Local resource competition affects sex allocation in a bird: experimental evidence

Zitan Song [a, b, 1], Yingqiang Lou [b, c, 1], Yiping Hu [b, e], Qiuxiang Deng [d], Wei Gao [f, †], Keqin Zhang [b, *]

[a] School of Nature Conservation, Beijing Forestry University, Beijing, China
[b] School of Zoological Science, Jilin Agricultural Science and Technology College, Jilin, China
[c] Institute of Zoology, Chinese Academy of Sciences, Beijing, China
[d] College of Chemistry and Biology, Beihua University, Jilin, China
[e] Department of Biology, Hainan Normal University, Haikou, China
[f] School of Life Sciences, Northeast Normal University, Changchun, China

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Sex allocation theory as applied to local resource competition (LRC) predicts that parents should skew investment towards philopatric offspring when local resources are abundant. Alternatively, parents should allocate resources to the dispersing sex when local resources are deficient in order to limit competition among relatives. Nest sites have been shown to be the primary factor limiting populations of secondary cavity-nesting birds. In this study, we manipulated nestbox density to test its effect on the sex allocation patterns of the great tit, Parus major, a species in which female offspring are more likely to disperse than male offspring. We also investigated the relationship between the brood sex ratio and the time of breeding, which has been shown in many studies to influence sex allocation. Consistent with the LRC prediction, parents invested more in male offspring and produced a male-biased sex ratio in the area where nestboxes were abundant. In our study, the reproductive success of great tits declined as the season progressed; however, the time of breeding had no effect on the sex ratio of the offspring. Overall, the results of our study suggest that nestbox availability can influence sex allocation in great tits, and may also represent a relatively common phenomenon in other secondary cavity-nesting birds.
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Sex allocation theory predicts that females are selected to bias offspring sex ratios through their ability to differentially invest and allocate resources between male and female offspring, thereby leading to an increase in reproductive success and fitness benefit (Charnov, 1979; Trivers & Willard, 1973). In most simultaneous hermaphroditic species, males of the highest quality and status will be successful in fighting and breeding (Fiske, Rintamäki, & Karvonen, 1998; West & Sheldon, 2002). Males often compete for territory and mates, and more dominant males are often more successful at defending territories (Wiley & Poston, 1996; Wong & Candolin, 2005) leading to higher rates of mating success (Møller, 1988; Smith, 1988). Hence parents in good condition should invest more in male offspring in order to have greater fitness return. Most current evidence supports sex allocation theory in invertebrates (West & Sheldon, 2002; West, Shuker, & Sheldon, 2005) while evidence in vertebrates, such as birds and mammals, is ambiguous (Cockburn, Legge, & Double, 2002). However, the scarcity of empirical evidence in vertebrates may be the result of multiple factors including the influence of longer and more complex life histories or variation in the environmental predictability of an individual's habitat (Booksmythe, Schwanz, & Kokko, 2013; Sheldon, 1998; West, Herre, & Sheldon, 2000; West et al., 2005).

There are two primary theoretical frameworks for sex allocation. (1) The Trivers − Willard hypothesis (TWH) states that higher quality females will produce higher quality offspring and male offspring, in particular, will have higher reproductive success than female offspring (Carranza, 2002). Therefore, females in good condition should favour a male-biased sex ratio (Trivers & Willard, 1973). The TWH has been confirmed in a wide range of vertebrate species, such as primates (Meikle, Tilford, & Vessey, 1984; Silk, Clark-Wheatley, Rodman, & Samuels, 1981), ungulates (Clutton-Brock, Albon, & Guinness, 1984, 1986), marsupials (Austad &

Sunquist, 1986; Cockburn, 1990) and birds (Kilner, 1998; Pike & Petrie, 2005). (2) The local mate competition (LMC) hypothesis postulates that parents should adjust the production of the dispersing sex to avoid local competition among kin for mates or resources. Hamilton (1967) first discussed the LMC hypothesis in which females selectively produce offspring of the dispersing sex, by favouring females in bird species and males in mammalian species (Greenwood, 1980). This hypothesis was subsequently extended to include other types of resources by modelling the competition among relatives for a limiting breeding resource and henceforth it was called local resource competition (LRC, Clark, 1978). There are some reports of LRC-related sex ratio adjustments among vertebrates, such as primates (Clark, 1978) and marsupials (Cockburn, Scott, & Dickman, 1985), but there have been very few studies conducted in birds. This is perhaps because birds rarely experience limitation of local resources because of their high mobility.

It has generally been argued that nest site availability limits the population and the reproduction of cavity-nesting birds (von Haartman, 1957; Newton, 1994), particularly in secondary cavity-nesting birds (Cody, 1985; Miller, 2010; Wiebe, 2011). Secondary cavity nesters, unlike other types of cavity nesters, do not excavate nests and rely on existing cavities, which makes them more likely to suffer from nest site limitation (Newton, 1994; Wiebe, 2011) and face inter- or intraspecific competition for the primary breeding resource (tree cavities). Although high nest site availability can locally increase breeding densities in many bird species (Aitken & Martin, 2008; Cockle, Martin, & Drever, 2010; Enemar & Sjöstrand, 1972; Sénéchal, Gauthier, & Savard, 2008), there is no evidence for an influence on brood sex ratio. According to the LRC hypothesis, females should produce a brood with male-biased sex ratio when nesting sites are abundant. However, the alternative LMC hypothesis suggests that because an increase in the local population occupies more nest sites, females should produce a female-biased brood sex ratio to avoid mate competition and inbreeding.

We investigated these sex allocation hypotheses through a nest site addition experiment in great tits, Parus major. Additionally, we examined the relationship between sex allocation and nest site limitation. The great tit is a monogamous species with limited breeding dispersal (only 34% of females dispersed less than 100 m compared to 74% of males) and female offspring often disperse further from their natal territory (Harvey, Greenwood, & Perrins, 1979). Additionally, male offspring often face territory competition with relatives, as the availability of nest sites is a vital resource for this species. In our study, we manipulated nestbox densities to test the effect of nest site availability on the sex allocation patterns of great tits. As female great tits are more likely to disperse and males are more philopatric (Andreu & Barba, 2006), we predicted that in areas where nest sites are more abundant, females should bias brood sex ratios towards males (LRC, Clark, 1978) or females (LMC, Hamilton, 1967). Additionally, we also tested whether the offspring sex ratio was influenced by parental body condition (TWH, Trivers & Willard, 1973). Because the timing of reproduction has been shown to influence reproductive success and sex ratios, we further tested whether the timing of breeding influenced the brood sex ratios to identify the primary factors affecting sex allocation in our population.

METHODS

Study Area and Subjects

The study area was located in the eastern Changbai Mountains in the Zuojia Nature Reserve (126°5′N, 44°6′E), in Jilin Province,

China, at elevations that ranged from 200 m to 500 m above sea level. The study area has an East monsoon climate characterized by short dry summers, long cold, snowy winters and secondary stage forests (approximately 50 years old). The mean minimum temperature occurs in January (−28 °C) and the annual precipitation in this area is 674 mm. Fieldwork was conducted on three study plots that were 2 km apart to avoid interactions between sites (Pearson, 1993) without a change in habitats; the area of plots a, b and c were 49, 21 and 5 ha, respectively. We checked tree cavities excavated by various woodpeckers and other excavator species from every tree in our study area before the experiment began and found that the density of natural nest cavities was similar in the three plots (4.45, 4.43 and 4.16/ha for plots a, b and c, respectively).

Experimental Design

We manipulated the nestbox density of the three study plots to alter this local breeding resource. Nestboxes (with internal dimensions of 12×12 cm and 26 cm high with a 4 cm diameter entrance hole) made of 1.5 cm thick untreated planks were hung on trees 3.5–4 m above the ground. Nestboxes were oriented to the east-southeast, similar to the typical cavities excavated by many cavity-nesting species (Conner, 1975; McEllin, 1979; Miller, 2010; Pinkowski, 1976). A total of 200 wooden nestboxes were allocated to the plots (100, 40 and 60 nestboxes for plots a, b and c, respectively). In the abundant (A) plot c, nestboxes were installed at intervals of 20 m, which represents a higher density than is found in the wild. In the scarce treatments (S), plots a and b, nestboxes were installed at intervals of 50 m. The occupation rate of natural holes was 3.61% in our population, which is significantly lower than that of the nestboxes (Zhao et al., 2011).

Data Collection

From April 2009 to July 2010, nestboxes were checked weekly to determine the onset of egg laying, clutch size, brood size and the number of fledging chicks. During incubation, because the great tit's body condition does not differ between males and females (Norte, Ramos, Sousa, & Sheldon, 2009), we randomly caught one parent during the last 3 days of incubation and measured the body mass and tarsus length, which were used to estimate individual body condition.

Prior to the expected hatch date, the nestbox was checked daily to determine the exact date of hatching. Nestling body condition was measured at 17–19 days after the last chick in a brood hatched, and blood was collected (ca. 5–10 μl) to determine the sex of each nestling.

Molecular Sexing

Great tit nestlings were sexed by using polymerase chain reaction (PCR) to amplify part of the CHD gene; primers P8 and P2 described by Griffiths, Double, Orr, and Dawson (1998) were used. The PCR products were visualized on a 2% agarose gel stained with ethidium bromide. Of all 198 nestlings sampled from 42 nests during 2009–2010, sex determination failed in only 12 cases (6%).

Statistical Analyses

The influence of study year, time of breeding and nestbox density on great tit reproductive success and the brood sex ratio (weighted by brood size) was analysed by fitting a general linear model to the data.

Body condition, which represents the health or quality of individuals in a given population, was evaluated using the residuals