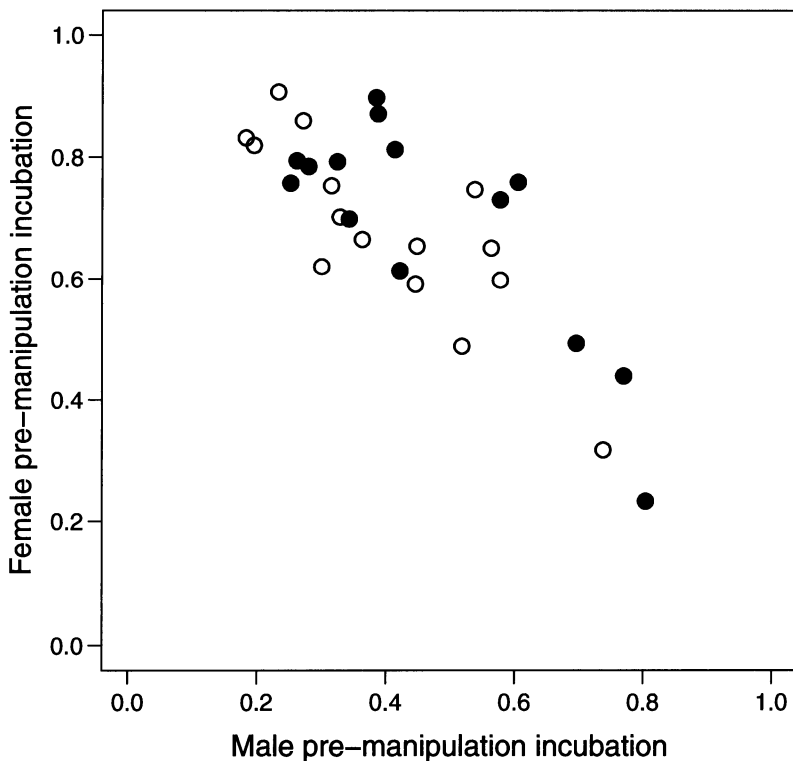

Figure 2. Pre-manipulation incubation of male and female zebra finch parents ($r = -0.79$, df $= 27$, $p < 0.0001$). Pre-manipulation incubation is the proportion of total observation time (6 h) that the male (or female) spent inside the nest box on day 8 of incubation. Filled circles represent couples in which the female was paired to her preferred male, and open circles represent pairs in which the female is paired with her least-preferred male.
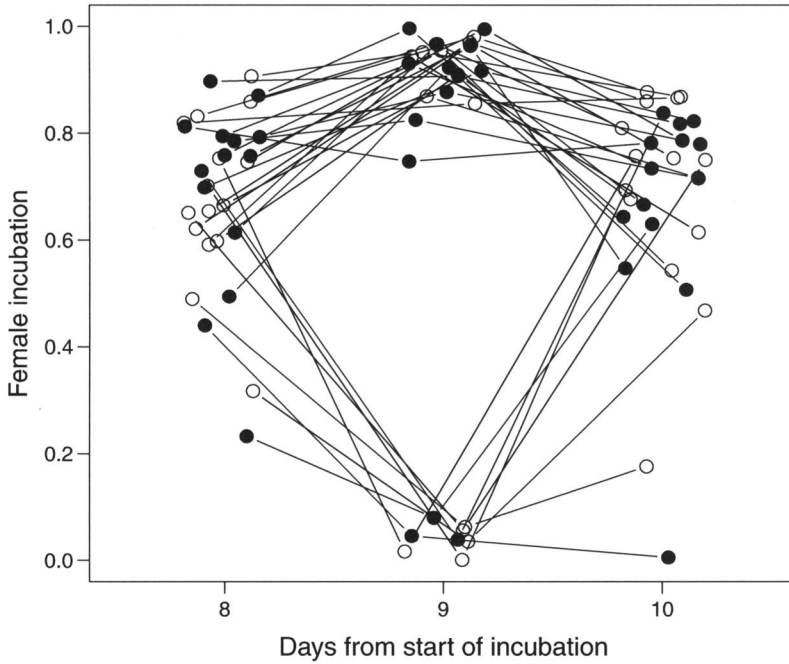
Figure 3. Incubation (proportion of 6 h observation time inside the nest) of zebra finch females on days 8–10 of incubation (pre-manipulation, male removal and post-manipulation). The male was removed on day 9 of incubation for the full period of behavioural recording. Filled circles represent females paired with their preferred and open circles represent females paired with their least-preferred male.

Female responses to mate restriction showed a bimodal distribution with some females increasing whereas others ceasing incubation during manipulation (Figure 3). Females mated with their preferred males were not more likely to increase their effort during mate restriction than females mated with their least-preferred males (GLM, mate preference: $\chi^2 = 0.05$, df $= 1$, $p = 0.821$). Females with high levels of pre-manipulation incubation were more likely increasing their effort during mate restriction than those females that had low levels of pre-manipulation incubation ($B = 7.05 \pm 3.20$, $\chi^2 = 6.71$, df $= 1$, $p = 0.010$).

Within the subset of 20 females that compensated for the loss of male care, mate preference did not explain the level of compensation (GLM, mate preference: $F_{1,17} = 0.17$, $p = 0.686$). The level of compensation decreased with increasing female pre-manipulation incubation ($B = -1.33 \pm 0.16$, $F_{1,17} = 66.34$, $p < 0.001$), possibly due to the 'ceiling effect'.

4. Discussion

Our experiment found no support for mating preferences to influence reproductive motivation and parental cooperation in zebra finches. Females paired with their preferred or least-preferred mates were not different in their propensity to start reproduction, and in their investment to egg-production. Moreover, reproducing experimental females were not different in their premanipulation incubation effort or in their compensatory responses to temporary mate restriction based on mate preference.

We suggest three, mutually non-exclusive explanation for our results. First, reproductive motivation and parental cooperation may be individually consistent behaviours in zebra finches. Studies focusing on the heritability of various forms of parental effort, including nest defence, food delivery rates and cooperative breeding have reported significant hereditary components in these behaviours (MacColl & Hatchwell, 2003; Dor & Lotem, 2010; Bize et al., 2012). The consistency of reproductive motivation and parental cooperation has not been addressed yet, and it is possible that, similar to other forms of parental behaviours, it is under strong genetic influence. Social learning of parental responses may also contribute to consistent parental behaviours (Hoppitt & Laland, 2013). For instance, the baseline relative share of parental effort between males and females often varies substantially (see also our results). If offspring learn from their same-sex parents how to respond to decreased or increased effort by the mate, this may result in little or no effect of the social environment (including mate quality) in their behavioural responses when reproducing as adults.

The second explanation of our findings involves the breeding ecology of zebra finches in nature. Zebra finches are socially monogamous, opportunistic breeders (Zann, 1996) with timing of breeding defined by rainfall. Therefore, low availability of sexually active unpaired individuals in the population coupled with an evolutionary history to start breeding whenever environmental conditions are favourable might have resulted in the evolution of less partner-quality-dependent parental behaviours. Also, due to social monogamy and the very low levels of extra-pair paternity (1.7%, Griffith et al., 2010) that makes the zebra finch one of the most genetically monogamous passerines, sexual conflict is expected to be low in this species (cf., Lessells, 2006). Because in such species male and female lifetime reproductive successes are tightly linked within a pair, we may expect partners to

compensate fully (or approaching full compensation) and independently of mate quality.

Finally, it is possible that parental cooperation is flexible with regard to mate preference, similar to other aspects of parental care in this species, including duration of parental care (Rehling et al., 2012). If so, our applied research paradigm was not adequate to detect this flexibility. Compensation during incubation for the loss of mate's effort has an upper bound, as individuals cannot possibly increase their effort during mate restriction once they have allocated most of their time to incubation. This effect is even more pronounced in females that had already high levels of pre-manipulation (baseline) incubation. Our statistical analysis found evidence for this, as the level of female compensation was negatively influenced by pre-manipulation incubation. Nevertheless, other response variables monitored in this study, including reproductive motivation and pre-manipulation effort showed also no effect of mate preference.

Parental cooperation tests often focus on feeding visits (Harrison et al., 2009), and factors influencing incubation received very little attention in general (Gorman et al., 2005). Instead of incubation, an alternative reproductive stage to monitor compensatory responses in our experiment would have been offspring provisioning. We note, however, that compensation during chick feeding has as much (or perhaps more) limitations as compensation during incubation. First, provisioning rates also have upper bounds by the maximum needs of young (i.e., parents cannot increase their feeding rates once young are well-fed). Second, parents are prone to respond to chick begging, so that monitoring the focal parent's behaviour during manipulation includes the combined effects of (possible) response to mate restriction and (changed) offspring begging behaviour.

Females in our experiment responded to the manipulation of mate effort by either increasing or ceasing their parental effort. This bimodal response was predicted by female pre-manipulation incubation; females with lower incubation effort before manipulation more likely ceased incubation during mate restriction. Similar to compensation for early life developmental deficits (Metcalfe & Monaghan, 2001; Fisher et al., 2006; Krause & Naguib, 2011), compensation for decreased partner effort may be costly. The bimodal response, therefore, may reflect a parental quality threshold, in that females of lower parental quality (or motivation) probably ceased care when forced to incubate alone, whereas females of higher parental quality (or motivation)

could compensate. The results are also in line with predictions of sexual conflict theory about manipulation between parents (Lessells, 2006; van Dijk et al., 2010). Our experimental design (maintaining acoustic and visual contact between pair members during mate restriction) may have resulted in females trying to manipulate their mate in vicinity to incubate by not compensating during mate restriction. Also, the same females probably decreased their pre-manipulation incubation already to get their mate working harder. It is also possible that females which ceased incubation followed a reproductive tactic in which the reproductive value (i.e., future benefits) of the given clutch did not overbalance the costs of caring alone. Finally, we cannot exclude the possibility that male behaviour (that we did not monitor during mate restriction) contributed to the variation in female responses to some extent.

We focused our study on females because female preference is more expressed and better established in behavioural tests than male preference. We note, however, that parental cooperation is a two player game, and it would be intriguing to investigate our research questions from the males' perspective, too.

In summary, our results suggest that reproductive motivation and parental cooperation are not flexible with regards to mate preference. We suggest two lines of further studies to gain a better understanding of the flexibility of parental cooperation. First, studies separating the genetic and non-genetic transmission of various forms of parental cooperation, which are lacking at the moment; and second, testing the repeatability or variation of parental cooperation along with change in various components of the social (and asocial) environment.

Acknowledgements

References

Barta, Z., Houston, A.I., McNamara, J.M. & Székely, T. (2002). Sexual conflict about parental care: the role of reserves. — Am. Nat. 159: 687-705.

Bennett, A.T.D., Cuthill, I.C., Partridge, J.C. & Maier, E.J. (1996). Ultraviolet vision and mate choice in zebra finches. — Nature 380: 433-435.

Bize, P., Diaz, C. & Lindstrom, J. (2012). Experimental evidence that adult antipredator behaviour is heritable and not influenced by behavioural copying in a wild bird. — Proc. Roy. Soc. Lond. B: Biol. Sci. 279: 1380-1388.

Bolund, E., Schielzeth, H. & Forstmeier, W. (2009). Compensatory investment in zebra finches: females lay larger eggs when paired to sexually unattractive males. — Proc. Roy. Soc. Lond. B: Biol. Sci. 276: 707-715.

Burley, N.T. (1986). Sexual selection for aesthetic traits in species with biparental care. — Am. Nat. 127: 415-445.

Burley, N.T. (1988). The differential-allocation hypothesis — an experimental test. — Am. Nat. 132: 611-628.

Caspers, B.A. & Krause, E.T. (2011). Odour-based natal nest recognition in the zebra finch (*Taeniopygia guttata*), a colony-breeding songbird. — Biol. Lett. 7: 184-186.

Clutton-Brock, T.H. (1991). The evolution of parental care. — Princeton University Press, Princeton, NJ.

Dor, R. & Lotem, A. (2010). Parental effort and response to nestling begging in the house sparrow: repeatability, heritability and parent-offspring co-evolution. — J. Evol. Biol. 23: 1605-1612.

Fisher, M.O., Nager, R.G. & Monaghan, P. (2006). Compensatory growth impairs adult cognitive performance. — PLoS Biol. 4: 1462-1466.

Forstmeier, W. & Birkhead, T.R. (2004). Repeatability of mate choice in the zebra finch: consistency within and between females. — Anim. Behav. 68: 1017-1028.

Gorman, H.E., Arnold, K.E. & Nager, R.G. (2005). Incubation effort in relation to male attractiveness in zebra finches *Taeniopygia guttata*. — J. Avian Biol. 36: 413-420.

Gowaty, P.A. (2003). Power asymmetries between the sexes, mate preferences, and components of fitness. — In: Evolution, gender and rape (Travis, C.B., ed.). MIT Press, Cambridge, MA, p. 61-86.

Gowaty, P.A. (2008). Reproductive compensation. — J. Evol. Biol. 21: 1189-1200.

Gowaty, P.A., Anderson, W.W., Bluhm, C.K., Drickamer, L.C., Kim, Y.K. & Moore, A.J. (2007). The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. — Proc. Natl. Acad. Sci. USA 104: 15023-15027.

Griffith, S.C., Holleley, C.E., Mariette, M.M., Pryke, S.R. & Svedin, N. (2010). Low level of extrapair parentage in wild zebra finches. — Anim. Behav. 79: 261-264.

Griffith, S.C., Pryke, S.R. & Buttemer, W.A. (2011). Constrained mate choice in social monogamy and the stress of having an unattractive partner. — Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 2798-2805.

Griggio, M., Matessi, G. & Pilastro, A. (2005). Should I stay or should I go? Female brood desertion and male counterstrategy in rock sparrows. — Behav. Ecol. 16: 435-441.

Harrison, F., Barta, Z., Cuthill, I. & Székely, T. (2009). How is sexual conflict over parental care resolved? A meta-analysis. — J. Evol. Biol. 22: 1800-1812.

Hoppitt, W. & Laland, K.N. (2013). Social learning: an introduction to mechanisms, methods and models. — Princeton University Press, Princeton, NJ.

Kosztolányi, A., Cuthill, I.C. & Székely, T. (2009). Negotiation between parents over care: reversible compensation during incubation. — Behav. Ecol. 20: 446-452.

Krause, E.T. & Naguib, M. (2011). Compensatory growth affects exploratory behaviour in zebra finches, *Taeniopygia guttata*. — Anim. Behav. 81: 1295-1300.

Krause, E.T., Krüger, O., Kohlmeier, P. & Caspers, B.A. (2012). Olfactory kin recognition in a songbird. — Biol. Lett. 8: 327-329.

Lack, D.L. (1968). Ecological adaptations for breeding in birds. — Methuen, London.

Lendvai, Á.Z., Barta, Z. & Chastel, O. (2009). Conflict over parental care in house sparrows: do females use a negotiation rule? — Behav. Ecol. 20: 651-656.

Lessells, C.M. (2006). The evolutionary outcome of sexual conflict. — Philos. Trans. Roy. Soc. Lond. B: Biol. Sci. 361: 301-317.

Liker, A. (1995). Monogamy in precocial birds: a review. — Ornis Hung. 5: 1-14.

MacColl, A.D.C. & Hatchwell, B.J. (2003). Heritability of parental effort in a passerine bird. — Evolution 57: 2191-2195.

Maynard Smith, J. (1977). Parental investment: a prospective analysis. — Anim. Behav. 25: 1-9.

McNamara, J.M. & Weissing, F.J. (2010). Evolutionary game theory. — In: Social behaviour: genes, ecology and evolution (Székely, T., Moore, A.J. & Komdeur, J., eds). Cambridge University Press, Cambridge.

McNamara, J.M., Houston, A.I., Barta, Z. & Osorno, J.L. (2003). Should young ever be better off with one parent than with two? — Behav. Ecol. 14: 301-310.

Metcalfe, N.B. & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? — Trends Ecol. Evol. 16: 254-260.

Pariser, E.C., Mariette, M.M. & Griffith, S.C. (2010). Artificial ornaments manipulate intrinsic male quality in wild-caught zebra finches (*Taeniopygia guttata*). — Behav. Ecol. 21: 264-269.

Pogány, Á., Heszberger, J., Szurovecz, Z., Vincze, E. & Székely, T. (2014). An infrared motion detector system for lossless real-time monitoring of animal preference tests. — Acta Biol. Hung. 65: in press.

R Core Team (2013). R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna.

Ratikainen, I.I. & Kokko, H. (2010). Differential allocation and compensation: who deserves the silver spoon? — Behav. Ecol. 21: 195-200.

Rehling, A., Spiller, I., Krause, E.T., Nager, R.G., Monaghan, P. & Trillmich, F. (2012). Flexibility in the duration of parental care: zebra finch parents respond to offspring needs. — Anim. Behav. 83: 35-39.

Royle, N.J., Hartley, I.R. & Parker, G.A. (2002). Sexual conflict reduces offspring fitness in zebra finches. — Nature 416: 733-736.

Sheldon, B.C. (2000). Differential allocation: tests, mechanisms and implications. — Trends Ecol. Evol. 15: 397-402.

Swaddle, J.P. & Cuthill, I.C. (1994). Preference for symmetrical males by female zebra finches. — Nature 367: 165-166.

van Dijk, R.E., Pogány, Á., Komdeur, J., Lloyd, P. & Székely, T. (2010). Sexual conflict predicts morphology and behavior in two species of penduline tits. — BMC Evol. Biol. 10: 107.

Waas, J.R. & Wordsworth, A.F. (1999). Female zebra finches prefer symmetrically banded males, but only during interactive mate choice tests. — Anim. Behav. 57: 1113-1119.

Whittingham, L.A., Dunn, P.O. & Robertson, R.J. (1994). Female response to reduced male parental care in birds — an experiment in tree swallows. — Ethology 96: 260-269.

Wright, J. & Cuthill, I. (1989). Manipulation of sex-differences in parental care. — Behav. Ecol. Sociobiol. 25: 171-181.

Zann, R.A. (1996). Zebra finch: a synthesis of field and laboratory studies. — Oxford University Press, Oxford.