



Animal personality can modulate sexual conflict over offspring provisioning

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Sexual conflict over parental investment is widespread among species with biparental care. Studies have indicated that a high degree of behavioural similarity between the two parents can increase offspring survival; however, it remains unclear how sexual conflict over parental care is resolved. In this study, we examined whether similarity of personality traits between the two parents plays an important role in affecting the provisioning behaviour of each sex in a wild population of the chestnut thrush, *Turdus rubrocanus*. First, as expected, the mating pairs with more similar personality traits had higher provisioning rates than those pairs with dissimilar traits. Moreover, we found that the similarity of personality traits can modulate the sexual conflict over provisioning in this species, as both parents with more similar partners had relatively higher and less divergent provisioning rates. A partner removal experiment revealed how the sole female or male parent responded when the level of conflict over care increased (the removed partner does not provide any care). The majority of males always reduced their provisioning investment, while females' decisions depended on the degree of similarity with their partners. Females compensated by provisioning more frequently in pairs of similar personality traits (i.e. accepting a high level of conflict), but reduced their provisioning investment in extremely dissimilar pairs. Our results promote a better understanding of the resolution of sexual conflict over provisioning and highlight the evolutionary significance of mating with similar partners based on certain personality traits.

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Biparental care, with both parents participating in offspring feeding, is relatively common in birds (Burley & Johnson, 2002; Lack, 1968). In this case, each parent would benefit from an increased investment by its partner, for example saving energy for future reproduction (Lessells & Parker, 1999). As increasing parental investment is generally costly for the partner in that it may affect its survivorship and future reproductive fitness (Houston, Székely, & McNamara, 2005), sexual conflict over the provision of parental investment may thus arise between parents (Parker, Royle, & Hartley, 2002), which should be detrimental to offspring survival (Royle, Hartley, & Parker, 2002).

In nature, individuals sometimes show certain nonrandom mating patterns, such as positive assortative mating, which occurs when males or females choose mates with similar traits to themselves (Delestrade, 2001; Shine, O'Connor, & Lemaster, 2001). Assortative mating can arise as a by-product of conflict between the two sexes (Jiang, Bolnick, & Kirkpatrick, 2013). For example, in the context of parental care, the similarity of a certain trait in two parents could be an important indicator of their caring ability. An individual with a similar trait may indicate a willingness to cooperate in parental care, which may in turn stimulate its partner to cooperate (Dall, Houston, & McNamara, 2004), resulting in a low level of conflict over parental investment. This can further enhance reproductive success by providing relatively high-quality care by both parents (Schuett, Tregenza, & Dall, 2010).

Animal personality, that is, consistent behaviour among individuals of the same species over time and across contexts (Dall et al., 2004; Sih, Bell, & Johnson, 2004), can function as a

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behavioural signal of willingness to provide parental care (Mutzel, Dingemanse, Araya-Ajoy, & Kempenaers, 2013; Royle, Schuett, & Dall, 2010). It may therefore influence conflict resolution over parental investment in those species with biparental care (Chira, 2014; David, Pinxten, Martens, & Eens, 2015). Some studies have indicated that pairs with similar exploratory and/or aggressive behaviour can raise offspring in better condition (David et al., 2015; Schuett, Dall, & Royle, 2011; Schuett et al., 2010), and that pairs with similar nest defence strategies have higher reproductive success (Burtka & Grindstaff, 2015). Nevertheless, it remains unclear how individuals respond (i.e. decide their investment in caring) when mated to partners of different personality types, which may further cause different levels of conflict over parental care.

In this study, to uncover the role of personality traits in modulating sexual conflict over provisioning, we investigated the relationships among two personality traits (i.e. activity and breathing rate) and provisioning behaviour (quantified as provisioning rate in each nest) in a wild population of chestnut thrush, *Turdus rubrocanus*. As an important personality trait, activity has been proposed to be related to the food intake rate, productivity and growth in various animal species (Biro & Stamps, 2008). Breathing rate has been used as another indicator of personality trait representing boldness (Carere & van Oers, 2004; Fucikova, Drent, Smits, & Oers, 2009). According to a previous study conducted in the same chestnut thrush population, activity and breathing rate are highly repeatable and observable traits (Zhao, Hu, Liu, Chen, & Sun, 2016).

Our specific aims in this study were twofold: (1) to investigate whether pair formation between individuals of similar personality traits can affect provisioning behaviour and reduce sexual conflict over provisioning; and (2) to investigate how each parent responds when sexual conflict over parental provisioning is intensified. The latter was studied experimentally by conducting a mate removal experiment during nestling provisioning and subsequently monitoring the change in provisioning investment by the remaining mate. We predicted that pairs with more similar personality traits would be more willing to provide parental care, which enables their offspring to get more food. We also predicted that pairs with more similar personality traits would be more likely to increase the provisioning rates in responding to a situation of intensified sexual conflict.

METHODS

Study Area and Subjects

Our study area is in the Lianhuashan National Nature Reserve, Gansu Province in central China (34°40'N, 103°30'E). Detailed descriptions of local climate and vegetation can be found in previous studies (Sun, Swenson, Fang, Klaus, & Scherzinger, 2003; Zhao et al., 2016). In our study area, chestnut thrushes begin to build nests in late April and form a breeding pair for just one breeding season. Males usually defend the nesting area, while females brood offspring (Zhao et al., 2016). Both males and females participate in food provisioning and nest cleaning, and females generally have higher provisioning rates than males. We systematically searched for nests of chestnut thrushes throughout our study area (approximately 200 ha) from April to late July in 2015 and 2016. We found most nests before egg laying (41), and the rest during incubation (20). All nests found during incubation were monitored daily to assess hatching date, and most nests were checked when the females were not in the nest. Females laid one egg per day and began incubation once they finished laying eggs. The incubation period averaged 13 days. Consequently, we were able to deduce the first egg-laying dates of the 20 nests detected during incubation. We defined hatching date as day 0 when ageing nestlings. To test

repeatability of different personality traits, we captured the birds using mist nets positioned 2 m from the nests at least twice during three separate periods: before clutch initiation, during the incubation period and during the nestling period. The interval between two mist net captures was at least 7 days (range 7–62 days with a mean of 25.8 days; Zhao et al., 2016). Each individual was uniquely marked by a metal band and colour bands. To facilitate identification of the two parents, females were colour banded on the left leg and males on the right leg. The sex of each captured individual was identified by checking the presence of a brood patch (since only females incubate the eggs in this species). The identity of social mating pairs was verified by video recordings (with a mean \pm SD duration of 27.9 \pm 26.8 h) taken during nestling provisioning.

Activity and Breathing Rate Measurement

We measured two personality traits, activity and breathing rate, in 2015 and 2016. Breathing rate of each individual was measured using the handling stress test (Carere & van Oers, 2004; Klueen, Siitari, & Brommer, 2014; Zhao et al., 2016) immediately after being captured. The total number of breast movements within 60 s was recorded (Zhao et al., 2016). Birds with relatively lower breathing rates should be bolder than those with higher rates in general (Carere & van Oers, 2004; Zhao et al., 2016). Activity was measured in a cage (60 \times 36 cm and 60 cm high) between 0900 and 1700 hours, following Zhao et al. (2016). After a 10 min acclimatization period after release into the cage, we began to record activity (i.e. walk, hop and fly) for a 5 min period. We used JWatcher (Blumstein, Evans, & Daniels, 2006) to analyse the activity data. To account for differences in energy expenditure between walking, hopping and flying, we calculated activity score as walks \times 1 + hops \times 2 + flights \times 3, following Zhao et al. (2016).

Monitoring Provisioning Behaviour

In 2016, for all experimental nests ($N = 21$) we recorded provisioning behaviour of both parents from 0700 to 1800 hours continuously using infrared cameras (Ltl6210MC). All cameras were positioned about 1 m from the nest. We collected food-provisioning data between 0800 and 0900 hours to assess the normal provisioning rate of each parent when both parents feed offspring together. Recordings were collected when the nestlings were 7 or 8 days old. The camera trigger interval was set at 0 s and recorded for 60 s to ensure recording of all nest-visiting behaviours (e.g. food delivery, faecal removal and brooding behaviour). For each observation period, we analysed food delivery rates (per h) for both males and females.

Removal Experiment

We conducted a partner removal experiment at 21 nests in 2016 when the nestlings were 7 or 8 days of age. All trials were conducted under good weather conditions (no rain or strong wind). For each nest, we temporarily removed both parents one after another, for 1 h to avoid nest abandonment. The interval between male removal and female removal at each nest was more than 2.5 h to enable the captured individual to recover from any induced stress resulting from capture. We continued with the experiment (i.e. capturing the other parent) until the previously removed parent returned to feed the offspring for at least 1.5 h. Each parent was removed only once in the breeding season. The removed parents resumed feeding the offspring 2.8 \pm 1.6 h (mean \pm SD) after being released, with only four (9.5% of total) exceeding 6 h. Most

trials were carried out on the same day ($N = 19$ nests, 90.5% of total), but trials at two nests were conducted on 2 consecutive days (i.e. the second parent removal was conducted the next day if we did not catch it the same day). We found no significant effect of removal order on variation in provisioning behaviour (see Results), which confirmed that the second trapped parent did not bias the effect of order.

During the removal period, the removed parent was kept in a small cotton bag. We assessed the changes in provisioning rate of the remaining parent immediately after removing one parent, which can be treated as a situation of artificially intensified conflict. As the provisioning rate may vary with time of day, we defined the hour before and after we caught the bird as period 1 (normal feeding by two parents) and period 2 (feeding by only one parent), respectively. The changes in provisioning behaviour were thus assessed between the two periods. Specifically, we calculated the relative change in provisioning rate (RC_p) for each parent to measure the differences during the experimental period. We used a relative change index $RC_p = \frac{p_2 - p_1}{p_1}$ following David et al. (2015), where p_1 and p_2 represent the provisioning rates of the same parent in periods 1 and 2, respectively. $RC_p > 0$ indicates the remaining parent compensated fully, $RC_p < 0$ that it did not. Immediately after completing each trial, we released the captured individual at the location where it was caught.

Data Processing and Statistical Analysis

We first tested for the presence of consistent individual differences by calculating the repeatability (r) of activity and breathing rate. Repeatability has been defined as the ratio of between-individual variance divided by the sum of this effect and residual variance (Nakagawa & Schielzeth, 2010). Here, we first constructed linear mixed models (LMMs) with individual identity (bird ID) as a random variable. In the model, activity scores were square-root transformed following Zhao et al. (2016), resulting in an approximate Gaussian distribution of residuals. To control for potential confounding factors, eight fixed factors were included: year, date (Julian date), sex, test sequence of activity and breathing rate (i.e. 1: first; 2: second; 3: third test), time of day (where 1200 = 0, 1300 = 1, 1100 = -1, etc.), temperature, context (i.e. 1: before breeding; 2: incubation; 3: nestling period) and body mass. Body mass was included in both models because it may affect personality traits such as breathing rate (Carere & van Oers, 2004). All continuous variables were mean centred and standardized. A likelihood ratio test (LRT) between the models with and without the random effect (bird ID) was used to test the statistical significance of the repeatability.

We then used these LMMs of activity and breathing rate to carry out 1000 simulations with the arm package. The averaged best linear unbiased predictors (BLUPs) for the intercepts of each individual were used as personality profiles (activity and breathing rate) in the following analysis. A recent study had indicated that utilizing the average BLUPs as estimates was less precise but unbiased (Dingemanse, Moiron, Araya-Ajoy, Mouchet, & Abbey-Lee, 2020). For simplicity, we refer to the average BLUPs of breathing rate and activity as 'breathing rate' and 'activity'. To measure the extent of personality trait similarity of a given breeding pair, we defined activity and breathing rate similarity indices (David et al., 2015) as activity similarity (AS) = $|\text{male activity} - \text{female activity}|$, and breathing rate similarity (BRS) = $|\text{male breathing rate} - \text{female breathing rate}|$.

As we did not measure the activity of one male parent within the 21 experimental breeding pairs, we used the data from 20 nests for the following analyses. To examine the effect of parents' personality on their provisioning behaviour, we first constructed a

generalized linear model (GLM), with the total provisioning rate (Poisson error structure) as the response variable. We included personality variables (i.e. activity and breathing rate of each parent, AS and BRS), brood size and body mass of each parent as independent variables. To assess the conflict over provisioning of a given breeding pair, we defined a divergence index as $\frac{p_F - p_M}{p_F + p_M}$, where p_F and p_M represent the food delivery rates (per h) of the female and male parent, respectively. Using this index allowed us to control for differences in total provisioning rate between pairs. We then constructed a linear model with the divergence index as the response variable and personality variables, brood size and body mass of each parent as independent variables. To avoid potential collinearity of the explanatory variables, we simplified these models using a stepwise backward approach to ensure that the variable inflation factor (VIF) values were less than 2.5 (Johnston, Jones, & Manley, 2018).

We also assessed the relationship between the provisioning rate of each sex and its personality traits by fitting a generalized linear mixed model (GLMM) with a Poisson error structure, with personality variables (i.e. activity and breathing rate of each parent, AS and BRS), brood size, sex and body mass included as fixed effects, and 'pair ID' as a random effect to control for the nonindependence of males' and females' behaviour within a pair. For partner removals, we assessed the relationships between the relative change in provisioning rate (RC_p) of each sex and personality variables using two LMMs. The log-transformed RC_p (calculated as $\log(RC_p + 2)$ to reach normality) was set as the response variable. As before, we included personality variables, brood size, sex and body mass as fixed effects and 'pair ID' as a random effect in the model. We also included the time of resuming food provisioning after being released and the removal order as another two fixed effects.

All LMMs and GLMMs were fitted with lmer and glmer functions from the lme4 package (Bates, Maechler, Bolker, & Walker, 2014), respectively. Wald chi-square tests were used to assess the significance of fixed effects in the LMMs and GLMMs. For each model, we also applied a bootstrapping method that would resample our data set with replacement 1000 times. We obtained the 95% confidence interval (CI) for estimates of our explanatory predictors to assess the effects of variation in the fixed factors. All statistical analyses were conducted using R (R Core Team, 2015).

Ethical Note

All procedures on chestnut thrushes complied with the ASAB/ABS and the local, institutional and national rules concerning the care and use of animal subjects. The birds were captured under a bird ringing licence from the China Bird Banding Centre and it was also permitted by the Animal Care and Use Committee of the Institute of Zoology, the Chinese Academy of Sciences (Permission No. 2013/108). Birds were caught only on days without rain and with low wind speed to reduce cooling during the capture and handling process. To reduce human disturbance during the incubation period, the nest was checked by one person only and the whole nest check took less than 1 min. We checked the nest only in the afternoon and in good weather conditions, when the temperature was relatively high. During incubation, nests were checked only when the female was absent. We could detect whether the females were present from over 4 m away, and none of them flew away at this distance. If the female was sitting on the eggs, we refrained from nest checks and tried another day when the female was absent. None of the nests that were checked and where the parents were caught during incubation were abandoned. To avoid nestling mortality, parents were caught when the nestlings were at least 6 days old, when they had feathers and were able to keep themselves warm. Birds were trapped and released within 70 min

near the trapping location. No adults or nestlings died during the experimental period.

RESULTS

Personality Test

In 2015 and 2016, we performed the breathing rate test 207 times in 166 birds (73 males and 93 females) and the activity test 169 times in 142 birds (61 males and 81 females). Of the measured individuals, 29 (11 males and 18 females) were tested twice or three times. Both personality traits were repeatable within individuals across time (Table 1). Body mass was significantly positively related to breathing rate, but not to activity: heavier individuals had a higher breathing rate than lighter individuals (see Appendix Table A1). We obtained average BLUP values of breathing rate and activity for 163 and 139 individuals, respectively. Three thrushes lacked body mass data, and thus we were unable to calculate the average BLUPs for them. There was no correlation between activity and breathing rate (Spearman rank correlation: $r_s = -0.084$, $N = 139$, $P = 0.327$).

Personality Similarity and Sexual Conflict over Provisioning

We found that pairs with more similar activity had higher total provisioning rates (Table 2, model TP ~ AS). Within a pair, the female parent generally had a higher provisioning rate than the male parent (Wilcoxon one-tailed signed-rank test: $V = 185.5$, $N = 20$, $P < 0.001$). The provisioning rate divergence between the two parents of a given pair was also affected by the within-pair activity similarity (Table 2, model PD ~ BRS + FBR + MAC + FM + AS): pairs with more similar activity showed less divergence in provisioning rates, potentially indicating a lower level of conflict.

Furthermore, as we found that sex had a significant effect on provisioning rate (Table 3) with females having higher rates than males (2.65 ± 1.14 (mean \pm SD) versus 1.20 ± 0.83), we assessed the provisioning rate of each sex in response to the activity similarity using separate GLMs. Both parents altered their provisioning rates significantly according to the degree of activity similarity rather than the personality traits of each parent (Fig. 1a and b, Table 3). They had higher provisioning rates in pairs with more similar activity (Fig. 1c).

Experimental Evidence of Sexual Conflict

Temporary partner removal revealed that the relative change in provisioning rate (i.e. RC_p) was strongly related to the sex and within-pair activity similarity (Table 4). Females increased provisioning rates within the more similar pairs, whereas males did not (Fig. 2). Furthermore, most males had negative values of RC_p , indicating that in most cases they reduced their provisioning rate after removal of their mate (Wilcoxon one-tailed signed-rank test: $V = 166.5$, $N = 20$, $P = 0.002$). Females in pairs with similar personality traits

increased provisioning rates after male removal (black points above the grey line in Fig. 2), but those in pairs with dissimilar personality traits reduced provisioning rates.

DISCUSSION

Animal personality has been proposed to play an important role in sexual selection and parental care (Schuett et al., 2010). We further hypothesized that the similarity of personality traits between two parents can modulate sexual conflict over offspring provisioning. In this study, we first showed that both activity and breathing rate are repeatable, but not correlated with each other in chestnut thrushes, which is consistent with our previous study (Zhao et al., 2016). We found evidence that pairs with more similar personality traits had lower levels of conflict over provisioning and higher provisioning rates.

Generally, mating with similar partners based on activity should be beneficial to chestnut thrushes (i.e. providing better parental care). This is consistent with other empirical studies on other taxa with assortative mating for different personality traits (Burtka & Grindstaff, 2015; Laubu, Dechaume-Moncharmont, Motreuil, & Schweitzer, 2016; Wiebke, Godin, & Dall, 2011). Nevertheless, the studies listed above did not give further evidence for how each parent responded to the level of personality similarity and how this can affect reproductive success. In this study, through video recording, we showed that the two parents within the more behaviourally similar pairs of chestnut thrush had less divergent provisioning rates and both male and female parents had higher provisioning rates. Personality trait can therefore modulate the degree of sexual conflict over offspring feeding in our population of chestnut thrushes. Furthermore, given that female thrushes generally have higher provisioning rates than males, the less divergent provisioning rates in pairs with more similar activity thus implies that males are willing to invest more on provisioning to reduce conflict when they mate with more similar partners. Males might therefore play a more dominant role in determining the level of conflict over provisioning than females in this species.

When facing a severe increase in sexual conflict through partner removal, chestnut thrushes generally responded strongly. Most males reduced their provisioning rate after removal of their partner regardless of personality similarity, while females' decisions depended on the similarity of their activity with their partner. Our results are thus in contrast to the hypothesis that similar pairs would have similar response rules while provisioning (Schuett et al., 2011), which predicts that parents with similar personalities would have similar responses to changes in effort by their partner. We suggest that this may be related to the division of labour in parental care between the two sexes (Royle, Smiseth, & Kolliker, 2012). Males normally dedicate more time to territory and nest defence than females (Sanz & Tinbergen, 2000), while provisioning and brooding behaviour are performed more by females in chestnut thrushes. In this case, when the level of conflict increases, males would rather conserve energy for remaking or future reproductive attempts by reducing provisioning in the current brood, because they might be unable to feed the nestlings until fledging on their own.

Female thrushes, however, showed divergent decisions depending primarily on the activity similarity with their mates. Female and male parents may be more likely to be trustworthy in pairs with similar activity than in dissimilar pairs (Royle et al., 2010). This may enable them to better coordinate their provisioning and share the burden of parental care (e.g. with less divergence in provisioning rate). In this situation, females may be in relatively good condition because of the help from their mate, which enables them to compensate for food provisioning reduction by their mate

Table 1
Repeatability and descriptive statistics of personality traits of the chestnut thrush

Trait	N_{ind}	Range	R	χ^2	P
Activity	139	0–18.815	0.738	19.819	< 0.001
Breathing rate	163	54–150	0.360	4.194	0.041

Activity is the square root of the number of movements in the simple cage test. Breathing rate is the number of breast movements during 60 s while being handled. The table shows the total number of individuals (N_{ind}), the range of traits and repeatability (R). Statistical significance of the repeatability was tested using a likelihood ratio test on the log likelihood of models with and without the random effect (bird ID). The LMMs of activity and breathing rate used to calculate the repeatability can be found in Table A1. Significant P values are shown in bold.

Table 2

The effects of personality variables and body mass on total provisioning rate (TP) and provisioning rate divergence (PD) of 20 breeding pairs of chestnut thrush

Models	Predictors	Estimates	SE	2.5% CI	97.5% CI
TP ~ AS	AS	-0.121	0.025	-0.180	-0.078
PD ~ BRS + FBR + MAC + FM + AS	BRS	-0.072	0.071	-0.235	0.039
	FBR	0.024	0.010	0.002	0.040
	MAC	0.032	0.017	0.001	0.062
	FM	0.009	0.009	-0.025	0.008
	AS	0.057	0.019	0.008	0.084

Using the stepwise backward approach, we carried out a GLM (Poisson error structure) of TP ~ AS, and LM of PD ~ BRS + FBR + MAC + FM + AS. 2.5% and 97.5% confidence intervals (CI) were calculated using a bootstrapping resampling method (each model resampled 1000 times). AS: activity similarity; BRS: breathing rate similarity; FBR: female breathing rate; MAC: male activity; FM: female body mass. Significant CIs are shown in bold.

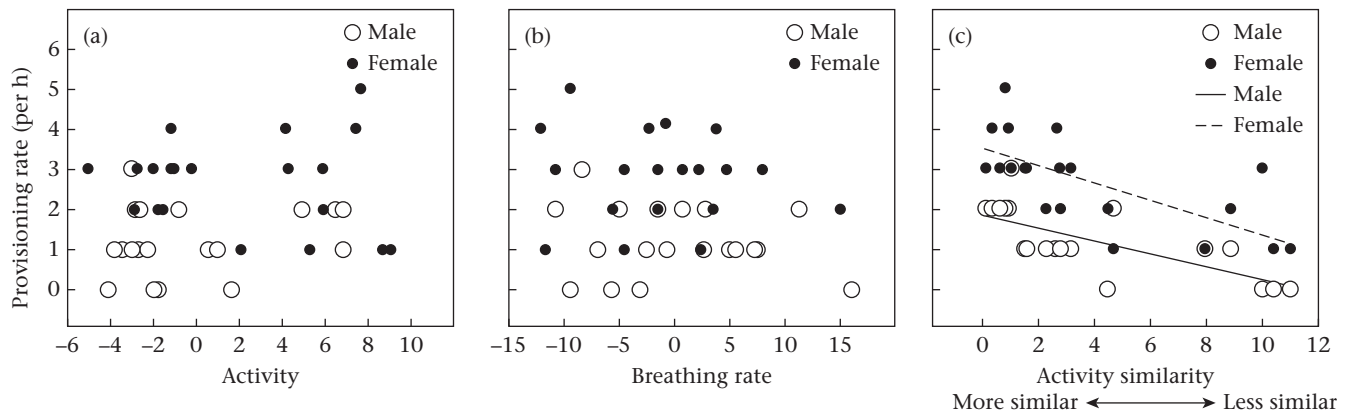


Figure 1. Relationships between the provisioning rate of each parent in chestnut thrushes and (a) each parent's activity (GLM: male: $z = 0.754, P = 0.451$; female: $z = -0.305, P = 0.760$), (b) each parent's breathing rate (GLM: male: $z = -0.479, P = 0.632$; female: $z = -0.560, P = 0.575$) and (c) within-pair activity similarity (GLM: male: $z = -2.253, P = 0.024$; female: $z = -2.032, P = 0.042$). We used the averaged BLUP values of activity and breathing rate as the personality traits of each individual. The significant regression lines are shown in (c).

and thus guarantee their offsprings' survival (Mcnamara, Houston, Barta, & Osorno, 2003; Royle et al., 2002). In contrast, females in dissimilar mating pairs may have already reached their physiological and/or psychological maximum without coordinated help from their mate. In this situation, when conflict intensifies in dissimilar pairs (e.g. when the male disappears as in the removal experiment), females may decide to reduce their provisioning rates or even to abandon the current brood to ensure their own survival and prepare for future reproduction (Szentirmai, Szekely, & Komdeur, 2007; Wolf, Doorn, Leimar, & Weissing, 2007). We suggest that more evidence in chestnut thrushes is still required to verify the hypothesis that female condition varies with the level of conflict in the pair. Moreover, further studies on other species are needed to test the generalizability of our findings about the effects

Table 3

The effects of personality variables and body mass on provisioning rate of each parent (20 males and 20 females), analysed using generalized linear mixed models with Poisson error structure

Predictors	Estimate	SE	2.5% CI	97.5% CI
AS	-0.116	0.047	-0.223	-0.042
Sex 2	0.734	0.258	0.245	1.270
AC	0.022	0.031	-0.036	0.087
BR	-0.010	0.019	-0.047	0.028
BRS	-0.021	0.027	-0.079	0.028
BS	0.004	0.163	-0.328	0.324
MP	0.007	0.017	-0.031	0.042

2.5% and 97.5% confidence intervals (CI) were calculated using a bootstrapping resampling method (each model resampled 1000 times). AS: activity similarity; AC: activity of each parent; BR: breathing rate of each parent; BRS: breathing rate similarity; BS: brood size; MP: mass of each parent. Significant CIs are shown in bold.

Table 4

The effects of personality variables and body mass on the log-transformed relative change in provisioning rate of each parent (20 males and 20 females), analysed using linear mixed models

Predictors	Estimate	SE	2.5%	97.5%
AS	-0.023	0.010	-0.043	-0.002
Sex 2	0.160	0.062	0.037	0.283
BRS	-0.005	0.006	-0.017	0.008
AC	-0.011	0.007	-0.026	0.003
BR	-0.002	0.004	-0.010	0.006
MP	-0.005	0.005	-0.014	0.006
BS	0.035	0.041	-0.043	0.115
RO 2	0.005	0.044	-0.084	0.092
TR	< -0.001	< 0.001	-0.001	0.001

2.5% and 97.5% confidence intervals (CI) were calculated using a bootstrapping resampling method (each model resampled 1000 times). AS: activity similarity; BRS: breathing rate similarity; AC: activity of each parent; BR: breathing rate of each parent; MP: mass of each parent; BS: brood size; RO: removing order; TR: time of resuming food provisioning after being released. Significant CIs are shown in bold.

of personality traits on modulating sexual conflict over provisioning.

Conclusions

In summary, chestnut thrush pairs with more similar personality had higher and less divergent provisioning rates. These results show that parents with similar personality traits in this species can effectively reduce sexual conflict over provisioning and improve their potential fitness. Furthermore, when intensity of sexual conflict increased in our study population, males reduced their provisioning investment while females' decisions depended on the

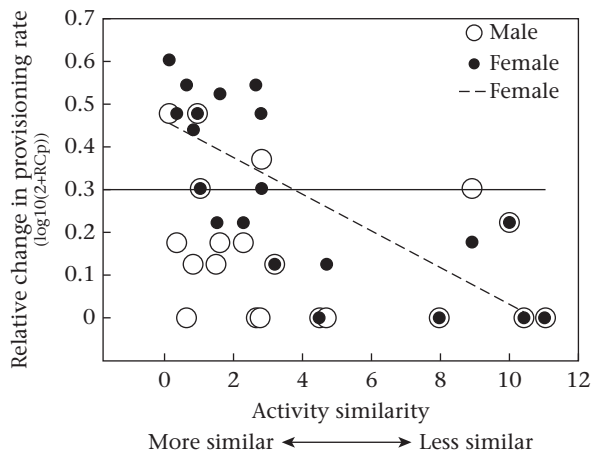


Figure 2. Relationships between the log-transformed relative change in provisioning rate ($\log_{10}(2 + RC_p)$) to nestlings before and after partner removal and within-pair activity similarity in chestnut thrushes (LM: male: $t = -1.496$, $P = 0.152$; female: $t = -4.744$, $P < 0.001$). The horizontal grey line shows the value of $\log_{10}(2)$, representing no change in provisioning rate between the two periods (i.e. when $RC_p = 0$). The dashed line is the significant regression line for females.

degree of personality similarity with their mate. Females compensated for the reduction in offspring feeding if they and their mate had similar personalities. Therefore, we conclude that females may be more likely to accept an increasing level of conflict over provisioning after mating with a partner with similar personality traits. Our findings further highlight the importance of animal personality within the context of sexual selection. We posit that pairing with similar partners based on personality traits may be a novel solution to sexual conflict over provisioning in species with biparental care.

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Appendix

Table A1

Results from the LMMs of activity and breathing rate to identify the effects of year, date, sex, test sequence of activity and breathing rate, time of day, temperature, context and body mass on personality traits in the chestnut thrush

	Predictors	Estimate	χ^2	df	P	
Activity (<i>N</i> = 139)	Temperature	0.718	2.013	1	0.156	
	Date	-0.847	2.978	1	0.084	
	Time of day	0.086	0.065	1	0.800	
	Order 2	0.115	1.158	3	0.763	
	Order 3	-1.344				
	Order 4	2.253				
	Context 2	0.261	0.064	2	0.969	
	Context 3	0.010				
	Sex 2	0.814	0.794	1	0.373	
	Year 2	-0.055	0.005	1	0.945	
	Body mass	-0.300	0.473	1	0.491	
	Breathing rate (<i>N</i> = 163)	Temperature	1.085	0.467	1	0.495
		Date	5.712	10.642	1	0.001
		Time of day	-0.512	0.164	1	0.686
Order 2		4.148	4.114	3	0.249	
Order 3						
Order 4						
Context 2		1.261	0.571	2	0.752	
Context 3						
Sex 2		14.715	27.443	1	< 0.001	
Year 2		3.643	1.823	1	0.177	
Body mass		3.063	4.708	1	0.030	

The effects of the predictors are presented as parameter estimates. Wald chi-square tests were used to assess the significance of fixed effects in the LMMs and GLMMs. Significant *P* values are shown in bold.