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Original Article

Breeding experience, but not mate retention, determines the breeding performance in a passerine bird

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Individuals that retain their former partners often perform better than conspecifics that switch partners. This may be due to high-quality individuals being more faithful to their partners and more productive. Investigations of the fitness benefits of mate retention that also control for potential confounding effects of individuals are scarce. We studied the influence of mate retention and breeding experience on breeding performance of the hair-crested drongo (*Dicrurus hottentottus*) by carrying out both cross-sectional and longitudinal analyses. Pairs with longer pair-bond duration did not fledge more young or fledglings of better body condition nor did they produce more or better fledglings than newly formed pairs consisting of at least 1 experienced breeder, that is, individuals that had bred before. Individuals produced fewer fledglings when they were paired with an inexperienced breeder, especially when females were paired with inexperienced males. Although clutch size was not affected by mate retention or breeding experience, pairs consisting of inexperienced breeder(s) had a relatively higher predation rate of eggs and/or nestlings because they may be less effective in nest defense. The onset of breeding was advanced in the year following mate retention, but not in the second year thereafter, when pairs still remained together. Furthermore, only the breeding experience of the male determined the onset of breeding: Pairs consisting of inexperienced males bred later in the season. Our results suggest that breeding experience, and particularly the breeding experience of the male, but not mate retention, is important in determining the breeding performance of hair-crested drongos.

Key words: **breeding experience, breeding performance, fledglings, laying date, mate retention, pair-bond duration.**

INTRODUCTION

Social monogamy is the predominant mating system in birds (Lack 1968; Bennett and Owens 2002; Griffith et al. 2002). Breeding pairs may remain together for 1 breeding season (seasonal monogamy) or continuously for several years (perennial monogamy) (Smith 1978). Breeding with the same mate repeatedly (perennial pair) may be favorable, because finding or fighting for a new mate and/or territory can be costly (Ens et al. 1996), and reproductive success may decrease after changing mates (Hatch and Westneat 2007; Gabriel and Black 2013). Most studies, comparing the mean breeding performance of pairs that breed either with the same or a different mate than the previous year, show that perennial pairs have a higher reproductive success than newly formed pairs (Perrins

and McCleery 1985; Black and Hulme 1996; Hatch and Westneat 2008, but see Pampus et al. 2005). However, in these studies, perennial pairs may consist of more individuals of high quality (older and more experienced) relative to newly formed pairs, which may also contribute to higher reproductive success (Black and Hulme 1996; van de Pol et al. 2006). The poor breeding performance of newly formed pairs may not be a consequence of partner switching, but a consequence of newly formed pairs consisting of young, inexperienced, low-quality birds, which have little chance of staying together and/or being less experienced in breeding (Ens et al. 1996; Hatch and Westneat 2007). Yet, this potentially confounding effect needs to be controlled for in the analyses of mate retention. This problem can be solved by comparing the breeding performance of individuals across 2 consecutive years, which either did or did not switch breeding partners in the second year (Ens et al. 1996; Llambías et al. 2008). However, investigations of the

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fitness benefit of mate retention using longitudinal analysis are rare (Llambías et al. 2008).

In this study, we investigated the influence of mate retention and breeding experience on breeding performance (for this study, this includes laying date, clutch size, survival of eggs to fledglings, number of fledglings, and body condition of the fledgling) of the hair-crested drongo (*Dicrurus hottentottus*), a migratory passerine, by carrying out both cross-sectional and longitudinal analyses. Individuals in this species form long-term socially monogamous pair-bonds and are highly faithful to their previous season's mate (Rocamora and Yeatman-Berthelot 2009). They also show extreme site-fidelity to their previous territories in that individuals build nests in trees in the vicinity of their previous nest tree, reuse the same nest tree, or sometimes even using the same tree branch. These characteristics allowed us to focus on the same individuals over consecutive years and examine the potential mechanisms that influence mate retention and breeding experience on breeding performance. First, we explored whether mate retention and breeding experience influenced the number of fledglings produced. Second, to determine whether perennial pairs performed better than newly formed pairs and whether individuals that had breeding experience performed better than first-time breeders, we compared differences in laying date, clutch size, and the proportion of eggs in the nest that survived to fledging. Third, we investigated the influence of pair-bond duration, that is, the number of years that the same individuals bred together, on both laying date and number of fledglings. Fourth, we examined the effects of mate retention and breeding experience on body condition of fledglings.

MATERIALS AND METHODS

Study site and species

We conducted this study at Dongzhai National Nature Reserve in the Dabieshan Mountains (Dongzhai, Henan Province, central China, 31.95°N, 114.25°E, elevation 100–840 m; for more information on the study site, see Li et al. 2009). The size of the study area is approximately 400 ha.

The hair-crested drongo is a medium-sized passerine with males being slightly larger and brighter than females (Chen and Luo 1998). Birds, which breed in central and southern China, are traditionally thought to overwinter in Indochina (Rocamora and Yeatman-Berthelot 2009). Hair-crested drongos arrive in late April on our study site and leave before the middle of November (Gao et al. 2006). They are highly faithful to their mates. In 2011–2014, 87.8% of the breeding pairs ($N = 98$) kept pair-bonds if both male and female returned. Adults also have high breeding site fidelity with 89.5% of males ($N = 143$) and 79.5% of females ($N = 146$) occupying the same territory as they did in the previous year. The average dispersal distance of those that moved to new territories was 131.9 ± 22.3 m (mean ± standard error [SE]) for males ($N = 12$) and 154.2 ± 28.6 m (mean ± SE) for females ($N = 29$; Lv L, unpublished data). Both parents participate equally in all breeding activities, including nest building, incubation, and feeding of offspring (Chen and Luo 1998). Clutch size varies from 3 to 5 eggs (3.93 ± 0.30, mean ± SE, $N = 276$) with a high hatching rate of 92.8% ($N = 484$; Lv L, unpublished data). Due to an abundance of food, no nestlings died of starvation if they did not fall victim to predation (2008–2014: 593 hatchlings from 166 nests of 105 males and 109 females were monitored until fledging; Lv L, unpublished data). The main reason for unsuccessful breeding is nest predation

by, for example, Eurasian jays (*Garrulus glandarius*) and besra sparrow hawks (*Accipiter virgatus*) (Lv L, personal observation). As both parents defend their nests aggressively against predators over the course of the breeding season, 66.2% of nests produce at least 1 fledgling ($N = 464$).

Data collection

Data collection took place from 2008 to 2014. Every year we located nests by checking the trees that had been used in previous years or by systematically searching the forest for nests. Adult drongos were captured by mist-netting either during incubation or the nestling-provisioning period in close proximity to nest trees. Birds were marked individually with a metal ring and a unique combination of color rings. None of the individuals we caught abandoned their nest after release. Sex of the adults was determined by the size of the brood patch, which is distinctively larger in females. The identity of parents at each nest was determined either through direct observation with a telescope or binoculars or indirectly through video recordings. The latter were taken by placing high-resolution cameras (Sony HDR-160E or Sony HDR-260E) at approximately 20 m from the nest. In cases where only 1 parent was ringed, we deduced the sex of the unringed parent by the sex of its ringed partner. Nests were checked every 1–3 days to determine laying date, clutch size, hatching date, number of nestlings, and number of fledglings. Nestlings were weighed to the nearest 0.1 g when they were between 14 and 18 days old (4 to 0 days before fledging) by using a digital balance. Each nestling was then ringed with a metal ring only.

In 2008 and 2009, the breeding performance of 38 and 37 pairs, respectively, of which 19.7% and 14.9% were ringed, was monitored. From 2010 to 2014, we studied the population more intensely with on average 76 pairs monitored each year and on average 77.5% of parents ringed. We presume that almost all nests present in the area were found over those years because we searched for nests extensively and 72.5% of nests ($N = 414$) were found before the onset of egg laying. Thus, from 2011 onwards, we consider all birds without rings to be recruited inexperienced first-time breeders due to 1) our study area being quite large and covering around 80 territories, 2) almost all nests having been located and most of adults having been ringed from 2010 onward, and 3) adult hair-crested drongos having high breeding site fidelity and small breeding dispersal distances.

Mating status and breeding experience classes

According to the ringing records, breeding pairs were classified into 5 types on the basis of whether each respective partner had previous breeding experience and whether pair partners had bred together in the past. Thus, pairs were categorized as 1) perennial pairs of mates retained (PP); 2) newly formed pairs consisting of an experienced male and an inexperienced female (EMIF); 3) newly formed pairs consisting of an inexperienced male and an experienced female (IMEF); 4) newly formed pairs consisting of 2 experienced breeders (EMEF); and 5) newly formed pairs consisting of 2 inexperienced breeders (IMIF). To study the effects of mate retention and breeding experience on breeding performance, 240 breeding attempts by 114 males and 122 females were examined. To avoid the potential influence of age on reproductive success (Reed et al. 2008; Nussey et al. 2013), only the first 2 consecutive years of perennial pairs were used in comparisons between pair categories. For newly formed breeding pairs consisting of an experienced

and an inexperienced breeder in a given year $X + 1$, we considered only year $X + 1$ in our analysis in cases in which any of the partners gained breeding experience (for the inexperienced breeder in year X) and paired with another inexperienced breeder in year $X + 2$ year to avoid pseudoreplication.

Data analyses

Because most nestlings (76.0%, $\mathcal{N} = 233$) were measured on days 15 and 16 after hatching, the total number of fledglings was equal to the number of nestlings sampled in the nest. At this point, nestlings already started to move out of the open nest and could be found standing on the nest branch or branches nearby. In order to control for annual variation, we standardized number of fledglings (total number of fledglings produced in 1 breeding season), clutch size, and proportion of eggs in the nest that survived to fledging (restricted to first clutches), respectively, by subtracting the mean of each parameter in any given year and subsequently dividing the difference by the standard deviation of that year. We also standardized laying date of each nest by subtracting the date of the first egg laid in any given year. As nestling body mass is correlated with age (Pearson's correlation coefficient $r = 0.153$, $P < 0.001$, $\mathcal{N} = 699$), we use the residuals from a regression of mass on age as true body mass of fledglings. The corrected body mass then was used as a measure of body condition at fledging (Magrath 1991; Naef-Daenzer et al. 2001).

To investigate the influence of mate retention and breeding experience on number of fledglings, we carried out both cross-sectional and longitudinal analyses. In the cross-sectional analyses, we carried out a Kruskal–Wallis analysis of variance (Anova) on ranks to compare the relative number of young fledged in all pair categories (PP, EMIF, IMEF, and EMEF), apart from the IMIF pair category, in a given year X. This was either the year before mate retention or the year before new pair-bonds formed. We then compared the relative number of fledglings in all 5 pair categories in year $X + 1$, that is, the first year of mate retention or the year of new pair formation. In the longitudinal analyses, we tested the relative number of fledglings produced by individuals before and when mates were retained or new pair-bonds formed over 2 consecutive years (year X and year $X + 1$) with Wilcoxon signed-rank tests within the pair categories PP, EMIF, and IMIF, respectively. For EMEF pairs, we performed individual Wilcoxon signed-rank tests depending on whether individuals newly paired with 1) experienced males or 2) experienced females in year $X + 1$ due to the fact that those experienced males or females came from different breeding pairs in year X or years prior to X. For newly formed pairs that consisted of an experienced and an inexperienced breeder (EMIF and IMEF) in year $X + 1$, and which remained bonded in year $X + 2$, we tested whether they produced more fledglings in year $X + 2$ than they did in year $X + 1$.

Following the procedures for testing mate retention and breeding experience on number of fledglings described above, we investigated how mate retention and breeding experience affected 1) laying dates, 2) clutch size, and 3) proportion of eggs in a nest that survived to fledging, respectively. All 3 of these breeding parameters were restricted to first clutches per breeding season only because hair-crested drongos generally are single brooded and only 18.3% of the breeding pairs ($\mathcal{N} = 120$) lay replacement clutches after their first clutch fails.

To investigate the effect of pair-bond duration on either laying date or number of fledglings, we employed linear mixed models with pair identity as a random factor, years as a covariant factor, and number of years retained with the same mate as a fixed factor. The denominator degrees of freedom in the analysis were obtained by using the "KRmodcomp" function from the R-package "pbkrtest" because our data were unbalanced (Kenward and Roger 1997; Halekoh and Højsgaard 2012).

To test the influence of mate retention and breeding experience on body condition of fledglings, we carried out linear mixed models with corrected body mass as the response variable. Nest ID was used as a random factor and pair category was used as a fixed factor. The effect of pair-bond duration on body condition of fledglings was also analyzed by fitting a linear mixed model with years as a covariant factor and number of years retained with the same mate as a fixed factor. Random effects were included for nest ID nested within breeding pair ID to control for covariances among breeding pairs and breeding attempts of each pair in different years. The denominator degrees of freedom in the analysis were obtained by using the "KRmodcomp" function whenever data were unbalanced.

All linear mixed models were performed in R.3.1.1 (R Core Team 2012), using the package lme4 (Bates et al. 2014). All the other analyses were performed using SPSS 19.0 (SPSS Inc., Chicago, IL). Parametric analyses were employed whenever data distribution fulfilled the normality assumptions (Shapiro–Wilks test); otherwise, nonparametric analyses were applied. All tests are given 2-tailed and α-level was set to $P < 0.05$.

RESULTS

Influence of mate retention and breeding experience on breeding performance

Number of fledglings

We found no significant difference in the number of fledglings produced by each of the 4 pair categories in year X (all except IMIF; Figure 1a). In year $X + 1$ that pairs remained together or formed new pair-bonds, pairs consisting of 2 inexperienced breeders (IMIF pairs) produced fewer fledglings than pair categories consisting of experienced males (PP, EMIF, and EMEF pairs; Mann–Whitney U-tests, all P values < 0.05; Figure 1a). In contrast, experienced females fledged more young only when they were paired with experienced males in comparison with females that paired with inexperienced males (Mann–Whitney U-test: $\mathcal{Z} = -2.004$; $P = 0.047$; Figure 1a). When comparing 2 consecutive years within each of the 4 pair categories (all except IMIF), experienced females tended to produce fewer fledglings when paired with inexperienced males relative to how many they produced in the previous year (Wilcoxon signed-rank test: $\mathcal{Z} = -1.680$, $P = 0.093$; Figure 1a). In contrast, experienced males tended to fledge more young than in the previous year if paired with experienced females in year $X + 1$ (Wilcoxon signed-rank test: $\mathcal{Z} = -1.660$, $P = 0.097$). Moreover, EMIF and IMEF pairs that retained their pair-bonds in year $X + 2$ produced more fledglings than they did in year $X + 1$, when bonds were newly formed (although this was marginally nonsignificant in IMEF pairs: Wilcoxon signed-rank test, EMIF: $\mathcal{Z} = -2.045$, $P = 0.041$; IMEF: $\mathcal{Z} = -1.753$, $P = 0.080$; Figure 1b).

Laying date

With respect to the onset of breeding, pairs consisting of 2 inexperienced breeders (IMIF pairs) bred later than pairs consisting
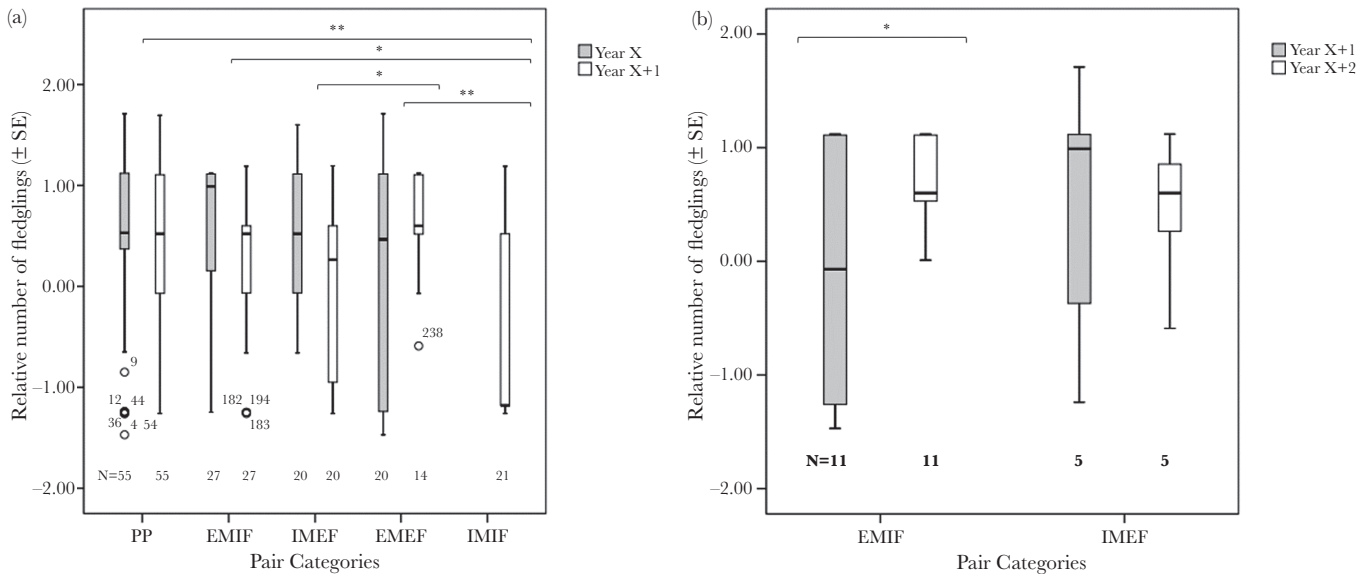
Figure 1
Influence of mate retention and breeding experience on the number of fledglings in hair-crested drongos: (a) relative number of fledglings (for definition, see below) produced by each pair category before (year *X*, filled bars) and the year of (year *X* + 1, open bars) mate retention or new pair-bonds formed; (b) relative number of young fledged in pairs that newly formed in year *X* + 1 (filled bars) consisting an experienced and an inexperienced breeder, and in year *X* + 2 (open bars) when they kept that bond. We use relative number of fledglings through standardizing the total number of fledglings produced by 1 breeding pair in 1 breeding season by subtracting the mean number of fledglings produced throughout the population of any given year and subsequently dividing the difference by the standard deviation of that year. Pair categories: PP, perennial pairs of mates retained; EMIF, newly formed pairs consisting of an experienced male and an inexperienced female; IMEF, newly formed pairs consisting of an inexperienced male and an experienced female; EMEF, newly formed pairs consisting of 2 experienced breeders; IMIF, newly formed pairs consisting of 2 inexperienced breeders. Boxplots show medians and quartiles, whiskers 10th and 90th percentiles, and circles 5th and 95th percentiles. Sample sizes are given above the *x* axis. *$P < 0.05$, **$P < 0.01$.

of experienced males (PP, EMIF, and EMEF pairs). Furthermore, pairs consisting of inexperienced males and experienced females (IMEF pairs) bred later than perennial pairs (PP) (Mann–Whitney *U*-test, all *P* values < 0.05; Figure 2). When comparing the laying date between years, the onset of breeding was advanced when mates were retained, but was delayed when females formed new pair-bonds with inexperienced males (Wilcoxon signed-rank test or *t*-test, respectively, both *P* values < 0.05; Figure 2).

Clutch size and the proportion of eggs in the nest that survived to fledging

Clutch size did not differ between or within pair categories (Kruskal–Wallis Anova or Wilcoxon signed-rank tests, respectively, all *P* values > 0.05). However, the proportion of eggs in the nest that survived to fledging in IMIF pairs was lower than in PP pairs and tended to be lower than in EMIF pairs (Mann–Whitney *U*-test, PP: $\mathcal{Z} = -2.572$, $P = 0.010$; EMIF: $\mathcal{Z} = -1.902$, $P = 0.057$; Figure 3a). In 2 consecutive years, the proportion of eggs in the nest that survived to fledging in IMEF pairs tended to decrease (Wilcoxon signed-rank test: $\mathcal{Z} = -1.792$, $P = 0.073$; Figure 3a). In contrast, the proportion of eggs in the nest that survived to fledging tended to increase both in EMIF and IMEF pairs when mates were retained in year *X* + 2 (Wilcoxon signed-rank test, EMIF: $\mathcal{Z} = -1.600$, $P = 0.110$; IMEF: $\mathcal{Z} = -1.753$, $P = 0.080$; Figure 3b).

Influence of pair-bond duration on the onset of breeding and number of fledglings

Over the study period, the average length of pair-bond duration was 2.69 ± 0.13 years (mean ± SE, $\mathcal{N} = 61$, range 2–6 years). Pair-bond duration had no effect on laying date or number of fledglings

produced (linear mixed model, laying date: $F = 1.01$, degrees of freedom [df] = 96.8, $P = 0.218$; number of fledglings: $F = 0.66$, df = 59.3, $P = 0.502$).

Influence of mate retention and breeding experience on body condition of fledglings

The body condition of fledglings did not differ between pair categories in year *X* (linear mixed model, $F = 0.18$, df = 83.7, $P = 0.910$) and in year *X* + 1 (linear mixed model, $F = 0.18$, df = 76.0, $P = 0.948$) when mates were retained or new pair-bonds were formed. Pair-bond duration also had no effect on the body condition of fledglings (linear mixed model, $F = 0.20$, df = 26.4, $P = 0.938$).

DISCUSSION

Influence of mate retention and breeding experience on reproductive success

Mate retention is the most common mating strategy in hair-crested drongos. If both mates survived to the next breeding season, only 13.1% of the total breeding pairs ($\mathcal{N} = 107$) split up to breed with a new partner. It has been suggested for other species that mate retention saves time and energy spent finding a new mate, which instead can be spent on reproduction (Black and Hulme 1996; Adkins-Regan and Tomaszycki 2007). Furthermore, by retaining one's mate, the coordination of reproductive behaviors such as behavioral synchrony and compatibility between partners may be improved, as mates are already familiar with one another (Griggio and Hoi 2011; van Rooij and Griffith 2013, but see Gabriel and Black 2013). This, in turn, contributes to a better breeding performance compared with newly formed pairs (Choudhury et al. 1996; Spoon et al. 2006, 2007, but see Lewis et al. 2009). In our study,
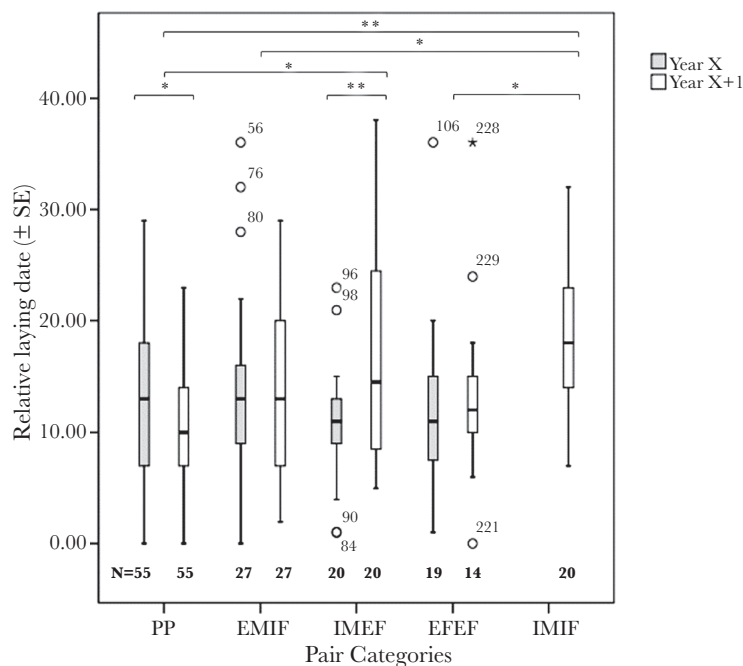
Figure 2
Relative laying date of each pair category before (year *X*, filled bars) and the year of (year *X* + 1, open bars) mate retention or formation of new pairs in hair-crested drongos. Relative laying date was used through standardizing laying date by subtracting the date of the first eggs laid in that specific year. Boxplots show medians and quartiles, whiskers 10th and 90th percentiles, and circles 5th and 95th percentiles. Sample sizes are indicated above the *x* axis. *$P < 0.05$, **$P < 0.01$.

however, hair-crested drongos did not perform better after mate retention in terms of reproductive success.

Hair-crested drongo pairs that remained together in the following year did not fledged more young than they did in the first year they bred together, which is consistent with other studies (McDonald et al. 2004; Pampus et al. 2005; Llambías et al. 2008). Furthermore, perennial pairs did not produce more fledglings than newly formed pairs, except if newly formed pairs consisted of 2 inexperienced breeders (IMIF pairs). Meanwhile, newly formed pairs that consisted of an experienced and an inexperienced breeder (IMEF and EMIF pairs, respectively) fledged more young in the following year if they remained together. However, this may be due to the cumulative breeding experience of the originally inexperienced breeders (Pampus et al. 2005; Hatch and Westneat 2008). Both experienced and inexperienced females that paired up with experienced males produced more fledglings than if they formed bonds with inexperienced males. This was also true in the longitudinal analysis, where females tended to fledge fewer young relative to the previous year, after they engaged in a new bond with an inexperienced male. This implies that the breeding experience of the male is critical in determining reproductive success. Inexperienced males can improve their prospective breeding performance during their first breeding experience. The breeding experience of females also influences the breeding performance of the pair with inexperienced females causing a reduced reproductive success, but the effect is much weaker than in the case of inexperienced males (Figure 1). The fact that there was no difference in the number of fledglings between pair categories before switching mates provides further evidence for the influence of breeding experience on breeding performance. In this species, most mate switches occur when a former mate die. Thus, most adults of these pair categories are experienced breeders before switching mates. Meanwhile, body condition of fledglings was not affected by mate retention or breeding experience, which suggested that, although the number of fledglings was different in some pair

categories (see above), the quality of fledglings was not different between pair categories. Therefore, both our cross-sectional and longitudinal results support the idea that breeding experience, and particularly the breeding experience of males, influences reproductive success in hair-crested drongos.

Influence of mate retention and breeding experience on the onset of breeding

The hair-crested drongo is a long-distance migrant with a relatively long period of postfledging parental care, which lasts for approximately 50 days (Rocamora and Yeatman-Berthelot 2009). Early breeding might improve reproductive success because offspring fledged earlier in the season will have more time to gain mass and increase their foraging skills before the fall migration. Additionally, parents of earlier clutches may have more chances to produce a successful replacement clutch in cases where the first clutch fails (Dhondt 1987; Naef-Daenzer et al. 2001; Becker and Zhang 2010). In our study, the laying date was advanced in the first year of mate retention, which is consistent with other studies (Fowler 1995; Black and Hulme 1996; Llambías et al. 2008). However, the laying date was not influenced by longer-term pair-bond duration. As we only used the first 2 consecutive years of perennial pairs to test whether the laying date changed when mates were retained relative to the year prior, it suggests that mate retention will advance the onset of breeding in the first year of mate retention, but not from the second year onwards.

Perennial pairs bred earlier than newly formed pairs, which matches patterns found in many other studies (Rowley 1983; Black and Hulme 1996; Pampus et al. 2005; Hatch and Westneat 2008, but see Llambías et al. 2008). However, contrary to many other studies where timing of breeding hinges on females (de Steven 1978; Hipfner et al. 1997; González-Solís et al. 2004; de Forest and Gaston 2014), we found that the onset of breeding of newly formed pairs depended on the breeding experience
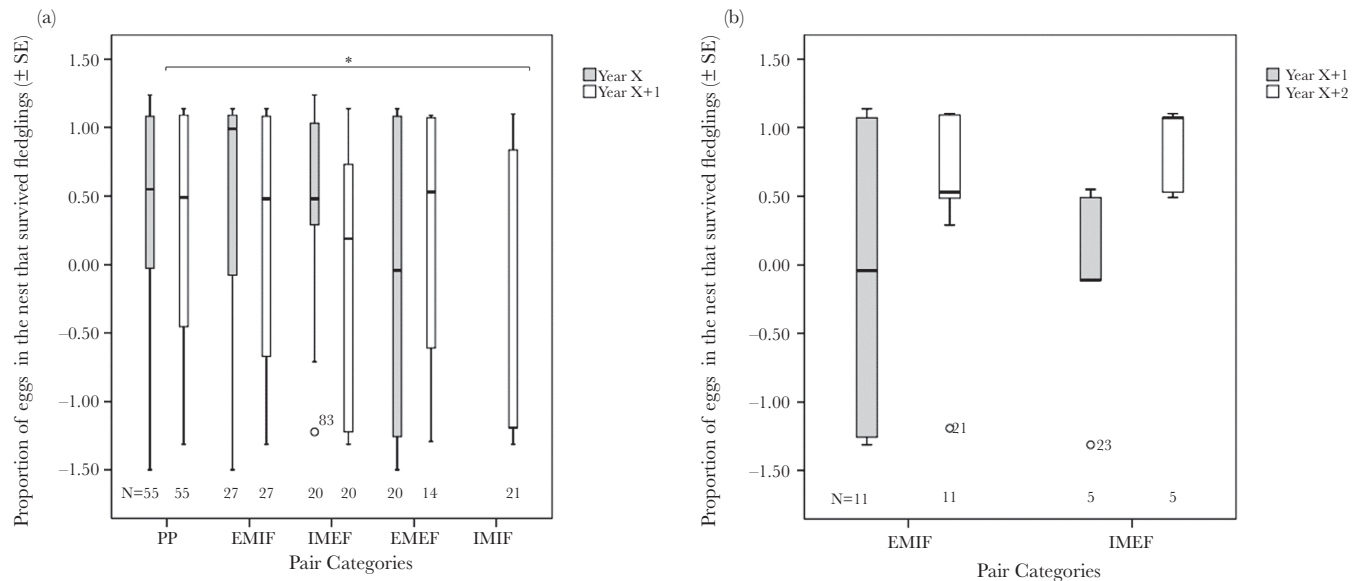
Figure 3

Influence of mate retention and breeding experience on the proportion of eggs in the nest that survived to fledging in hair-crested drongos: (a) proportion of eggs surviving to fledging in each pair category before (year X, filled bars) and the year of (year $X + 1$, open bars) mate retained or pairs newly formed; (b) proportion of eggs in the nest that survived to fledging in pairs that newly formed in year $X + 1$ (filled bars) consisting an experienced and an inexperienced breeder, and in year $X + 2$ (open bars) when they remained paired. The proportion of eggs in the nest that survived to fledging was restricted to the first clutch and was standardized by subtracting the mean proportion of eggs in the nest that survived to fledging throughout population of any given year and subsequently dividing the difference by the standard deviation of that year. Boxplots show medians and quartiles, whiskers 10th and 90th percentiles, and circles 5th and 95th percentiles. Sample sizes are indicated above the x axis. *$P < 0.05$.

of males. Newly formed pairs that consisted of inexperienced males initiated breeding attempts later than did pairs that consisted of experienced males, regardless of the breeding experience of females. Furthermore, females that paired up with inexperienced males bred later than they did in the previous year. Laying date, however, was not delayed if experienced males paired with inexperienced females. Younger and inexperienced males usually arrive later because they may be in poorer physical condition and migrate more slowly relative to older and experienced males (Lundberg and Alatalo 1992; Dittmann and Becker 2003; Mitrus 2007). Hair-crested drongos behave like many other passerines in that males establish the territory and attract females. Young and inexperienced males that attempt to breed for the first time may need more time to find suitable females and establish territories to breed since they suffer from aggression and competition of early-arriving older and experienced males (Hill 1989). However, this may not be the case for young and inexperienced female hair-crested drongos because widowed experienced males usually retain their former territories and engage in attracting first-time breeding females. Thus, the arrival date and the time needed for establishing a territory might be the reason why the breeding age and experience of males, but not females, matters in hair-crested drongos. Future studies with detailed information of arrival date and pair formation date will offer a good opportunity to investigate the male phenotypic contribution to laying date, a trait classically attributed to the female.

Influence of mate retention and breeding experience on other breeding performance parameters

The size of the first clutch produced in any given year was not influenced by mate retention or breeding experience. The proportion of

eggs in the nest that survived to fledging was similar for perennial pairs and newly formed pairs consisting of at least 1 experienced breeder. However, the proportion of eggs that survived to fledging tended to be lower when females paired up with inexperienced males. In contrast, the proportion of eggs in the nest that survived to fledging in newly formed pairs consisting of an experienced and an inexperience breeder (EMIF and IMEF pairs) tended to increase when mates were retained in the following year. This implies that the cumulative breeding experience of inexperienced breeders from the first-time breeding leads to a higher reproductive success. Hatching success is high in hair-crested drongos and the main reason for nest failure is predation on eggs and/or nestlings. This may well be the reason for a lower reproductive success of pairs consisting of inexperienced breeders, as inexperienced breeders are usually less skilled in protecting eggs or nestlings from predators (Forslund and Pärt 1995). Furthermore, male hair-crested drongos are slightly larger than females and take more responsibility in defending nests from predators (Rocamora and Yeatman-Berthelot 2009); therefore, rendering the breeding age and experience of males is more important in determining the reproductive success.

Replacement clutches may reduce the negative effect of nest predation on breeding performance (Arnold 1993; Amat et al. 1999; Hipfner et al. 1999; Arnold et al. 2010). In our study, the 3 breeding pairs consisting of 2 experienced breeders, successfully renested after the failure of their first clutches and produced at least 1 fledgling. In contrast, of the 11 breeding pairs consisting of 2 inexperienced breeders, only 2 produced replacement clutches after failure of first clutches, and only 1 of those successfully fledged young from the replacement clutch. Fledging young from replacement clutches might be the reason why pairs consisting of 2 experienced breeders produced more fledglings than those pairs consisting of 2 inexperienced breeders.

Influence of pair-bond duration on breeding performance

Several studies have shown that individuals optimize the onset of breeding and breeding performance through repeated breeding attempts with the same partner (Bradley et al. 1995; van de Pol et al. 2006; Naves et al. 2007; Nisbet and Dann 2009, but see McDonald et al. 2004). In our study, however, neither the onset of breeding nor number of fledglings were influenced by pair-bond duration. This, combined with the fact that perennial pairs and newly formed pairs of 2 experienced breeders did not differ in these 2 variables, suggests that hair-crested drongos do not benefit from mate retention in terms of breeding performance. It is interesting to note that all previous studies that reported an improved breeding performance, when pair-bonds lasted over extended periods, occurred in long-lived birds (Bradley et al. 1995; Black 2001; van de Pol et al. 2006; Naves et al. 2007; Nisbet and Dann 2009). In contrast, the average length of pair-bond duration in the hair-crested drongo was less than 3 years, which is much shorter than in previous studies. Improved breeding performance in this relatively short-lived species, which usually happened from the first year of breeding to the second year of keeping pair-bonds, may be prolonged in long-lived birds during the pair-bond and therefore show an obvious pattern of improving breeding performance.

Why might hair-crested drongos engage in mate retention although they do not improve their breeding performance?

Mate retention may be a by-product of breeding site fidelity if it results from both male and female returning to their previous breeding site (Burger 1974; Morse and Kress 1984; Cuthbert 1985; Pietz and Parmelee 1994; Ens et al. 1996; Naves et al. 2007; Bai and Severinghaus 2012, but see Bried et al. 2003; Robert and Paiva 2014). In hair-crested drongos, 92.3% of males ($N = 39$) and 71.4% of females ($N = 28$), whose initial mates of the previous year were presumed dead as they were not recorded over 2 consecutive years, reused the same breeding sites as in the previous year. This suggests that both male and female hair-crested drongos are quite faithful to their breeding sites. This, in turn, might lead to pairs breeding together again. If so, the evolution of mate retention in hair-crested drongos may not be related to fitness benefits of long-term partnerships. Nonetheless, 75% of recruited breeding birds ($N = 8$), which were ringed as fledglings, were produced by perennial pairs, whereas the rest was produced by all other pair categories combined (Lv L, unpublished data). As the total number of fledglings produced by perennial pairs was similar to the number of fledglings from all 4 other pair categories combined over the 2011–2014 period (perennial pairs: 242 fledglings; other pair categories: 224 fledglings), it suggests that fledglings from perennial pairs may have a higher chance of surviving until breeding. This, however, may also be explained by a correlation between high-quality breeding sites combined with high site fidelity. If individuals are more faithful to high-quality breeding sites compared with low-quality ones (Newton 1993; Bried and Jouventin 1999, but see Jiménez-Franco et al. 2013; Bollinger et al. 2014), it may lead to pairs in high-quality sites being more likely to remain paired. Thus, the higher survival rate of fledglings from perennial pairs may have been caused by better growth conditions of high-quality breeding sites. Only by clarifying the relationship between breeding site fidelity and mate retention, while considering the influence of breeding site quality and individual quality, can the underlying benefits and mechanisms of mate retention be uncovered.

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