Condition mediates context-dependent breeding strategies and consequences
Lyu, Lei

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Chapter 5

Do hair-crested drongos reduce prospective territory competition by dismantling their nest?

Lei Lv, Jianqiang Li, Jan Komdeur, Chang Gao, Sjouke A. Kingma, Yong Wang, and Zhengwang Zhang
Abstract

Animal species which breed seasonally usually prefer to use the same territory where they successfully produced young previously. However, intra-specific competition may be intense for those suitable territories. Therefore, it is predicted that natural selection favours behaviour of territory owners to reduce such competition. Hair-crested drongos, *Dicrurus hottentottus*, a territory faithful passerine, dismantle their nests after breeding. As most of the nests that were not dismantled remain intact till the next breeding season, we hypothesized that nest-dismantling serves a purpose of reducing territory competition from conspecifics that use the presence of a nest as a cue to select suitable territories for the next year. Here, we provide the first experimental test of this territory competition hypothesis. Our results showed that successful pairs, which usually reuse their territories in the next year, were more likely to dismantle their nests and dismantle their nests faster compared to failed breeding pairs which often moved out from their original territories. Experimentally strengthened nests that were placed in successful territories attracted prospectors and tended to result in a higher reuse rate of territories in the next year. However, the replacement rate of strengthened-nest owners in the next year was low and not higher than pairs that dismantled their nest. Furthermore, strengthened-nest owners did not initiate breeding later or produce fewer fledglings due to the potential higher territory competition. Altogether, our results partially support the territory competition hypothesis. We suggest that nest-dismantling may only be beneficial to hair-crested drongos when territory competition is very intense.
Introduction

Breeding in the same territory over consecutive years is a widespread phenomenon in the animal kingdom (Greenwood 1980; Switzer 1993; Newton 2008; Piper 2011). This kind of territory fidelity can benefit individuals because of their experience with local conditions (Beletsky and Orians 1991; Pärt 1995). Such experience consists of prior knowledge of local food resources, predator habits or predator refuges and support from familiar neighbours, which often leads to higher foraging efficiency, better breeding performance and higher survival rates (Hinde 1956; Stamps 1995; Grabowska-Zhang et al. 2012). Furthermore, the phenomenon of territory fidelity usually follows good breeding performance at a particular territory (Gavin and Bollinger 1988; Switzer 1997; Haas 1998; Robert and Paiva 2014). Individual former breeding performance can provide an indirect assessment of habitat or territory quality when habitat, predation or food conditions are temporally and spatially predictable (Boulinier and Danchin 1997; Doligez et al. 2003). Thus, the optimal strategy for animals is to remain faithful to the territory where their past reproductive success was high (Nowak and Sigmund 1993; Switzer 1993; Schmidt 2001).

Individuals that prefer to reuse a successful territory may face territory competition from conspecifics, especially when individuals use the past breeding performance of other pairs as a cue to assess the quality of the territory. There is indeed substantial evidence that prospectors, which are generally immatures, failed or non-breeders, gather information on local patch quality to select the optimal territory for the future (reviewed in Ponchon et al. 2013). Territory competition may have a large impact on the fitness of individuals not only because they may lose their preferred territories, but also in terms of time, energy expenditures and risks of injury incurred during aggression (Eason and Hannon 1994; Marler et al. 1995; Cleveland 1999). Therefore, behaviour to reduce prospective territory competition is predicted to be favoured by natural selection. Indeed, in common loons, Gavia immer, where prospecting individuals use the presence of chicks as a cue to locate good territories and usurp it in the subsequent year (Piper et al. 2000; Piper et al. 2006), the territory owners show a tendency to conceal chicks from prospecting individuals, perhaps to avoid future territory take-overs (Piper et al. 2006).

The hair-crested drongo, Dicrurus hottentottus, a insectivorous passerine distributed in East and South Asia, exhibits a unique behaviour in that most parents dismantle their nests within two weeks after breeding (Li et al. 2009). Since nests
are solidly built with mainly of fine grass stems and rootlets, it is time and energy consuming to dismantle it. However, it is unclear whether this behaviour is adaptive. A previous study proposed that nest-dismantling may reduce the possibility that conspecifics are triggered by the presence of a nest to compete for the territory in the following breeding season (territory competition hypothesis; Li et al. 2009). This is likely, because, first of all, adult drongos show high fidelity to their territories (Lv et al. 2016). Meanwhile, the nest of drongos, which is conspicuously attached to tree crotches with a limited number of leaves, is easy to locate and therefore may be used as a cue by prospectors in searching for prospective territories. Studies on other species have also shown that the presence of a nest may indicate the suitability of the territory for successful nesting to conspecifics. For example, in the Eurasian penduline tit, *Remiz pendulinus*, males use old nests as a cue to select suitable territories (Gergely et al. 2009), and similarly, many hole nesters prefer nest boxes containing old nests over nest boxes without nests (Thompson and Neill 1991; Davis et al. 1994; Mazgajski 2003; Mazgajski 2007). In hair-crested drongo, it has been observed that some non-breeding yearlings obtained a territory in the subsequent year nearby the territory where they had been seen in the previous year (L. Lv, personal observation). Therefore, by dismantling the nest, drongos may conceal their successful territories from other individuals and avoid or reduce the potential costs of territory competition in the following year.

Here we consider a number of predictions and assumptions of the territory competition hypothesis. First, nests should remain intact until the next breeding season if they were not dismantled. Second, if failed breeders are less likely to reuse the territory in the following year, they may be less motivated to dismantle their nest than successful individuals. Third, experimentally strengthened nests, which remained intact until the next breeding season, should attract conspecifics to the territory and lead to higher territory reusing rate and higher replacement rate of territory owners in the following year. Finally, strengthened nests placed in successful territories should lead to reduced breeding performance of owners in the following year due to the cost of competition for retaining or even losing the previous territory. By using observational and experimental data, this study provides the first experimental test of the territory competition hypothesis.
Materials and methods

Study Site and Study Population
We conducted this study in a 400ha area in the Dongzhai National Nature Reserve (31.95° N, 114.25° E, elevation 100-840 m) in central China (for more information on the study site see Li et al. 2009). The hair-crested drongo is a socially monogamous passerine which forms long-term pair bonds. Most of the birds that breed in southern and eastern China, including our study site, winter in Indochina (Rocamora and Yeatman-Berthelot 2009). At our study site, drongos arrive in late April and leave before mid-October (Gao et al. 2006). The data used in this study were collected between 2010 and 2016 with on average 77 (range 47-86) breeding pairs monitored each year, and almost 80% of the adults were ringed with a unique set of colour rings. We caught individuals by mist-netting in close proximity to the nest trees during incubation or nestling-provisioning period. None of the caught individuals abandoned their nest after release.

Hair-crested drongos are territorial during the breeding period with most of their territories spread continuously over the study area. Birds defend their territory vigorously from conspecific intruders and raptors. They prefer to nest in larger hardwood trees or Chinese water firs (*Metasequoia glyptostroboides*) in our study area (Cantrell et al. 2016). The cup-shaped nest attaches firmly in a tree crotch (Du and Zhang 1985; see Figure 5.1), which located near the end of a branch in the middle canopy of the tall tree with an average ± SE nest height of 8.28 ± 0.55 m (*N* = 50; Cantrell et al. 2016). Both parents participate in all breeding activities, including nest building, incubation and feeding of offspring. Modal clutch size is four (range 3-5) and is featured of high hatching success (Lv et al. 2016). The main reason for unsuccessful breeding is nest predation by predators such as Eurasian Jays (*Garrulus glandarius*) and Besra Sparrow Hawks (*Accipiter virgatus*) (L. Lv personal observation). The species is generally single-brooded with about two thirds of all nests producing at least one fledgling. Few breeding pairs lay replacement clutches after their first clutch failed (Lv et al. 2016).

Data Collection and Field Procedures
We searched for nests by checking trees which had been used previously and potential nesting sites in the forest. After a nest was located, we determined the identity of the nest owners either through direct observation with a telescope or binoculars, or indirectly through video recording, where video cameras (Sony HDR-160E, Sony HDR-260E or Samsung F40) were placed 10-30 m from the nest.
To determine the breeding stage (nest-building, egg-laying, incubation and nestling) and the fate (successful or failure) of each nest, we checked the nest every two or three days by mirroring over nests or climbing trees. During the nest-dismantling period (started from the first check of nest failure or after the young fledged), we took pictures of the nest every two or three days to record the proportion of remaining nest material.

To test whether the nest of drongos can remain intact until the next breeding season under natural conditions, we performed a nest intactness experiment. In July 2010, we collected ten nests by cutting the nest branch from the base after fledging of the young. We then placed these nests individually at a site in the study area that consists of low shrubs. Drongos usually occur in the canopy of the forest and were rarely observed at the site where the experimental nests were situated. We placed all nests in their natural position with the base of the nest branch tied to shrub branches of similar thickness. Nests were 1 m above the ground with a distance of 0.5 m to 4 m from each other. We photographed each nest after it was fixed and checked its condition again at the beginning of the next breeding season (middle May 2011).

To investigate whether the territory reuse was affected by previous breeding performance, we determined the rate of reusing successful territories (at least one young fledged) and failed territories for which both male and female breeder were identified. We defined an individual as reusing the same territory if it built a nest in the same tree as in the previous year or in a tree within 106 m (the average distance between two nearest nest trees in 2014, $N = 80$) from the nest tree that it used in the previous year. Considering the utilization history of territories, we defined individuals as ‘changed territory’ when they bred in their direct neighbour’s nest tree that was less than 106 m from their previous nest tree.

To examine whether drongos dismantled their nest according to breeding performance, we monitored the nest-dismantling of successful nests and failed nests. As some breeding pairs produced replacement clutches after their first breeding attempt failed and they might dismantle their first nest to use nest material for building a new nest (L. Lv, personal observation), failed nests of breeding pairs who subsequently produced a replacement clutch were not included in the analyses. We used photographs of the nest, which were taken during nest checks, to define the stage of the nest-dismantling (Figure 5.1). Four stages were used according to how much of the nest material was left (stage 4 ≥ 75%, 3 = 50-75%, etc.; see Figure 5.1). All nests were assessed by the same observer (L. Lv). We defined the duration of nest-dismantling as the average duration (in days) when more than 50%
of the nest and more than 75% of the nest was dismantled (i.e. from dismantling onset to the first recording date of stage 2 and stage 1), respectively. From 2011 to 2014, drongos were present until October (2011: 11 October; 2012: 10 October; 2013: 12 October; 2014: 9 October). Therefore, we defined nests, which still had more than one fourth of nest material left in late October, as not dismantled.

To test whether the existence of a nest in a territory affected territory reuse in the following breeding season, we carried out a nest-hanging experiment by using successful nests for which both male and female breeder were identified. Nests in the experimental group were collected by cutting the nest branch from the base and strengthened by using grey Dyneema PE fishing line (line number: 8.0; diameter: 0.50 mm) to make the nests indestructible for drongos. All nests were stitched in the same manner by the same experimenter (C. Gao). Within two days after the nests were collected, we re-attached strengthened nests to the similar position and orientation of its original location by fixing the base of the nest branch to a similar sized branch with steel wire.

To test whether drongos accept experimentally strengthened nests and treat them as natural nests, we compared the nest visitation rates of nest owners and conspecifics between strengthened nests and natural nests in the nest-dismantling period, respectively. In 2011, all strengthened nests (N = 11) in the experimental group were monitored by motion-triggered infrared cameras (Scoutguard SG550) which each was set about 0.4 m from the strengthened nest. We set cameras to the video mode with zero seconds after each trigger. Video length was set to 60 seconds. Only the recordings for which nests had been monitored for the entire day (5:30 to 19:30) in the first month of monitoring were used in the analysis. On average, each nest was monitored 7.45 ± 2.88 days (mean ± SE, N = 11). Meanwhile, we recorded the nest visits of eleven natural nests that succeeded in producing fledglings through filming in the nest-dismantling period (from the dismantling onset until at least one fourth of nest material was left). Each nest was monitored on average ± SE: 25.56 ± 15.47 hours (N = 11). All owners of nests that were monitored by infrared cameras or video cameras were individually ringed with a unique combination of colour rings before monitoring.

As the nest visitation rates of nest owners and conspecifics were the same for the strengthened nests and natural nests (Mann-Whitney U test: nest owners: Z = -0.962, N1 = N2 = 11, p = 0.336; conspecifics: Z = -1.194, N1 = N2 = 11, p = 0.232), we considered that drongos treated strengthened nests as natural nests. All nests in the control group, but none in the experimental group, were dismantled by drongos.
in $9.82 \pm 1.69$ days (average $\pm$ SE, $N = 39$). Thus, nests in experimental group attracting conspecifics for a much longer period (about three months from early July till the migration time in September and October) than nests in control group. For this reason, we assume that nests in experimental group attract more conspecifics’ visiting and are consequently experiencing a higher nest competition in the following year than nests in control group. We considered that the owners of a territory were replaced if both of the territory owners in the next year were not previous owners. Territory owners who moved to other territories were also recorded. And we assumed that a territory owner was died if it was not recorded in our study area for two years. All the hung nests were removed at the end of the breeding season (August) in the following year.

Figure 5.1. An example of hair-crested drongo nest-dismantling stages: (A) stage 4 of full nest; (B) stage 2 of between 25% and 50% of nest material left; (C) stage 1 of less than 25% of nest material left.

**Statistical Analyses**

We tested whether the number of nests that were still intact and the number of nests that were incomplete in the following year of the nest intactness experiment were significantly different from the expectation that all nests were intact by using Fisher’s exact test. Subsequently, we used the same statistical method to investigate whether the return rate and the territory reusing rate of territory owners were influenced by their breeding performance in the previous year. Furthermore, we explored whether the occurrence of nest dismantling behaviour was related to breeding performance. For nests which were dismantled, Mann-Whitney $U$-test was used to compare the speed of dismantlement between successful and failed nests.

To investigate whether territories were more likely to be reused and territory owners were more likely to be replaced when nests were experimentally caused to persist in the territory, we fitted ‘year’, ‘treatment’ (experimental versus control)
and ‘number of fledglings produced in the previous year’ as explanatory variables in (separate) generalized linear models (GLMs) with binomial error and logit link function. ‘Reused or not’ and ‘replaced or not’ were set as binomial response variables. We also analysed the influence of nest hanging experiment on reproductive success of males and females, respectively, by fitting GLMs with binomial error and logit link function. Number of fledglings was used as an index for reproductive success with low reproductive success defined as producing none or one fledgling and high reproductive success defined as producing more than one fledglings (from 2 to 5). 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, except for ‘treatment’ or ‘number of fledglings produced in the previous year’, if doing so resulted in a lower AICc score, which were obtained by using the “AICcmodavg” package (Mazerolle 2011). Two two-way interactions between ‘year’ and ‘treatment’, and between ‘treatment’ and ‘number of fledglings produced in the previous year’, were tested in all analyses, but not significant and therefore not reported.

The effect of the nest-hanging experiment on the timing of breeding was analysed by fitting general linear models, using laying date of breeding pair of male ID or female ID as response variables, respectively. ‘Treatment’ was used as a predictor and laying date in the previous year was used as a covariate.

Laying date of each nest was standardized by subtracting the date of the first egg laid in any given year. Only the laying date of the first breeding attempt in that season was used. Laying dates were log transformed to meet the assumption of normality of the model residuals.

All analyses were conducted in either SPSS 19.0 (SPSS Inc., Chicago, IL, USA) or R.3.1.1 (R Core Team 2012) package lme4 (Bates et al. 2014). All tests were given two-tailed and significance was assessed at $p = 0.05$.

**Ethical Note**

The experimental protocols used in this study abided by the Law of the People’s Republic of China on the Protection of Wildlife (27 August 2009) and were approved by the Administration Bureau of Dongzhai National Nature Reserve. During the study period, we did not observe any fledglings returning to the nest for resting. Therefore, collecting nests after the young fledged will not influence the survival rate of fledglings. As drongos occasionally reuse the same branch in the next breeding season and there are many similar branches on the nest tree, we
presume that cutting one nest branch has no or little influence on the subsequent breeding activity.

**Results**

**Nest Intactness Experiment**

Nests that were removed and stored elsewhere were still intact in 8 of 10 cases in the following breeding season. It was not significantly different from our expectation that all nests would be intact in the next year (Fisher’s exact test, \( p = 0.474 \)). For the two incomplete nests, the nest material dropped from the branches and nothing left.

**Figure 5.2.** Return rate and territory reusing rate of the hair-crested drongo after (A) successful or (B) failed breeding attempt to produce fledglings in the previous year.
Figure 5.3. Mean duration of nest-dismantling ± SE in hair-crested drongo nests which produced fledglings (successful nest) or not (failed nest). Numbers above bars indicate sample sizes.

Figure 5.4. How territories were used by their former owners in the next year when successful nests were experimentally strengthened to persist in the territories (treatment). Blank: not used; changed: replaced by new birds, but former owners not seen; usurped: replaced by new birds and former owners seen; same: used by former owners. Numbers above bars indicate sample sizes.
Return Rate, Territory Reusing Rate and Nest-Dismantling

There was no difference in the probability that successful males or failed males to return the study area in the next year (Fisher's exact test, $p = 1.000$; Figure 5.2), but fewer females returned if they failed in the previous year (Fisher's exact test, $p = 0.025$; Figure 5.2). Both males and females were less likely to reuse the territories if they failed in the previous year (Fisher's exact test, both $p < 0.015$; Figure 5.2). Nine of the 83 failed nests (10.8%) and five of the 187 successful nests (2.7%) were not dismantled, so that failed nests were significantly less likely to be dismantled than successful nests (Fisher's exact test, $p = 0.013$). Furthermore, failed nests were dismantled on average 2.97 days longer than successful nests (Mann-Whitney $U$ test: $Z = -1.958$, Mean$_{\text{failed}} = 12.61 \pm 1.35$ days, Mean$_{\text{successful}} = 9.64 \pm 0.70$ days, $N_{\text{failed}} = 67$, $N_{\text{successful}} = 174$, $p = 0.050$; Figure 5.3).

Nest-hanging Experiment

Experimentally strengthened nests tended to increase the reuse rate of territories in the next year (Table 5.1). Also territories that produced more fledglings in the previous year also tended to result in a higher reusing rate of territories (Table 5.1). However, the replacement of territory owners was not affected by the persistence of strengthened-nest or the number of fledgling produced in the previous year (Table 5.1). Furthermore, laying date (Table 5.2) and reproductive success of returned nest owners (both male and female; Table 5.3) were also not significantly influenced by the nest hanging treatment.

Table 5.1. Two generalized linear models for analysing whether the persistence of experimentally strengthened nests (treatment) and the number of fledglings produced in the previous year influence the reuse of territories and the replacement of territory owners.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Territory reused or not reused ($N = 79$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>1.186</td>
<td>0.639</td>
<td>1.855</td>
<td>0.064</td>
</tr>
<tr>
<td>Fledglings</td>
<td>0.586</td>
<td>0.316</td>
<td>1.857</td>
<td>0.063</td>
</tr>
<tr>
<td>Nest owners replaced or not replaced ($N = 63$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.346</td>
<td>0.719</td>
<td>-0.482</td>
<td>0.630</td>
</tr>
<tr>
<td>Fledglings</td>
<td>-0.422</td>
<td>0.365</td>
<td>-1.157</td>
<td>0.247</td>
</tr>
</tbody>
</table>
Table 5.2. Two general linear models for analysing whether laying date of breeding pairs (female ID and male ID, separately) were influenced by the persistence of experimentally strengthened nests (treatment) with laying date of the previous year as covariates.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Breeding pair of female</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(N = 38)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.121</td>
<td>0.090</td>
<td>-1.339</td>
<td>0.189</td>
</tr>
<tr>
<td>Laying date of previous</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>0.498</td>
<td>0.222</td>
<td>2.246</td>
<td>0.031</td>
</tr>
<tr>
<td>Breeding pair of male</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(N = 46)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.047</td>
<td>0.073</td>
<td>-0.646</td>
<td>0.522</td>
</tr>
<tr>
<td>Laying date of previous</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>year</td>
<td>0.340</td>
<td>0.149</td>
<td>2.277</td>
<td>0.028</td>
</tr>
</tbody>
</table>

Laying dates were log transformed to meet the assumption of normality of the model residuals. Significant values are in bold.

Table 5.3. Summaries of two generalized linear models for analysing whether reproductive success of territory owners (female ID and male ID, separately) were affected by the persistence of experimentally strengthened nests (treatment) or the number of fledglings that they produced in the previous year.

<table>
<thead>
<tr>
<th></th>
<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>p</th>
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<tbody>
<tr>
<td>Breeding pair of female</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(N = 38)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.417</td>
<td>0.774</td>
<td>-0.539</td>
<td>0.590</td>
</tr>
<tr>
<td>Fledglings</td>
<td>-0.587</td>
<td>0.477</td>
<td>-1.232</td>
<td>0.218</td>
</tr>
<tr>
<td>Breeding pair of male</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(N = 47)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>-0.150</td>
<td>0.701</td>
<td>-0.214</td>
<td>0.830</td>
</tr>
<tr>
<td>Fledglings</td>
<td>-1.501</td>
<td>0.691</td>
<td>-2.172</td>
<td>0.030</td>
</tr>
</tbody>
</table>

Reproductive success was defined as low if individuals produced none or one fledgling and as high if individuals produced from two to five fledglings. Significant values are in bold.
Discussion

Our results showed that most hair-crested drongo nests were still intact in the next breeding season if they had not been dismantled. Therefore, they have the potential to serve as cues for suitable territories to other individuals. Consistent with the prediction of the territory competition hypothesis (Li et al. 2009), we found that successful breeders were more likely to dismantle their nest and dismantled faster than failed breeders as territory reusing rate was higher after successful breeding attempts. Although strengthened nests, which were experimentally caused to persist in successful territories, attracted conspecifics and tended to result in a higher reusing rate of territories than other territories with nests which were dismantled, the replacement rate of territory owners in the following breeding season was not affected by this experimental treatment. Furthermore, nest owners did not initiate breeding later or produce fewer fledglings due to the potential higher territory competition after this treatment. Therefore, our results only partially support the prediction that nest-dismantling is an adaptive behaviour for hair-crested drongos to reduce territory competition from conspecifics in the following breeding season.

Influence of Breeding Dispersal on Nest-Dismantling

Drongos that had failed to produce fledglings in the previous year were more likely to change their territory than individuals that had succeeded (Figure 5.2). This is also found in other studies which demonstrated current breeding performance has a strong impact on breeding dispersal with high breeding dispersal probability after breeding failure (Alcock 1993; Switzer 1993; Haas 1998; Apollonio et al. 2003; Hoover 2003). Therefore, if individuals benefit from nest-dismantling in terms of reduced territory competition in the following year, failed breeding pairs that were more likely to disperse should be less motivated to dismantle their nest. Furthermore, there is substantial evidence that failed breeding individuals prospect the breeding performance of others to locate the high quality territories where they preferentially settle to breed in the following year (Eadie and Gauthier 1985; Cadiou et al. 1994; Doligez et al. 2004; Ward 2005; Calabuig et al. 2010; Schuett et al. 2012). As prospecting mainly occurs at the end of the breeding season (Arlt and Pärt 2008; Betts et al. 2008), which is normally the similar time after the breeding failure, failed drongos may prefer to engage in prospecting rather than in nest-dismantling behaviour. This may explain the less occurrence and low speed of nest dismantling in failed breeders.
Nest-Dismantling and Prospective Territory Competition

The territory competition hypothesis predicts that prospectors use the presence of nests as a cue in selecting potential territories and compete for these territories in subsequent year (Li et al. 2009). Indeed, our nest-hanging experiment revealed that experimentally strengthened nests did attract prospectors. However, it did not lead to a higher replacement rate of strengthened-nest owners in the next year. When prospectors competed for territories that were selected based on the assessment of the previous year, prior residency of territory owners often confers an advantage in maintaining ownership of a territory regardless of who occupies it first. For example, when prospectors compete with individuals who already retained their previous territories, residents consistently dominate opponents in aggressive interactions within their familiar areas (the ‘resident advantage’; reviewed by Kokko et al. 2006). Even if prospectors had occupied the territory before the owners from the previous year arrived, most of them were subsequently evicted when the owners from the previous year returned (Nolan 1978; Jakobsson 1988; but see Arcese 1987). For instance, a study on the northern wheatear, *Oenanthe oenanthe*, found that individuals selected the territories that they had prospected in the previous year, but the probability of successfully acquiring these territories was strongly dependent on the survival of the original owners (Pärt et al. 2011). In our study population, we also observed that new breeding pairs were replaced by pairs with at least one bird from the previous year during the nesting period (L. Lv, unpublished data). Therefore, the advantage of the original nest owners in retaining territories may have led to the relatively low replacement rates of nest owners in both of experimental and control groups, and the small difference between these two groups. In fact, only 10 out of 63 (15.9%) reused territories in the experimental and control group together were replaced by new birds in the next year (Figure 5.4; 7 of 10 using the same nest tree and the other three nested in trees 11, 17 and 43 meters away from the original nest tree, respectively). Among them, 7 territories (70.0%) were usurped and led to most of the replaced owners nesting near their old territories (Figure 5.4). This result suggests that territory competition does exist in our study population. However, the intensity of territory competition may be too weak to motivate drongos to reduce the prospective cost of territory competition by dismantling their nest. Furthermore, both the timing of breeding and the fledgling number of territory owners was not influenced by the strengthened nests hung in their territories in the previous year. These results suggest that potential territory competition as incurred by the strengthened nest did not lead to reduced breeding performance in drongos. Therefore, there was no or little cost for drongos if they...
did not dismantle their nest under conditions of weak territory competition.

In addition to the territory competition hypothesis, it has also been proposed that nest-dismantling may be an adaptive behaviour that benefited hair-crested drongos in the past, i.e. the “once-beneficial hypothesis” (Li et al. 2009). Previous limitation of territories may have forced drongos to monopolize a territory but the restrictive factor has disappeared with environmental change or when entering a new breeding range. In this case, the nest-dismantling behaviour, assuming that the energetic cost to the breeding pair is low, has been retained but is no longer adaptive. From this point, the once-beneficial hypothesis may supplement the territory competition hypothesis when territory competition is weak in the population. Thus, it would be interesting to test whether drongos benefit from nest-dismantling when or where territory competition is more intense.

**Reusing Rate of Territory**

Although the replacement rate of territory owners was not differed between experimental group and control group, territories in experimental group tended to have a higher chance of being reused in the next year. For these territories that had not been reused, they were caused by former territory owners did not return (most likely died) or moved to other territories (number of territories that former owners did not return or moved to other territories; in experimental group: 2 and 3, in control group: 6 and 5). Nest hanging experiment may not increase the return rate of territory owners, but it may contribute to enhancing territory owners being more faithful to their former territories. As territory owners in experimental group have to spend more time in defending their territories due to more visiting of other conspecifics that are attracted by the strengthened nests, they may be more motivated to reuse their former territories in the next year. Further studies with larger sample size are needed to test this idea.

Many studies reported that the number of fledglings was used by prospectors to assess the quality of the territory (e.g. Ward 2005; Parejo et al. 2007). Therefore, more chicks produced in the territory may attract more competing prospectors and consequently lead to a higher replacement rate of former territory owners in the next year. However, this was not supported in our study. As a contrast, territories, where more chicks fledged in the previous year, tended to be reused in a higher chance. Since the number of fledglings in the territory did not influence the replacement of former territory owners, this was most likely due to a higher territory reusing rate of former owner in territories where more young fledged in the last year. Therefore, these results suggested that territory owners, who produced
more fledglings in the previous year, performed better in retaining their former territories even with potential intense competition from conspecifics. This may cause by the variation of phenotypic quality or conditions among territory owners. High-quality individuals may be more productive and consistently dominate the inter-specific territory competition (Pierotti and Annett 1994; Bearhop et al. 1999; Renison et al. 2003). Meanwhile, better breeding performance also enhances territory fidelity (Gavin and Bollinger 1988; Switzer 1997; Haas 1998; Robert and Paiva 2014). All of this can contribute to a higher chance of territories being reused by these former owners who produced more chicks in the previous year.

Conclusion
Altogether our results only partially support the territory competition hypothesis that hair-crested drongos dismantle their nests to reduce territory competition in the following breeding season. Territory owners that succeeded in producing fledglings were more likely to dismantle nests and dismantle them faster if they prefer to reuse the territories in the following year. Prospectors may use the information of nest location in selecting preferred territories for the following breeding season. However, due to the advantage of original territory owners in retaining their territory, few prospectors may be able to usurp territories. Furthermore, owners did not seem to suffer from territory competition in terms of breeding performance. One potential alternative explanation is that nest-dismantling may benefit drongos only when territory competition is very intense in the population, a hypothesis that remains to be tested. As of now, however, the exact function of nest-dismantling remains a mystery.

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A male Asian paradise flycatcher (*Terpsiphone paradisi*)

Black-throated tit (*Aegithalos concinnus*)

*Photo: Peng Zhang*