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

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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 &

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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

from a linear regression of body mass against tarsus length (Johnson, Krapu, Reinecke, & Jorde, 1985). We used general linear mixed-effects models (GLMMs) to assess the effects of chick sex, nestbox density, breeding date and brood size on nestling body condition, with nestbox identity entered as a random factor. The GLMMs were fitted using the 'lme4' package, and we used Satterthwaite's approximation to calculate the degrees of freedom. The sex ratio departures from Fisher's equal sex ratio (Fisher, 1930) were analysed using a G test, and Fisher's exact test was used to compare the occupation rate of different treatments. All analyses were performed in R version 3.1.1 (R Development Core Team, http://cran.r-project.org/).

Ethical Note

The nestbox we used in this study was specifically designed for great tits and has been shown not to negatively influence reproduction (Liu, 2005). Adult great tits were caught in nests during the last 3 days of incubation to make sure the nest was not abandoned and were released immediately after the body condition measurements were collected. Blood samples of nestlings (17–19 days old) were collected from the brachial vein, which does no harm to the nestlings (all 198 nestlings fledged successfully).

RESULTS

Great tits occupied a total of 108 artificial nestboxes during 2009–2010 in our study area (50, 31 and 27 boxes in plots a, b and c, respectively). The occupation rate of nestboxes was not significantly different between the two treatment areas (A: 27/120; S: 81/280; Fisher's exact test: $P = 0.185$), but the nests in the abundant patch (2.7 nests/ha) were much denser than in the scarce patch (0.58 nests/ha).

Reproductive Success

Parental body condition had no effect on great tit reproduction (Table 1) and was not correlated with nestbox density or breeding date (density: $F_{1, 29} = 0.797$, $P = 0.379$; breeding date: $F_{1, 23} = 0.389$, $P = 0.596$). Great tit nests were more likely to be destroyed in 2010 (nest success rate: 2009: 87%, $N = 61$; 2010: 62%, $N = 47$; Table 2), and more chicks survived to fledging in 2009 (mean ± SE: 2009: 7.426 ± 0.480, $N = 61$; 2010: 5.745 ± 0.709, $N = 47$; Table 1). In addition, the nest success rate (determined by whether one or more chicks in a clutch were alive at the fledging age), clutch size, brood size and the number of fledglings were not influenced by local nestbox density (Table 1). There was a seasonal decline in great tit

Table 2
Models for the effects of parental body condition, year (2009, 2010), nestbox density (abundant, scarce) and time of breeding (Julian day) on great tit brood sex ratio and nest success rate (1/0)

	Brood sex ratio[a]			Nest success rate		
	df	F	P	df	Z	P
Parental body condition	1,17	0.717	0.717	1,29	1,479	0.139
Year	1,40	1.450	0.236	1,106	−2.924	**0.003**
Density	1,40	6.003	0.019	1,106	−0.260	0.795
Time of breeding	1,38	0.392	0.535	1,92	0.117	0.907
Year[b]	1,38	1.610	0.212	1,104	−0.573	0.566
Density[b]	1,38	5.208	**0.028**	1,104	0.338	0.736
Year * density[b]	1,38	1.209	0.279	1,104	−0.338	0.736
Time of breeding[c]	1,35	0.228	0.636	1,89	0.381	0.703
Density[c]	1,35	5.050	**0.031**	1,89	0.463	0.644
Time of breeding * density[c]	1,35	1.488	0.231	1,89	−0.394	0.694

Models were fitted with the general linear model. Significant relationships are in bold.
[a] Brood sex ratio was weighted with the brood size.
[b] Function of year, nest density and their interaction.
[c] Function of time of breeding, nest density and their interaction.

reproductive success, and this relationship remained significant when nestbox density was entered as a covariate (Table 1, Fig. 1).

Sex Allocation with LRC

We found that great tits breeding in the area with abundant nest sites produced a male-biased sex ratio (sex ratio: 0.646, $G = 5.636$, $P = 0.018$); however, there were no sex biases in the areas where nest sites were scarce (sex ratio: 0.489, $G = 0.106$, $P = 0.744$). The brood sex ratio showed a positive association with nestbox density (Fig. 2). The parental body condition, year and time of breeding had no influence on the brood sex ratio in our experiment (Table 2).
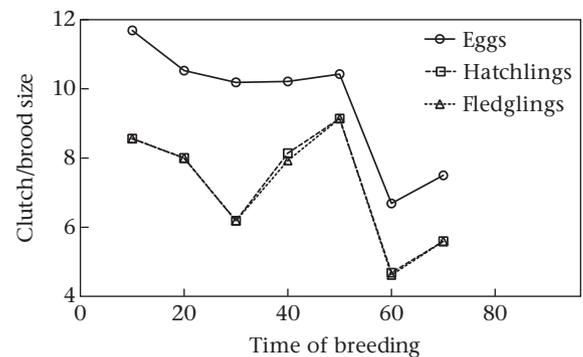
Figure 1. Association between reproductive success and the time of breeding in 2 years; the time of breeding was calculated as the Julian day.

Table 1
Models for the effects of parental body condition, year (2009, 2010), nestbox density (abundant, scarce) and time of breeding (Julian day) on great tit reproductive success

	Clutch size			Brood size			Fledging number		
	df	F	P	df	F	P	df	F	P
Parental body condition	1,29	0.499	0.486	1,29	2.544	0.122	1,29	2.544	0.122
Year	1,106	0.010	0.920	1,106	3.889	0.051	1,106	4.119	**0.045**
Density	1,106	0.153	0.696	1,106	0.426	0.515	1,106	0.571	0.452
Time of breeding	1,92	36.100	**<0.0001**	1,92	6.68	0.011	1,92	6.959	**0.001**
Year[a]	1,104	0.010	0.920	1,104	3.858	0.052	1,104	4.098	**0.046**
Density[a]	1,104	0.145	0.704	1,104	0.094	0.760	1,104	0.161	0.689
Year * density[a]	1,104	2.727	0.102	1,104	1.076	0.302	1,104	1.313	0.254
Time of breeding[b]	1,89	31.815	**<0.0001**	1,89	5.966	0.017	1,89	6.242	**0.014**
Density[b]	1,89	0.522	0.472	1,89	0.009	0.923	1,89	0.046	0.831
Time of breeding * density[b]	1,89	0.274	0.602	1,89	0.150	0.700	1,89	0.123	0.726

Models were fitted with the general linear model. Significant relationships are in bold.
[a] Function of year, nest density and their interaction.
[b] Function of time of breeding, nest density and their interaction.
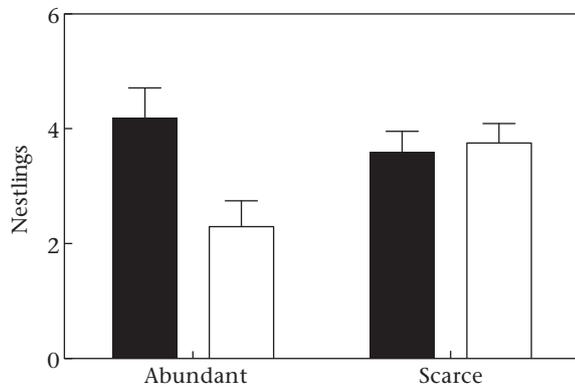
Figure 2. The mean ± SD number of sons (black bars) and daughters (white bars) in broods when nest sites were abundant or scarce.

Table 3
Generalized linear mixed models (GLMMs) of nestlings' body condition

Parameter	df	χ^2	P	Estimate	SE
Sex	1,146.02	5.096	**0.024**		
		Male		0.179	0.139
		Female		−0.073	0.112
Nestbox density	1,19.44	4.468	**0.035**		
		Abundant		0.413	0.260
		Scarce		−0.136	0.146
Sex∗Nestbox density	1,145.15	9.145	**0.010**		
		Male: abundant		0.559	0.221
		Female: abundant		0.155	0.267
		Male: scarce		−0.007	0.312
		Female: scarce		−0.192	0.315
Parental body condition	1,13.82	0.002	0.552	0.080	0.134
Time of breeding	1,19.02	0.283	0.595	−0.005	0.009
Brood size	1,17.97	0.317	0.574	−0.037	0.066
Brood sex ratio	1,18.00	0.002	0.962	−0.034	0.711

Models were fitted with the general linear mixed model, and nestbox ID was entered as a random effect. Significant relationships are in bold.
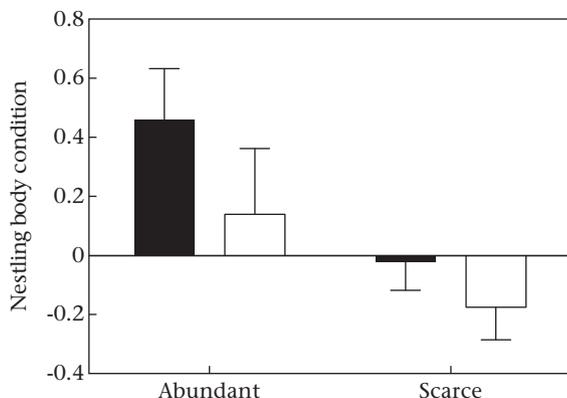
Nestling Body Condition

Sons in a brood possessed better body condition than daughters, and nestlings raised in the abundant patch were heavier than those from the scarce patches for a given tarsus length (Fig. 3, Table 3). Additionally, nestling body condition was significantly associated with the interaction between chick sex and nestbox density (Table 3). Lastly, male offspring in the abundant area had better body condition than daughters of the same brood (Fig. 3, Table 3).

DISCUSSION

Great tits responded to greater nest site availability by producing more philopatric male offspring and investing more in offspring in the area with more vacant nestboxes that could provide potential breeding opportunities, supporting the LRC hypothesis.

Previous studies of sex allocation in response to local resources in vertebrates primarily focused on the resource enhancement provided by cooperative relatives (Komdeur, Daan, Tinbergen, & Mateman, 1997; Packer & Pusey, 1987; West, 2009), whereas few studies related their findings to LRC and LMC (West et al., 2005), especially in birds (Gowaty, 1993, but criticized by Weatherhead & Montgomerie, 1995; Palmer, 2000). Selection for sex allocation depends on LRC and will be driven by competition over limited resources (Clark, 1978). However, many previous studies focused on natal dispersal (Gowaty, 1993) and the quality of the territory (West et al., 2005) which can become confounding if LRC is occurring. The occupation rate of nestboxes in our study areas (A: 22.5%; S: 28.9%)

Figure 3. The body condition (mean ± SD) of sons (black bars) and daughters (white bars) in broods when nest sites were abundant or scarce.

was much higher than that of natural nest cavities (3.61%), and the breeding density was much greater in our patches, indicating that the density of nestboxes was the primary resource limiting great tit breeding.

Like most passerines, great tit females are natal dispersers (Andreu & Barba, 2006; Greenwood & Harvey, 1982). Therefore, parents will benefit from producing male offspring in a breeding territory with less local competition, particularly competition for potential breeding opportunities. In addition, the reduction of competition over nest sites could possibly benefit male great tits more than females as males establish and defend territories (Hinde, 1952). Thus, the male-biased brood sex ratio in the area with high levels of nest site availability in our study is consistent with the LRC hypothesis of sex allocation theory. Additionally, male offspring from the abundant patch were in better condition, which also supports the LRC hypothesis.

Abundant nestboxes have the potential to increase the great tit breeding population. Additionally, since male great tits have higher natal philopatry (Andreu & Barba, 2006), male-biased broods also have the potential to increase population sizes the following year. However, great tits did not adjust the pattern of sex allocation according to the LMC hypothesis, which suggests that females should bias the sex ratio towards the more dispersing female offspring in order to reduce competition for mates and avoid inbreeding. LMC will occur in species in which natal dispersal is very small (Cremer & Heinze, 2002; Hasegawa & Yamaguchi, 1995) and the philopatric sex faces more competition over mates. Sex allocation in response to LMC is rare in vertebrates, although common in invertebrates (West et al., 2005), which may be due to their greater mobility and reduced sex-biased natal dispersal. In addition, the mating of vertebrates is controlled by complex mate choice and is less limited by population density, so that the LMC may be driven less by selection.

Another potential explanation for our observation is that the area with highest nest site availability had greater occupancy by high-quality parents. A male-biased brood sex ratio would, therefore, be a response to condition-dependent sex allocation (TWH), as high-quality parents would favour the production of more costly male offspring (Bradbury & Blakey, 1998; Pike & Petrie, 2006; Trivers & Willard, 1973). However, we did not find support for condition-dependent sex allocation in our study, as parental body condition did not affect the brood sex ratio, and the parental body condition showed no difference between the two treatments. In addition, there was no difference in reproductive success and parental body condition between the two treatments, which also

revealed territory quality (Högstedt, 1980; Johnson, 2007). The density of nestboxes therefore has an influence on the competition for nest sites by male great tits in the following year, but does not affect territory quality.

The seasonal decline in reproductive success observed in our study is relatively common in avian ecology (Decker, Conway, & Fontaine, 2012); individuals that breed early in the season may have greater experience (Nol & Smith, 1987), more abundant food (Siikamäki, 1998) and greater offspring survivorship (Smith, 1993). However, in our study, the brood sex ratio and nestling body condition were not correlated with the time of breeding, which suggests that great tits do not manipulate patterns of sex allocation in response to the time of breeding. Great tit reproduction was more successful in 2009, perhaps because of inclement weather in the winter of 2009 and spring of 2010 in our study areas. The snow cover during the winter and spring was over twice that of the previous year (Yang, Chen, Lu, & Yang, 2010), and the temperature in 2010 was much lower than in 2009 (http://www.jlqx.gov.cn). Great tits in our study area foraged on the ground half the time (Gao, Xiang, Feng, Deng, & Zhao, 1996), and it is likely that the snow cover before breeding reduced food availability, negatively affecting reproductive success. On the other hand, higher temperatures lead to greater food abundance (Bale et al., 2002), probably favouring more successful reproduction. Additionally, past studies suggest that great tits will change their laying date in response to a warmer spring (McCleery & Perrins, 1998). In our study, laying date was 14 days earlier in 2009 than 2010, and earlier laying is often associated with higher fledging success (Decker et al., 2012).

Nest site availability is the primary factor limiting the reproduction of secondary cavity-nesting birds (Miller, 2010; Newton, 1994; Wiebe, 2011), with great tits favouring male offspring in the area with abundant nest sites. To our knowledge, no study has previously investigated this pattern of sex allocation in birds. The density of nestboxes provides an excellent opportunity to manipulate potential competition for nest sites between relatives in secondary cavity-nesting species, and more studies sampling a wider range of locations and species would provide an excellent means of further investigating this pattern.

Acknowledgments

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