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Chapter 4

The trade-off between paternal care and pursuing additional matings is mediated by direct opportunities for extra-pair mating in a socially monogamous bird

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Abstract

In socially monogamous species with bi-parental care, males may face a trade-off between parenting effort and pursuing extra-pair matings. The “parental-mating trade-off” hypothesis predicts that males who are more successful at obtaining extra-pair matings (high quality) should provide less parental care. However, former studies have largely ignored potential confounding effect of availability of extra-pair mating opportunities for males in testing this hypothesis. Therefore, we explore whether the variation in paternal care is explained by the interaction between male quality and the number of local fertile females in the socially monogamous hair-crested drongo (*Dicrurus hottentottus*). We found males with longer tarsi were heavier and more likely to sire extra-pair offspring. In agreement with the “parental-mating trade-off” hypothesis, longer-tarsus males incubated less, but they only did so above a threshold number of local females being fertile. Females incubated more to compensate for the reduced incubation attendance of their partners, but this compensation was not dependent on male tarsus length (rejecting the “positive differential allocation” hypothesis). Our results highlight the need for future studies to quantify available mating opportunities when investigating how individual quality shapes the optimal investment allocation for males between parenting and mating efforts, and reveals the mechanism of how female parental care is affected by the quality of their partners.

Introduction

Paternal care, where males invest time and energy in raising offspring, is a widespread phenomenon in socially monogamous animals (Clutton-Brock 1991; Ketterson and Nolan 1994). Males may benefit from caring for their offspring, but in contrast to females their fitness can also be strongly determined by the extent to which they can achieve additional fertilizations (Bateman 1948). Therefore, males in such species may be confronted with a trade-off between allocating resources (e.g. time and energy) in providing parental care and trying to obtain additional fertilizations by extra-pair matings (“parental-mating trade-off” hypothesis, Magrath and Komdeur 2003; Stiver and Alonzo 2009). This is especially the case when extra-pair mating opportunities for males coincide with periods in which they provide parental care (Grafen 1990; Andersson 1994), and which of these two strategies prevails in such periods depends on the relative fitness benefits of paternal care versus pursuing additional matings.

If females mate with extra-pair males to obtain good genes for their offspring (Griffith and Immler 2009; Puurtinen et al. 2009), males’ extra-pair matings success would depend on traits that reflect their genetic quality (attractiveness), like size, age or ornaments (Akçay and Roughgarden 2007; Bitton et al. 2007; Cleasby and Nakagawa 2012). Meanwhile, if males compete for extra-pair mating opportunities (McKinney et al. 1983; Castro et al. 1996; Kempenaers et al. 1997; Westneat and Stewart 2003), traits that determine the outcome of male-male competition, such as tarsi length (Vedder et al. 2010), would determine males’ ability in gaining extra-pair matings (competitiveness). Variation in such traits, reflecting the potential for extra-pair mating success, may therefore define the optimal investment between providing parental care and pursuing extra-pair mating of different males. It can be expected that high quality males (more attractive and/or competitive), who have a higher chance of obtaining extra-pair matings, should invest more in mating effort and less in parenting effort. However, tests of this “parental-mating trade-off” hypothesis have provided contrasting results (Kokko 1998; Nakagawa et al. 2007; Diniz et al. 2015; Grunst and Grunst 2015).

One reason for this inconsistency may be that the influence of the availability of fertile females, and thus male extra-pair mating opportunities is often overlooked (Magrath and Komdeur 2003; Stiver and Alonzo 2009; Hill et al. 2011). However, due to variation in local density and breeding synchrony, the number of fertile females in the vicinity often varies spatially and temporally (Westneat and Sherman 1997; Chuang et al. 1999; Richardson et al. 2001; Mayer and Pasinelli 2013),

which may affect extra-pair mating opportunities for males and thus the effort and time they should invest in seeking such matings. Thus, studies aimed at testing the “parental-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 mating. To our knowledge, there is only one study that considered the influence of available extra-pair mating opportunities when investigating the relation between male quality and paternal care. Smith and Montgomerie (1992) reported that the incubation attendance of male barn swallows (*Hirundo rustica*) was not affected by their quality (tail length), the availability of extra-pair mating opportunities, or their interaction. However, in their study system, male care seems to have limited fitness consequences (on average males contributed only 9% of total incubation), which, in combination with modest sample size ($N = 16$), likely resulted in insufficient power to draw firm conclusions about the “parental-mating trade-off” hypothesis (Magrath and Elgar 1997).

Another, more conceptual problem with the parental-mating trade-off hypothesis is that the “positive differential allocation” hypothesis also predicts a negative relationship between male quality and paternal care (Burley 1986; Sheldon 2000). It states that females investing more resources in offspring sired by high quality males when such offspring are of genetically higher quality. If this is the case, females liberate their high quality partners from providing care, who may search for extra-pair matings instead, but in such cases reduced paternal care is not a direct effect of an optimal parental-mating trade-off by males. Thus, testing the “parental-mating trade-off” hypothesis without considering the “positive differential allocation” hypothesis may lead to a misinterpretation of the underlying mechanism in the relationship between male quality and paternal care. By investigating whether the presence of fertile females drives male investment in parental care in addition to quality may circumvent this problem, because paternal care in relation to male quality should be independent of the number of nearby fertile females if high quality males’ partners are willing to contribute more in parental care. However, if the link between male quality and his paternal effort depends on the availability of fertile females, it strongly suggests that compensation by females is the result of male behaviour, rather than differential allocation by females.

Here we test the “parental-mating trade-off” hypothesis during the incubation period of the socially monogamous hair-crested drongo (*Dicrurus hottentottus*), a territorial songbird with bi-parental care. Males contribute on average 40.9% (191 breeding attempts of 110 males) of the total incubation attendance. During this

period, males also seek extra-pair matings and most (58.3%) of extra-pair fertilizations ($N = 12$) occur during this relatively brief period (L. Lv, unpublished data). In this study, we investigate whether male hair-crested drongos trade off incubation attendance and mating effort according to their own quality and the availability of extra-pair mating opportunities. We hypothesize that high quality males incubate less, but only when they have more extra-pair mating opportunities. Additionally, we investigate whether the social partner compensates for the males' reduced investment and whether variation in female investment depends on male quality or is a direct response to reduced paternal care. Thus we test the parental-mating trade-off hypothesis while considering the often overlooked opportunities for males in pursuing extra-pair mating. Additionally, we make inferences on whether female care adjusted to male quality (the "positive differential allocation" hypothesis) may be an alternative explanation for a relationship between male care and his quality.

Materials and methods

Study Site, Population and Field Procedures

We collected data for this study yearly from 2010 to 2014 in a natural population of hair-crested drongo 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). Each year, between 47 and 86 breeding pairs were present within the study area of approximately 400 ha. Almost 80% of the adults were ringed with a unique set of colour rings.

The hair-crested drongo is a medium-sized migratory passerine with long-term socially monogamous pair bonds and exhibits high adult breeding site fidelity (84.4% of the surviving breeders ($N = 289$) returned to the same breeding site in the next year; L. Lv, unpublished data). At our study site, hair-crested drongos arrive from their wintering ground (Indochina; Rocamora and Yeatman-Berthelot 2009) in late April and leave before mid-October (Zhenjian Gao et al. 2006). They typically use the same nest tree as the previous year and actively defend their territory against conspecifics. Both parents participate almost equally in all breeding activities, including nest building, incubation and feeding of offspring (Chen and Luo 1998). Modal clutch size is four (75.6%, range 3-5, $N = 275$) and the median incubation period is 17 days (from the laying of the last egg to hatching of the last chick). During breeding, parents aggressively defend their nests from predators, which leads to about two thirds of the nests producing at least one fledgling. The species

is generally single-brooded but 18.3% of the breeding pairs ($N = 120$) laid replacement clutches after their first clutch failed (L. Lv, unpublished data).

Each year, we searched for nests by checking trees which had been used previously as nest trees, and potential nesting sites in the forest. Nests were checked every one to three days to determine laying date, clutch size, hatching date, and number of nestlings and fledglings. We captured adults by mist-netting in close proximity to the nest trees during incubation or nestling-provisioning. Sex of the adults was determined by the size of the brood patch (Chen and Luo 1998), which was distinctively larger in females and in cases where only one parent was ringed, we determined the sex of the unringed parent based on the sex of its ringed partner. Standard morphological measurements such as bill length, bill-head length, tarsus length, wing length, tail length, body length and weight were taken by using callipers or rulers to the nearest 0.01 or 0.1 mm, or scales to the nearest 0.1g. The characteristic long hair-like feathers, which sprang from the forehead and extended over the hind crown and upper back, were also measured or counted for the length of the longest, the average length of the longest three and the number of hairs. We collected a blood sample from each adult via venepuncture of the brachial vein and sopped up the sample with alcohol (95%) soaked cotton swabs. The blood samples of nestlings were collected in the same way when they were 16 or 17 days old (one or two days before fledging). Tissue samples of dead nestlings that were found directly beneath nests were also collected.

During 2011-2014, all nests with at least one ringed parent were filmed during the incubation period to determine the incubation attendance of both individuals. For nests used in this study, most (68.9%, $N = 167$) were filmed on the fifth or sixth day of incubation (range 1st to 14th). Each nest was filmed either in the morning (6 am to 12 am) or in the afternoon (14 pm to 19 pm) for at least 3h (mean \pm SE: 195.6 ± 3.6 min, $N = 167$). Video cameras (Sony HDR-160E, Sony HDR-260E or Samsung F40) were fixed on tripods and placed on the ground or tied on another tree nearby the nest tree with 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 behaviour. As a precaution, however, we excluded the period before a bird first visited the nest after the installation of the camera from analyses.

Molecular parentage analyses

We extracted DNA from blood or tissue samples of both parents and nestlings via a salt extraction procedure (Richardson et al. 2001). Eleven microsatellite markers

were utilized to genotype parents and nestlings and they were amplified in three independent multiplex PCR reactions. Eight markers were newly developed for the hair-crested drongo by All Genetics & Biology SL (A Coruña, Spain), and amplified in multiplex 1 (Dh14, Dh27, Dh32 and Dh54) and multiplex 2 (Dh8, Dh9, Dh31 and Dh52). Multiplex 3 consisted of three markers previously developed for other bird species: Mjg1 (Li et al. 1997), Pocc8 (Bensch et al. 1997) and Pdo6 (Griffith et al. 1999). The reaction conditions were the same for all multiplex reactions, and were carried out in a 10 µl volume (containing 20-50 ng DNA) using a QIAGEN Multiplex PCR Kit and manufacturer protocol. The PCR program was one cycle of 95 °C for 15 min, then 30 cycles of 94 °C for 30 s, 56 °C for 1.5 min and 72 °C for 1 min, followed by eight cycles of 94 °C for 30s, 52 °C for 1.5min and 72 °C for 1 min, and a final cycle of 60 °C for 30 min. Fluorescently labelled PCR products were sized on an AB3730 DNA analyser. Subsequently, allele lengths were scored with GeneMapper 4.0 software (Applied Biosystems).

The genotype of the nestlings matched their social mother in 99.3% of the cases ($N = 690$, five unmatched nestlings were excluded from analyses). Using Cervus 3.0 (Kalinowski et al. 2007), the combined sire exclusion probability of the eleven markers was calculated to be 0.99632 for the first parent and 0.99988 for the second parent (given the genotype of mother). By comparing the genotypes of each nestling with its social father, a nestling was assigned as an extra-pair offspring if there were at least two mismatches between the genotype of the social father and the nestling. For all extra-pair offspring, we attempted to assign paternity to one of all the breeding males sampled during that year or in previous years, using Cervus. Extra-pair paternity was assigned when one of the sampled males in the population matched all of the offspring's paternal alleles given the mother's genotype. A total of 64 extra-pair offspring (9.3%) were identified from 690 offspring belonging to 228 broods (16.7% of broods contained at least one extra-pair offspring). Among them, 35 extra-pair offspring (54.7%) were successfully assigned paternity to, in total, 13 genetic fathers. Males who obtained extra-pair paternity were only rarely cuckolded themselves: only in one of the 13 cases a male who had gained extra-pair paternity was cuckolded himself also.

Data Analyses

We used the video recordings to score the incubation attendance of both parents. Six incubation parameters were used in this study: male incubation attendance (min/h), male incubation absence (min/h, 60 min - male incubation attendance), female incubation attendance (min/h), overall nest incubation attendance (%),

average duration of male incubation bouts (min), and average duration of male recess periods (min).

Last incubation bouts were almost always not fully covered in the recording period, because incubating parents left the nest when we removed the filming equipment or the cease of filming, and consequently lead to an underestimation in the average length of incubation bouts. Therefore, the last incubation bout was not included in calculating average duration of incubation bouts, but included in calculating incubation attendance, if the male incubated less than 24.94 min or the female incubated less than 40.60 min in that bout (resembling the average durations of incubation bouts of 52 undisturbed males and 56 females, respectively). As incubation bouts of both male and female are repeatable ($R_{\text{male}} = 0.154 \pm 0.084$, $N = 52$, $p = 0.023$; $R_{\text{female}} = 0.649 \pm 0.056$, $N = 56$, $p < 0.001$; Lessells and Boag 1987), complete incubation bouts of short-bout individuals are more likely has already been covered in the recording period. Meanwhile, long incubation bouts (9.0% of incubation bouts was longer than 60 min, in total $N = 465$) which are interrupted at the end of the recording period for long-bout individuals can be saved. This method likely accurately reflects the average duration of incubation bouts.

We compared 10 morphological traits (mentioned in the method before) between males who gained extra-pair paternity ($N = 12$, excluding the male who also lost paternity in its own brood) with males who did not ($N = 140$). For all morphological traits, only the tarsus length was significantly different (tarsus length: t-test, $t = 2.284$, $p = 0.024$; other traits: t-test or Mann-Whitney U -test, all: $p > 0.177$), as males who gained extra-pair paternity (26.69 ± 0.23 mm, mean \pm SE) had 2.2% longer tarsi than males who did not (26.11 ± 0.07 mm, mean \pm SE). Although it was not significant if α -value was set as 0.005 according to Bonferroni corrections for 10 comparisons (Bland et al. 1995), extra-pair males had longer tarsi than within-pair males they cuckolded (pair t-test, $t = 3.458$, $p = 0.003$, $N = 19$). Therefore, it suggested that males who gained extra-pair paternity differed in tarsus length with males who did not. Thus, male tarsus length was used as a proxy for a male's likelihood to obtain an extra-pair mating (male quality).

Extra-pair mating opportunity was quantified for each male by 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'). 216 and 570 metres constituted the average and maximum distance between the nests where male hair-crested drongos gained extra-pair paternity and their own nests, respectively. Furthermore, most extra-pair offspring (74.3%, $N =$

26) were sired by males within 216 m of a female (L. Lv, unpublished data). As the shortest period of sperm storage in birds reported by Birkhead et al. (1992) was five days, we assumed that the fertile period of a female hair-crested drongo extended from five days before laying the first egg to the day the penultimate egg was laid (Møller and Gregersen 1994). Few males had more than 3 fertile females ($N = 9$, range = 3-5) in the 'circle' area. In order to meet homogeneity in sample sizes between compared groups, these males were pooled into a single group (3+). Accordingly, the number of fertile females for each male in the area of 'annulus' was also grouped into four categories: 0-1, 2-3, 4-5, and ≥ 6 fertile females, respectively. Twenty-two breeding pairs (18.3% of total pairs, $N = 120$) produced second clutches after their first clutches failed. However, these were excluded from the analyses.

To investigate whether male quality and extra-pair mating opportunities influence the incubation attendance of hair-crested drongos, we applied linear mixed models with normal error structure. We first examined whether 'male incubation attendance' was affected by male tarsus length 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 circle or annulus), 'number of nests' (in the area of circle or annulus), 'male tarsus length', 'laying date', 'number of days from filming date to laying date', 'temperature of filming date', 'recording time' (morning or afternoon) as fixed effects. In addition, the two-way interaction between 'male tarsus length' and 'number of fertile females' was included. 'Year' and 'male ID' were included as random effects in the model to control for year differences and the non-independence of repeated measurements of individuals, respectively. If male incubation attendance was affected, we determined how male tarsus length and the number of fertile females influenced 'duration of male average incubation bouts' and 'duration of male average recess periods', respectively, by using the same model structure. Thereafter, we tested whether 'female incubation attendance' was also affected by the interaction between male tarsus length and number of fertile females as a response to the changed incubation attendance of their partners with the same model structure. Finally, we assessed whether females responded to the decreased incubation attendance of their partners differently when 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 and adding 'male incubation absence' as a fixed effect. The interaction between fixed effects ('male tarsus length' and 'number of fertile females') was

replaced by two two-way interactions between male incubation absence and the number of fertile females, and between male incubation absence and male tarsus length. If female incubation fully compensated for the absence of the male, the expected regression coefficient between these variables should not differ from 1 ($\beta_{\text{male incubation absence}} \approx 1$). To test this, we performed parametric bootstrap simulations and compared the 95% confidence intervals for overlap with this expected slope.

To test whether male incubation attendance influenced the proportion of eggs in a nest that survived to nestlings of hair-crested drongos, we applied generalized linear mixed models with a binomial error structure (hatched vs unhatched or predated eggs). The full model included ‘male incubation attendance’, ‘clutch size’, ‘laying date’, ‘male age’ as fixed effects; ‘Year’ and ‘male ID’ as random effects.

We used an Information-Theoretic (IT) model selection approach, based on the Akaike information criterion (Burnham and Anderson 2002) with the Hurvich and Tsay (1989) correction for finite sample size (AICc). Models parameters were dropped if doing so resulted in a lower AICc score, which were obtained by using the “AICcmodavg” package (Mazerolle 2011). All interactions still present in the final model were temporarily dropped for the estimation of main effects.

‘Duration of male incubation bouts’ was square-root transformed, and ‘duration of male recess periods’ was log-transformed to meet the assumptions of normality and homoscedasticity of residuals. Daily temperature was obtained from ‘China Meteorological Data Sharing Service System’, station 57297 (32.13°N, 114.05°E), which was the closest station (~30km distance) from our study site. Statistical analyses were conducted using SPSS 19.0 (SPSS Inc., Chicago, IL, USA), with the exception of mixed model analyses that were performed in R.3.1.1 (R Core Team 2014), using the package lme4 (Bates et al. 2014). Confidence intervals for the parametric bootstraps were obtained using the package boot (Canty and Ripley 2015). All tests are given two-tailed and α -level was set to $p < 0.05$.

Results

Male Incubation Attendance

Fertile females present in circle area: Male incubation attendance decreased significantly with male tarsus length, but only when there were at least two fertile females (overall interaction effect, $\chi^2 = 12.46$, $p = 0.006$; Table 4.1a, Figure 4.1a). However, the main effects, male tarsus length and the number of fertile females, did not influence male incubation attendance (tarsus: t value = 0.04, $p = 0.972$; number of fertile females: overall effect, $\chi^2 = 5.96$, $p = 0.114$).

Fertile females present in annulus area: Male incubation attendance was not correlated with male tarsus length (t value = 0.06, $p = 0.956$) and the number of fertile females (overall effect, $\chi^2 = 2.78$, $p = 0.428$). Additionally, there was no significant interaction between male tarsus length and the number of fertile females (overall effect, $\chi^2 = 2.29$, $p = 0.514$; Table 4.2).

Since only the extra-pair mating opportunities in the circle area was associated with male incubation attendance, hereafter all analyses focus only on the number of fertile females present in the circle area.

Male Incubation Recesses and Bouts

Although the duration of male recess was not affected by male tarsus length (t value = -0.27, $p = 0.789$) nor by the number of fertile females ($\chi^2 = 6.36$, $p = 0.095$) as the main effects, males with longer tarsi recessed longer when there were at least two fertile females (Table 4.1c, Figure 4.1b, overall interaction effect, $\chi^2 = 16.63$, $p < 0.001$). However, males' average duration of incubation bouts did not change with their tarsus length (t value = -0.52, $p = 0.603$) or the number of fertile females ($\chi^2 = 3.66$, $p = 0.301$). Also, the relationship between the average duration of male incubation bouts and male tarsus length did not depend on the number of fertile females (overall interaction effect, $\chi^2 = 5.35$, $p = 0.148$; Table 4.1b).

Female Incubation Attendance

Although the interaction between male tarsus length and the number of fertile females was not significant (overall interaction effect, $\chi^2 = 6.46$, $p = 0.092$; Table 4.1d), females who mated with longer-tarsus males tended to incubate more when there were at least two fertile females (Table 4.1d, Figure 4.1c). In an additional analysis, in which the number of fertile females was set at two levels by grouping no more than one fertile female and at least two fertile females, respectively, the

interaction between male tarsus length and the number of fertile females was significant (overall interaction effect, $\chi^2 = 5.13$, $p = 0.023$). However, in both analyses, female incubation attendance was not affected by the tarsus length of their mates or by the number of fertile females when their interactions were not included (all: $p > 0.096$).

Male Incubation Absence and Female Incubation Compensation

Females incubated significantly more when males were absent longer (Table 4.3, Figure 4.1d). However, this pattern was not dependent on the number of fertile females or the tarsus length of their partners (number of fertile females: overall effect, $\chi^2 = 4.08$, $p = 0.253$, male tarsus length was dropped from the full model; Table 4.3, Figure 4.1d). Females did not fully compensate for male incubation absence (bootstrapped 95% confidence intervals: 0.699 to 0.891) and 79% of male incubation absence was compensated (Table 4.3).

Male Incubation Attendance and Eggs Survival Rate

The proportion of eggs in a nest that survived to nestlings was not influenced by male incubation attendance ($\chi^2 = 2.69$, $p = 0.101$).

Table 4.1. Summary of four linear mixed models testing whether the incubation effort of hair-crested drongos was influenced by male quality (tarsus length), the number of fertile females within 216 meters from their nests and their interactions. ‘Duration of male incubation bouts’ was square-root transformed, and ‘duration of male recess periods’ was log-transformed. Males who had three or more fertile females ($N = 9$, range = 3-5) within 216 meters from their nest tree were pooled into a single group. Significant effects are denoted in bold face.

Fixed effects	Estimates	SE	<i>t</i> -value	<i>p</i> -value
(a) Male incubation attendance (min/h, $N = 167$):				
# fertile female (1)	32.29	59.95	0.54	0.591
# fertile females (2)	329.30	120.39	2.74	0.007
# fertile females (≥ 3)	265.22	108.28	2.45	0.015
Male tarsus length	1.72	1.47	1.18	0.242
Recording time (pm)	-3.27	1.63	-2.01	0.047
# fertile female (1) \times Male tarsus length	-1.09	2.28	-0.48	0.634
# fertile females (2) \times Male tarsus length	-12.67	4.61	-2.75	0.007
# fertile females (≥ 3) \times Male tarsus length	-9.91	4.13	-2.40	0.018
(b) Duration of male average incubation bouts (min, $N = 162$):				
# fertile female (1)	16.17	9.30	1.74	0.084
# fertile females (2)	26.29	17.28	1.52	0.130
# fertile females (≥ 3)	24.49	18.05	1.36	0.177
Male tarsus length	0.22	0.22	0.96	0.338
# fertile females (1) \times Male tarsus length	-0.60	0.35	-1.69	0.092
# fertile females (2) \times Male tarsus length	-0.99	0.66	-1.49	0.138
# fertile females (≥ 3) \times Male tarsus length	-0.94	0.69	-1.37	0.172
(c) Duration of male average recess periods (min, $N = 166$):				
# fertile females (1)	5.05	3.28	1.54	0.125
# fertile females (2)	-16.82	6.10	-2.76	0.007
# fertile females (≥ 3)	-13.69	6.49	-2.11	0.037
Male tarsus length	-0.03	0.08	-0.37	0.712
Recording time (pm)	0.28	0.09	3.11	0.002
# fertile female (1) \times Male tarsus length	-0.20	0.12	-1.59	0.115
# fertile females (2) \times Male tarsus length	0.65	0.23	2.79	0.006
# fertile females (≥ 3) \times Male tarsus length	0.51	0.25	2.06	0.041

(d) Female incubation attendance (min/h, $N = 149$):

# fertile female (1)	-8.16	63.98	-0.13	0.899
# fertile females (2)	-209.00	136.89	-1.53	0.130
# fertile females (≥ 3)	-217.32	108.57	-2.00	0.048
Male tarsus length	-1.34	1.53	-0.88	0.381
Recording time (pm)	1.09	1.83	0.60	0.550
Laying date	-0.42	0.19	-2.21	0.029
# fertile females (1) \times Male tarsus length	0.13	2.43	0.05	0.957
# fertile females (2) \times Male tarsus length	8.01	5.25	1.53	0.130
# fertile females (≥ 3) \times Male tarsus length	8.08	4.13	1.96	0.053

Table 4.2. Summary of a linear mixed model testing whether the incubation attendance (min/h, $N = 167$) of male hair-crested drongos was affected by male quality (tarsus length), the number of fertile females in the annulus between the concentric circles radii of 216 and 570 meter and their interactions. Number of fertile females for each male in the annulus was grouped into four levels: 0 to 1, 2 to 3, 4 to 5, and at least 6 fertile females, respectively.

Fixed effects	Estimate s	SE	<i>t</i> -valu e	<i>p</i> -valu e
# fertile females (2-3)	72.49	65.16	1.11	0.268
# fertile females (4-5)	-47.28	81.72	-0.58	0.564
# fertile females (≥ 6)	-10.89	169.7 1	-0.06	0.949
Male tarsus length	0.50	1.55	0.32	0.747
Recording time (pm)	-2.97	1.73	-1.72	0.089
# fertile females (2-3) \times Male tarsus length	-2.70	2.48	-1.09	0.278
# fertile females (4-5) \times Male tarsus length	1.93	3.11	0.62	0.536
# fertile females (≥ 6) \times Male tarsus length	0.37	6.42	0.06	0.955

Table 4.3. Summary of a linear mixed model testing whether female incubation attendance by 149 hair-crested drongos was influenced by the incubation absence of their partners considering the influence of their social male's/partners' quality (tarsus length) and the number of fertile females within 216 meters.

Fixed effects	Estimates	SE	<i>t</i> -value	<i>p</i> -value
Male absence	0.79	0.05	16.60	< 0.001
# fertile female (1)	-1.35	1.18	-1.14	0.258
# fertile females (2)	2.03	1.79	1.13	0.259
# fertile females (≥ 3)	1.03	2.15	0.48	0.633
Temperature	-0.76	0.23	-3.36	0.001
Recording time (pm)	-1.23	1.07	-1.15	0.252

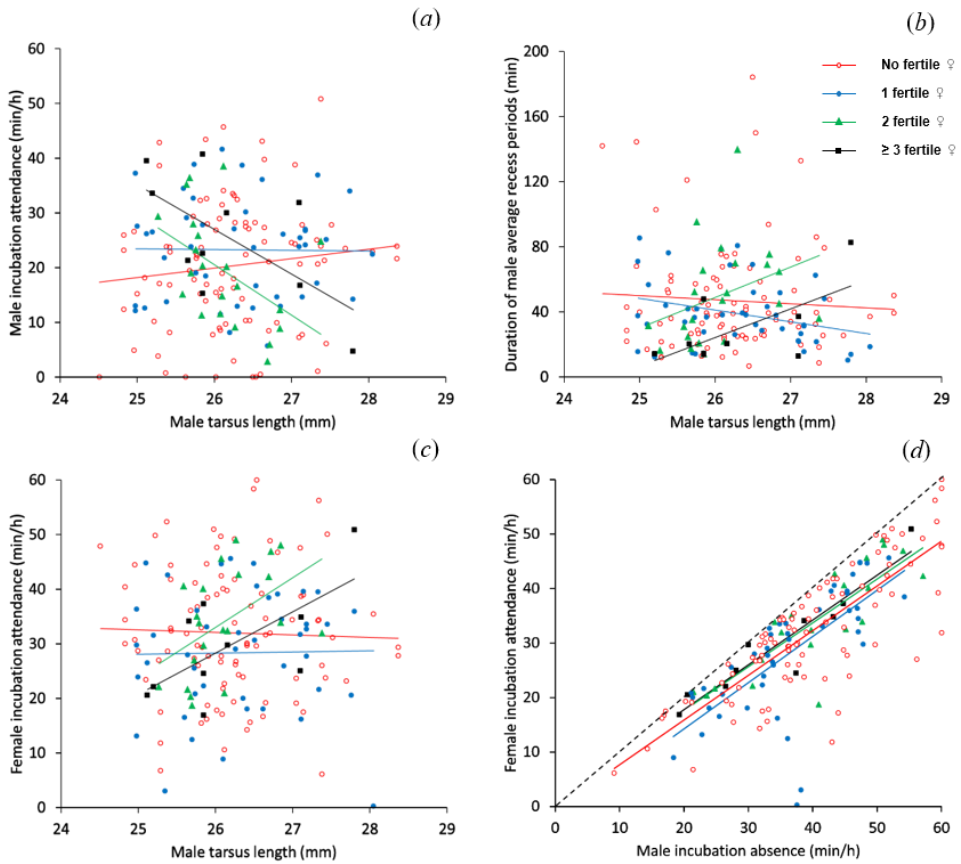


Figure 4.1. The influence of male quality (tarsus length) and number of fertile females within 216 meters on (a) male incubation attendance, (b) duration of male average recess period and (c) female incubation attendance in hair-crested drongos, and (d) the effect of male incubation absence on female incubation attendance when the number of fertile females within 216 metres from their nests varies. Lines are regression lines with the raw data. The slope of the dashed line in (d) indicates the null hypothesis that females fully compensate for a reduction in male incubation attendance.

DISCUSSION

In agreement with the “parental-mating trade-off” hypothesis, we found that high quality male hair-crested drongos incubated less by recessing longer. However, this was only the case above a threshold number of nearby fertile females. This effect was not the consequence of improved incubation by females paired with high quality males. Females compensated for 79% of the decreased incubation attendance of their partners, irrespective of male quality. Breeding pairs did not suffer from lower proportion of eggs in a nest that survived to nestlings when males incubated less and were not fully compensated by their partners. We discuss these findings and their implications below.

Paternal Care, Extra-pair Mating Opportunities and Male Quality

High quality male hair-crested drongos incubated less only when there were at least two fertile females present nearby (within 216 meters from male’s nest). This suggests that there is a threshold of available extra-pair mating opportunities for high quality males to spend more time off the nest. As males contribute to almost half of the incubation, they presumably play an important role in ensuring good conditions for development of embryos and egg protection against predators. Our result suggests that the availability of mating opportunities is important in determining the trade-off between parenting and extra-pair mating effort in males, which may explain why high quality males do not decrease their provisioning rate in many socially monogamous bird species with short breeding season (high breeding synchrony) (e.g. Komdeur et al. 2005; Limbourg et al. 2013; Grunst and Grunst 2015). In species with high breeding synchrony, the number of local fertile females is typically high during the incubation period, but low during the nestling period (Magrath and Komdeur 2003; Canal et al. 2012). Thus, the temporal conflict between parenting and mating, for males, may be lower during the nestling period (Kokko 1998; Stiver and Alonzo 2009).

For male hair-crested drongos, the trade-off between incubation and extra-pair mating was affected by the number of fertile females within 216 meters, not in the area between 216 and 570 meters. 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 from close neighbours and the probability of obtaining extra-pair paternity decreases with distance (Petrie and Kempenaers 1998; Pedersen et al. 2006; Canal et al. 2012). A recent study on the extra-territorial forays of blue tits (*Cyanistes caeruleus*) revealed that males were more likely to

visit direct neighbouring females than females present two territories away during the extra-pair mating period (Schlicht et al. 2015). Also in the hair-crested drongos, the accessible extra-pair mating opportunities for males are, to a large extent, restricted to their close neighbours. The average distance between two nearest nest trees is 87.5 ± 5.9 meters (mean \pm SE, $N = 123$). Therefore, males who seek extra-pair copulations further than 216 meters away have to cross other territories and have a higher chance of being discovered and attacked by other territory owners.

When more extra-pair mating opportunities were available, incubation attendance of male hair-crested drongos was negatively correlated with their quality as measured by tarsus length. This is likely due to the higher chance of obtaining extra-pair fertilizations for males with longer tarsi. In male hair-crested drongos, extra-pair males had longer tarsi than the within-pair males they cuckolded or males who did not get extra-pair paternity. Similar relationships were also found in other studies (blue tit: Kempenaers et al. 1997; red bishop: Friedl and Klumpp 2002; pied flycatcher: Canal et al. 2011, but see Savi's warblers: Neto et al. 2010). In hair-crested drongos, males who have longer tarsi are also heavier and tend to have longer bill-head (Pearson's correlation coefficient, body weight: $r = 0.240$, $p = 0.004$; bill-head length: $r = 0.155$, $p = 0.065$, $N = 143$). 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). From the other side, as morphological size is to a large extent heritable (e.g. Henrik 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. 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.

High quality male hair-crested drongos with more extra-pair mating opportunities recessed longer in-between incubation bouts, but did not incubate shorter in each bout. This is consistent with the idea that such males alternate incubation bouts with extra-territorial forays. A similar pattern, but without considering the influence of male quality, was documented for colonial fairy martins (*Hirundo ariel*) where male incubation attendance decreased with an increasing proportion of fertile females in the colony, which resulted primarily from recessing longer, but not from shorter incubation bouts (Magrath and Elgar 1997). In hair-crested drongos, the duration of incubation bouts was repeatable in

both males and females. Therefore, males may also show behavioural consistency with regarding to the duration of incubation bouts even when they have more extra-pair mating opportunities, although repeatability is much lower for males than for females. Instead of shortening the duration of incubation bouts, males increased the duration of recess periods. Males who recess longer may have a higher chance of gaining extra-pair copulations. A study on the extra-territorial movements of common yellow throats (*Geothlypis trichas*) showed that males who intruded into their neighbour's territories with fertile female owners behaved covertly and never sang during intrusions (Pedersen et al. 2006). Similar studies on song sparrows (*Melospiza melodia*) and Seychelles warblers (*Acrocephalus sechellensis*) showed that intruding males were always chased away if they were detected by the territory owners (Komdeur et al. 1999; Akçay et al. 2012). Both studies suggest that males may have to stay cryptic and wait for the proper time to engage in extra-pair copulations during intrusions. However, further studies are needed to test this idea by tracking the movements of male hair-crested drongos during the incubation period.

Female Compensation

Incubation attendance of female hair-crested drongos was not affected by their partner's quality when extra-pair mating opportunities were rare. This indicates no support for the "positive differential allocation" hypothesis, which predicts that females increase their breeding investment when paired with high quality males (Burley 1986; Sheldon 2000). However, females did compensate for the lack of male investment, but this compensation was not affected by partners' quality or by the number of nearby fertile females. Furthermore, presumably due to constraints on self-maintenance, females compensated for only 79% 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). Interestingly, although reduced male incubation attendance was not fully compensated by their partners, male incubation attendance had no significant influence on the proportion of eggs in a nest that survived to nestlings. This result suggests that reduced male incubation attendance may not lead to a reduced hatching success or an increased predation rate of eggs.

Conclusion

This study demonstrates how extra-pair mating opportunities for males interact

with male quality in determining paternal care in a bi-parental species. The adaptive response to this trade-off for males is dependent on both male quality and number of nearby fertile females. Moreover, this result sheds light on the mechanism behind improved female parental care if females mate with high quality partners, which appears to be a response to the reduced time of high quality males spend on incubating, rather than to the quality of the male itself. Our results highlight the need for quantifying available mating opportunities in investigating how individual quality influence males trading off parental care and pursuing additional matings, and improves our understanding of how and why females' adjust parental care to the quality of their partners.

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