

Becoming more like your mate: hormonal similarity reduces divorce rates in a wild songbird



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In animals with biparental care, maintaining a pair bond is of adaptive value because it increases reproductive success and reduces costs, such as energy and time, for finding a new mate. Hormones are important mediators of social behaviours as well as parental care, and endocrine mechanisms are therefore likely to be involved in the decision whether to stay with the same mate or separate after a breeding season. Because behavioural compatibility has been shown to increase fitness and hormones have been shown to regulate behavioural traits, here we examined whether the degree of endocrine similarity is also related to reproductive success and pair bond longevity. We used a 3-year study on free-living great tits, *Parus major*, to test whether mates had similar hormone levels during the parental phase. We tested specifically whether the metabolic hormone corticosterone was related to pair bond longevity and reproductive success. Baseline, but not stress-induced, corticosterone concentrations were highly correlated among members of a pair and became more similar among members of pairs that stayed together for multiple years. Pairs that increased their hormonal similarity within a season (from pre-breeding to breeding) had the highest reproductive success. Pairs with more similar baseline corticosterone levels and higher reproductive success were also more likely to remain together after the breeding season. The results of this study suggest that pair bond longevity is related to endocrine similarity and reproductive success, and raise the possibility that hormonal mechanisms may be under sexual selection.

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Reproductive success can vary considerably among pairs in a population (Lack, 1964). In biparental species, reproductive success depends not only on individual quality but also on pair-specific characteristics, such as the degree of compatibility and coordination among parents (Hirschenhauser, Möstl, & Kotrschal, 1999; Mariette & Griffith, 2012; Marzluff & Balda, 1988; Spoon, Millam, & Owings, 2006). For example, disassortative mating based on boldness behaviour in guppies, *Poecilia reticulata*, decreases reproductive success (Ariyomo & Watt, 2013). Stable, long-term pair bonds have high reproductive success (Adkins-Regan & Tomaszycki, 2007; Black, 2001; Sánchez-Macouzet, Rodríguez, & Drummond, 2014), whereas unsuccessful pairs can separate, which in turn results in physiological costs and reduced reproductive success (Angelier, Moe, Clement-Chastel, Bech, & Chastel,

2007; Black, 2001; Choudhury, 1995). These costs result from a lack of coordination among new pair members or from the stress associated with forced or natural pair separation (Catry, Ratcliffe, & Furness, 1997; Dhondt & Adriaensen, 1994; Remage-Healey, Adkins-Regan, & Romero, 2003). Physiological mechanisms are likely to mediate decisions on mate selection and pair bond maintenance, as well as costs associated with these decisions.

Hormones are coordinators of reproductive and social behaviours in a wide range of vertebrate species (Adkins-Regan, 2005), and are influenced by the environment and social circumstances, such as the social mate. A study in greylag geese, *Anser anser*, showed that pairs with highly correlated testosterone levels throughout many years were more likely to nest in a given year and had larger clutches and heavier eggs (Hirschenhauser et al., 1999). However, testosterone is associated with courtship behaviour and can be a male-biased trait (Hau, 2007). In contrast, glucocorticoids (corticosterone in birds) are regulated year-round in both sexes with higher levels in birds during the breeding season than at other times of the

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year (Romero, 2002). Corticosterone levels are also directly related to parental effort (Bonier, Moore, & Robertson, 2011; Ouyang, Sharp, Quetting, & Hau, 2013), can predict individual reproductive success (Bonier, Moore, Martin, & Robertson, 2009; Ouyang, Hau, & Bonier, 2011; Patterson, Hahn, Cornelius, & Breuner, 2014) and therefore are candidate mechanisms by which pair bond longevity may be achieved through the modulation of parental behaviour. Evidence from a few studies indicates that pair separation or mating with an unattractive partner increases circulating levels of corticosterone (Angelier et al. 2007; Griffith, Pryke, & Buttemer, 2011; Ramage-Healey et al. 2003). Higher levels of faecal corticosterone metabolites (Moreno et al. 2010) and baseline corticosterone (Villavicencio, Apfelbeck, & Goymann, 2014) are also found to be associated with a greater loss of paternity in males. In white-throated sparrows, *Zonotrichia albicollis*, during the parental/nestling phase white-striped morph males have higher levels of baseline corticosterone than tan-striped males (Horton & Holberton, 2010; Swett & Breuner, 2008), and white-striped males also have more extrapair fertilizations and provide less parental care than the tan-striped males (Tuttle, 2003). Moreover, females of both morphs have baseline corticosterone levels comparable to the tan-striped males with which they prefer to mate (Horton & Holberton, 2010). Pair similarity in corticosterone levels could therefore, via behavioural compatibility or sexual selection (van Oers, Drent, Dingemans, & Kempenaers, 2008), provide a proximate explanation for the variation in levels of extrapair paternity. This idea has been confirmed in parrots, in which a high degree of behavioural compatibility, as defined by an inverse relationship between affiliation and aggression, was found to decrease extrapair paternity and increase pair bond longevity (Spoon, Millam, & Owings, 2007).

These studies raise the question whether a greater similarity in hormone levels, as a cause or result of behavioural similarity, provides benefits to members of a pair. Therefore, we used a multiyear study to examine the relationship between endocrine similarity in corticosterone concentrations, pair bond status and reproductive success in a wild population of great tits, *Parus major*, to answer the following questions. (1) Is pair similarity in corticosterone levels related to pair bond duration? (2) Is corticosterone similarity related to reproductive success? (3) Is extrapair fertilization related to hormonal similarity, and potentially associated with pair bond longevity?

METHODS

Study Site and Standard Protocols

This study was carried out between March 2009 and July 2011 in Möggingen, southern Germany (47°N, 8°E, see Ouyang, Quetting, & Hau, 2012 for a detailed description of the study site and standard protocols). Our breeding population was established in February of 2009, and in 2009 the vast majority of breeders were first-year birds. Great tits are socially monogamous cavity nesters with biparental care, in which both sexes provide food to the nestlings (Lack, 1964). Nests were monitored regularly so that the date of the first egg and the date of hatch (as day 1) could be determined. Nestlings were then monitored every 5 days until fledging and the total number of fledglings was recorded for each nest.

We videorecorded feeding rates for one 2 h period between 0800 and 1200 hours (i.e. noon) in 2009 and 2010 when the adults were feeding their 12-day-old young. The number of local recruits from each nest was also determined as the number of offspring present in the study population the next breeding season.

For 2 weeks in March of 2009 and 2010 (about 2 weeks before the first egg was laid in the population, hereafter termed 'pre-breeding'), adults were captured in mist nets at feeding stations. All

adults were marked with a numbered aluminium ring and Darvic bands with a unique colour combination for individual identification. In May–June of 2009 and 2010 (hereafter termed 'breeding'), both members of a breeding pair were captured on the same day in their nestbox between 0800 and 1200 hours with a manually triggered metal trap that closed the entrance hole after birds entered it to feed their 8- or 9-day-old chicks. A blood sample (80–120 µl) was taken within 3 min of capture (mean ± SD; 2009: 1.8 ± 1.0 min, $N = 89$; 2010: 1.9 ± 0.9 min, $N = 149$) for later determination of hormone concentrations. Birds were then placed in a cloth bag for a standard capture and restraint procedure (Ouyang, Hau, et al., 2011; Wingfield et al. 1982) and another blood sample (<50 µl) was taken at 30 min post capture to determine stress-induced corticosterone concentrations. Blood samples were immediately stored on ice and centrifuged (822 × g, 10 min) within 4 h; the plasma was then removed and stored at –80 °C. The remaining red blood cells were stored in Queen's lysis buffer for later DNA extraction. While the adults were being held in bags for blood sampling, we weighed all chicks to the nearest 0.1 g while keeping them on warming pads, took a small blood sample (10 µl) and then returned them immediately to the nest. We released the adults after taking the second blood sample and measuring body mass (nearest 0.1 g) and tarsus length (nearest 0.1 mm). Adult age was scored by plumage appearance as a first-year breeder or older (Jenni & Winkler 1994), or from previous banding records.

Hormone Analysis

Plasma corticosterone concentrations were determined using an enzyme immunoassay kit (Cat. No. 901-097; 80-0045, Assay Designs, Ann Arbor, MI, U.S.A.), following a double diethyl ether extraction of 5 µl plasma sample aliquots following Ouyang, Hau, et al. (2011). Samples, along with a blank buffer and two separate, stripped-chicken plasma standards (at 20 ng/ml) were then redissolved in assay buffer at a 1:80 dilution and reconstituted overnight. The next day, 100 µl of each sample (in duplicate) were added randomly to individual wells on an assay plate. For comparative purposes, we added 10% to the final concentrations to account for recoveries (average extraction efficiency after double diethyl ether extraction: 89.7 ± 6.1%; Ouyang, Hau, et al., 2011). The average intraplate coefficient of variation was 10.7% (two replicate standards per plate), and the interplate coefficient of variation was 5.1% ($N = 29$ plates).

Extrapair Paternity

We obtained extrapair paternity data for 338 offspring from 57 nests (total $N = 453$) in 2010. DNA for the adults was extracted using a DNA isolation robot (Qiagen, Venlo, The Netherlands). Paternity analysis was performed for all nestlings that were present at 8–9 days after hatching. Genomic DNA from both the nestlings and the parents were isolated using the PureGene DNA Isolation Kit (Gentra Systems, Minneapolis, MN, U.S.A.), and a polymerase chain reaction (PCR) was carried out using the Multiplex PCR kit (Qiagen). Five microsatellite regions (PmaTAGAn71, PmaGAn27, PmaTGAn33, PmaC25, PmaD105; Kawano, 2003; Saladin, Bonfils, Binz, & Richner, 2003) were amplified. PCR products were run on an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems, Foster City, CA, U.S.A.) with a molecular size standard (GeneScan-500 LIZ, Applied Biosystems). Sizes of the amplification products were determined using commercial software (GeneMapper 4.0, Applied Biosystems), and parentage was assigned using CERVUS 3.0 (Kalinowski, Taper, & Marshall, 2007; Marshall, Slate, Kruuk, & Pemberton, 1998). Critical values were calculated by using the following parameters in CERVUS: 10 000 cycles, 98% of loci typed, error rate 0.001%, 120

candidate parents. In this way the tolerance of mismatches was set to accept mismatches up to LOD scores of 2.73 (95%) and 1.09 (85%). An individual was categorized as extrapair if there were one or more mismatches and CERVUS-based analyses did not recognize the social father as the most likely father. Combined exclusion probability for the five markers together on 453 individuals was 0.998.

Statistics

Statistical tests were performed in the R environment, version 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>). The difference in behavioural traits and hormone concentrations between members of a pair was calculated as the absolute value of the male trait minus the female trait. We used a general linear mixed model (GLMM) to test whether the focal individual's hormone level was correlated with its mate's hormone level, while including the following covariates: body condition, clutch size, lay date, habitat quality, age (first year or older) and year. We analysed the likelihood a pair will separate (separate and find new partners in the next year) using a GLMM with binomial errors and a logit link function with the following independent variables: hormonal similarity, extrapair paternity rates, fledging success and year. We used a GLMM with a zero-inflated Poisson distribution to estimate fledging output because of the excess of the number of zero fledglings, while including the following independent variables: hormonal similarity between a pair, body condition and year. In all GLMMs, individual identity was included as a random effect to control for repeated sampling of individuals.

A paired *t* test was used to analyse whether hormonal traits were different from one time point to the next (i.e. from pre-breeding to breeding). For pairs that stayed together for 2 or more years, we used a repeated measures ANOVA to look for changes in pair similarity of corticosterone levels from one year to the next.

To test whether pair combinations of extreme hormone levels (high–high and low–low) were different from other pair combinations (high–low or intermediate), we calculated a similarity index (van Oers et al., 2008). We transformed baseline corticosterone levels by subtracting the mean value of all individuals from each of the individual values. We then summed the transformed scores from both pair members. Therefore, low values indicated pairs in which both partners had low corticosterone values, and high values indicate pairs with high corticosterone values in each mate. For example, if the population mean value is 10 ng/ml, a pair of two low-value birds (uncorrected hormone levels of 2 and 3 ng/ml) will get a value of $-8 + -7 = -15$, and a pair of two high-value birds (20 and 22) will get a score of $10 + 12 = 22$. A pair of intermediate birds (11 and 10) will get a score of $1 + 0 = 1$.

Because there were many more within-pair offspring (WPO) than extrapair offspring (EPO), we ran a Monte Carlo simulation in which the status of being either EPO or WPO was randomized within each nest with mixed paternity ($N = 28$) to compare the weights of EPO and WPO. We calculated the mean weights of chicks assigned as EPO and WPO and got a pairwise character and a *t* value. We repeated this procedure 10 000 times, giving 10 000 *t* values. We then compared the observed *t* value derived from the pairwise *t* test of the means of the EPO and the WPO with the distribution of the simulated *t* values, giving the *P* value. To compare the recruitment rates of EPO and WPO, we ran the same procedure, but used a Fisher's exact test to calculate the *P* value.

Data on relationships among absolute hormone levels, parental feeding rates and fitness measures were previously reported by Ouyang, Sharp, et al. (2013). In this paper, we analysed hormone similarities within pairs to examine whether similarity in hormone

levels can explain pair bond longevity and variation in fitness of pairs (which has not been previously reported). Data on extrapair paternity have also not been reported previously.

Ethical Note

All parts of the study were conducted in Germany at the Max Planck Institute for Ornithology in Radolfzell, with permission by the appropriate authority, the animal welfare and nature conservation departments of the regional council (Regierungspräsidium Freiburg, permit number 35-9185.81/G-09/02). These authorities grant animal experimentation permits according to the Animal Welfare Law and the Nature Conservation Law of Germany, and are compliant with the legislation of the European Union. No nest was disturbed for more than 45 min during capture of the parents. We collected the smallest amount of blood possible and used highly sensitive assay techniques that allowed us to detect stress hormones in small sample volumes. While the adults were held captive, chicks were placed on heating pads to ensure they were sufficiently warm. No parents deserted the nest after capture in 2009 and 2011, but owing to a cold and wet breeding season, desertion rate was 36% in 2010 (Ouyang et al., 2012).

RESULTS

Hormone Similarities During Breeding (May)

During breeding, baseline corticosterone concentrations of both members of a pair were positively correlated (regression coefficient $\beta = 0.43$, SE = 0.08, $df = 93$, $t = 5.06$, $P < 0.0001$; Fig. 1), but stress-induced corticosterone concentrations were not correlated ($P > 0.10$). Clutch size, age, year, body condition and habitat quality did not explain significant variation in the model ($P_s > 0.10$). The pairs that had greater discrepancies in their feeding rates also had larger discrepancies in their baseline corticosterone levels ($r_{85} = 0.37$, $P = 0.0005$), which is probably because baseline corticosterone levels are positively correlated with feeding rates in both sexes in this population (Ouyang, Sharp, et al., 2013).

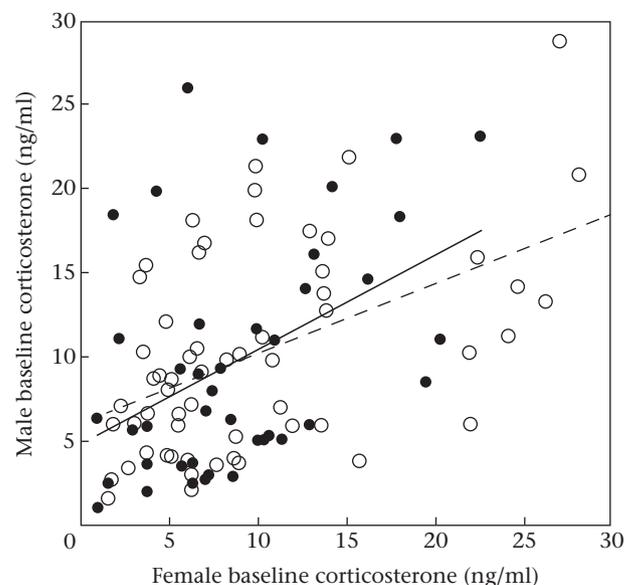


Figure 1. Baseline corticosterone concentration correlations for members of a pair. Solid circles and solid regression line are for 2009 and open circles and dashed regression line are for 2010.

Pairs with more similar baseline corticosterone levels ($\beta = -0.14$, $SE = 0.06$, $z = -1.98$, $N = 103$, $P = 0.04$; Fig. 2) and more fledglings ($\beta = 0.23$, $SE = 0.09$, $z = 2.55$, $N = 103$, $P = 0.01$) were more likely to remain paired the next year, whereas pairs with less similar baseline corticosterone levels and fewer fledglings were more likely to separate. EPO rates and year did not relate to whether the pairs stayed bonded ($P_s > 0.10$). Degree of similarity between pair members in hormone levels and body condition during breeding did not predict fledgling output ($P_s > 0.05$).

Because the analysis revealed a significant relationship between baseline corticosterone similarity and pair bond longevity, the calculated similarity index was added to the above models but remained nonsignificant, indicating that absolute corticosterone levels did not affect pair bond dynamics, i.e. birds that remained together had similar levels regardless of whether they were high–high or low–low partners/pairings.

Hormone Similarities During Prebreeding (March)

We caught 12 pairs of male and females during the prebreeding and breeding periods in 2009 and 2010. Pair differences in baseline corticosterone level were greater during the prebreeding period than they were during breeding ($t_{11} = 2.41$, $N = 12$, $P = 0.02$; Fig. 3). Pairs that increased baseline corticosterone similarity from prebreeding to breeding produced more fledglings than pairs with baseline corticosterone levels that grew more dissimilar (year: $\beta = -2.48$, $SE = 0.92$, $z = -2.6$, $P = 0.009$; change in baseline corticosterone: $\beta = -0.33$, $SE = 0.11$, $z = -2.90$, $P = 0.004$; Fig. 4).

Hormone Similarity Across Years

Over the years, males and females that remained paired became more similar (repeated measures ANOVA; $N = 46$, $df = 2$, $F = 8.40$, $P = 0.002$; Fig. 5). This increase in similarity was not due to absolute levels of baseline corticosterone being lower in 2010 because baseline corticosterone levels did not differ between years for females (Mann–Whitney: $z = -0.806$, $N_{2009} = 46$, $N_{2010} = 72$, $P = 0.42$) or for males ($z = -0.73$, $N_{2009} = 46$, $N_{2010} = 72$, $P = 0.46$).

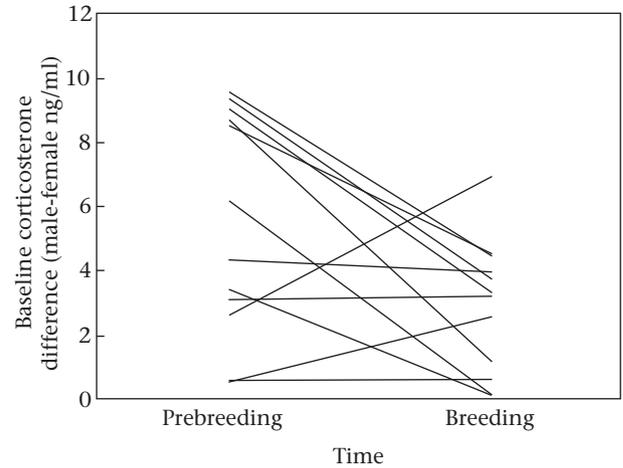


Figure 3. Baseline corticosterone difference (absolute value of male–female levels) for pairs caught during both prebreeding and breeding.

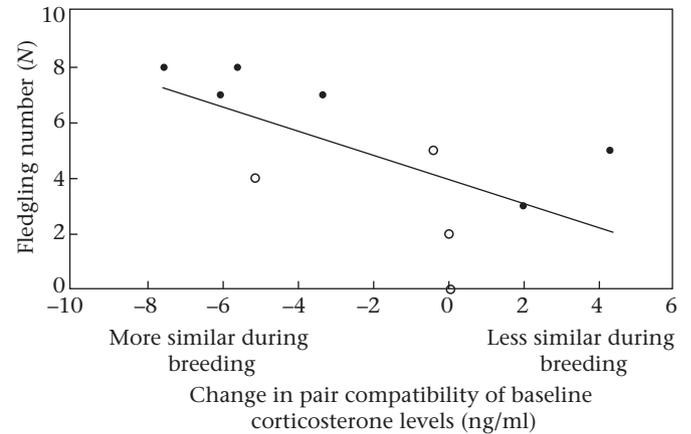


Figure 4. The change in similarity of baseline corticosterone concentrations (breeding differences between pairs in corticosterone levels – prebreeding differences between pairs in corticosterone levels) from prebreeding to breeding in relation to the number of fledglings produced. Closed circles are pairs from 2009 and open circles are pairs from 2011.

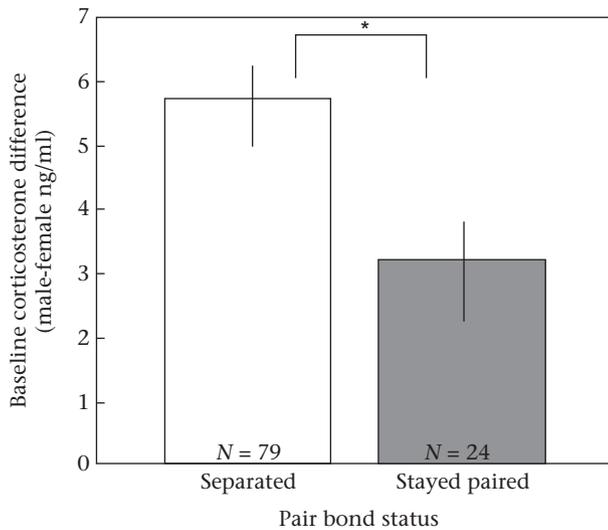


Figure 2. Differences in baseline corticosterone (absolute value of male–female levels) between members of a pair with respect to pair bond status (Cohen’s $d = 0.60$, plotted are mean \pm SE: separated = 5.7 ± 0.5 ; stayed paired = 3.2 ± 0.7). * $P < 0.05$.

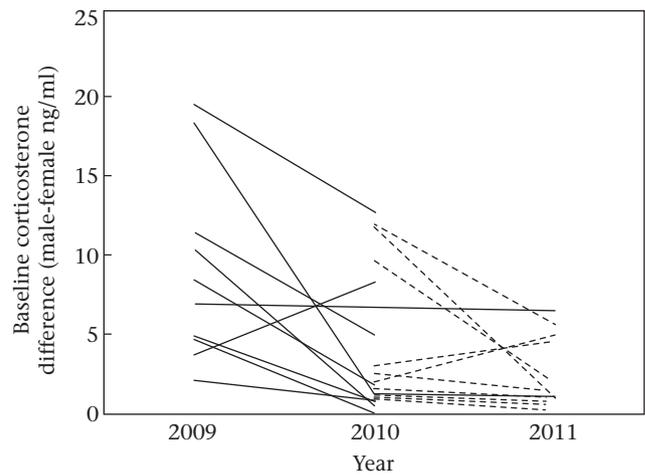


Figure 5. Baseline corticosterone differences between members of a pair (absolute value of male–female levels) over the 3 years of the study. Solid lines are pairs that stayed bonded in 2009 and 2010 and, for two pairs, in 2011 as well. Dashed lines are pairs that stayed bonded in 2010 and 2011.

Individuals that re-paired had greater dissimilarity in corticosterone levels with their new partner the next year than individuals that stayed with the same partner ($\beta = -2.90$, $SE = 1.1$, $df = 54$, $z = -2.6$, $P = 0.009$). Age, year, lay date and clutch size were not related to changes in corticosterone similarity between years ($P > 0.3$). Individuals that separated did not differ in their fledgling output in the next year compared to individuals that stayed together ($P > 0.05$). However, separated individuals fledged more offspring with their new partner in the following year than they did with their previous partner (paired t test: $t_{34} = -2.44$, $P = 0.01$; fledglings_{old partner} = 4.61 ± 0.38 , fledglings_{new_partner} = 5.85 ± 0.34). If individuals separated from a pair mate, they did not re-pair with a mate the next year with more similar baseline corticosterone levels than their previous partner (paired t test: $P = 0.4$).

Extrapair Paternity

Of the 57 nests in 2010, 32 (56.1%) contained a total of 58 extrapair offspring (17.4% extrapair paternity rate). The number of extrapair young within a nest was not correlated with any hormonal trait during breeding except that low female stress-induced corticosterone levels were correlated with high numbers of extrapair young ($r_{54} = -0.38$, $P = 0.004$; all other P s > 0.05). Extrapair young did not recruit at a higher rate than their half-sibs ($P = 0.44$), nor were they heavier than their half-sibs ($P = 0.38$). Numbers of extrapair offspring in a given nest were not related to the similarity in male and female baseline corticosterone levels during breeding ($\beta = -0.04$, $df = 46$, $t = -1.22$, $P = 0.23$), nor to similarity in stress-induced corticosterone ($\beta = -0.02$, $df = 44$, $t = -1.59$, $P = 0.12$) when we controlled for habitat quality, clutch size and lay date. The feeding rate difference between members of a pair was not related to the proportion of extrapair young in the nest ($r_{34} = 0.01$, $P = 0.96$).

DISCUSSION

Baseline corticosterone levels in wild great tits were correlated between members of a pair and baseline corticosterone levels of members of stable pairs became more similar over subsequent years. By contrast, pairs that separated were more dissimilar in their baseline corticosterone levels and also had fewer fledglings prior to separation than pairs that stayed together. Pairs that became more similar in hormone levels from before egg laying to breeding in a given year had greater reproductive output. Extrapair fertilizations were not related to endocrine similarity or pair bond longevity. Although studies have found associations between absolute hormone levels of males and the chance of gaining or losing fertility due to extrapair paternity, to our knowledge no one has tested the link between hormone similarity and extrapair paternity. In our population of great tits, extrapair paternity was not associated with pair bond longevity or with similarity in corticosterone levels.

Baseline corticosterone levels of males caught during March correlated with those of their female partner, raising the possibility that individuals of similar quality and/or reproductive state may pair bond associatively (Black, 2001; Weiss, Kotschal, Mostl, & Hirschenhauser, 2010). Moreover, baseline corticosterone is often thought to be associated with individual quality or be an indicator of the ability for later investment (Bonier et al. 2011; John-Alder, Cox, Haenel, & Smith, 2009; Kitaysky, Wingfield, & Piatt, 2001; Ouyang, Sharp, Dawson, Quetting, & Hau, 2011), further suggestive of an assortative mating strategy. Alternatively, hormone profiles of males and females might become more correlated after pairing, which could have happened before we sampled birds in the pre-breeding period and/or afterwards.

Indeed, as the breeding season progressed, hormone levels of pairs became more similar. This increase in similarity could be due to the pair raising the same number of offspring and/or experiencing similar environmental conditions at the nesting site (Ouyang, Sharp, et al., 2013), on their territory and in their foraging locations. Surprisingly, hormone levels became more similar even over the years for members of a pair that remained mated. Long-term pair associations could lead to a general decrease in corticosterone levels (Adkins-Regan, 2008), such that endocrine similarity is a result of pair bond stability/or duration, but cause and effect of this relationship cannot be disentangled here. Endocrine similarity between pair members could also happen over time simply because of increased similarity in behaviour, either as a result of breeding in the same territory or learning from past experiences. Indeed, we found that pairs that stayed together also had higher fledging success than pairs that separated, which could be explained by nest site fidelity which further facilitates mate fidelity (Hoover, 2003).

The discrepancy in baseline corticosterone could be a mechanism that precipitates pair separation (Catty et al., 1997); pairs with divergent baseline corticosterone tended to separate. This finding is in line with the 'incompatibility hypothesis,' which suggests that if inequalities exist in parental effort, such that one sex compensates for the other, pair separation is more likely (Choudhury, 1995). Endocrine asynchrony could cause pair bond instability, in which one member of the pair finds a new mate the next year with more similar behavioural/endocrine traits owing to possible fitness consequences associated with having to compensate for the previous mate. Indeed, we found that individuals that separated had higher reproductive success with their new partners the next year, which could also be a result of increased parental experience and/or age from one breeding season to the next (Bouwhuis, Charmantier, Verhulst, & Sheldon, 2010; Bouwhuis, Sheldon, Verhulst, & Charmantier, 2009). Individuals select mates based on a suite of behavioural and morphological traits, and it is likely that baseline corticosterone levels mediate one or a suite of these sexually selected traits (Almasi, Roulin, & Jenni, 2013; Fairhurst, Dawson, Oort, & Bortolotti, 2014; Lattin & Romero, 2013). For example, baseline corticosterone is positively related to parental care (Bonier et al. 2011; Ouyang, Sharp, et al., 2013), and if individuals select mates based on the ability to provide care, they may also be selecting individuals with high baseline corticosterone levels, which modulate a suite of other behavioural traits (Henderson, Heidinger, Evans, & Arnold, 2013; Lendvai, Giraudeau, Németh, Bakó, & McGraw, 2013; Saino et al., 2013). Indeed, in this great tit population, high baseline corticosterone levels during the prebreeding period are indicative of high parental effort during breeding (Ouyang, Muturi, Quetting, & Hau, 2012).

Although most bird species are socially monogamous, many species show a considerable variation in both pair bond longevity and proportion of extrapair paternity, which may represent behavioural strategies by which individuals paired with low-quality mates can improve their breeding status (Cezilly & Nager, 1995; Ramsay, Otter, Mennill, Ratcliffe, & Boag, 2000). Intra- and interspecific studies have shown an association between separation rate and frequency of extrapair paternity (Choudhury, 1995; Heg, Ens, Burke, Jenkins, & Kruijt, 1993). However, in our population, the number of extrapair fertilizations was not related to endocrine similarity nor to the likelihood of separation. Instead, pair separation could be related to dissimilarity in behavioural strategies that may be modulated by baseline corticosterone (Baugh et al., 2012). As in other studies, we did not find that extrapair offspring recruited at a higher rate or had higher body condition than biological offspring (Lubjuhn, Strohbach, Brün, Gerken, & Epplen, 1999; Strohbach, Curio, Bathen, Epplen, & Lubjuhn, 1998).

Although there were extrapair fertilizations, they did not seem to have an effect on pair bond longevity.

We often think of variation in reproductive success at an individual level; however, in biparental species, it takes the coordination of both members of a pair to successfully raise offspring (Lessells, 2012). We have shown that the degree of endocrine similarity has implications for reproductive success and pair bond longevity, and we suggest that the mechanisms regulating pair bond formation and mating strategies should be evaluated in the context of sexual selection.

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