University of Groningen

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

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

Published in:
 Behavioral Ecology and Sociobiology

DOI:
[10.1007/s00265-017-2422-1](https://doi.org/10.1007/s00265-017-2422-1)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
 Publisher's PDF, also known as Version of record

Publication date:
 2018

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Lv, L., Li, J., Kingma, S. A., Gao, C., Wang, Y., Komdeur, J., & Zhang, Z. (2018). Do hair-crested drongos reduce prospective territory competition by dismantling their nest after breeding? *Behavioral Ecology and Sociobiology*, 72(1), [12]. <https://doi.org/10.1007/s00265-017-2422-1>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

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

Lei Lv^{1,2,3} · Jianqiang Li⁴ · Sjouke A. Kingma² · Chang Gao¹ · Yong Wang^{1,5} · Jan Komdeur² · Zhengwang Zhang¹

Received: 28 September 2017 / Revised: 3 December 2017 / Accepted: 8 December 2017 / Published online: 27 December 2017
© Springer-Verlag GmbH Germany, part of Springer Nature 2017

Abstract

Animals that breed seasonally often use the same territory where they successfully produced young previously. Intra-specific competition may be intense for these high-quality territories, and therefore, natural selection should favour behaviour of territory owners to reduce such competition. Hair-crested drongos, *Dicrurus hottentottus*, a territory-faithful migratory passerine, dismantle their nests after breeding. As undissembled nests usually remain intact until the next breeding season, we hypothesised that nest dismantling serves the purpose of reducing territory competition from conspecifics that may use the presence of a nest as a cue to select suitable territories in the next year. Here, we provide the first experimental test of this “territory competition hypothesis”. Our results show that successful pairs, who often reuse their territories in the next year, were more likely to dismantle their nests and tended to dismantle faster compared to failed breeding pairs who often moved to another territory in the next year. Strengthened natural nests that were experimentally placed in successful territories attracted prospectors. However, the usurpation rate of those territories in the following year was low and not higher than that of territories where nests were dismantled. Furthermore, returned strengthened-nest owners did not initiate breeding later or produce fewer fledglings suggesting that potential higher territory competition did not affect their reproduction. Altogether, our results only partially support the “territory competition hypothesis”. We suggest that nest dismantling may only be beneficial to drongos in years when territory competition is very intense.

Significance statement

Seasonal-breeding animals may face intra-specific competition for high-quality territories. Successful individuals often reuse their territory, but whether they can reduce prospective territory competition through hiding breeding locations (e.g. nests) has rarely been studied. We conducted an experiment to test whether a medium-sized passerine reduces the potential costs of territory competition by destroying their nest after breeding, concealing their selection of territory to other individuals. Territory owners invested more in nest dismantling if they were more likely to reuse the territory. However, they were still able to retain their previous territory and did not have a lower reproductive success if their nest was not dismantled. We suggest that individuals may only benefit from masking public information of breeding habitat selection from conspecifics by dismantling their nest when territory competition is very intense.

Keywords Nest dismantling · Hair-crested drongos *Dicrurus hottentottus* · Territory competition · Adaptive behaviour · Prospector

Communicated by J. A. Graves

✉ Jan Komdeur
j.komdeur@rug.nl

✉ Zhengwang Zhang
zzw@bnu.edu.cn

¹ Ministry of Education Key Laboratory for Biodiversity and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing, People's Republic of China

² Behavioural and Physiological Ecology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

³ School of Life Sciences, Sun Yat-sen University, Guangzhou, People's Republic of China

⁴ College of Nature Conservation, Beijing Forestry University, Beijing, People's Republic of China

⁵ Department of Biological and Environmental Sciences, College of Agriculture, Life, and Natural Sciences, Alabama A&M University, Normal, AL, USA

Introduction

In many animals, individuals occupy the same territory over consecutive years (Greenwood 1980; Switzer 1993; Newton 2008; Piper 2011). This kind of territory fidelity can benefit individuals because of 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, territory fidelity usually follows good breeding performance in a particular territory (Gavin and Bollinger 1988; Switzer 1997; Haas 1998; Robert and Paiva 2014), because breeding performance provides an indirect assessment of 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 potential competitors use the past breeding performance of other pairs as a cue to assess the quality of the territory. There is substantial evidence that prospectors, which are immature individuals, failed breeders or non-breeders, gather information on local patch quality at the end of a breeding season to select the optimal territory for the next season (reviewed in Reed et al. 1999; Ponchon et al. 2013). Territory competition may impact the fitness of individuals not only because they may lose their preferred territory but also because of time loss, energy expenditures and risks of injury incurred during fights (Eason and Hannon 1994; Marler et al. 1995; Cleveland 1999). Therefore, behavioural tactics to reduce prospective territory competition are predicted to be favoured by natural selection. Indeed, in common loons, *Gavia immer*, where prospecting individuals use the presence of fledglings as a cue to locate good territories and usurp it in the subsequent year (Piper et al. 2000, 2006), territory owners show a tendency to conceal chicks from prospecting individuals, perhaps to avoid future territory takeovers (Piper et al. 2006). Apart from chicks, the presence of a nest may also indicate the suitability of the territory for breeding to conspecifics. In the Eurasian penduline tit, *Remiz pendulinus*, males use old nests as a cue to select suitable territories (Gergely et al. 2009), and many cavity nesters prefer nest boxes containing old nests over nest boxes without nests (Thompson and Neill 1991; Davis et al. 1994; Mazgajski 2003, 2007). Therefore, it

can be expected that, in species with high territory fidelity, nest owners who reproduced successfully aim to mask cues that signal suitable territories, in order to reduce territory competition in the next year.

The hair-crested drongo, *Dicrurus hottentottus*, a migratory insectivorous passerine, exhibits a nest-dismantling behaviour in that most parents dismantle their nests within two weeks after breeding (Li et al. 2009). Apart from this species, this behaviour has only been observed in two Indian laughing thrushes (Nilgiri laughing thrush, *Garrulax cachinnans*, and white-breasted laughing thrush, *Garrulax jerdoni*; Islam 1989) and greater racket-tailed drongos (*Dicrurus paradiseus*, LL, personal observations). Why birds dismantle their nest after breeding has never been tested. In hair-crested drongos, nests are solidly built (consisting of mainly fine grass stems and rootlets) and, in combination with opportunity-costs, nest dismantling is likely to be energetically costly. 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 adult drongos show high fidelity to their territories (Lv et al. 2016). Secondly, the conspicuous nest of drongos is easy to locate and therefore may be used as a cue by prospecting individuals in searching for future territories. Thirdly, some non-breeding yearlings obtained a territory in the subsequent year nearby the territory where they had been ringed (LL, unpubl. data). It indicated that yearlings were prospecting at that moment, and prospecting occurs in the local area which covers several nearby territories. Thus, by dismantling the nest, drongos may conceal their high-quality territories from other individuals and avoid or reduce the potential costs of territory competition and losing their territory in the following year.

Here, we consider a number of predictions and assumptions of the “territory competition hypothesis”. First, we expected that nests remain intact until the next breeding season if they were not dismantled. Second, we predicted that, if failed breeders were less likely to reuse the territory in the following year, they were less motivated to dismantle their nest than successful individuals. Third, we prospecting that experimentally strengthened nests, which remained intact until the next breeding season, should attract conspecifics to the territory and lead to a higher usurpation rate of territories in the following year. Finally, we predicted that 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 400 ha 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 that forms long-term pair bonds. Most of the birds that breed in China, including in 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 (2010, 47; from 2011 to 2016, range 75–86) 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 the nestling-provisioning period. None of the caught individuals abandoned their nest after release. Since our study involved focal animals in the field, it was not possible to record data blind with respect to the hypotheses we tested.

Drongos are territorial during the breeding period, and most of their territories are clustered in our study area with each territory abutting at least one other territory. Birds defend their territory vigorously from conspecific intruders and raptors. They nest in larger hardwood trees or Chinese water firs, *Metasequoia glyptostroboides*, in our study area (Cantrell et al. 2016). The cup-shaped nest is built firmly in a tree crotch (Du and Zhang 1985; Fig. 1), which is located near the end of a branch in the middle canopy of the tall tree with an average $\pm$ SE nest height of 8.28 ± 0.55 m ($n = 50$; Cantrell et al. 2016). Both parents participate in nest building, incubation and offspring feeding. Modal clutch size is four eggs (75.64%, range 3–5, $n = 275$) and hatching success is high (92.8%, 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* (LL, personal observation). Drongos are generally single-brooded with ca. two thirds of all nests producing at least one fledgling. Only 18.3% of the breeding pairs ($n = 120$) lay replacement clutches after their first clutch failed (Lv et al. 2016).

Data collection and field procedures

We searched for nests by checking trees that 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 observations with a telescope

or binoculars, or 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 nests 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 located 1 m above the ground with a distance of 0.5 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 territory reuse was affected by previous breeding performance, we determined the rate of re-use of successful territories (at least one young fledged) and failed territories for which both male and female breeders 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 62 m of the former nest tree (the average radius that was calculated based on the area of intensive use at 60% isopleth of five home ranges in 2009 with fixed kernel methods (Worton 1989; Börger et al. 2006)). Some individuals moved to the nest tree where the adjacent pair had bred in the previous year, which was also less than 62 m from their original nest tree; we defined those as having “changed territory”.

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 (LL, unpubl. data), failed nests of breeding pairs who subsequently produced a replacement clutch were not included in the analyses. We used photographs of the nest that were taken during nest checks to define the stage of the nest dismantling. Four stages were used according to how much of the nest material was left (stage 4, $\geq 75\%$; stage 3, 50–75%; etc.; Fig. 1).

Fig. 1 An overview of hair-crested drongo nest-dismantling stages: **a** stage 4, full nest; **b** stage 2, between 25 and 50% of nest material left; **c** stage 1, less than 25% of nest material left

All nests were assessed by the same observer (LL). 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 were 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 9–12 October. Therefore, we defined nests that still had more than one fourth of nest material left in mid-October as not dismantled.

To test whether the existence of a nest in a territory affected territory competition in the following year, we carried out a nest-hanging experiment by using successful nests for which both male and female breeders were identified from 2011 to 2013. Eighty-five nests were randomly assigned to a control or an experimental group after the young fledged. Nests in the experimental group ($n = 38$) were collected by cutting the nest branch from the base and strengthened using a grey Dyneema PE fishing line (line number, 8.0; diameter, 0.50 mm) to make the nests indestructible for drongos (Fig. 2). All nests were stitched densely in the same manner by the same experimenter (CG). Within two days after the nests were collected, we re-attached strengthened nests to a similar position and orientation of its original location by fixing the base of the nest branch to a similar-sized branch with steel wire.

Fig. 2 A natural nest of hair-crested drongo strengthened with fishing line

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 (e.g. prospectors) between strengthened nests and natural nests in the nest-dismantling period, respectively. In 2011, nine strengthened nests in the experimental group were monitored by motion-triggered infrared cameras (Scoutguard SG550), each set about 0.4 m from the strengthened nest. We set cameras to the video mode with 0 s interval after each trigger. Video length was set to 60 s. 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 8.67 ± 1.00 days (mean $\pm$ SE, $n = 9$). We also recorded the nest visits of ten 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 $\pm$ SE: 48.90 ± 33.55 h ($n = 10$). All owners of nests that were monitored by infrared cameras or video cameras were individually ringed with a unique combination of colour rings. Nest owners and conspecifics visited the strengthened nests and natural nests, and there was no significant difference in visitation rates between these two types of nests, despite an apparent trend (nest visitation rates of parents: strengthened nests = 0.07 ± 0.11 times/h (mean $\pm$ SE), natural nests = 0.16 ± 0.19 times/h (mean $\pm$ SE), $t = 1.30$, $p = 0.212$; nest visitation rates of conspecifics: strengthened nests = 0.10 ± 0.12 times/h (mean $\pm$ SE), natural nests = 0.18 ± 0.18 times/h (mean $\pm$ SE), $t = 1.22$, $p = 0.238$; $n_{\text{strengthened nests}} = 9$, $n_{\text{natural nests}} = 10$). Therefore, we assume that drongos treated strengthened nests as natural nests.

In the nest-hanging experiment, all nests in the control group, but none in the experimental group (all nests were complete), were dismantled by drongos in 9.82 ± 1.69 days (mean $\pm$ SE, $n = 39$). Thus, nests in the experimental group did persist longer (about 3 months from early July till the migration time in September and October) and consequently attracted conspecifics for a much longer period than nests in the control group. Therefore, it was legitimate to predict that experimental territories experienced a higher territory competition in the following year than territories in the control group.

To test this prediction, we measured the territory competition by checking the occurrence of territory usurpation in the experimental group and control group. We considered that the territory was usurped if both territory owners in the next year were new breeders and the former territory owner(s) survived (whether the bird was resighted in our study area in any given year during the next 3-year period). Given that the resighting probability of birds breeding in our study area is very high (0.941, $n = 795$; LL, unpubl. data), a missing bird can be reliably considered as having died. No strengthened nests were used by breeders, and they were removed at the end of the breeding season (August) in the following year.

Statistical analyses

We tested whether the return rate and the territory reusing rate of territory owners were influenced by their breeding performance in the previous year. Furthermore, we also explored whether the nest's being dismantled (less than 25% of nest material left) or not (more than 25% of nest material left) was related to reproductive success (yes or no). For nests which were dismantled, we compared the speed of dismantlement (in number of days) between successful and failed nests. Additionally, we tested whether prospecting events were influenced by the timing of breeding and breeding performance by fitting a general linear model (LM). The nest visitation rate of conspecifics during the dismantling period (number of visits per hour) was used as a response variable, and laying date and number of fledglings (range from 1 to 4) were used as predictors.

To investigate whether territories were more likely to be usurped 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 a generalised linear model (GLM) with binomial error and logit link function. “Usurped or not” was set as binomial response variables. By using the same model structure, we also analysed the influence of the nest hanging experiment on reproductive success of females and males, respectively. 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 two to five fledglings (grouping into 0 and 1–5 gave the same result), because the number of fledglings was distributed more like in U shape (model clutch size is four, around one third of all nests were predated and few nests were partially predated). We used Akaike's information criterion corrected for small sample size (AICc) to determine the combination of variables that best explained the data with minimal parameters (Burnham and Anderson 2002).

Model selection was performed by backward stepwise elimination, and the fit of each new model was assessed by comparison of AICc values. Model 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 were not significant and therefore not reported.

The effect of the nest-hanging experiment on the timing of breeding of females and males, respectively, was analysed by fitting general linear models, using the laying date of the breeding pair as the response variable. “Treatment” was used as a predictor and laying date in the previous year was used as a covariate.

The laying date of each nest was standardised 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. Standardised 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 $p = 0.05$.

Data availability statement The datasets generated during and/or analysed during the current study are available in the figshare repository, <https://figshare.com/articles/Nest-dismantling/5611303>.

Results

Nest intactness experiment

Nests that were removed and stored elsewhere were still intact in eight of ten cases in the following breeding season. It indicated that most nests survived until the next year if they were not dismantled by drongos. For the two incomplete nests, the nest material dropped from the branches and nothing was left.

Return rate, territory reusing rate and nest dismantling

There was no difference in the probability that successful males or failed males returned to the study area in the next year (chi-square test, $\chi^2 = 0.06$, $p = 0.812$; Fig. 3), but fewer females returned if they failed in the previous year (chi-square test, $\chi^2 = 5.57$, $p = 0.018$; Fig. 3). Both males and females were less likely to reuse the territories if they failed in the previous year (chi-square test, both $p < 0.007$; Fig. 3). Nine

Fig. 3 Return rate and territory reusing rate of hair-crested drongo territories after a pair was **a** successful ($n = 109$) or **b** failed to produce fledglings ($n = 27$) in the previous year. Individuals who did not return most likely died

of the 83 failed nests (10.8%) and five of the 187 successful nests (2.7%) were not dismantled, indicating that failed nests were significantly less likely to be dismantled than successful nests (chi-square test, $\chi^2 = 7.80$, $p = 0.005$). Furthermore, nest dismantling of failed nests took on average 2.97 days longer than that of successful nests (failed nested = 12.61 ± 1.35 days (mean $\pm$ SE, $n = 67$), successful nests = 9.64 ± 0.70 days (mean $\pm$ SE, $n = 174$), $t = 1.96$, $p = 0.053$).

Nest-hanging experiment

The nest visitation rate of conspecifics was not affected by the laying date nor by the number of fledglings (LMs: laying date, $F_{19} = 0.47$, $p = 0.501$, $\Delta\text{AICc} = +2.33$; number of fledglings, $F_{19} = 0.68$, $p = 0.582$, $\Delta\text{AICc} = +8.83$; $r^2_{\text{full model}} = 0.12$). Furthermore, the usurpation rate of territories was not affected by whether the territory contained a strengthened nest or not (GLM with binomial error: $z_{74} = 0.40$, $p = 0.686$) or the number of fledglings produced in the previous year (GLM with binomial error: $z_{74} = -0.75$, $p = 0.453$, $r^2_{\text{final model}} = 0.03$). Furthermore, laying date (LMs: females: $t_{38} = -1.34$, $p = 0.189$, $r^2_{\text{final model}} = 0.16$; males: $t_{46} = -0.65$, $p = 0.522$, $r^2_{\text{final model}} = 0.11$) and reproductive success of returned nest owners (GLMs with binomial error: females: $z_{38} = -0.54$, $p = 0.590$, $r^2_{\text{final model}} = 0.09$; males: $z_{47} = -0.21$, $p = 0.830$, $r^2_{\text{final model}} = 0.35$) were also not significantly influenced by the nest-hanging treatment.

Discussion

Our results show that most drongo nests were still intact at the beginning of the next breeding season if they had not been dismantled. Therefore, they have the potential to serve as cues of 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 nests and tended to dismantle faster than failed breeders as the territory reusing rate was higher after successful breeding attempts. Although nests that were experimentally strengthened so they persisted until the next breeding season attracted prospectors, the usurpation rate of territories 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 potentially higher territory competition after this treatment. Thus, our results only partially support the prediction that nest dismantling is an adaptive behaviour for drongos to reduce territory competition from conspecifics in the following breeding season.

The effect of breeding dispersal on nest dismantling

Drongos that failed to produce fledglings in the previous year were more likely to change their territory than individuals that had succeeded (Fig. 3), a finding that echoes what others have reported (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 in other species that individuals, who failed in their own breeding, 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). In drongos, nests were visited nearly always by conspecifics during the dismantling period (rarely in other periods; each year in total only one or two conspecifics were observed during the period when the breeding pair was actively attending the nest (either during nest building, incubation or nestling-provisioning period; at least 40 nests in each stage)), which suggests that prospecting occurred. Failed

drongos may gain an adaptive benefit by prospecting rather than dismantling their nests. This may explain the lower occurrence and low speed of nest dismantling in failed breeders.

Nest dismantling and prospective territory competition

In agreement with the “territory competition hypothesis”, our experimental presentation of strengthened nests revealed that these indeed attract prospectors. As the prospecting frequency of conspecifics was not affected by the laying date nor by the number of fledglings produced in the prospected territory, territories with strengthened nests should experience a higher territory competition in the following year than territories in the control group due to the longer period of attracting conspecifics in a similar prospecting frequency. However, the experiment did not demonstrate a higher usurpation rate of strengthened nest territories 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 the ownership of a territory regardless of who occupies it first. If prospectors compete with individuals who already retained their previous territories, it has been reported that residents consistently dominate opponents in aggressive interactions within their familiar areas (the “resident advantage”; reviewed by Kokko et al. 2006). Besides, 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*, revealed 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 settled new breeding pairs were replaced by pairs consisting of at least one bird from the previous year during the nest-building period (LL, unpubl. data). Therefore, the advantage of the original territory owners in retaining territories may have led to the relatively low usurpation rates of territories in both of the experimental and control groups, and the small difference between these two groups. As a consequence, prospectors may not benefit from prospecting in terms of getting access to high-quality territories. In fact, only 7 out of 74 (9.5%) territories in the experimental and control groups together were usurped by new birds in the next year (4 of 7 using the same nest tree and the other 3 nested in trees 11, 17 and 43 m away from the original nest tree, respectively). Most of former owners, who moved, bred near their old territories. This result suggests that territory competition did exist in our study population during the study period, but the intensity may be too weak to motivate drongos to reduce

the prospective cost of territory competition by dismantling their nest.

If former territory owners do not return (most likely died), strengthened nests may attract prospectors and lead to a higher occupation rate of territories. However, although the sample size was small due to limited mortality, territories with an experimental nest were not occupied more often than territories without strengthened nests (33.3%, 1 of 3 versus 25.0%, 2 of 8 territories, respectively). To properly investigate whether the presence of used nests attracts drongos, one should position used nests in suitable areas without drongos present and subsequently monitor whether this results in a higher probability of drongos occupying these areas compared to empty suitable areas without experimental nests. Our result indicates that unoccupied high-quality territories existed in the breeding area, and the low occupation rate (only 3 of 11 territories) may mean that territory competition is relatively low in the population. Furthermore, both the timing of breeding and reproductive success of territory owners were not influenced by the strengthened nest placed in their territory in the previous year, which suggested that potential territory competition induced by the presence of a (strengthened) nest did not lead to reduced breeding performance in drongos. Therefore, we suggest that there would be no or little conceivable costs for drongos if they would not dismantle their nest under conditions of weak territory competition.

Competition may be higher in high-quality territories. We have indications that territory quality varies across the study area: in 25 territories (31.2%, 25/80), breeding pairs consistently succeeded in producing fledglings in at least 4 years during our study period (more than half of our study period). Although this success may be attributed to territory owners being more experienced, it may also reflect differences in territory quality. In contrast, territories that failed to produce fledglings in one or two breeding seasons were usually not occupied anymore afterwards (Fig. 3). We quantified the frequency of prospecting visits for some 25 territories and found that the prospecting visits were not more common in high-quality territories (high-quality territories = 0.10 ± 0.09 times/h (mean $\pm$ SE, $n = 5$), low-quality territories = 0.21 ± 0.22 times/h (mean $\pm$ SE, $n = 14$), $t = -1.08$, $p = 0.296$; LL, unpubl. data). However, this analysis was based on limited sample size, inhibiting to find a statistical difference; future work on testing the effect of territory quality on territory competition may provide valuable insights into whether nest dismantling is shaped by territory competition.

Conclusion

Altogether, our results only partially support the “territory competition hypothesis” that 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 tended to dismantle them faster because they were more often reusing the territories in the following year. Prospectors may use the information about nest locations 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. However, the exact function of nest dismantling needs further study.

Acknowledgements We are grateful to Luis Biancucci, Peng Zhang, Zheng Chen, Matt Lerow, Matthew Slaymaker, Andrew Cantrell, Xu Luo, Hang Zhang, Etienne Melese, Samuel S. Snow, Gabriele Cavallini, Constance Fastré, Yifeng Zhong, Zhi Zheng, Sebastian Orue and Elsa D. Lake who helped with the fieldwork and Dongzhai National Reserve for the permission and assistance to the work. We thank three anonymous reviewers for their comments on previous versions of this manuscript.

Funding ZZ was supported by the National Key Programme of Research and Development, Ministry of Science and Technology (2016YFC0503200), and the “985 Project” of Beijing Normal University; JL by National Natural Science Foundation of China (No. 31101644; 31472011); JK by the Netherlands Organisation for Scientific Research (NWO: VICI grant 865.03.003, and ALW grant 823.01.014); and SAK by NWO (VENI grant 863.13.017).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statement This study abided by the Law of the People's Republic of China on the Protection of Wildlife (27 August 2009) and was approved by the Administration Bureau of Dongzhai National Nature Reserve. The banding of birds was licensed by the National Bird Banding Centre of China (No. 20090003). During the study period, we did not observe any fledglings returning to the nest for resting. Therefore, collecting nests after the young fledged have not influenced the survival rate of fledglings. As drongos occasionally reuse the same branch in the next year 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.

References

- Alcock J (1993) Differences in site fidelity among territorial males of the carpenter bee *Xylocopa varipuncta* (Hymenoptera: Anthophoridae). *Behaviour* 125(3):199–217. <https://doi.org/10.1163/156853993X00245>
- Apollonio M, Scotti M, Gosling LM (2003) Mating success and fidelity to territories in a fallow deer lek: a female removal experiment. *Naturwissenschaften* 90(12):553–557. <https://doi.org/10.1007/s00114-003-0475-7>
- Arcese P (1987) Age, intrusion pressure and defence against floaters by territorial male song sparrows. *Anim Behav* 35(3):773–784. [https://doi.org/10.1016/S0003-3472\(87\)80114-8](https://doi.org/10.1016/S0003-3472(87)80114-8)
- Bates D, Maechler M, Bolker B (2014) Package “lme4”: linear mixed-effects models using Eigen and S4. R package version 1:1–7 <https://CRAN.R-project.org/package=lme4>
- Beletsky LD, Orians GH (1991) Effects of breeding experience and familiarity on site fidelity in female red-winged blackbirds. *Ecology* 72(3):787–796. <https://doi.org/10.2307/1940581>
- Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006) Effects of sampling regime on the mean and variance of home range size estimates. *J Anim Ecol* 75(6):1393–1405. <https://doi.org/10.1111/j.1365-2656.2006.01164.x>
- Boulinier T, Danchin E (1997) The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evol Ecol* 11(5):505–517. <https://doi.org/10.1007/s10682-997-1507-0>
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media, New York
- Cadiou B, Monnat JY, Danchin E (1994) Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment. *Anim Behav* 47(4):847–856. <https://doi.org/10.1006/anbe.1994.1116>
- Calabuig G, Ortego J, Aparicio JM, Cordero PJ (2010) Intercolony movements and prospecting behaviour in the colonial lesser kestrel. *Anim Behav* 79(4):811–817. <https://doi.org/10.1016/j.anbehav.2009.12.007>
- Cantrell A, Lv L, Wang Y, Li J, Zhang Z (2016) Evaluation of nest site preferences of a nest dismantler, the hair-crested drongo (*Dicrurus hottentottus*) in Dongzhai national nature reserve of central China. *Avian Res* 7:1–7
- Cleveland A (1999) Energetic costs of agonistic behavior in two herbivorous damselfishes (*Stegastes*). *Copeia* 1999(4):857–867. <https://doi.org/10.2307/1447962>
- Davis WH, Kalisz PJ, Wells RJ (1994) Eastern Bluebirds prefer boxes containing old nests. *J Field Ornithol* 65:250–253
- Doligez B, Cadet C, Danchin E, Boulinier T (2003) When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim Behav* 66(5):973–988. <https://doi.org/10.1006/anbe.2002.2270>
- Doligez B, Pärt T, Danchin E (2004) Prospecting in the collared flycatcher: gathering public information for breeding habitat selection? *Anim Behav* 297:457–466
- Du J, Zhang J (1985) Ecology observation on the summer ecology of the hair-crested drongo *Dicrurus hottentottus*. *Sichuan J Zool* 4:20–21
- Eadie JM, Gauthier G (1985) Prospecting for nest sites by cavity-nesting ducks of the genus *Bucephala*. *Condor* 87:528–534
- Eason P, Hannon SJ (1994) New birds on the block: new neighbors increase defensive costs for territorial male willow ptarmigan. *Behav Ecol Sociobiol* 34(6):419–426. <https://doi.org/10.1007/BF00167333>
- Gao Z, Du Z, Wang X, Huang H, Wang K, Yang C (2006) The nest-site selection of hair-crested drongo at Dongzhai Nature Reserve. *Chinese J Zool* 41:69–73
- Gavin T, Bollinger E (1988) Reproductive correlates of breeding-site fidelity in bobolinks (*Dolichonyx oryzivorus*). *Ecology* 69(1):96–103. <https://doi.org/10.2307/1943164>
- Gergely Z, Mészáros LA, Szabad J, Székely T (2009) Old nests are cues for suitable breeding sites in the Eurasian penduline tit *Remiz pendulinus*. *J Avian Biol* 40(1):2–6. <https://doi.org/10.1111/j.1600-048X.2008.04582.x>
- Grabowska-Zhang AM, Sheldon BC, Hinde CA (2012) Long-term familiarity promotes joining in neighbour nest defence. *Biol Lett* 8(4):544–546. <https://doi.org/10.1098/rsbl.2012.0183>

- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28(4):1140–1162. [https://doi.org/10.1016/S0003-3472\(80\)80103-5](https://doi.org/10.1016/S0003-3472(80)80103-5)
- Haas C (1998) Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. *Auk* 115(4):929–936. <https://doi.org/10.2307/4089511>
- Hinde R (1956) The biological significance of the territories of birds. *Ibis* 98:340–369
- Hoover JP (2003) Decision rules for site fidelity in a migratory bird, the prothonotary warbler. *Ecology* 84(2):416–430. [https://doi.org/10.1890/0012-9658\(2003\)084\[0416:DRFSFI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0416:DRFSFI]2.0.CO;2)
- Islam MA (1989) Nest destruction and cannibalistic behaviour of laughing thrushes, *Garrulax* spp. (Aves: Muscicapidae). *Bangladesh J Zool* 17:15–17
- Jakobsson S (1988) Territorial fidelity of willow warbler (*Phylloscopus trochilus*) males and success in competition over territories. *Behav Ecol Sociobiol* 22(2):79–84. <https://doi.org/10.1007/BF00303541>
- Kokko H, Lopez-Sepulcre A, Morrell L (2006) From hawks and doves to self-consistent games of territorial behavior. *Am Nat* 167(6):901–912. <https://doi.org/10.1086/504604>
- Li J, Lin S, Wang Y, Zhang Z (2009) Nest-dismantling behavior of the hair-crested drongo in central China: an adaptive behavior for increasing fitness? *Condor* 111(1):197–201. <https://doi.org/10.1525/cond.2009.080051>
- Lv L, Komdeur J, Li J, Scheiber IBR, Zhang Z (2016) Breeding experience, but not mate retention, determines the breeding performance in a passerine bird. *Behav Ecol* 27(4):1255–1262. <https://doi.org/10.1093/beheco/arw046>
- Marler CA, Walsberg G, Moore MLW (1995) Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behav Ecol Sociobiol* 37(4):225–231. <https://doi.org/10.1007/BF00177401>
- Mazerolle MJ (2011) AICcmodavg: model selection and multimodel inference based on (Q) AIC (c). R Package version 1:16 <https://CRAN.R-project.org/package=AICcmodavg>
- Mazgajski TD (2003) Nest site choice in relation to the presence of old nests and cavity depth in the starling *Sturnus vulgaris*. *Ethol Ecol Evol* 15(3):273–281. <https://doi.org/10.1080/08927014.2003.9522672>
- Mazgajski TD (2007) Effect of old nest material on nest site selection and breeding parameters in secondary hole nesters—a review. *Acta Ornithol* 42(1):1–14. <https://doi.org/10.3161/068.042.0107>
- Newton I (2008) Migration ecology of birds. Academic Press, London
- Nolan V (1978) The ecology and behavior of the prairie warbler *Dendroica discolor*. Ornithological Monographs 26, American Ornithologists' Union, Washington
- Nowak M, Sigmund K (1993) A strategy of win-stay, lose-shift that outperforms tit-for-tat in the prisoner's dilemma game. *Nature* 364(6432):56–58. <https://doi.org/10.1038/364056a0>
- Pärt T (1995) The importance of local familiarity and search costs for age- and sex-biased philopatry in the collared flycatcher. *Anim Behav* 49(4):1029–1038. <https://doi.org/10.1006/anbe.1995.0132>
- Pärt T, Arlt D, Doligez B, Low M, Qvarnström A (2011) Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *J Anim Ecol* 80(6):1227–1235. <https://doi.org/10.1111/j.1365-2656.2011.01854.x>
- Piper WH (2011) Making habitat selection more “familiar”: a review. *Behav Ecol Sociobiol* 65(7):1329–1351. <https://doi.org/10.1007/s00265-011-1195-1>
- Piper WH, Tischler KB, Klich M (2000) Territory acquisition in loons: the importance of take-over. *Anim Behav* 59(2):385–394. <https://doi.org/10.1006/anbe.1999.1295>
- Piper WH, Walcott C, Mager JN, Perala M, Tischler KB, Harrington E, Turcotte AJ, Schwabenlander M, Banfield N (2006) Prospecting in a solitary breeder: chick production elicits territorial intrusions in common loons. *Behav Ecol* 17(6):881–888. <https://doi.org/10.1093/beheco/arl021>
- Ponchon A, Grémillet D, Doligez B, Chambert T, Tveraa T, González-Solis J, Boulinier T (2013) Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives. *Methods Ecol Evol* 4(2):143–150. <https://doi.org/10.1111/j.2041-210x.2012.00259.x>
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.cran.r-project.org>
- Reed JM, Boulinier T, Danchin E, Oring LW (1999) Informed dispersal: prospecting by birds for breeding site. *Curr Ornithol* 15:189–259
- Robert A, Paiva V (2014) Nest fidelity is driven by multi-scale information in a long-lived seabird. *Proc R Soc B* 281(1793):20141692. <https://doi.org/10.1098/rspb.2014.1692>
- Rocamora G, Yeatman-Berthelot D (2009) Family Dicruridae (drongos). In: del Hoyo J, Elliot A, Christie DA (eds) Handbook of the birds of the world, 14th edn. Lynx Edicions, Barcelona, pp 172–271
- Schmidt KA (2001) Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. *Evol Ecol Res* 3:633–648
- Schuett W, Laaksonen J, Laaksonen T (2012) Prospecting at conspecific nests and exploration in a novel environment are associated with reproductive success in the jackdaw. *Behav Ecol Sociobiol* 66(9):1341–1350. <https://doi.org/10.1007/s00265-012-1389-1>
- Stamps J (1995) Motor learning and the value of familiar space. *Am Nat* 146(1):41–58. <https://doi.org/10.1086/285786>
- Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. *Evol Ecol* 7(6):533–555. <https://doi.org/10.1007/BF01237820>
- Switzer PV (1997) Past reproductive success affects future habitat selection. *Behav Ecol Sociobiol* 40(5):307–312. <https://doi.org/10.1007/s002650050346>
- Thompson CF, Neill AJ (1991) House wrens do not prefer clean nestboxes. *Anim Behav* 42(6):1022–1024. [https://doi.org/10.1016/S0003-3472\(05\)80157-5](https://doi.org/10.1016/S0003-3472(05)80157-5)
- Ward MP (2005) Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. *Oecologia* 145(4):650–657. <https://doi.org/10.1007/s00442-005-0179-0>
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70(1):164–168. <https://doi.org/10.2307/1938423>