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Original Article

Extra-pair mating opportunities mediate parenting and mating effort trade-offs in a songbird

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In socially monogamous species with bi-parental care, males may face a trade-off between providing parental care and pursuing extra-pair matings. The "parenting-mating trade-off" hypothesis predicts that high-quality males—who have greater potential to gain extra-pair matings, for example, larger males usually win the competition for extra-pair mating—should reduce parental care and spend more time looking for extra-pair matings. However, the trade-off between parenting and mating efforts may be complicated by variation in the availability of extra-pair mating opportunities. By using field data of hair-crested drongos (*Dicrurus hottentottus*), a species exhibiting bi-parental incubation behavior, collected in central China from 2010 to 2017, we tested whether the potential negative relationship between male quality and paternal care was dependent on the number of nearby fertile females. We found that male drongos mainly seek extra-pair matings during the incubation period and high-quality individuals (males with longer tarsi) are more likely to sire extra-pair offspring. In agreement with the "parenting-mating trade-off" hypothesis, high-quality males incubated less by recessing longer between incubation bouts. However, this was only the case when sufficient fertile females nearby for extra-pair mating opportunities. Females compensated for reduced male care, but this was independent of male quality. This suggests that the reduction in care by high-quality males might be a direct response to extra-pair mating opportunities rather than facilitated by differential allocation of females. Our results indicate that individual quality and available mating opportunities may shape the optimal trade-off between parental care and seeking additional matings for males.

Lay Summary: How do individual quality and the number of potential extra-pair mates influence the optimal trade-off between parental care and engaging extra-pair courtship in animals? In hair-crested drongos, high-quality males, who are more successful in obtaining extra-pair fertilizations, reduced their share in incubation, but only when they had sufficient extra-pair mating opportunities. Females partially compensate for the reduced incubation of their partners, but the compensation was not affected by male quality.

Key words: parental care, extra-pair mating opportunity, trade-off, male quality, incubation attendance.

INTRODUCTION

In socially monogamous animals, males can enhance their fitness by providing paternal care to their preexisting offspring (i.e., increase the survival probability of offspring; Clutton-Brock 1991; Ketterson and Nolan 1994), and also by pursuing extra-pair matings and producing a greater number of offspring (Bateman 1948). However, as extra-pair mating opportunities for males may coincide with the period in which they provide parental care (Grafen 1990; Andersson 1994), males face a trade-off between allocating resources (e.g., time and energy) in providing parental care to their own brood and seeking extra-pair matings (the "parenting-mating trade-off" hypothesis; Westneat et al. 1990; Magrath and Komdeur 2003; Stiver and Alonzo 2009). The optimal parenting-mating trade-off depends on the relative fitness benefits of engaging in extra-pair matings (siring extra-pair offspring) and the potential costs of reducing paternal care, such as reduced survival of young if mates do

not compensate for the reduction in care. Overall, males should be selected to maximize their fitness by optimizing their allocation of effort to these two components in each breeding attempt.

Male traits may reflect their probability of gaining extra-pair matings through female choice and male-male interactions. Females may actively engage in extra-pair matings in order to obtain good genes for their offspring (i.e., "good-genes" hypothesis; Griffith and Immler 2009; Puurtinen et al. 2009). In this case, males' extra-pair mating success (extra-pair copulations resulting in the production of extra-pair young) would depend on traits that reflect their genetic quality (attractiveness), such as ornaments, age or body size (Akçay and Roughgarden 2007; Bitton et al. 2007; Cleasby and Nakagawa 2012). Additionally, males' extra-pair mating success may also be determined by male-male interactions. Males who have higher social rank (Otter et al. 1998) or larger body size (e.g., tarsus length; Vedder et al. 2010) may be more likely to win the male-male competition (i.e., higher competitiveness) and should, therefore, have better chances of gaining extra-pair matings. Thus, it can be predicted that high-quality males (more attractive and/or competitive) should invest more in mating effort and less in parental care due to their high potential for extra-pair mating success. Several empirical studies support the "parenting-mating trade-off" hypothesis by showing that high-quality males provide less parental care than low-quality males (e.g., Mitchell et al. 2007; Engqvist 2011; Diniz et al. 2015). Additionally, males whose attractiveness was experimentally reduced increased their paternal care in several species (e.g., Sanz 2001; Hasegawa and Arai 2015). However, other studies did not find support the "parenting-mating trade-off" hypothesis (e.g., Nakagawa et al. 2007; Grana et al. 2012), or found that trade-offs were context-dependent (e.g., existed during the incubation period but not during the nestling stage; Grunst and Grunst 2015).

One reason for this inconsistency may be that the influence of the availability of fertile females, and thus the males' opportunity for extra-pair mating, is often overlooked in tests of the "parenting-mating trade-off" hypothesis (Kokko 1998; Magrath and Komdeur 2003; Stiver and Alonzo 2009). Due to variation in local breeding density and breeding synchrony, the number of fertile females for focal males often varies spatially and temporally (Westneat and Sherman 1997; Chuang et al. 1999; Richardson et al. 2001; Mayer and Pasinelli 2013). Therefore, studies aimed at testing the "parenting-mating trade-off" hypothesis should incorporate both

the effects of male quality and the availability of fertile females on males' relative investment in parental care and pursuing extra-pair matings. To our knowledge, only one study examined the relationships between male quality and paternal care also considered the influence of the number of fertile females. Smith and Montgomerie (1992) found that the incubation attendance of male barn swallows (*Hirundo rustica*) was not affected by their quality, the number of available fertile females, or their interaction. However, males contributed only 9% of total incubation on average, which, in combination with modest sample size ($N = 16$ males), may have resulted in limited power to draw firm conclusions about the "parenting-mating trade-off" hypothesis (Magrath and Elgar 1997).

Another, more conceptual problem with the "parenting-mating trade-off" hypothesis is that the "differential allocation" hypothesis also predicts a negative relationship between male quality and paternal care (Burley 1986; Sheldon 2000). This hypothesis states that females invest more resources into offspring sired by high-quality males. In such cases, reduced paternal care is not a direct effect of an optimal parenting-mating trade-off by males. Thus, testing the "parenting-mating trade-off" hypothesis without considering the "differential allocation" hypothesis may lead to a misinterpretation of the underlying mechanism in the relationship between male quality and paternal care (Mitchell et al. 2007; Stiver and Alonzo 2009; Diniz et al. 2015). However, these two hypotheses can be differentiated by investigating whether the negative correlation between male quality and paternal care is determined by the number of nearby fertile females. If high-quality males' partners are willing to compensate for reduced paternal care (i.e., "differential allocation" hypothesis), the correlation between male quality and paternal care should be negative and independent of the number of nearby fertile females (Figure 1b). However, if the negative relationship between male quality and paternal care depends on the presence of nearby fertile females or depends on the number of nearby fertile females (Figure 1a), this would provide support for the "parenting-mating trade-off" hypothesis and rule out the "differential allocation" hypothesis, in that high-quality males reduce paternal care in order to seek extra-pair matings.

Lastly, in addition to parenting and mating efforts, males also allocate time to self-maintenance activities, such as foraging (Magrath and Komdeur 2003). Males that are confronted with extra-pair mating opportunities may choose to reduce such self-maintenance
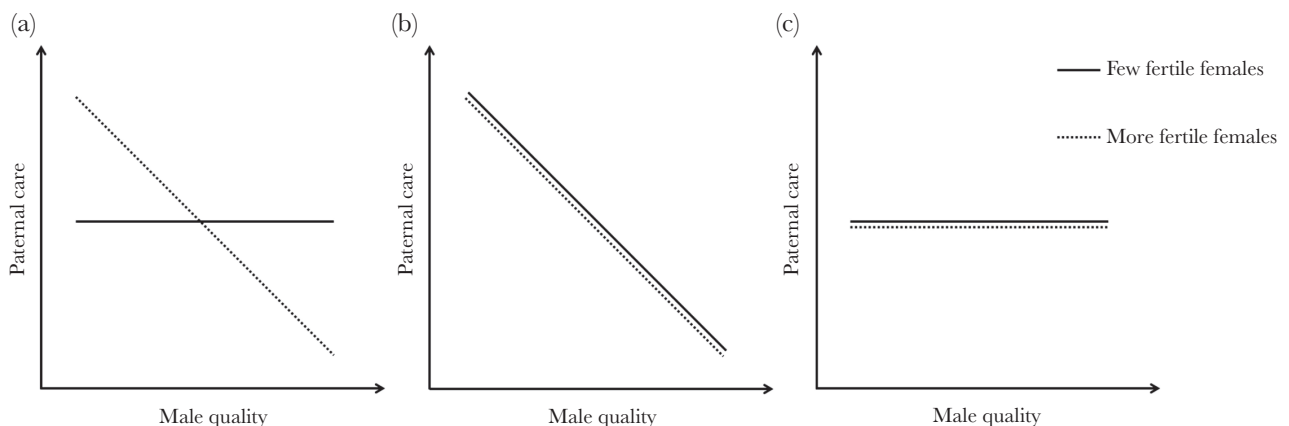
Figure 1
The correlation between male quality and paternal care under low or high number of mating opportunities (i.e., few or more fertile females present nearby) according to the predictions of the "parenting-mating trade-off" hypothesis (a), the "differential allocation" hypothesis (b), and when males invest more in mating efforts at the expense of self-maintenance (c). Male quality reflects male's ability to gain extra-pair matings. The solid and dotted lines in the figure just indicate the relationship between male quality and paternal care, not indicating the different values of paternal care between two lines.

activities, rather than reduce paternal care. This seems especially likely for high-quality males in good body condition who would suffer few long-term fitness consequences of temporary reductions in self-maintenance (reviewed in Santos and Nakagawa 2012; Bleu et al. 2016). As such, a lack of negative relationship between paternal care and male quality whenever the number of fertile female present nearby is low or high (Figure 1c) cannot be considered as evidence against the "parenting mating trade-off" hypothesis.

In this correlational study, we test the "parenting-mating trade-off" during the incubation period in the socially monogamous hair-crested drongo (*Dicrurus hottentottus*), a territorial songbird with bi-parental care. We use individual incubation attendance as a measurement of parental care. Males contribute, on average, nearly half of the incubation attendance, and therefore, male incubation attendance may play an important role in determining the hatching success of the clutch. However, males also seek extra-pair matings at this phase. Most males that gained extra-pair paternity did so during their social mate's incubation period (55.6%, overall $N = 18$ males) and not during their social mate's nestling period (5.6%, overall $N = 18$ males; Lv L, unpublished data). Therefore we focused on the incubation period to investigate a trade-off between paternal effort and mating effort. Furthermore, males who gained extra-pair paternity had significantly longer tarsi (as a proxy for body size) than 1) males that did not gain extra-pair paternity and 2) the males they cuckolded (Supplementary Material), which suggests that male size corresponds to extra-pair matings success. Therefore, this study system is ideal for investigating whether male hair-crested drongos trade-off incubation attendance and mating effort according to their own quality (i.e., size) and extra-pair mating opportunities. We test whether males who engage in extra-pair matings increase their reproductive success by siring more offspring and whether there is a cost of reducing paternal care with reduced hatching success in hair-crested drongos. We also explicitly considered whether the potential negative relationship between male quality and male incubation attendance depends on extra-pair mating opportunities (i.e., number of nearby fertile females) and explore whether this relationship is influenced by differential allocation or by males seeking extra-pair matings.

METHODS

Study population

We collected data from 2010 to 2017 in a natural population of hair-crested drongos breeding in the Dongzhai National Nature Reserve (31.95° N, 114.25° E) in central China (for more information about the study site see Li et al. 2009). The reserve is located in the transitional area between subtropical and temperate zones. Each year, we monitored between 47 and 86 breeding pairs (mean = 76 pairs) within the study area of approximately 400 ha.

The hair-crested drongo is a medium-sized (body length is around 30 cm) migratory passerine with sexual size dimorphism (males: mean tarsus length ± SE: 26.19 ± 0.07 mm, $N = 134$; female: mean tarsus length ± SE: 25.69 ± 0.08 mm, $N = 146$; 1.9% difference; $t = 4.87$, $P < 0.001$; Lv L, unpublished data). Individuals start breeding at 2 years of age, except for two breeding yearling females during our study period (not included in this study). Adults breed in pairs and form long-term pair bonds (Lv et al. 2016). They are highly faithful to their territories across years (Rocamora and Yeatman-Berthelot 2009; Lv et al. 2016). Hair-crested drongos arrive in Dongzhai National Nature Reserve from their wintering grounds in Indochina in late April (Rocamora and Yeatman-Berthelot 2009). The birds breed from early May through August

and depart before mid-October (Gao et al. 2006). The species is generally single-brooded with only 18.3% of pairs ($N = 120$ pairs) laying replacement clutches after their first clutch failed (Lv et al. 2016). All females in the population lay within a period of around one month in each season (mean ± SE: 30.12 ± 0.92 days, $N = 8$ seasons) and 71.5% of them during a 11-day period (overall $N = 617$ nests), which indicate a high breeding synchrony of this species. Modal clutch size is four (75.6%, overall $N = 275$ nests, range: 3–5 eggs), the median incubation period is 17 days (from the day the penultimate egg is laid to hatching) and all eggs hatch within 1–3 days. Both parents participate in all breeding activities, including nest building, incubation, and feeding of offspring (Chen and Luo 1998). Nest success was high with 66.2% of the nests producing at least one fledgling ($N = 464$ nests; Lv et al. 2016).

Field methods

Birds in our study area usually nest in high trees, such as hardwood trees and Chinese water firs (*Metasequoia glyptostroboides*). Each year we monitored nesting behavior. Once nests were found, they were checked every 1–3 days to determine laying date, clutch size, hatching date, and number of nestlings and fledglings. To collect morphological measurements and blood samples of studied individuals, we captured adults by mist-netting during incubation or nestling-provisioning, and we handled nestlings at the nest when they were 14–18 days post-hatching. During the study period, we ringed 80.3% of breeding individuals (overall $N = 1208$ adult-seasons) with unique set of color rings. For all adults, we took standard morphological measurements such as wing length, tarsus length, and body mass by using calipers or rulers to the nearest 0.01 or 0.1 mm, or scales to the nearest 0.1 g. We also measured the characteristic long hair-like feathers, which grow from the forehead and extend over the hind crown and upper back, for the average length (to the nearest 0.1 mm) of the longest three "hairs." Blood of captured adults and nestling was sampled via the brachial vein. If nestling were found dead (due to predation; 1.6% of all nestling samples, $N = 1172$ nestlings), we collected the tissue samples. For daily mean temperature, we obtained recordings from "China Meteorological Data Sharing Service System" (http://www.cma.gov.cn/2011qxfw/2011qsjgx), station 57297 (32.13°N, 114.05°E), which was the closest station (~30 km distance) to this study site.

Incubation behavior

To measure the incubation attendance of both parents, we filmed the nests with at least one ringed parent during the incubation period from 2011 to 2014. In cases where only one parent was ringed, we inferred the sex of the unringed parent based on the sex of its ringed partner (no same-sex pairs were recorded in this species). We filmed each nest only once for at least 3 h (mean ± SE: 195.6 ± 3.6 min, $N = 167$ nests, 101 males), either in the morning (6 AM to 12 AM; 61.1%) or in the afternoon (2 PM to 7 PM; 38.9%). Most of the observed within-pair matings occurred in the afternoon (83.3%, 5 of 6 matings of four breeding pairs; Lv L, unpublished data). This suggests that the afternoon might be more important than the morning for males looking for extra-pair matings. Additionally, the temperature is usually higher in the afternoon than in the morning, and, therefore, reducing incubation attendance may be less costly for males in terms of egg hatching success. Thus, we expect that males who seek extra-pair matings incubate less in the afternoon than in the morning. To compare the incubation attendance in the morning and in the afternoon between nests on similar days of incubation, we filmed 68.9% of nests on days 5–6 of incubation

(among them 59.1% of nests in the morning, overall $\mathcal{N} = 115$ nests; Supplementary Figure S1). We filmed other nests between days 1–4 of incubation or between days 7–14 of incubation due to the shortage of cameras for filming in the field. However, excluding these nests that did not film not on days 5–6 of incubation gave very similar results. Therefore, we kept these nests in the analyses. Additionally, nests with different laying dates had similar chance of being filmed in the morning or in the afternoon (Supplementary Figure S2). We fixed video cameras (Sony HDR-160E, Sony HDR-260E, or Samsung F40) on tripods and placed on the ground or tied on another tree nearby the nest tree at a distance of 10 to 30 meters from the nest. Adult birds returned to the nest soon after the observer left and we did not detect any apparent effects of the cameras or tripods on incubation behavior (e.g., returned adults did not pay any attention to cameras or tripods). As a precaution, however, we excluded the time period from the initiation of camera recording to the time when a bird first visited the nest from our analyses (mean ± SE: 13.3 ± 0.9 min, $\mathcal{N} = 167$ observations, 101 males).

To measure the incubation attendance of both parents, we scored video recordings and calculated the duration of each incubation bout (in min) as the time between when a bird was on and off the nest during incubation. We defined a male incubation recess as the duration (in min) between the end of one incubation bout to the start of its next incubation bout (its partner may incubate during this period). All birds in our video recordings could be identified and birds never incubated together. Incubation attendance (min/h) was calculated as the sum of individual incubation bouts (min) divided by the total duration of the recording period (h). In total, we used five measurements of incubation behavior in this study: male incubation attendance (min/h; $\mathcal{N} = 167$ observations, 101 males), male incubation absence (min/h; 60 min - male incubation attendance), female incubation attendance (min/h; $\mathcal{N} = 149$ observations, 97 females), average duration of male incubation bouts (min; $\mathcal{N} = 162$ observations, 98 males), and average duration of male recess periods (min; $\mathcal{N} = 167$ observations, 101 males). Sample sizes differed between incubation parameters because male did not incubate in five observations (not included in calculating average duration of male incubation bouts). Females who were not ringed were not included in calculating female incubation attendance because the random effect of individual ID (see below) was used to control the repeated measurements of incubation attendance for the same individual in the analyses. Additionally, since the last incubation bouts in the recording period were not fully covered (battery died or interrupted by observer), we only included these in calculating incubation attendance, but not in calculating the average duration of incubation bouts. We restricted all analyses to first clutches of each pair.

Molecular parentage analyses

We extracted DNA from blood or tissue samples of both parents ($\mathcal{N} = 760$ parents) and nestlings ($\mathcal{N} = 1172$ nestlings) via a salt extraction procedure (Richardson et al. 2001). To genotype parents and nestlings, we used 10 polymorphic microsatellite markers and amplified them in three multiplex PCR reactions. All Genetics & Biology SL (Coruña, Spain) developed seven new markers for the hair-crested drongo (see details of 7 microsatellites in Supplementary Table S1), and amplified them in multiplex 1 (Dh14, Dh27, Dh32, and Dh54) and multiplex 2 (Dh8, Dh9, and Dh52). Multiplex 3 consisted of three markers previously developed for other bird species: Mjg1 (Mexican jay *Aphelocoma ultramarine*; Li et al. 1997), Pocc8 (crowned leaf warbler *Phylloscopus occipitalis*; Bensch et al. 1997) and Pdo6 (house sparrow *Passer domesticus*; Griffith et al. 1999). We use

the same reaction conditions for all multiplex reactions, and carried out them in a 10 μL volume (containing 20–50 ng DNA) using a QIAGEN Multiplex PCR Kit and following the manufacturer's protocol. The PCR program was one cycle of initial denaturation for 15 min at 95°C, then 30 cycles of denaturation for 30 s at 94°C, annealing for 1.5 min at 56°C and extension for 1 min at 72°C, followed by eight cycles of denaturation for 30 s at 94°C, annealing for 1.5 min at 52°C and extension for 1 min at 72°C, and a final cycle of extension for 30 min at 60°C. We sized fluorescently labeled PCR products on an DNA analyzer (ABI 3730) and scored allele lengths with GeneMapper 4.0 software (Applied Biosystems).

All individuals were, on average, genotyped for 99.6% of all loci and the genotyping error rate was low with 0.005 of alleles incorrectly genotyped across loci. The genotype of the nestlings matched their social mother in 99.1% of the cases (overall $\mathcal{N} = 1172$ nestlings). The 10 nestlings that mismatched the genotype of their social mother could either be the result of intra-specific egg parasitism or error in genotyping. We, therefore, excluded them from later analyses. The combined exclusion probability of the 10 markers is 0.99595 for the first parent and 0.99987 for the second parent (given the genotype of mother) by using Cervus 3.0 (Kalinowski et al. 2007). To prevent false extra-pair assignments due to genotyping error or 0-alleles, we manually compared the genotypes of each nestling with its social father and conservatively assigned a nestling as extra-pair offspring if it has 2 or more mismatches with its social father and not with one mismatch. For each extra-pair offspring, we attempted to assign paternity to one of all the breeding males present in the population, which were sampled in the population during that year or in previous years. We used Cervus to find a male that perfectly matched all of the offspring's paternal alleles (i.e., zero mismatches) given the mother's genotype. Thus, we were conservative in our extra-pair assignment method by not allowing any mismatches between extra-pair offspring and extra-pair father. If one of the sampled males matched the genotype of the extra-pair offspring, this male was then assigned as the extra-pair father. If none of the sampled males matched, the extra-pair father was not assigned. We never observed more than one male match the genotype of the extra-pair offspring.

Extra-pair mating opportunities

To test whether the trade-off between providing parental care and pursuing extra-pair matings of males is limited by the distance from the focal male's nest to the nest of extra-pair mates, we measured extra-pair mating opportunities at different distance-categories. The average radius of hair-crested drongo territories is 62.0 ± 8.8 meters (mean ± SE, $\mathcal{N} = 5$ territories; Lv et al. 2018), which was calculated based on the area of 60% isopleth of home ranges with fixed kernel methods (Worton 1989; Börger et al. 2006). Since most nests were located in this study area (Lv et al. 2016), we could measure the extra-pair mating opportunities for each focal male by counting the number of fertile females nearby. The average and maximum distance between their own nests and the nests where male hair-crested drongos gained extra-pair paternity are 216 and 570 meters, respectively. And the majority of nests containing a male's extra-pair offspring was found within 216 meters of its own nest (74.3%, 26 of 35; Lv L, unpublished data). Therefore, we used the software MapSource to count the number of fertile females within 216 meters from its nest (hereafter "circle") and in the annulus between the concentric circles radii of 216 and 570 meters (hereafter "annulus") during the date we recorded incubation behavior. By comparing whether males respond to the number of fertile females

located in the area of the circle and in the annulus area differently, we tested whether extra-pair mating opportunities for male hair-crested drongos were limited by distance. The number of fertile females for 29 males whose territory were located nearby the edge of this study area may be underestimated (17.4% of all males, overall $N = 167$ males). However, excluding these males from the analyses gave very similar result. Therefore, we kept them in the analyses. As the shortest period of sperm storage in birds reported by Birkhead et al. (1992) is 5 days, we made the conservative assumption that the fertile period of a female hair-crested drongo extended from 5 days before laying the first egg to the day the penultimate egg was laid (Møller and Gregersen 1994). Few males had more than two fertile females in the circle area ($N = 9$ males, range: 3–5 females). In order to reduce heterogeneity in sample sizes between compared groups ($N_{0 \text{ fertile female}} = 92$ males; $N_{1 \text{ fertile female}} = 44$ males; $N_{2 \text{ fertile females}} = 22$ males), we pooled these males into a single group (3+ fertile females). Accordingly, we also grouped the number of fertile females for each male in the area of annulus into four categories: 0–1 ($N = 84$ males), 2–3 ($N = 48$ males), 4–5 ($N = 24$ males), and 6+ fertile females ($N = 11$ males, range: 6–13 females), respectively. It is worth to mention that the results of setting the number of fertile females into four levels are very similar with the results obtained by using the actual number of fertile females without considering heterogeneity and grouping (Supplementary Table S2).

Statistical analyses

To investigate whether male quality and extra-pair mating opportunities influence the incubation behavior of male and female hair-crested drongos, we applied linear mixed models with normal error structure. Male incubation attendance is affected by both average duration of male incubation bouts and average duration of male recess periods. For example, less male incubation attendance could attribute to shorter incubation bout, longer recess periods, or a combination of both. Thus, we first examined whether male incubation attendance was associated with male tarsus length (see details of using tarsus length as an index of male quality in Supplementary Material) and the number of fertile females (in the area of the circle and of the annulus, respectively). The full model included number of fertile females (in the area of the circle or of the annulus), male tarsus length, laying date, day of incubation, ambient temperature of filming date, video recording time (morning or afternoon) as fixed effects. In addition, we also included the two-way interaction between male tarsus length and number of fertile females. We included year and male ID as random effects in the model to control for year differences and the non-independence of repeated measurements of individuals, respectively. Subsequently, we used the same set of fixed effects and random effects to explore whether male tarsus length and number of fertile females affected 1) average duration of male incubation bouts and average duration of male recess periods; 2) female incubation attendance (to test whether females incubated more if they mated with high-quality males; male ID was replaced by female ID). We also assessed whether females responded to the decreased incubation attendance of their partners differently when the number of fertile females varied and whether females responded to the decreased incubation attendance of their partners according to the tarsus length of their partners, by setting: female incubation attendance as a response variable; year, male ID and female ID as random effects; and male incubation absence, number of fertile females, male tarsus length, laying date, day of incubation, ambient temperature of filming date and video recording time as fixed effects. We also included two two-way interactions of male

incubation absence: number of fertile females and male incubation absence: male tarsus length. When females fully compensated for the absence of the male during incubation, the expected regression coefficient between female incubation attendance and male incubation absence should not differ from 1 ($\beta_{\text{male incubation absence}} \approx 1$). To test for female compensation, we performed parametric bootstrap simulations and compared the 95% confidence intervals for overlap with this expected slope by using the package "boot" with 1000 iterations and normal method (Canty and Ripley 2015).

To test whether there is a cost for males who decrease incubation attendance and seek extra-pair matings, we examined if male incubation attendance influenced the proportion of eggs in a nest that survived until hatching (combined effects of egg predation and hatching success) by applying a generalized linear mixed model with a binomial error structure (hatched vs. predated or unhatched eggs). The full model included male incubation attendance, clutch size, and laying date as fixed effects; year and male ID as random effects.

To test whether males produced more offspring through extra-pair mating in each year, we compared the annual mean number of fledglings sired by males who gained extra-pair paternity and males who did not gain extra-pair paternity by using a Mann-Whitney U test. Additionally, we compared the annual mean number of fledglings in each male's brood (social partner) between males who sired extra-pair young and males who did not.

We conducted statistical analyses using SPSS 19.0 (SPSS Inc., Chicago, IL), with the exception of linear mixed model analyses, which we performed in R.3.5.2 (R Core Team 2018), using the package "lme4" (Bates et al. 2014). For linear mixed models, we assessed collinearities between predictor variables by calculating variance inflation factors (VIF). All VIF values were well below a threshold of three, indicating low collinearity (Zuur et al. 2009). We also checked the normality model residuals—both visually and by Shapiro-Wilk test—and assessed linearity by visual inspection of residuals plotted against model fitted values and predictors. To meet the assumptions of normality of residuals, we square-root transformed the average duration of male incubation bouts, and log-transformed the average duration of male recess periods (Shapiro-Wilk tests after data transformed: both $P > 0.120$). All tests were two-tailed and α-level was set to $P < 0.05$.

For model selection, we compared all possible combinations of fixed effects and a null model with an intercept but no fixed effects. The models were compared by Akaike's information criterion corrected for small sample size (AICc; Hurvich and Tsai 1989), which penalizes more complex models (Burnham and Anderson 2002), by using the "dredge" function in "MuMIn" package (Bartoń 2018). We chose the model with the lowest AICc value for parameter inference and estimated main effects from models with interaction terms removed.

RESULTS

Extra-pair paternity

A total of 109 extra-pair offspring (9.4%) were identified from 1162 offspring. The extra-pair offspring were from 62 broods (16.7%, overall $N = 372$ broods) and 80.6% of these broods contained only one or two extra-pair offspring (range: 1–4 nestlings). Furthermore, 64 extra-pair offspring (58.7%, overall $N = 109$ extra-pair offspring, from 35 broods) were assigned paternity to a total of 23 extra-pair fathers. All extra-pair offspring within a brood were sired by only one male. Males that obtained extra-pair paternity were rarely cuckolded by their social females (13.0%, overall $N = 23$ extra-pair fathers).

Male incubation attendance

Male incubation attendance decreased significantly with male tarsus length in hair-crested drongos, but only when at least two fertile females were present in the circle area (within 216 meters; Table 1a, Supplementary Table S2a, Figure 2a). Males incubated 12.6% less in the afternoon than males in the morning (mean ± SE: 19.59 ± 1.32 min/h, $\mathcal{N}$ = 65 observations vs. 22.41 ± 1.09 min/h, $\mathcal{N}$ = 102 observations; Table 1a). However, male incubation attendance was neither correlated with male tarsus length nor with the number of fertile females present in the annulus area (between the concentric circles radii of 216 and 570 meters; Table 2, Supplementary Table S3). Additionally, there was no significant interaction between male tarsus length and the number of fertile females present in the annulus area (Table 2, Supplementary Table S3). Since only the extra-pair mating opportunities in the circle area were associated with male incubation attendance, hereafter all analyses focus only on the number of fertile females present in the circle area.

Male incubation bouts and recesses

Average duration of male incubation bouts was not associated with their tarsus length, the number of nearby fertile females, or their interaction (Table 1b, Supplementary Table S2b). However, average duration of male recess periods was significantly positively correlated with their tarsus length, but only when at least two fertile females were present nearby (Table 1c, Supplementary Table S2c, Figure 2b). Males with longer tarsi had longer incubation recess periods. Additionally, males recessed 20.3% longer in the afternoon than males in the morning (mean ± SE: 51.68 ± 4.22 min, $\mathcal{N}$ = 65 observations vs. 41.20 ± 2.92 min, $\mathcal{N}$ = 102 observations; Table 1c).

Female incubation attendance and female incubation compensation

Females with at least two fertile females present nearby tended to incubate more if they were mated with longer-tarsus males (Table 1d, Supplementary Table S2d, Figure 2c). Female incubation attendance decreased with date of laying (Table 1d).

Females whose partners were absent for a longer period and experienced lower ambient temperature incubated significantly more (Table 3, Supplementary Table S4, Figure 2d). This pattern was independent of the number of nearby fertile females or the tarsus length of their partners (Table 3, Supplementary Table S4, Figure 2d). Additionally, females provided 80% compensation for male incubation absence (bootstrapped mean (95% confidence interval) = 0.8 (0.700 to 0.894)).
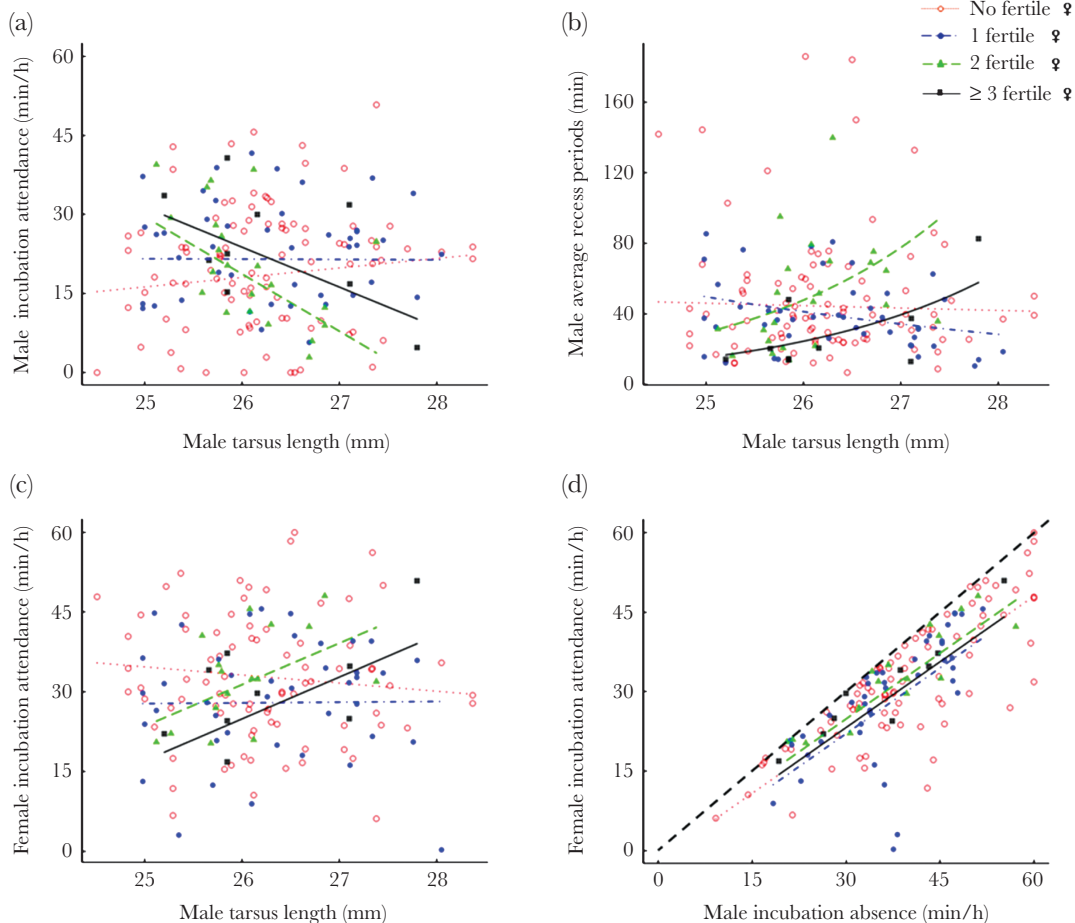
Figure 2
The relationship between male quality (tarsus length) and number of fertile females within 216 meters of a male's nest on (a) male incubation attendance, (b) average duration of male recess periods, (c) female incubation attendance in hair-crested drongos, and (d) the association between male incubation absence and female incubation attendance as the number of fertile females within 216 meters from their nests varies. Lines show the model predicted mean responses for groups with different numbers of fertile females. Predictions for average duration of male recess periods (b) were back-transformed from a log-scale. The slope of the dashed line in (d) indicates the null hypothesis that females fully compensate for a reduction in male incubation attendance.

Table 1

Summary of final best-fit linear mixed models testing whether the incubation behavior of male (a–c) and female (d) hair-crested drongos was influenced by male quality (tarsus length), the number of fertile females within 216 meters from their nests, and their interaction

Fixed effects	β	SE	t	P-value
(a) Male incubation attendance (min/h, N = 167 observations, 101 males):				
Number of fertile females (relative to 0): 1	29.54	59.96	0.49	0.623
2	362.76	112.16	3.23	**0.001**
≥3	243.20	119.34	2.04	**0.043**
Male tarsus length	1.69	1.47	1.15	0.251
Video recording time (relative to morning)	−3.30	1.63	−2.02	**0.045**
Number of fertile females (relative to 0): 1 × Male tarsus length	−0.98	2.28	−0.43	0.667
Number of fertile females (relative to 0): 2 × Male tarsus length	−13.93	4.30	−3.24	**0.001**
Number of fertile females (relative to 0): ≥3 × Male tarsus length	−9.09	4.53	−2.01	**0.047**
(b) Average duration of male incubation bouts (min, N = 162 observations, 98 males):				
Number of fertile females (relative to 0): 1	0.43	0.29	1.46	0.146
2	0.42	0.38	1.10	0.274
≥3	−0.13	0.57	−0.23	0.817
Male tarsus length	−0.09	0.18	−0.53	0.601
(c) Average duration of male recess periods (min, N = 167 observations, 101 males):				
Number of fertile females (relative to 0): 1	5.05	3.28	1.54	0.125
2	−16.82	6.10	−2.76	**0.007**
≥3	−13.69	6.49	−2.11	**0.037**
Male tarsus length	−0.03	0.08	−0.37	0.712
Video recording time (relative to morning)	0.28	0.09	3.11	**0.002**
Number of fertile females (relative to 0): 1 × Male tarsus length	−0.20	0.12	−1.59	0.115
Number of fertile females (relative to 0): 2 × Male tarsus length	0.65	0.23	2.79	**0.006**
Number of fertile females (relative to 0): ≥3 × Male tarsus length	0.51	0.25	2.06	**0.041**
(d) Female incubation attendance (min/h, N = 149 observations, 97 females):				
Number of fertile females (relative to 0): 1	−4.37	63.85	−0.07	0.946
2	−228.75	125.59	−1.82	0.071
≥3	−229.68	120.52	−1.91	0.059
Male tarsus length	−1.30	1.52	−0.85	0.396
Video recording time (relative to morning)	1.14	1.83	0.62	0.535
Laying date	−0.42	0.19	−2.23	**0.028**
Number of fertile females (relative to 0): 1 × Male tarsus length	−0.01	2.42	−0.01	0.996
Number of fertile females (relative to 0): 2 × Male tarsus length	8.76	4.83	1.81	0.072
Number of fertile females (relative to 0): ≥3 × Male tarsus length	8.54	4.56	1.87	0.064

Significant effects are denoted in bold. Candidate models show in Supplementary Table S3. The overall effect of interaction between number of fertile females and male tarsus length is χ^2 = 13.71, P = 0.003 in (a); χ^2 = 16.28, P < 0.001 in (c); χ^2 = 7.10, P = 0.069 in (d). The overall effect of number of fertile females is χ^2 = 4.28, P = 0.233 in (a); χ^2 = 3.06, P = 0.383 in (b); χ^2 = 6.28, P = 0.099 in (c); χ^2 = 5.66, P = 0.789 in (d).

Table 2

Summary of the final best-fit linear mixed model testing whether the incubation attendance of male hair-crested drongos (min/h, N = 167 observations, 101 males) was associated with male quality (tarsus length), the number of fertile females present in the annulus between the concentric circles radii of 216 and 570 meters from a male's nest, and their interactions

Fixed effects	β	SE	t	P-value
Number of fertile females (relative to 0–1): 2–3	72.49	65.16	1.11	0.268
4–5	−47.28	81.72	−0.58	0.564
6+	−10.89	169.71	−0.06	0.949
Male tarsus length	0.50	1.55	0.32	0.747
Video recording time (relative to morning)	−2.97	1.73	−1.72	0.089
Number of fertile females (relative to 0–1): 2–3 × Male tarsus length	−2.70	2.48	−1.09	0.278
Number of fertile females (relative to 0–1): 4–5 × Male tarsus length	1.93	3.11	0.62	0.536
Number of fertile females (relative to 0–1): 6+ × Male tarsus length	0.37	6.42	0.06	0.955

Candidate models show in Supplementary Table S4. The overall effect of interaction between number of fertile females and male tarsus length is χ^2 = 2.29, P = 0.514, and the overall effect of number of fertile females is χ^2 = 2.78, P = 0.428.

Male incubation attendance and fitness

Males contributed 40.8 ± 1.6% (mean ± SE, N = 167 observations, 101 males) of incubation attendance. However, the proportion of eggs in a nest that survived until hatching was not influenced by male incubation attendance (generalized linear mixed model: χ^2 = 2.69, P = 0.101, N = 155 nests of 98 males).

Extra-pair paternity and fitness

Males who gained extra-pair paternity sired more fledglings in each year (median = 3.5, range: 0.0–4.0 fledglings, N = 23 males) than males who did not gain extra-pair paternity (median = 2.5, range: 0.0–5.0 fledglings, N = 178 males; U = 1133, P < 0.001). However, for each male's brood (social partner), males who gained extra-pair

Table 3

Summary of the final best-fit linear mixed model testing whether female incubation attendance (min/h, N = 149 observations, 97 females) by hair-crested drongos was influenced by the incubation absence of their partners considering the influence of their partners' quality (tarsus length), and the number of fertile females within 216 meters from their nests

Fixed effects		β	SE	t	P-value
Male absence		0.80	0.05	16.58	**<0.001**
Number of fertile females (relative to 0):	1	−1.40	1.18	−1.19	0.237
	2	2.07	1.78	1.16	0.248
	≥3	1.02	2.15	0.48	0.634
Ambient temperature		−0.76	0.23	−3.39	**0.001**
Video recording time (relative to morning)		−1.19	1.07	−1.12	0.267

Significant effects are denoted in bold. Candidate models show in Supplementary Table S5. The overall effect of number of fertile females is $\chi^2 = 4.17$, $P = 0.243$.

paternity did not produce more fledglings than males who did not sire extra-pair offspring (median = 3.0, range: 0.0–4.0 fledglings, $N = 23$ males vs. median = 3.0, range: 0.0–5.0 fledglings, $N = 178$ males; $U = 1842$, $P = 0.429$).

DISCUSSION

The "parenting-mating trade-off" hypothesis predicts that males face a trade-off between providing parental care and seeking extra-pair matings. It is predicted that males should invest more in finding extra-pair mates and provide less parental care if they are more successful at obtaining extra-pair matings (high-quality individuals) (Westneat et al. 1990; Magrath and Komdeur 2003; Stiver and Alonzo 2009). In agreement with the "parenting-mating trade-off" hypothesis, we found that high-quality male hair-crested drongos (as inferred from tarsus length) incubated less than low-quality males by recessing longer between incubation bouts during the recorded period of around 3 h. However, this was only the case when sufficient number of fertile females were present nearby. Females compensated for around 80% of the decreased incubation attendance of their partners, irrespective of male quality. Despite reduced male incubation and only partial compensation by the females, these breeding pairs may not suffer from lower proportion of eggs in a nest that survived until hatching. Additionally, males gained fitness benefit by engaging in extra-pair mating in terms of siring more offspring in each year.

Paternal care, extra-pair mating opportunities, and male quality

High-quality male hair-crested drongos incubated less than low-quality males, only when more fertile females were present nearby (within 216 meters from the male's nest; Table 1a). As males contribute almost half of all incubation, they presumably play an important role in ensuring good conditions for the development of embryos and egg protection against predators. However, they also benefit considerably from gaining extra-pair matings, since males who gained extra-pair paternity sired significantly more fledglings during the breeding season. Additionally, males who seek extra-pair matings during the incubation period of their own nest have no potential cost of losing their within-pair paternity, because their social partners had already completed their clutch. Thus, by trading off the potential cost of decreasing paternal care and the benefit of pursuing additional matings, high-quality males only spend more time off the nest when the chance of gaining extra-pair matings is high. These results may explain why high-quality males do not

decrease their provisioning rate in many socially monogamous bird species with short breeding seasons (i.e., high breeding synchrony; e.g., Komdeur et al. 2005; Limbourg et al. 2013; Grunst and Grunst 2015). Due to high breeding synchrony, the number of local fertile females is generally low during the nestling period, since most females will have completed their clutch, and extra-pair mating opportunities for males are therefore restricted to the incubation period (Magrath and Komdeur 2003; Kaiser et al. 2017). Thus, the potential temporal conflict between parenting and mating efforts, for high-quality males, is probably low during the nestling period (Kokko 1998; Stiver and Alonzo 2009). Our result suggests that the number of fertile females may play an important role in determining male's optimal trade-off between providing incubation attendance and pursuing additional matings.

For the high-quality males of hair-crested drongos, the trade-off between incubation and extra-pair mating was associated with the number of fertile females present within 216 meters (the circle area; Table 1a), not in the area between 216 and 570 meters (the annulus area; Table 2). This result suggests that males may be limited by distance to obtain extra-pair matings. In territorial avian species, males usually obtain extra-pair paternity with close neighbors and the probability of obtaining extra-pair paternity decreases with distance (e.g., Petrie and Kempenaers 1998; Schlicht et al. 2015; Kaiser et al. 2017). In hair-crested drongos, the average distance between two nearest nests is 88 meters ($N = 123$ nests; Lv L, unpublished data). Therefore, males who seek extra-pair matings farther than 216 meters away have to cross other territories and may have a greater chance of being discovered and attacked by other territory owners. Our results highlight that spatial accessibility needs to be considered when measuring extra-pair mating opportunities for males, since the optimal investment between parenting and mating efforts for males may be affected by the availability of extra-pair mating opportunities.

When more nearby fertile females were available, incubation attendance of male hair-crested drongos was negatively correlated with their quality as measured by tarsus length (Table 1a). This is likely due to the greater chance of obtaining extra-pair matings for males with longer tarsi. Extra-pair sires had significantly longer tarsi than the within-pair males they cuckolded or males who did not get extra-pair paternity. Similar relationships have been found in several other species, for example, blue tit *Parus caeruleus* (Kempenaers et al. 1997), red bishop *Euplectes orix* (Friedl and Klumo 2002), red-backed shrike *Lanius collurio* (Schwarzová et al. 2008) and pied flycatcher *Ficedula hypoleuca* (Canal et al. 2011). Larger individuals typically have an advantage in male-male competition and consequently may be more competitive in obtaining extra-pair matings

(Enquist and Leimar 1983; Bolund et al. 2007). Alternatively, as morphological size is to a large extent heritable (e.g., Smith 1993; Merilä 1997), females might choose large males as extra-pair partners because their offspring will inherit good competitive abilities from the father. Although female hair-crested drongos seem unlikely to assess tarsus lengths directly from the males, this biometric could be related to other traits not considered in this study, such as song features and ornamentation. For example, studies on other songbirds reported that males with longer tarsi also had larger repertoire size (Doutrelant et al. 2000; Hesler et al. 2012). Further studies are needed to investigate whether larger male hair-crested drongos are more likely to gain extra-pair matings due to their male-male competition advantage, preference of females in choosing larger extra-pair partners, or a combination of both.

Contrary to predictions of the "parenting-mating trade-off" hypothesis, our data suggests that males with shorter tarsi who had more nearby fertile females incubated more than other males with shorter tarsi whose extra-pair mating opportunities were rare (see the left-hand side in Figure 2a). If so, this could partly have explained the significant interaction effect between males' tarsus length and number of nearby fertile females on male incubation attendance (i.e., low male incubation attendance of males with longer tarsi). However, in an additional analysis, we found that the incubation attendance by short-tarsi (< population mean) males was not significantly different when few or many fertile females around ($t = -1.67$, $P = 0.098$; Figure 3). In contrast, and in line with our original explanation, males with longer tarsi (>population mean) who had many nearby fertile females incubated less than males with longer tarsi who had few nearby fertile females ($t = 2.29$, $P = 0.025$; Figure 3). This result suggests that the negative correlation between male incubation attendance and male tarsus length when

more nearby fertile females were available can mainly be attributed to males with longer tarsi incubating less.

High-quality males decreased incubation attendance through prolonging duration of each incubation recess period (Table 1c), rather than shortening duration of each incubation bout (Table 1b). Furthermore, all males recessed longer in the afternoon, which was associated with less incubation attendance in the afternoon than in the morning (Table 1c). As most matings occurred in the afternoon in this species, males who recessed longer in the afternoon may have a greater chance of gaining extra-pair matings. Finding the fertile female and displaying to her would take time for males who seek extra-pair matings. Additionally, shorter morning recess times could be related to lower morning temperatures and more incubation attendance by males which might be necessary to ensure good conditions for the development of embryos.

Although high-quality males decreased incubation attendance when there were more fertile females present nearby, our analyses could not rule out the possibility that males may also simultaneously decrease the effort of self-maintenance (e.g., foraging). Measuring the effort that allocates to self-maintenance activities are difficult in the field, especially for forest birds. Future work should test the potential paternal cost as a consequence of reduced efforts in self-maintenance during the incubation period on subsequent breeding effort (e.g., reduced chick provisioning rate).

Female compensation

Incubation attendance of female hair-crested drongos was not associated with their partner's quality when the number of nearby fertile females was low (Table 1d). This indicates no support for the "differential allocation" hypothesis, which predicts that females
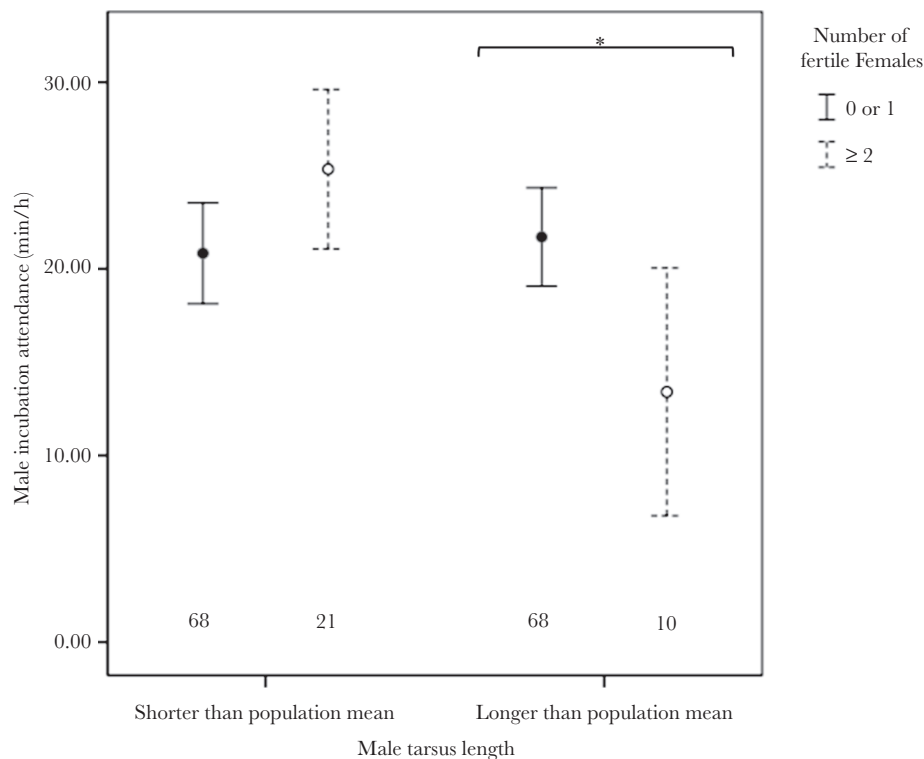
Figure 3
The effect of male quality (tarsus length) and the number of fertile females within 216 meters of a male's nest on male incubation attendance. Error bars show mean value and 95% confidence intervals. Sample sizes are indicated above the x axis. * = $P < 0.05$.

increase their breeding investment when paired with high-quality males (Burley 1986; Sheldon 2000). Females did compensate for the lack of male investment, but this compensation was not influenced by partners' quality or by the number of nearby fertile females (Table 3). Thus, our result suggests that female compensation may be triggered by male behavior (high-quality males invest less), but not by male quality. It may offer an alternative explanation for the positive relationship between female care and the quality of their partners. Presumably, due to constraints on self-maintenance, females compensated for 80% of male absence. This result is consistent with most game-theoretic models of bi-parental care, which predict that partial compensation is the most evolutionarily stable strategy (e.g., Houston and Davies 1985; McNamara et al. 1999).

Female hair-crested drongos incubated more during male recess periods when ambient temperature was low (Table 3). This suggests that incubation is more important to ensure the survival and development of embryos in low temperatures. Additionally, females who started breeding later may also incubate less as a consequence of low individual quality and/or low territory quality, which need further exploring.

The costs of extra-pair mating

Although reduced male incubation attendance was not fully compensated by their partners, we did not detect an effect of reduced male incubation attendance on the proportion of eggs in a nest that survived until hatching. This result suggests that reduced male incubation attendance did not lead to a cost in reproductive success. This is either because males are optimizing when they are incubating and when they leave the nest to have the least impact on egg survival, or because females compensate for reduced male incubation attendance through incubating the eggs more effectively. It is also worth noting that a male's opportunities for extra-pair matings, and therefore his reduction in paternal care, is probably not constant over the whole incubation period. As the fertile period of females (7–9 days) is shorter than the incubation period (around 17 days), the coincident fertile periods of different nearby females (at least 2) for a focal male is short (mean ± SE: 2.53 ± 3.38 days, range: 0–13 days, $\mathcal{N}$ = 121 males). Therefore, high-quality males who incubated less when they had access to more nearby fertile females may increase their attendance when extra-pair mating opportunities become scarce. As a consequence, the potential negative effect of short-term reduced male incubation attendance on hatching success and egg predation is probably weak. To detect this potential effect, a more appropriate method for future studies could be investigating the influence of male incubation attendance within a relative longer incubation period (e.g., male incubation attendance across several days rather than within about 3 h as in this study) on the proportion of eggs in a nest that survived until hatching.

CONCLUSION

This correlational study indicates that male quality and extra-pair mating opportunities may jointly influence the optimal trade-off between providing parental care and pursuing additional matings for males. Our results support the "parenting-mating trade-off" hypothesis, but do not support the "differential allocation" hypothesis. It suggests that the driver of increased female parental care, for females with high-quality partners, might be a response to the reduced parenting efforts of high-quality males, rather than to the quality of the male itself. Our results highlight the need for quantifying available mating opportunities and considering female compensation for reduced male care in testing the "parenting-mating trade-off" hypothesis.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

REFERENCES

Akçay E, Roughgarden J. 2007. Extra-pair paternity in birds: review of the genetic benefits. Evol Ecol Res. 9:855–868.

Andersson MM. 1994. Sexual selection. Princeton (NJ): Princeton University Press.

Bartoń K. 2018. MuMIn: Multi-Model Inference. R package version 1.43.6. Available from: https://cran.r-project.org/package=MuMIn.

Bateman A. 1948. Intra-sexual selection in Drosophila. Heredity. 2:349–368.

Bates D, Maechler M, Bolker B. 2014. Package "lme4": linear mixed-effects models using Eigen and S4. R package version 1.1–7.

Bensch S, Price T, Kohn J. 1997. Isolation and characterization of microsatellite loci in a Phylloscopus warbler. Mol Ecol. 6:91–92.

Birkhead TR, Møller AP, Quinn D. 1992. Sperm competition in birds: evolutionary causes and consequences. London: Academic Press.

Bitton PP, O'Brien EL, Dawson RD. 2007. Plumage brightness and age predict extrapair fertilization success of male tree swallows, *Tachycineta bicolor*. Anim Behav. 74:1777–1784.

Bleu J, Gamelon M, Sæther BE. 2016. Reproductive costs in terrestrial male vertebrates: insights from bird studies. Proc R Soc B Biol Sci. 283:20152600.

Bolund E, Schielzeth H, Forstmeier W. 2007. Intrasexual competition in zebra finches, the role of beak colour and body size. Anim Behav. 74:715–724.

Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T. 2006. Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol. 75:1393–1405.

Burley N. 1986. Sexual selection for aesthetic traits in species with biparental care. Am Nat. 127:415–445.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer.

Canal D, Potti J, Dávila JA. 2011. Male phenotype predicts extra-pair paternity in pied flycatchers. Behaviour. 148:691–712.

Canty A, Ripley B. 2015. boot: Bootstrap R (S-Plus) functions. R Package. version 1.3-1-7.

Chen F, Luo S. 1998. Fauna Sinica: Aves, Passeriformes Bombycillidae-Prunellidae. Vol. 9. Chinese Academy of Sciences Chinese Animal Editorial Committee, editor. Beijing (China): Science Press.

Chuang H, Webster M, Holmes R. 1999. Extrapair paternity and local synchrony in the black-throated blue warbler. Auk. 116:726–736.

Cleasby IR, Nakagawa S. 2012. The influence of male age on within-pair and extra-pair paternity in passerines. Ibis. 154:318–324.

Clutton-Brock TH. 1991. The evolution of parental care. Princeton (NJ): Princeton University Press.

Diniz P, Ramos DM, Macedo RH. 2015. Attractive males are less than adequate dads in a multimodal signalling passerine. Anim Behav. 102:109–117.

Doutrelant C, Blondel J, Perret P, Lambrechts MM. 2000. Blue Tit song repertoire size, male quality and interspecific. J Avian Biol. 31:360–366.

Engqvist L. 2011. Male attractiveness is negatively genetically associated with investment in copulations. Behav Ecol. 22:345–349.

Enquist M, Leimar O. 1983. Evolution of fighting behavior: decision rules and assessment of relative strength. J Theor Biol. 102:387–410.

Friedl TWP, Klumo GM. 2002. Extrapair paternity in the red bishop (*Euplectes orix*): is there evidence for the good-genes hypothesis ? Behaviour. 139:777–800.

Gao Z, Du Z, Wang X, Huang H, Wang K, Yang C. 2006. The nest-site selection of Spangled Drongo at Dongzhai Nature Reserve, Henan. Chinese J Zool. 41:69–73.

Grafen A. 1990. Biological signals as handicaps. J Theor Biol. 144:517–546.

Grana SC, Sakaluk SK, Bowden RM, Doellman MA, Vogel LA, Thompson CF. 2012. Reproductive allocation in female house wrens is not influenced by experimentally altered male attractiveness. Behav Ecol Sociobiol. 66:1247–1258.

Griffith SC, Immler S. 2009. Female infidelity and genetic compatibility in birds: the role of the genetically loaded raffle in understanding the function of extrapair paternity. J Avian Biol. 40:97–101.

Griffith SC, Stewart IRK, Dawson DA, Owens IPF, Burke T. 1999. Contrasting levels of extra-pair paternity in mainland and island populations of the house sparrow (*Passer domesticus*): is there an 'island effect'? Biol J Linn Soc. 68:303–316.

Grunst AS, Grunst ML. 2015. Context-dependent relationships between multiple sexual pigments and paternal effort. Behav Ecol. 26:1170–1179.

Hasegawa M, Arai E. 2015. Experimentally reduced male ornamentation increased paternal care in the barn swallow. J Ornithol. 156:795–804.

Hesler N, Sacher T, Mundry R, Bairlein F, Dabelsteen T, Coppack T. 2012. Song repertoire size correlates with measures of body size in Eurasian blackbirds. Behaviour. 149:645–665.

Houston AI, Davies NB. 1985. The evolution of cooperation and life history in the Dunnock, *Prunella modularis*. In: Sibly RM, Smith RH, editors. Behavioural ecology: ecological consequences of adaptive behaviour. Oxford: Blackwell Scientific Publications. p. 471–487.

Hurvich C, Tsai CL. 1989. Regression and time series model selection in small samples. Biometrika. 76:297–307.

Kaiser SA, Risk BB, Sillett TS, Webster MS. 2017. Ecological and social factors constrain spatial and temporal opportunities for mating in a migratory songbird. Am Nat. 189:283–296.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16:1099–1106.

Kempenaers B, Verheyen GR, Dhondi AA. 1997. Extrapair paternity in the blue tit (*Parus caeruleus*) : female choice, male charateristics, and offspring quality. Behav Ecol. 8:481–492.

Ketterson ED, Nolan Jr. V. 1994. Male parental behavior in birds. Annu Rev Ecol Syst. 25:601–628.

Kokko H. 1998. Should advertising parental care be honest? Proc R Soc B Biol Sci. 265:1871–1878.

Komdeur J, Oorebeek M, van Overveld T, Cuthill IC. 2005. Mutual ornamentation, age, and reproductive performance in the European starling. Behav Ecol. 16:805–817.

Li SH, Huang YJ, Brown JL. 1997. Isolation of tetranucleotide microsatellites from the Mexican jay *Aphelocoma ultramarina*. Mol Ecol. 6:499–501.

Li J, Lin S, Wang Y, Zhang Z. 2009. Nest-dismantling behavior of the haircrested drongo in central China: an adaptive behavior for increasing fitness? Condor. 111:197–201.

Limbourg T, Mateman AC, Lessells CM. 2013. Parental care and UV coloration in blue tits: opposite correlations in males and females between provisioning rate and mate's coloration. J Avian Biol. 44:17–26.

Lv L, Komdeur J, Li J, Scheiber IBR, Zhang Z. 2016. Breeding experience, but not mate retention, determines the breeding performance in a passerine bird. Behav Ecol. 27:1255–1262.

Lv L, Li J, Kingma SA, Gao C, Wang Y, Komdeur J, Zhang Z. 2018. Do hair-crested drongos reduce prospective territory competition by dismantling their nest after breeding? Behav Ecol Sociobiol. 72:12.

Lv L, Zhang Z, Groenewoud F, Kingma SA, Li J, van der Velde M, Komdeur J. (2019). Data from: extra-pair mating opportunities mediate parenting and mating effort trade-offs in a songbird. Behav Ecol. https://doi.org/10.5061/dryad.ht76hdrb8

Magrath MJL, Elgar MA. 1997. Paternal care declines with increased opportunity for extra-pair matings in fairy martins. Proc R Soc B Biol Sci. 264:1731–1736.

Magrath MJL, Komdeur J. 2003. Is male care compromised by additional mating opportunity? Trends Ecol Evol. 18:424–430.

Mayer C, Pasinelli G. 2013. New support for an old hypothesis: density affects extra-pair paternity. Ecol Evol. 3:694–705.

McNamara JM, Gasson CE, Houston AI. 1999. Incorporating rules for responding into evolutionary games. Nature. 401:368–371.

Merilä J. 1997. Expression of genetic variation in body size of the collared flycatcher under different environmental conditions. Evolution. 51:526–536.

Mitchell DP, Dunn PO, Whittingham LA, Freeman-Gallant CR. 2007. Attractive males provide less parental care in two populations of the common yellowthroat. Anim Behav. 73:165–170.

Møller AP, Gregersen J. 1994. Sexual selection and the barn swallow. Oxford: Oxford University Press.

Nakagawa S, Ockendon N, Gillespie DO, Hatchwell BJ, Burke T. 2007. Does the badge of status influence parental care and investment in house sparrows? An experimental test. Oecologia. 153:749–760.

Otter K, Ratcliffe L, Michaud D, Boag PT. 1998. Do female black-capped chickadees prefer high-ranking males as extra-pair partners? Behav Ecol Sociobiol. 43:25–36.

Petrie M, Kempenaers B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. Trends Ecol Evol. 13:52–58.

Puurtinen M, Ketola T, Kotiaho JS. 2009. The good-genes and compatible-genes benefits of mate choice. Am Nat. 174:741–752.

R Core Team. 2018. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing; 2018. Open access available from http//cran. r-project. org.

Richardson DS, Jury FL, Blaakmeer K, Komdeur J, Burke T. 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*). Mol Ecol. 10:2263–2273.

Rocamora G, Yeatman-Berthelot D. 2009. Family Dicruridae (drongos). In: del Hoyo J, Elliot A, Christie DA, editors. Handbook of the birds of the world. 14th ed. Barcelona (UK): Lynx Edicions. p. 172–271.

Santos ES, Nakagawa S. 2012. The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. J Evol Biol. 25:1911–1917.

Sanz JJ. 2001. Experimentally reduced male attractiveness increases parental care in the pied flycatcher *Ficedula hypoleuca*. Behav Ecol. 12:171–176.

Schlicht L, Valcu M, Kempenaers B. 2015. Spatial patterns of extra-pair paternity: beyond paternity gains and losses. J Anim Ecol. 84:518–531.

Schwarzová L, Šimek J, Coppack T, Tryjanowski P. 2008. Male-biased sex of extra pair young in the socially monogamous red-backed shrike *Lanius collurio*. Acta Ornithol. 43:235–239.

Sheldon BC. 2000. Differential allocation: tests, mechanisms and implications. Trends Ecol Evol. 15:397–402.

Smith HG. 1993. Heritability of tarsus length in cross-fostered broods of the European starling (*Sturnus vulgaris*). Heredity. 71:318–322.

Smith HG, Montgomerie R. 1992. Male incubation in barn swallows: the influence of nest temperature and sexual selection. Condor. 94:750–759.

Stiver KA, Alonzo SH. 2009. Parental and mating effort: is there necessarily a trade-off? Ethology. 115:1101–1126.

Vedder O, Schut E, Magrath MJL, Komdeur J. 2010. Ultraviolet crown colouration affects contest outcomes among male blue tits, but only in the absence of prior encounters. Funct Ecol. 24:417–425.

Westneat DF, Sherman PW. 1997. Density and extra-pair fertilization in birds: a comparative analysis. Behav Ecol Sociobiol. 41:205–215.

Westneat DF, Sherman PW, Morton ML. 1990. The ecology and evolution of extra-pair copulations in birds. Curr Ornithol. 7:331–369.

Worton BJ. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology. 70:164–168.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009. Mixed effects models and extensions in ecology with R. New York: Spring Science and Business Media.