Chapter 1

General introduction

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A general introduction

Individuals vary in traits associated with reproduction (McNamara and Houston 1996; Cam and Monnat 2000). For example, some individuals may be in better physiological condition, have more breeding experience and/or higher quality than conspecifics. The causes and consequences of such between-individual heterogeneity have been a central aspect in studies of animal ecology and evolution. This is because individuals of a given species are rarely equally adapted to their environments and thus show heterogeneity in breeding performance, which in turn may have a profound influence on population dynamics (Newton 1989; Smith 2004; Hochachka 2006). Furthermore, if a given trait is heritable, heterogeneity in breeding performance may lead to a genetic covariance between the trait and fitness (Falconer and Mackay 1996). Therefore, phenotypic evolution can be expected in that trait. For example, the parturition date of red squirrels (*Tamiasciurus hudsonicus*) appears to be under consistent directional selection, where earlier breeders obtain a better breeding performance (Réale et al. 2003). As a result, population-level breeding has been shown to commence progressively earlier due to individual plasticity and the genetic changes among generations (Réale et al. 2003). These results indicate that estimating the variation among individuals in the expression of traits associated with individual fitness is critical in understanding population dynamics, population genetic structure, and evolutionary change.

Individuals may also experience different environmental and/or social contexts, which may influence their breeding strategies. With regard to environmental contexts, one common pattern in the seasonal environment is the deterioration of environment across the time of the breeding season due to, for example, lower food availability and/or increased predation pressure over time (Hedgren and Linman 1979; H G Smith 1993; Naef-Daenzer et al. 2001; Verboven, Tinbergen, Verhulst, et al. 2001; Gotmark 2002; Grüebler and Naef-Daenzer 2008). Individuals that are in better condition and have the ability to breed earlier may prefer to breed earlier (Møller et al. 2004; Ninni et al. 2004), because they can breed in a better environment in terms of more food and less predation. Moreover, the benefit of the selected breeding strategy for individuals may also depend on the decision made by other conspecifics (Smith 1974; Dominey 1984). If most individuals in the population select the same time to breed, it may lead to high competition during that period, which may be disadvantageous for individuals that are less competitive. Furthermore, breeding at the same time may also be disadvantageous for low
quality males because they may have a higher likelihood of being cuckolded since extra-pair mating may increase with high levels of breeding synchrony (Stutchbury and Morton 1995). For example, a study on ground tits (Parus humilis) reports that breeding synchrony on the individual-level (between female and her extra-pair partner), but not on the population level, predicts the probability of extra-pair paternity (Wang and Lu 2014).

Once the breeding has commenced, males may also face an energetic and temporal trade-off between different breeding activities, such as caring for their own brood or seeking extra-pair matings (mate-parenting trade-off hypothesis, reviewed in Magrath and Komdeur 2003, Stiver and Alonzo 2009). High quality males may spend more effort in seeking extra-pair matings than low quality males, because they probably are less likely to be cuckolded by their partners and, by doing this, they can achieve relatively greater reproductive success. This is supported by many studies that demonstrate reduced paternal care in males with experimentally-increased attractiveness (e.g. Qvarnström 1997), or increased paternal care in males with experimentally-reduced attractiveness (e.g. Sanz 2001; Hasegawa and Arai 2015). Meanwhile, social context can also influence whether and to what extent males engage in extra-pair mating efforts, since potential extra-pair mating opportunities are influenced by breeding density and the degree of breeding synchrony in the local population (Chuang et al. 1999; Richardson and Burke 2001; Wang and Lu 2014). Therefore, individuals may determine their breeding strategy based on both their own condition and the contexts they experience (McNamara and Houston 1996). Natural selection should favour those individuals who can adopt the best breeding strategy for themselves in order to maximize their fitness.

**Aim of the study**

In this thesis, I studied how individual body condition, breeding experience and male quality influenced the breeding strategy of a migratory Asian passerine, the hair-crested drongo (Dicrurus hottentottus), under different environmental and social contexts. I focused on the determination and influence of the timing of breeding, the effect of mate retention and breeding experience on breeding performance, and the trade-off between caring for own brood and seeking additional extra-pair matings in males. I also experimentally investigated the cost of (potential) territory competition from conspecifics as the proximate reason for a unique behaviour, nest-dismantling (parents dismantle their nest after breeding).
The aims of this study was: (i) to understand whether hair-crested drongos adopted the best breeding strategy based on their own condition and the environmental and/or social contexts that they experience, and (ii) to explore whether individuals benefited from their breeding strategy in terms of obtaining a higher fitness. The specific aims of each chapter will be explained in more detail in the thesis outline below.

**Study area and species**

This study was conducted at Dongzhai National Nature Reserve in the Dabieshan Mountains, in central China (Dongzhai, Henan Province, 31.95° N, 114.25° E, elevation 100-840 m, Figure 1.1). The field-based data were collected every year from early May to early August between 2008 and 2015 in a broadleaf forest of approximately 400 ha.

Hair-crested drongos are medium-sized insectivorous songbirds in which males are slightly larger and brighter than females (Chen and Luo 1998) (Figure 1.2). The species is distributed in the eastern South Asia, southern and eastern East Asia and Southeast Asia (Figure 1.1). The breeding population in central and southern China (including our study site), is thought to overwinter in Indochina (Rocamora and Yeatman-Berthelot 2009). Birds arrive in late April at our study site, and leave before the middle of October (Z Gao et al. 2006). They have high breeding site fidelity with 91.7% of males (N = 134) and 82.5% of females (N = 120) reusing the same breeding site upon returning the next year. Individuals build nests either in trees in the vicinity of the previous nest tree, reuse the same nest tree, or sometimes even the same tree branch. Hair-crested drongos are highly faithful to their mates and form relatively long-term socially monogamous pair bonds (average length of pair-bond duration: 2.69 ± 0.13, mean ± SE, N = 61, range 2-6 years). If both mates survive to the next breeding season, only 13.1% of the total breeding pairs (N = 107) split up to breed with a new partner (L. Lv, unpublished data). Females are faithful to their social partners and 90.7% of offspring are produced by the social father (690 offspring of 228 broods; L. Lv, unpublished data).

Breeding starts about one week after arrival at the breeding site. Both parents participate almost equally in all breeding activities, including nest building, incubation and feeding of offspring (Chen and Luo 1998). The cup-shaped nest (Figure 1-2) is built near the end of a branch in the middle canopy of the tree with an average nest height of 8.3 ± 0.6 m (mean ± SE, N = 50; A. Cantrell unpublished data). The nest, which is made mainly of fine grass stems and rootlets, is attached
firmed in a tree crotch (Du and Zhang 1985). Modal clutch size is four (75.6%, range 3-5, $N = 275$), and both median incubation period and nestling period are around 17 days (L. Lv, unpublished data). The hatching rate was high (92.8%, $N = 484$ eggs, L. Lv, unpublished data) and, due to an abundance of food, no nestlings died of starvation in our study population if they were not predated over the period of study (208 nests monitored from hatching to fledgling). The main reason for unsuccessful breeding is nest predation by e.g. Eurasian Jays ($Garrulus glandarius$) and Besra Sparrow Hawks ($Accipiter virgatus$) (L. Lv 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 one fledgling ($N = 464$). The species is generally single-brooded but 18.3% of the breeding pairs (in total, $N = 120$) engage in another breeding attempt if their first clutch fails. Breeding pairs sometimes reuse their first nest and lay replacement clutches, but in most cases (72%, $N = 25$) they will rebuild a new nest on the same nest tree or another tree nearby. Furthermore, individuals will reuse the nest material for building the replacement nest.

After the chicks fledge, birds live in a family group and parents keep feeding fledglings for up to 50 days (Rocamora and Yeatman-Berthelot 2009). After the breeding attempt has finished, either through nestling fledging or nest failure, breeding pairs show a unique behaviour of nest-dismantling, which has rarely been reported in other species (Islam 1989). It takes about two weeks and both of the parents participate. The interesting feature of this behaviour is that parents always dismantle their nest when breeding has finished (no more replacement clutches) and do not reuse the nest material for a new nest (see more in chapter 5). Birds leave the study area in late September and early October. The latest records of birds present in the study area are from mid-October (L. Lv unpublished data).
Figure 1.1 The distribution of the hair-crested drongo (*Dicrurus hottentottus*) and the location of study site. The wintering area of the studied population is also indicated.

Figure 1.2 Hair-crested drongo and its nest with clutch.
Thesis outline

In Chapter 2, we find a consistent negative relation between timing of breeding and breeding performance among years in the hair-crested drongo. We test whether this negative relationship is due to the deteriorating breeding environment over a breeding season (the “date hypothesis”), or to individuals of better quality breeding earlier (the “quality hypothesis”), or to a combination of both. A novel comparative method, which compares the reproductive success of the same perennial pair (pairs of mate retention over years) in the year of their earlier breeding with the reproductive success in the year of later breeding, is used.

In Chapter 3, we examine whether perennial pairs, breeding with the same mate from previous year, perform better than newly formed pairs, and if so, whether this is due to perennial pairs consisting of more individuals of better condition than newly formed pairs. In addition, we explore how the condition of new male or female mates, breeding experience, influences the breeding performance. We also test whether breeding pairs perform better if they have longer pair-bond duration.

In Chapter 4, we investigate how male quality influences the trade-off between parenting and mating efforts considering the availability of extra-pair mating opportunities. If the parental-mating trade-off hypothesis, which proposes that high quality males should provide less parental care when they have additional mating opportunities, is supported, we would expect to see how males adjust their incubation behaviour to spend more time in mating efforts. We also test how the females respond in terms of incubation time to the decreased incubation attendance of their high quality partners.

In Chapter 5, we test whether hair-crested drongos dismantle their nest in order to decrease the potential intra-specific competition for territories from conspecifics that use the presence of a nest as a cue to select suitable territories for the next year. We discuss how breeding performance is related to the probability of reusing territories, and therefore influences the decision and speed of nest dismantling. We test whether experimentally strengthened nests can lead to higher competition for territories in the following breeding season and thereafter negatively influence the previous territory owners reusing the territories and their subsequent breeding performance.

In Chapter 6, I provide a synthesis to summarize and discuss the main results of this thesis and suggest potential areas for future research.