

Original Article

# Do sex-specific densities affect local survival of free-ranging great tits?

Stephanie P.M. Michler,<sup>a</sup> Marion Nicolaus,<sup>b</sup> Richard Ubels,<sup>a</sup> Marco van der Velde,<sup>a</sup> Christiaan Both,<sup>a</sup> Joost M. Tinbergen,<sup>a</sup> and Jan Komdeur<sup>c</sup>

<sup>a</sup>Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, the Netherlands, <sup>b</sup>Department of Behavioural Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology, Eberhard-Gwinner-Strasse 7-8, 82305 Starnberg, Germany, and <sup>c</sup>Behavioural Ecology and Self-Organisation, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, the Netherlands

Competition within sexes is expected when resources are sex specific, whereas competition between sexes can occur when similar resources are exploited. Local population density and sex ratio will determine the amount of sex-specific interactions and thus the potential degree of sex-specific competition. In contrast, high densities and the density of same-sex individuals may also positively influence survival, for example, by facilitating the exploitation of resources. The population density and sex ratio may therefore differently affect survival of males and females and thus also affect the expected fitness gains of producing a certain offspring sex. In this paper, we investigate experimentally whether and how sex-specific local densities affected sex-specific annual local survival of juvenile and adult great tits. We manipulated the density and sex ratio of fledgling great tits in 12 forest plots during 3 consecutive breeding seasons and monitored local survival until the next breeding season. We found no negative effects of the number of same- or opposite-sex competitors on juvenile local survival. Instead, local survival of juveniles of both sexes increased with the density of same-sex fledglings. Adult local survival was negatively affected by an experimental increase in density of nestlings, yet associated positively with the natural breeding pair density in a plot. Juvenile local survival related negatively to breeding pair density. Our results reveal experimental evidence for both negative effects of density on adult local survival and positive sex-specific effects on juvenile local survival, which shape sex-specific fitness prospects and might thus also alter optimal sex allocation decisions. *Key words:* between-sex competition, density dependence, intra specific competition, social environment, social interactions, within-sex competition. [*Behav Ecol* 22:869–879 (2011)]

## INTRODUCTION

Social interactions are mostly in the form of competition for resources, such as food, suitable nest sites, mating partners, territories, or roosting sites with negative effects on individual performance (Begon and Mortimer 1981; Begon et al. 1996; Newton 1998). However, positive effects of social interactions can also be observed. For instance, aggregations of individuals in flocks outside the breeding season can be beneficial for exploitation of food sources (Krebs et al. 1972) or to reduce predation risk (Caraco et al. 1980). Generally, individuals differ in traits, such as sex, size, age, ornamentation, resident status, or explorative behavior that affect their dominance, social status, and consequently their competitive ability (Ketterson 1979; Wilson 1992; Liker and Barta 2001; Dingemanse and de Goede 2004). Therefore, the relative advantage of an individual within a population will depend on the number and the traits of the other individuals present (Begon et al. 1996; Newton 1998). For instance, if resources are sex specific, competition within the sexes in a given species is expected to depend on the number of each sex in the local population. If resources are

not sex specific, the more competitive sex is expected to have an advantage. Therefore, not only the number but also the sex ratio of conspecifics at a local scale should determine the fitness prospects of males and females and thus affect for instance the intensity of sexual selection (Fitzze and Le Galliard 2008; Dreiss et al. 2010) or optimal sex allocation decisions (Alonzo and Sheldon 2010).

Key fitness components and major sources of individual variation in lifetime reproductive success are offspring survival until first reproduction and adult annual survival (Clutton-Brock 1988; Newton 1989). For numerous species, experimental approaches have shown that survival relates negatively to intraspecific competition. Density effects on juvenile survival (Ekman et al. 1981; Tinbergen et al. 1985; White and Bartmann 1998; Gundersen et al. 2002; Gunnarsson et al. 2006) and also adult survival (Ekman et al. 1981; Karels and Boonstra 2000) have been shown for several species of mammals and birds. However, other studies suggested that density-dependent survival is only found at certain spatial scales (Both and Visser 2000; Brouwer et al. 2006), which implies that competition regularly takes place at a smaller scale than the whole population. Studies that investigate survival effects of sex-specific local competition are still rare and showed negative effects of increasing same-sex densities on recruitment (Wolff et al. 2002; Wauters et al. 2004) and adult survival (Wauters et al. 2004) but also negative effects of opposite-sex densities on survival of females (Le Galliard et al. 2005). There is some evidence that females suffer from

Address correspondence to S.P.M. Michler. E-mail: s.p.m.michler@gmail.com.

Received 14 October 2010; revised 31 March 2011; accepted 6 April 2011.

competition with males, for example, females lost weight due to restricted access to high-quality wintering habitats (Marra and Holmes 2001) or feeding sites (Dunbar and Crook 1975) or showed restricted feeding rates due to high levels of competitive interactions (Benkman 1997). Positive effects of the density of same- or opposite-sex conspecifics are hardly reported in the literature. An experimental study on Townsends voles (*Microtus townsendii*) showed that the presence of same-sex siblings can have positive effects on recruitment (Lambin 1994). In summary, the current literature provides mixed evidence for sex-specific density-dependent survival; females and males might be negatively affected by competition with members of the same sex but also by competition with members of the other sex and might even benefit from high numbers of the same sex. Therefore, an experiment is needed to investigate both sex-specific and sex-unspecific density-dependent effects on survival of males and females.

The aim of our study was to test experimentally whether survival of juveniles and adults depends on age- and sex-specific densities in a wild population of great tits (*Parus major*). For this purpose, we manipulated the local social environment (density and sex ratio of fledgling great tits) at the level of forest plots during 3 consecutive breeding seasons from 2005–2007. We analyzed local survival of juvenile and adult males and females to the next year's breeding population in relation to plot density and sex ratio treatment, sex-specific competitor densities, fledgling, and adult densities.

Great tits roam around in family groups after fledging of the young (Kluyver 1951) and in late summer birds aggregate in large flocks of up to 50 (Hinde 1952) or even 60 individuals (Michler S, personal observation). There is scope for competition between and within the sexes, but the extent of both may vary with season. Male great tits engage in territorial behavior already in autumn (Kluyver 1951; Drent 1983). At this time, territory owners (Drent 1983) or birds, which had prior residency in aviary experiments, (Sandell and Smith 1991) win competitive interactions more often than birds without territory or later arriving birds. This is probably the reason why in this territorial species, males show higher natal philopatry than females (Greenwood 1980). Therefore, male juvenile great tits should be more strongly affected by higher local numbers of territorial (male) birds than female juveniles (Greenwood et al. 1979). As pair formation can take place in autumn and winter (Hinde 1952), females might compete for potential partners during this period.

During competitive interactions in autumn and winter flocks, males are dominant over females within age classes, but adults are dominant over juveniles irrespective of sex (Saitou 1979b; Drent 1983). Also during competition for artificial food (Kluyver 1957; Drent 1983; Wilson 1992) and roosting sites in winter (Kluyver 1957), males generally dominate females. Males also generally show higher levels of aggressive behavior

(Saitou 1979b; Drent 1983; Wilson 1992). This means that high local numbers and a male-biased local sex ratio are likely to relate to high levels of competition for both sexes, where juveniles are probably more affected than adults. High densities may also have positive effects on great tit survival by providing protection from predators (Götmark and Andersson 2005) or possibly facilitating the exploitation of food when individuals learn already depleted or potential new food sources by observing the behavior of others (Krebs et al. 1972).

We manipulated the density and sex ratio of nestlings to achieve biased plot compositions of fledglings (Table 1, Supplementary Material, Supplementary Figure S1). We wanted to investigate density-dependent survival in a natural population, which meant that individuals were free to move after fledging. The type, timing, and extent of resource competition or social information our manipulations created were, therefore, not under our control. The sign of the effects will however allow us to speculate about the mechanisms that contributed to the patterns in juvenile and adult local survival.

## METHODS

### Study area

The study was conducted in the Lauwersmeer area, which is situated in the northeast of The Netherlands (lat 53°23' N, long 6°14' E). In February 2005, we extended the existing study area (see Tinbergen 2005) by establishing 12 nest-box plots (Figure 1), where in some woodlots, existing boxes were rearranged, whereas in others, they were newly put up. Consequently, each of the 12 plots consisted of 50 nest-boxes in a regular 50 m grid (50 m in-between all adjacent boxes), they thus had equal nest-box densities. The woodlots were primarily deciduous forests (about 30-year old plantations of oak [*Quercus robur*], poplar species [*Populus* spp.], birch [*Betula pubescens*], maple [*Acer platanoides*], ash [*Fraxinus excelsior*], and elder [*Alnus glutinosa*]) and were separated by at least 300 m of open grassland or forest patches without boxes (Figure 1).

### Field and lab methods

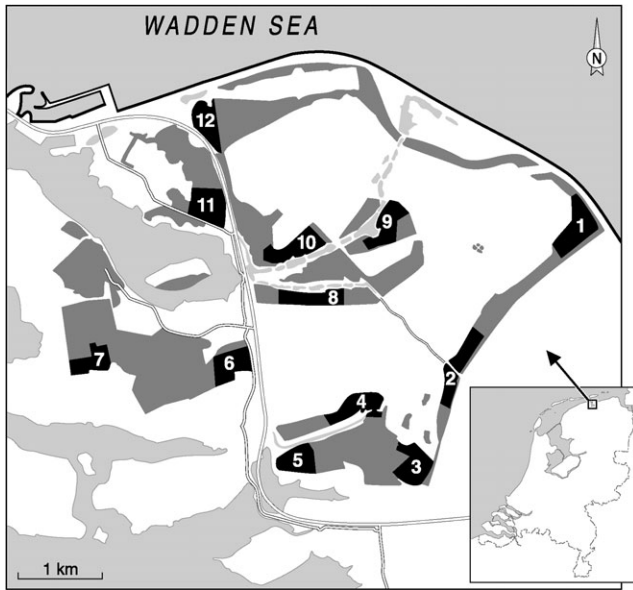
From the beginning of April, nest-boxes were checked weekly to establish the start of egg laying (back calculated assuming 1 egg was laid per day, Kluyver 1950), and the clutch size was determined after the onset of incubation. Before the expected hatching date, nest-boxes were checked daily to determine hatching date (day 0). We sampled a small quantity of blood (ca. 5–10 µl) of all nestlings when they were 2 days old by piercing their tarsal vein (with a Microlance 0.3 × 13 mm, 30G ½) and clipped the end of their toenails in a unique combination (nail clipping code) for later identification of individuals (St Louis et al. 1989). Blood was collected with

**Table 1**

**Plot sex ratio (left columns) and plot density (right columns) of nestlings at nestling age 6, 14 and at fledging per sex ratio and density treatment category**

	Female-biased plot sex ratio	Control plot sex ratio	Male-biased plot sex ratio	Kruskal–Wallis test	High-density treatment	Low density treatment	Independent <i>t</i> -test
	Mean ± SD, <i>N</i>			$\chi^2$ , df, <i>P</i>	Mean ± SD, <i>N</i>		<i>t</i> , df, <i>P</i>
Nestlings day 6	0.24 ± 0.01, 12	0.49 ± 0.01, 12	0.75 ± 0.01, 12	16.0, 2, <b>&lt;0.001</b>	156.0 ± 35.2, 18	127.1 ± 37.0, 18	–2.52, 34, <b>0.02</b>
Nestlings day 14	0.23 ± 0.02, 12	0.49 ± 0.02, 12	0.77 ± 0.03, 12	24.0, 2, <b>&lt;0.001</b>	126.0 ± 36.1, 18	107.1 ± 26.2, 18	–1.80, 34, 0.08
Fledglings	0.23 ± 0.02, 12	0.49 ± 0.03, 12	0.76 ± 0.03, 12	24.0, 2, <b>&lt;0.001</b>	118.3 ± 36.3, 18	101.1 ± 23.9, 18	–1.68, 34, 0.10

Differences between treatment categories were tested using Kruskal–Wallis for the plot sex ratio treatment and independent *t*-test for the density treatment. Statistically significant *P* values (at the 0.05 level) are given in bold.



**Figure 1**  
Map of the study area in the Lauwersmeer (lat 53°23'N, long 6°14'E), NL. Each numbered black area (1–12) represents a forest plot with 50 nest-boxes. Water is indicated in light gray, woodlots in dark gray, and open grass-land or agricultural areas in white.

heparinized capillaries (Hirschmann, 60 µl volume, 75 mm length) and directly transferred to 100% ethanol (1.5 ml tubes). Blood sampling of nestlings that are 2 days old or younger so far has not shown adverse effects on nestling survival (Lessells et al. 1996). Between day 3 and 5, molecular sex determination was performed such that on day 6, after hatching, the sex of all nestlings was known to allow accurate sex ratio manipulation of the broods (see below). DNA was extracted using the Chelex method described by Walsh et al. (1991). Sex of the young was determined following Griffiths et al. (1998). The polymerase chain reaction products were separated by electrophoresis on a 2% agarose gel.

On day 6, nestlings received a uniquely numbered aluminum band (issued by the Dutch “Vogeltrekstation”) and were exchanged between broods of the same age to achieve brood and plot level manipulations (see experimental design below). Nestlings were transported within 30 min by car in small boxes and were kept warm using cotton wool and heat packs. We exchanged at least one nestling per brood to have comparable levels of disturbance. On day 7, parents were caught using spring traps in the nest-boxes, and they were fitted with an aluminum band and a unique combination of 3 color bands if they were previously unbanded. At day 14, all nestlings were additionally provided with 3 color bands in a unique combination with the aluminum band. Nestlings leave the nest approximately 20 days after hatching, thus we performed nest-box checks every second day from day 19 onward to determine successful fledging of nestlings and to identify dead individuals that remained in the nest-box.

**Experimental design**

*Plot level manipulation*

We simultaneously manipulated density (number of nestlings) and sex ratio (proportion of male) of nestling great tits in 12 plots over 3 years (2005, 2006, and 2007) by manipulating broods within plots at day 6 of nestling age (see below under brood level manipulation). The aim of the experiment was to

PLOT TREATMENTS		BROOD TREATMENTS		
Plot sex ratio (males %)	Plot density	% of brood size treatments within plots		
Female biased 25%	low	FR: 60%	FC: 20%	FE: 20%
	high	FR: 20%	FC: 20%	FE: 60%
Balanced sex ratio 50%	low	BR: 60%	BC: 20%	BE: 20%
	high	BR: 20%	BC: 20%	BE: 60%
Male biased 75%	low	MR: 60%	MC: 20%	ME: 20%
	high	MR: 20%	MC: 20%	ME: 60%

**Figure 2**  
Experimental treatments applied to plots during the 3 years (2005–2007) combining sex ratio and density of juvenile great tits. The density treatment at the plot level was achieved by manipulating 60% of the broods within a plot toward the desired treatment keeping 40% of the nests as controls for the other treatments. Sex ratio treatment for all broods within a plot was in the direction of the plot treatment. F: female-biased brood, B: balanced (control) sex ratio brood, and M: male-biased brood; R: reduced brood size, C: control brood size, and E: enlarged brood size.

manipulate both the number and the sex ratio of fledglings per plot to create different social environments that juveniles experience after leaving the nest. Plot sex ratio treatments were either male biased (75% male young), female biased (25% males) or control (50% males), and the plot density treatments were high (increased number of young) or low density (reduced number of young). We had 6 different combinations of plot sex ratio and plot density treatments, thereby creating a gradient from female-biased low density to male-biased high-density environments (Figure 2). Each treatment combination occurred in 2 replicates per year and was semi-randomly allocated to plots each year (not allowing for a plot to have the same combination in consecutive years). The randomization of plot treatments in every year ensured that treatment effects were not obscured by plot effects, such as plot quality, the distance to other plots, or the degree of isolation.

The plot sex ratio treatment resulted in 3 categories that differed in final nestling sex ratio at day 6, 14 and in fledgling sex ratio (Table 1). The natural plot sex ratio and the final experimental plot sex ratio at day 6 did not correlate (Spearman rank correlation,  $r_s = 0.23$ ,  $n = 24$ ,  $P = 0.280$ ). The density treatment categories significantly differed in final nestling density at day 6, but due to mortality in the nest, low- and high-density plots did not differ significantly in the density of nestlings at day 14 and of fledglings (Table 1). The experimental plot density of nestlings at day 6 and of fledglings was correlated with the natural density of nestlings at day 6 within a year (Table 3). This was mainly because not all broods were biased in the direction of the plot treatment (Figure 2, see also METHODS under “brood level manipulation”).

Observation of color-banded juveniles in the post-fledging period in 2005 and 2006 (June–October) revealed that the experiment had produced differences between female-biased and male-biased plots in the number of male juveniles that were visible at least until September in both years (Supplementary Material, Supplementary Figure S1). The number of female juveniles observed in the post-fledging phase in and around nest-box plots differed for the plot sex ratio treatment categories in June but disappeared in later months (Supplementary Material, Supplementary Figure S1). This is probably because female young move larger distances than male young from the natal habitat already shortly after fledging (Dhondt 1979; Drent 1984).



### Brood level manipulation

To achieve the plot treatments, first broods (broods that started less than 30 days after the start of the very first brood in that year) within plots were manipulated on day 6 after hatching to receive the brood treatment that corresponded to the plot treatment (Figure 2). For the sex ratio, this meant that all broods within a plot were manipulated in the direction of the plot treatment (Figure 2), and thus, broods were manipulated to contain on average 25% male young in female-biased plots, 50% in control plots, and 75% in male-biased plots. The plot density manipulation was achieved by manipulating 60% of the broods within plots in the desired direction (Figure 2), for example, for a high-density plot treatment, most broods in the plot were increased, and we kept 20% of broods per plot as opposite brood treatment controls (reduced brood size for high-density plots) and 20% as real controls (average brood size for a year). In this way, the brood size treatment effect could be estimated independently from the plot density treatment effect. Brood size treatments were assigned to nests within plots before clutch completion such that treatment groups were equally distributed over the season but were otherwise randomly assigned to nest-box numbers. The brood sizes were based on the average yearly brood size for control broods and a manipulation of  $\pm 3$  young for enlarged or reduced broods, respectively (Supplementary Material, Supplementary Table S1). Nestlings of the corresponding sex were chosen randomly for exchange between broods based on their nail clipping code. For further details on the experimental manipulation, see also Nicolaus et al. (2009). Average brood sex ratio, brood size, plot density, and plot sex ratio before and after manipulation (at day 6) per year and per brood or plot treatment category are given in Supplementary Material, Supplementary Table S1. Second broods and replacement broods of known first broods after failure were left unmanipulated. The general handling of birds and the experiments complied with the current Dutch law (DEC nr. 4114B).

### Data selection and analyses

We analyzed annual local survival probability for all first brood juvenile great tits that were known to have fledged ( $n = 3950$ ) and for all adults that were identified as social parents (attending parents) of a first brood in 2005–2007 ( $n = 1233$ ). Individuals were scored as being alive in the subsequent breeding season (2006–2008) if they were recorded as a breeder in our study area. Breeding dispersal between plots in our population was low (5%). The resighting probability for adults over the years 2005–2008 (estimated with program MARK) differed between the sexes (Supplementary Material, Supplementary Table S2, model 4 vs. model 5) but did not vary between years (Supplementary Material, Supplementary Table S2, model 4 vs. model 2). Adult females had a resighting probability of  $1 \pm 0.000001$  and adult males of  $0.89 \pm 0.05$  (estimates from model 1, Supplementary Material, Supplementary Table S2). Given the low adult breeding dispersal ( $125 \text{ m} \pm 237$  standard deviation [SD]) and the high adult resighting probabilities, our mixed model estimates of adult annual local survival are probably close to actual survival. Natal dispersal of juveniles between plots was high (70%). The mean natal dispersal distance over the years 2006–2008 was  $1281 \text{ m} \pm 1051$  SD (females:  $1450.42 \text{ m} \pm 68.69$  standard error [SE], males:  $1106.46 \text{ m} \pm 69.58$  SE, see also Supplementary Material, Supplementary Table S3). Although our study area is relatively large (ca.  $33 \text{ km}^2$ ) and rather isolated (next biggest forest, ca. 4 km away) the estimates of local survival will thus probably be lowered by dispersal out of the study area. The randomi-

zation of a plot's treatment between years and the 2 treatment replicates within years should however have minimized the dispersal effects due to specific properties of the plots.

Our data set has a hierarchical structure with individuals nested within broods, within cohorts (all broods within a plot in a given year), and within plots. Therefore, we used a mixed model approach in MLwiN 2.0 (Rasbash et al. 2004) to analyze individual local survival probability as binomial response variable with a logit link error function with individual, brood, cohort, and plot as random effects. For the analysis of adult local survival, the male and the female parent of the same brood were nested within brood. Adults can enter the data set as a breeder in more than 1 year ( $n = 251$ ), and therefore, we selected 1 breeding event randomly for each individual for the analysis on local adult survival ( $n = 982$ ). This random sampling procedure was repeated 3 times, and all analyses gave qualitatively the same results. Individuals from first broods that were not manipulated ( $n = 53$  juveniles,  $n = 46$  adults) were not included in the analyses.

Our aim was to investigate whether density and sex composition of plots after fledging affected local survival of juvenile and adult great tits and whether males and females were differently affected. We were thus not only interested in whether our experiment in general affected local survival but more specifically also in how the social environment we had created influenced local survival. The social environment after fledging however is composed of both natural and experimental variation in plot density and sex ratio.

Thus, to estimate sex-unspecific effects of the experimental treatments, we analyzed the plot density and sex ratio treatment (manipulation at day 6) as categorical variables. Furthermore, we analyzed several variables as different aspects of the social environment after fledging. Plot breeding pair density (based on the number of incubated first broods per plot) and plot fledgling density were analyzed as sex-unspecific aspects of the social environment. Both are probably directly experienced by fledglings and adults after leaving the nest and could affect local survival to the next year through negative or positive effects of social interactions. The breeding pair density was significantly correlated with the number of fledglings as well as with the natural and final experimental nestling density at day 6 (Table 2) but not with the density treatment (density as treatment categories; Spearman rank correlation:  $r_s = -0.158$ ,  $n = 36$ ,  $P = 0.358$ ; experimental change in nestling density, see Table 2).

To investigate the importance of the sex-specific social environment, we calculated the density of opposite-sex fledglings per plot (number of males for females and vice versa, only first brood young were used) and the density of same-sex fledglings per plot for each adult and juvenile. Same- and opposite-sex fledgling densities consist of experimental variation in plot sex ratio and plot density and natural variation in plot density of fledglings. The plot sex ratio of nestlings after manipulation at day 6 (and thus also the sex ratio treatment) correlated significantly with the same- and opposite-sex fledgling densities, but the change in nestling density (density treatment) did not correlate with same- or opposite-sex fledgling density (Table 2). Therefore, effects of same- and opposite-sex fledgling density on local annual survival can to a large part be interpreted as a causal experimental effect, although some of the variation in these measures is due to differences in natural plot density of fledglings.

We applied a stepwise forward selection procedure where year was controlled for as a factor to analyze local annual survival probability. We tested for sex (categorical with female as reference), plot density and sex ratio treatment (categorical with low and control as reference respectively), breeding pair density, fledgling density, same- and opposite-sex fledgling

**Table 2**  
**Overview of correlation coefficients between the various plot density and plot sex ratio variables from 3 years of data (2005–2007) for a Dutch great tit population**

Variables	Original nestling density d6	Change in nestling density d6	Final nestling density d6	Fledgling density	Final nestling sex ratio d6	Change in nestling sex ratio d6	No of male fledglings	No of female fledglings
Breeding pair density	$r_c = \mathbf{0.785}$ , $P < \mathbf{0.001}$	$r_c = 0.133$ , $P = 0.440$	$r_c = \mathbf{0.761}$ , $P < \mathbf{0.001}$	$r_c = \mathbf{0.365}$ , $P = \mathbf{0.029}$	$r_s = -0.179$ , $P = 0.295$	$r_s = -0.215$ , $P = 0.209$	$r_c = 0.101$ , $P = 0.559$	$r_c = 0.227$ , $P = 0.183$
Original nestling density d6	—	$r_c = -0.138$ , $P = 0.424$	$r_c = \mathbf{0.773}$ , $P < \mathbf{0.001}$	$r_c = \mathbf{0.466}$ , $P = \mathbf{0.004}$	$r_s = -0.091$ , $P = 0.598$	$r_s = -0.279$ , $P = 0.100$	$r_c = 0.084$ , $P = 0.624$	$r_c = 0.325$ , $P = 0.053$
Change in nestling density d6	—	—	$r_c = \mathbf{0.521}$ , $P = \mathbf{0.001}$	$r_c = 0.297$ , $P = 0.079$	$r_s = -0.162$ , $P = 0.344$	$r_s = -0.080$ , $P = 0.644$	$r_c = 0.076$ , $P = 0.657$	$r_c = 0.189$ , $P = 0.270$
Final nestling density d6	—	—	—	$r_c = \mathbf{0.591}$ , $P < \mathbf{0.001}$	$r_s = -0.183$ , $P = 0.286$	$r_s = -0.272$ , $P = 0.108$	$r_c = 0.122$ , $P = 0.479$	$r_c = \mathbf{0.400}$ , $P = \mathbf{0.016}$
Fledgling density	—	—	—	—	$r_s = -0.152$ , $P = 0.377$	$r_s = -0.180$ , $P = 0.294$	$r_c = 0.242$ , $P = 0.155$	$r_c = \mathbf{0.649}$ , $P < \mathbf{0.001}$
Final nestling sex ratio d6	—	—	—	—	—	$r_s = \mathbf{0.904}$ , $P < \mathbf{0.001}$	$r_s = \mathbf{0.835}$ , $P < \mathbf{0.001}$	$r_s = -\mathbf{0.843}$ , $P < \mathbf{0.001}$
Change in nestling sex ratio d6	—	—	—	—	—	—	$r_s = \mathbf{0.809}$ , $P < \mathbf{0.001}$	$r_s = -\mathbf{0.847}$ , $P < \mathbf{0.001}$
No of male fledglings	—	—	—	—	—	—	—	$r_c = -\mathbf{0.581}$ , $P < \mathbf{0.001}$

Variables analyzed are residuals corrected for year ( $n = 36$ ). Correlation coefficients given are Spearman rank correlation ( $r_s$ ) for final nestling sex ratio at day 6 (d6) and change in nestling sex ratio d6 with other variables and Pearson correlation coefficient ( $r_c$ ) for all other correlations. Statistically significant  $P$  values (at the 0.05 level) are given in bold.

density as continuous variables (all per plot within a year, centered on their population averages). We also tested interactions between sex and all continuous variables such as between sex and the density and plot sex ratio treatment. Moreover, we tested whether the brood size treatment (3 categories with control as reference) significantly affected local annual survival. Because the sex ratio of all broods within a plot was biased in the same direction, we used the variation in relative experimental brood sex ratio within plots (deviance of final brood sex ratio to final plot sex ratio at day 6) to control for the brood sex ratio manipulation. The relative experimental brood sex ratio was not significantly correlated with the original sex ratio of the brood (generalized linear model corrected for year: likelihood ratio  $\chi^2 = 3.36$ , degrees of freedom [df] = 1,  $P = 0.067$ ).

Explanatory variables that were significantly correlated with each other (Table 2) were tested separately in the models. It did not occur that more than one such variable was significant when tested individually. Wald test was applied to determine the significance of explanatory variables as they were added to the model (Rasbash et al. 2009). In some analyses, variation for some of the specified random effects could not be estimated. This indicates that there was too little variation in survival on these levels or that the underlying levels took over all the variation. Excluding levels with zero estimates from the analysis did not change the results so we always kept them in the models.

**Spatial and temporal scale of the experiment**

We manipulated sex ratio and density of nestling birds on the scale of nest-box plots with an average size of 10.29 ha  $\pm$  1.39 SD. The maximal distance between 2 plots was 5968.45 m, and the average distance between all pairs of plots was 2599 m  $\pm$  915 SD. Adjacent plots were on average 1209 m  $\pm$  291 SD apart. During the nestling phase, great tit parents were previously shown to have feeding ranges of 0.33–0.44 ha (Naef-Daenzer 2000), and during the post-fledging dependency phase, families had home ranges of around 8.3

ha (Naef-Daenzer and Gruebler 2008; Matthysen et al. 2010). Within a breeding season, we thus expected competition to take place mainly within plots because activities such as foraging during feeding of nestlings and during the first part of the post-fledging dependency phase mainly take place within nest-box plots (Michler S, personal observations). The mean natal dispersal distance was 1281 m  $\pm$  1051 SD with a maximum of 4726 m. Natal dispersal in our study site thus mostly took place between neighboring plots (Nicolaus M, Michler SPM, Jalvingh KM, Ubels R, van der Velde M, Komdeur J, Both C and Tinbergen JM, unpublished data) We therefore consider it likely that yearling birds could experience competition and gathered information on a larger scale than a single plot.

**RESULTS**

**Juvenile survival**

Juvenile local survival varied significantly between years from an average of 0.07  $\pm$  0.007 SE in the period 2005–2006 to 0.18  $\pm$  0.012 SE in 2006–2007 and to 0.10  $\pm$  0.008 SE in the period 2007–2008 (Table 3, Figure 3). Local juvenile survival was significantly affected by the brood size manipulation where nestlings from reduced broods had higher and those from enlarged broods lower survival compared with control broods (Table 3). Additionally, survival was negatively related to the number of breeding pairs in the plot of fledging (Table 3, Figure 3). The local survival of both juvenile sexes increased with the density of same-sex fledglings in the plot (Table 3, Figure 4). There was no significant interaction between year and breeding pair density (tested in final model, year  $\times$  breeding pair density:  $\chi^2 = 4.75$ , df = 2,  $P = 0.093$ ; year  $\times$  same-sex density:  $\chi^2 = 2.04$ , df = 2,  $P = 0.361$ ; and year  $\times$  brood size treatment:  $\chi^2 = 2.56$ , df = 4,  $P = 0.635$ ). We found no effect of opposite-sex fledgling density, fledgling density, the plot density treatment, or the plot sex ratio treatment on local survival, and none of these variables showed a sex-specific effect

Table 3

Model summaries of analysis on juvenile local survival, examining the effects of juvenile sex, breeding pair density, fledgling density, same-sex fledgling density, opposite-sex fledgling density, plot density, and sex ratio treatment for the 3 study years 2005–2007

Explanatory variables	$\beta$ (SE)	$\chi^2$	df	<i>P</i>
<b>Final model</b>				
Intercept	-2.49 (0.15)	273.85	1	<b>&lt;0.001</b>
Year 2006	0.73 (0.18)	20.70	2	<b>&lt;0.001</b>
Year 2007	0.53 (0.18)			
Brood size reduced	0.18 (0.14)	10.35	2	<b>0.006</b>
Brood size enlarged	-0.25 (0.14)			
Breeding pair density	-0.05 (0.01)	11.94	1	<b>&lt;0.001</b>
Same-sex fledgling density	0.004 (0.002)	6.40	1	<b>0.011</b>
Random effects $\sigma^2$ (SE)				
Plot	0.01 (0.03)	0.19	1	0.663
Cohort	0.03 (0.04)	0.56	1	0.454
Nest	0.23 (0.10)	5.40	1	0.020
<b>Rejected terms</b>				
Sex	-0.01 (0.11)	0.004	1	0.949
Sex $\times$ breeding pair density	-0.002 (0.01)	0.02	1	0.885
Sex $\times$ same-sex fledgling density	0.002 (0.004)	0.24	1	0.621
Fledgling density <sup>a</sup>	0.003 (0.003)	1.39	1	0.237
Sex $\times$ fledgling density <sup>a</sup>	0.002 (0.003)	0.37	1	0.545
Opposite-sex fledgling density <sup>b</sup>	-0.001 (0.002)	0.11	1	0.730
Sex $\times$ opposite-sex fledgling density <sup>b</sup>	0.005 (0.005)	1.02	1	0.312
Plot sex ratio female bias <sup>b</sup>	-0.002 (0.16)	0.02	2	0.987
Plot sex ratio male bias <sup>b</sup>	-0.02 (0.16)			
Sex $\times$ plot sex ratio female bias <sup>b</sup>	-0.11 (0.28)	0.59	2	0.746
Sex $\times$ plot sex ratio male bias <sup>b</sup>	0.12 (0.28)			
Density treatment	0.18 (0.14)	1.76	1	0.185
Sex $\times$ density treatment	0.06 (0.22)	0.07	1	0.787

Survival was corrected for year differences and the brood size treatment. Explanatory variables were tested sequentially, and correlated variables were not tested in the same model. Summaries are derived from the binomial response mixed-modeling procedure in MLwiN,  $n = 3950$ . Statistically significant *P* values are given in bold.

<sup>a</sup> Tested in model correcting for the factors year and brood size treatment.

<sup>b</sup> Tested in model correcting for the factors year, breeding pair density, and brood size treatment.

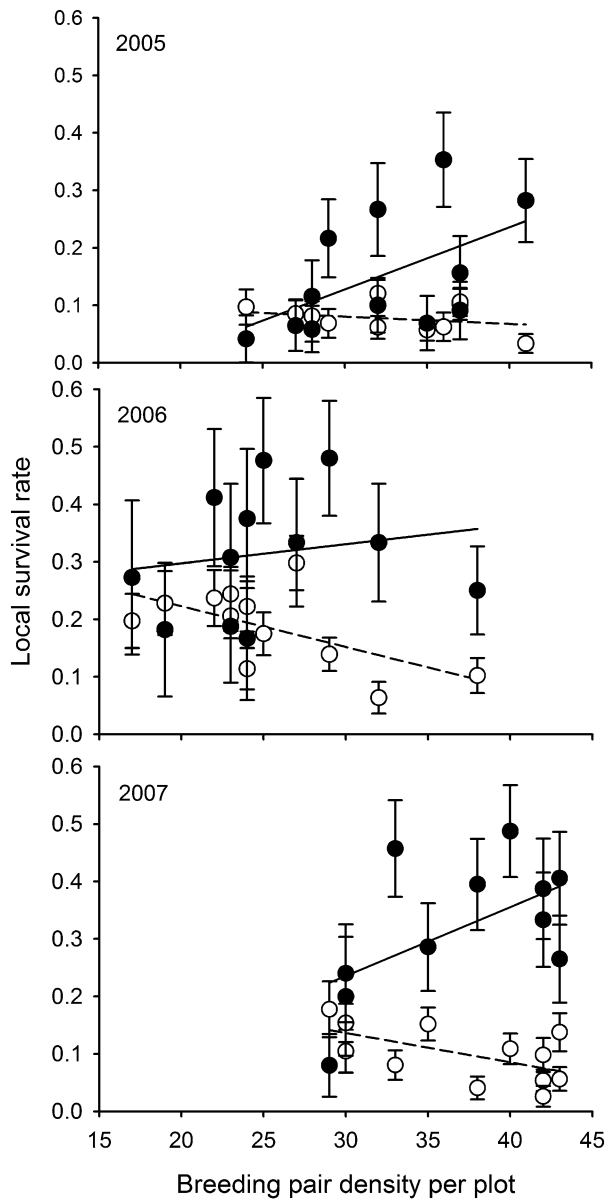
(Table 3). The relative experimental brood sex ratio did not significantly affect survival (in final model:  $\beta = 0.18 \pm 0.62$  SE,  $\chi^2 = 0.09$ ,  $df = 1$ ,  $P = 0.768$ ) and did not change the importance of variables in the final model (same-sex fledgling density:  $\chi^2 = 4.06$ ,  $df = 1$ ,  $P = 0.044$ ; breeding pair density:  $\chi^2 = 11.88$ ,  $df = 1$ ,  $P = 0.001$ ; and brood size treatment:  $\chi^2 = 10.38$ ,  $df = 2$ ,  $P = 0.005$ ). In summary, juvenile annual local survival was negatively affected by an increase in brood size, negatively related to the density of adult birds but positively related to the density of fledglings of their own sex, and there were large differences between years.

An analysis of natal dispersal distance (Supplementary Material, Supplementary Table S3) showed that females had significantly larger natal dispersal distances than males within our study area, but natal dispersal distance was not related to fledgling density, breeding pair density, same-sex fledgling density, opposite-sex fledgling density, plot sex ratio, or plot density treatment, and none of these variables significantly interacted with sex. This suggests that our results on local survival are not simply caused by selective dispersal out of the study area.

### Adult survival

Adult local survival to the next breeding season varied significantly between years ranging from an average of  $0.16 \pm 0.02$  SE during the period 2005–2006 to  $0.32 \pm 0.03$  SE from 2006–2007 and to  $0.35 \pm 0.02$  SE from 2007–2008 (Table 4, Figure 3). The experimental plot density treatment affected both male and female adult local survival negatively

(Table 4). When we controlled for the brood size treatment, the manipulation that was used to create differences in densities, the effect of plot density treatment remained almost significant ( $\beta = -0.34 \pm 0.19$  SE,  $\chi^2 = 3.36$ ,  $df = 1$ ,  $P = 0.066$ ). The brood size treatment effect alone had no significant effect on survival of adults (reduced:  $\beta = 0.30 \pm 0.20$  SE, enlarged:  $\beta = -0.21 \pm 0.21$  SE;  $\chi^2 = 2.20$ ,  $df = 2$ ,  $P = 0.332$ ). Therefore, the negative effect of the density treatment on adult survival might to a small extent be due to the fact that the majority of broods in plots with increased density of nestlings received additional young in the nest, which generated some survival costs for parents. The survival to the next year for both adult sexes was significantly positively related to the breeding pair density of the plot in which an adult had bred (Table 4, Figure 3). Both the relation with breeding pair density and the effect of the density treatment did not vary between years (tested in final model, year  $\times$  breeding pair density:  $\chi^2 = 4.18$ ,  $df = 2$ ,  $P = 0.124$ ; year  $\times$  density treatment:  $\chi^2 = 0.37$ ,  $df = 2$ ,  $P = 0.832$ ). Adult survival did not vary significantly with the plot fledgling density, same- or opposite-sex fledgling density, or the plot sex ratio treatment (Table 4). There were no sex-specific effects of the plot density and the plot sex ratio treatment and no difference between the sexes in the correlation of adult local survival with breeding pair density, fledgling density, and same-sex or opposite-sex fledgling density (Table 4). Including the nonsignificant relative experimental brood sex ratio ( $\beta = -0.46 \pm 0.80$  SE,  $\chi^2 = 0.32$ ,  $df = 1$ ,  $P = 0.570$ ) did not change the final model. Thus, adult annual local survival was positively related to high densities of adults, negatively affected by an increase in density of nestlings and varied strongly between years.



**Figure 3**  
Local survival rate to the next year's breeding season per study year (2005–2007) for adult (filled circles, solid line) and juvenile (open circles, dashed line) great tits in relation to the breeding pair density per plot. Raw data are presented, and error bars give SE for each plot. Linear regression line is based on raw data.

**DISCUSSION**

**Experimental density effects on survival**

We tested whether local survival of juvenile and adult great tits was affected by sex-specific and sex-unspecific local densities. We found that juveniles of both sexes showed lower local survival to the next year when unmanipulated breeding pair densities were high. The density and the sex ratio treatment (manipulation of nestlings) in the plot had no effect on juvenile annual local survival. However, survival of both male and female juveniles increased with the local density of fledglings of the same sex. In contrast to juveniles, adult local survival for both sexes related positively to high breeding pair densities and was negatively affected by an experimental increase in nestling density (density treatment).

**Table 4**

**Model summaries of analysis on adult local survival examining the effects of adult sex, breeding pair density, fledgling density, same-sex fledgling density, opposite-sex fledgling density, plot density, and plot sex ratio treatment for 3 study years 2005–2007**

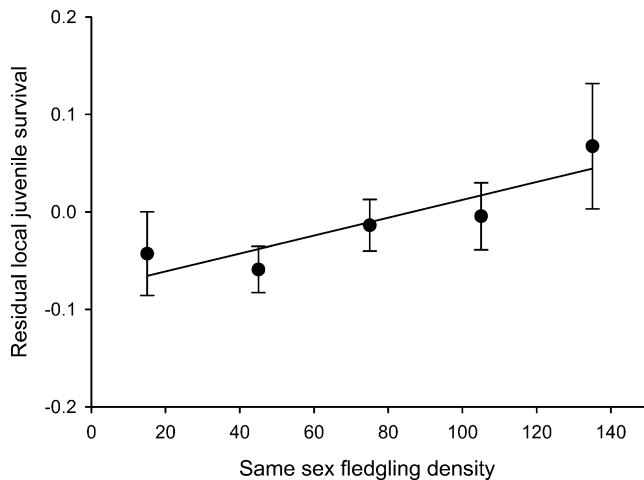
Explanatory variables	$\beta$ (SE)	$\chi^2$	df	<i>P</i>
<b>Final model</b>				
Intercept	-1.49 (0.17)	73.61	1	<b>&lt;0.001</b>
Year 2006	1.21 (0.25)	29.03	2	<b>&lt;0.001</b>
Year 2007	0.80 (0.22)			
Breeding pair density	0.04 (0.02)	5.79	1	<b>0.016</b>
Density treatment	-0.38 (0.17)	4.94	1	<b>0.026</b>
Random effects $\sigma^2$ (SE)				
Plot	—	—	—	—
Cohort	0.05 (0.06)	0.84	1	0.360
Nest	—	—	—	—
<b>Rejected terms</b>				
Sex	-0.29 (0.15)	3.69	1	0.054
Sex $\times$ breeding pair density	-0.005 (0.02)	0.05	1	0.816
Sex $\times$ plot density treatment	-0.06 (0.30)	0.04	1	0.830
Fledgling density <sup>a</sup>	0.005 (0.003)	2.64	1	0.104
Sex $\times$ fledgling density <sup>a</sup>	0.002 (0.005)	0.21	1	0.646
Same-sex fledgling density	-0.002 (0.003)	0.50	1	0.480
Sex $\times$ same-sex fledgling density	-0.004 (0.006)	0.53	1	0.467
Opposite-sex fledgling density	0.003 (0.003)	1.68	1	0.195
Sex $\times$ opposite-sex fledgling density	0.004 (0.004)	0.94	1	0.331
Plot sex ratio female bias	0.37 (0.19)	3.51	2	0.173
Plot sex ratio male bias	0.20 (0.21)			
Sex $\times$ plot sex ratio female bias	0.69 (0.37)	3.54	2	0.170
Sex $\times$ plot sex ratio male bias	0.34 (0.38)			

Survival was corrected for year differences, and variables were tested sequentially. Correlated variables were not tested in the same model. Summaries are derived from the binominal response mixed-modeling procedure in MLwiN, *n* = 982. Statistically significant *P* values are given in bold.

<sup>a</sup> Tested while correcting for the factors year and density treatment.

Our primary aim was to manipulate fledgling densities to create substantial differences in competitive pressure to affect both juvenile and adult survival negatively. We thus need to explain why juvenile survival was not affected by the density treatment (change in density of nestlings) while parental survival was. One explanation is that the manipulation was not sufficiently strong. The density treatment had an effect on the number of nestlings, but the number of fledglings hardly differed between high and low density plots (Table 1). Lower adult survival in high-density plots might then rather be attributed to the cost of raising an enlarged brood which is more often the case in high than low density plots (supported by the reduction of density treatment effect when brood size treatment is included in the model) or to the cost of competition with neighbors who are more likely to have a large brood in high-density plots and thus need to search for nestling food at higher rates (Stoehr et al. 2001; Neuenschwander et al. 2003). However, it is also possible that adults are more affected by local changes in fledgling densities because they





**Figure 4**

Local juvenile survival probability increased with the number of same-sex fledglings per plot. Residual survival was obtained per individual from a model correcting for year, breeding pair density, and brood size treatment. For graphical representation, we present averaged residuals with SE (and fitted regression line) for 5 groups of same-sex fledgling densities (note analysis was done with same-sex fledgling densities as continuous variable). The groups were obtained by averaging at intervals of 30 units. The sample sizes of individual per group in order of increasing same-sex density are 400, 1337, 1210, 735, and 268.

may not have the option to disperse; they generally show less dispersal than juveniles (Hinde 1952; Saitou 1979a).

Juvenile survival was negatively affected by brood size enlargement which is in line with the findings of another study in our population by Nicolaus et al. (2009) which showed that brood size enlargement negatively affected fledgling mass, wing length, and nestling survival. Thus, increased competition in the nest also translated into reduced recruitment. This is probably mediated via condition as it has often been shown that lower condition results in lower local survival (Tinbergen and Boerlijst 1990; Naef-Daenzer et al. 2001; Perrins and McCleery 2001; Monros et al. 2002).

#### Negative sex-specific effects

We found no negative effects of the number of same-sex competitors on male and opposite-sex competitors on female juvenile survival, even though the biology of the species supports such predictions (see INTRODUCTION). We also found no difference between the sexes in how fledgling density, breeding pair density, same-sex fledgling density, opposite-sex fledgling density, plot density, or plot sex ratio treatment affected survival of both juveniles and adults to the next year's breeding population.

Previous experimental studies found negative effects of adult female densities for juvenile survival in gray-tailed voles (*M. canicaudus*, Wolff et al. 2002) and negative effects of same-sex density for female fitness in western mosquito fish (*Gambusia affinis*, Smith and Sargent 2006; Smith 2007). In common lizards (*Lacerta vivipara*), females had lower fitness in male-biased environments (Le Galliard et al. 2008). It is possible that in our study system, sex-specific behaviors of juveniles, especially aggressive ones, only manifested themselves after molt in late summer and autumn. By this time, the plot biases in number of male and female juveniles were weakened due to movements of birds between plots (Supplementary Material, Supplementary Figure S1). However, as the positive ef-

fect of same-sex fledgling density is indeed a sex-specific effect, another explanation is more likely, namely that juveniles in our study population distributed themselves after fledging in a way to reduce sex-specific local competition (Michler SPM, Nicolaus M, Ubels R, van der Velde M, Komdeur J, Both C and Tinbergen JM, unpublished data). In an analysis on post-fledging movements, we found that female juveniles dispersed further from male-biased plots than male juveniles in the period when males start to become territorial. This movement might allow individuals to reduce negative effects of competition. For adults, the lack of any sex-specific effects on survival might primarily be explained with their general dominance over juveniles at least until molt (Drent 1983). One would probably need to alter sex-specific adult densities to detect an effect on survival of this age class (e.g., see Le Galliard et al. 2005; Smith 2007).

Several studies of birds or mammals speculated that the evolutionary result of avoidance of harmful intersexual interactions are segregation of seasonal foraging habitats by sex (Ketterson 1979; Ardia and Bildstein 1997; Marra 2000; Breed et al. 2006), the formation of sex-specific winter flocks (Benkman 1997), or sex-specific foraging tactics (Noske 2003; Steer and Burns 2008). Although the subordinate sex may suffer negative consequences from, for example, choosing a suboptimal foraging habitat (Marra and Holmes 2001), behavioral adaptations may explain why there is only little evidence for direct negative effects of intersexual interactions on survival of the subordinate sex (Dunbar and Crook 1975; Le Galliard et al. 2006).

#### Positive sex-specific effects

The explanation for the positive effect of same-sex density on local survival of young great tits is mainly speculative. Any effect will depend on the type of interactions individuals engage in and the type of resources they compete for, in which period competition takes place and also on how long the experimental change in plot composition lasted. In addition, the effect was rather weak with 30 extra same-sex individuals per plot needed to increase survival by 10%–11%.

The first explanation is based on a descriptive model presented by Tinbergen et al. (1987). Although adult males generally succeed in defending their territories in autumn (Drent 1983), Tinbergen et al. (1987) suggested that at given densities of territorial adult males, the number of candidate males (local young or immigrants) that can settle in an area is positively related to increasing numbers of their own type. They argued that this might be because the cost for adult males to defend a large territory increases with increasing number of candidates (more competitive encounters). Consequently, established adult males should reduce the size of their territory, which would create "empty" space and allow more candidates to settle (Tinbergen et al. 1987). Therefore, local survival of young males could be enhanced when there are more individuals of their own age and sex in the local area. This may come about by 2 processes. The first requires that the sex-biased composition of the plots lasted until the territorial phase in autumn, which was the case at least for some of our study years (Supplementary Material, Supplementary Figure S1). The second entails that during post-fledging movements, males stayed together in male-biased flocks which is possible because it was shown previously that members of a summer flock can also aggregate together in autumn and winter flocks (Saitou 1979a). Although females generally do not engage in territorial activities (Drent 1983), there also can be severe skirmishes between females before the breeding period (Both C, personal observation), thus the same explanation might also apply to young females. Same-sex



associations between unrelated individuals have been reported for meadow voles *M. pennsylvanicus* (Beery et al. 2009), African wild dogs *Lycaon pictus* (de Villiers et al. 2003), and various nonhuman primate species (Vanhooff and Vanschaik 1994; Parish 1996).

A second explanation for the positive effect of same-sex densities on survival might be that growing up in a same-sex environment makes you a better competitor. Early and frequent interactions with individuals of the same sex may shape sex-specific competitive abilities of juveniles. This process may require behavioral and physiological changes in juveniles that enhance their performance in competition with older same-sex individuals or immigrants during territory establishment, fighting for food or when competing for a partner. In birds, it has been shown that early social interactions are necessary for the development of normal behavioral patterns (Groothuis and van Mulekom 1991; Groothuis 1992) and can determine subsequent social dominance (Hansen and Slagsvold 2004). However, it still needs to be established whether an increase of encounters with same-sex individuals improves sex-specific competitive performance. Although we do not know which mechanism shaped our results, our experimental study showed that the presence of conspecifics of the same age-sex class enhanced juvenile local survival.

### Natural density effects

The negative relationship between juvenile survival and local breeding pair densities and the positive relationship between adult survival and local breeding pair density were apparent in all years, although annual densities varied extensively (Figure 3).

In large herbivores, density dependent survival of yearlings is very common (Gaillard et al. 2000; Bonenfant et al. 2009) and also for various bird species, it was found that juvenile survival rates decrease with increasing population density (Arcese et al. 1992; Perdeck et al. 2000; Nicoll et al. 2003; Armstrong et al. 2005; Dimond and Armstrong 2007) and that the number of juvenile local settlers is negatively related to the density of adults (Van Balen 1980; Drent 1983; Newton and Marquiss 1986). In many of these studies, adult local survival was not correlated with population density (Newton and Marquiss 1986; Arcese et al. 1992; Nicoll et al. 2003; Dimond and Armstrong 2007), and in some, the relationship was negative (Van Balen 1980; Armstrong et al. 2005). Surprisingly, in our study, adult survival correlated positively with local densities of breeding pairs. This might be explained by plot quality traits (high food abundance, low predator density) that correlated with plot breeding pair densities and also improved local survival. We have indications that plots, which showed generally higher breeding pair densities are situated close to villages where artificial winter food is provided (Nicolaus M, 2009). If winter food or general plot quality enhances local survival, this should also apply to juveniles. It is however likely that artificial food might be easier accessed by adults as they probably have previous knowledge of food sources from earlier years or because they simply dominate juveniles in competitive interactions (Saitou 1979b; Drent 1983; Hogstad 1989). It has been shown experimentally in willow tits (*P. montanus*) that juveniles can suffer reduced survival in mixed age groups (Ekman et al. 1981) probably due to displacement by dominant adults from good foraging areas (Ekman and Askenmo 1984). Alternatively, high density of local adults may have negatively affected survival of juveniles by altering competition for nonfood related resources (roosting places or territories). In territorial species, the number of territories occupied by adults sets limits on the number of juveniles that can settle in an area as shown by adult removal experiments (Krebs

1971), and this can consequently affect juvenile survival rates (Klomp 1980). However, care needs to be taken in which period such removal is carried out as juveniles seem not always equally susceptible to competition with adults (Dimond and Armstrong 2007). Manipulating adult densities during different phases within and outside the breeding season might provide more clarity about the mechanisms involved in competition between age-classes and whether juveniles mainly suffer from competition with dominant adults for food or whether the territorial behavior of adults limits juvenile settlement.

### CONCLUSIONS

Our results confirm that not all individuals in a population are equally affected by density-dependent mechanisms and that sex-specific densities are important in determining fitness prospects of individuals. We detected a positive link between annual local survival and the densities of same-sex fledglings that can be considered causal, but the underlying mechanisms remain elusive. We therefore suggest that future studies continue to study sex-specific and sex-unspecific density effects by use of experiments and investigate the dynamics of behavioral interactions between individuals of all age and sex classes and their consequences for fitness.

### SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

### FUNDING

Grant from the Netherlands Organisation for Scientific Research (NWO-VICI, 86503003) awarded to J.K. as well as by the University of Groningen.

This study was part of S.P.M.M.'s and M.N.'s PhD work. R.U. assisted in fieldwork and managed the database. M.v.d.V. performed the molecular sexing of the nestlings. C.B. and J.M.T. collected data in the field and were involved in planning and discussion as was J.K. We thank Luc te Marvelde and Kim Meijer for assistance in the lab. Karen Bouwman and Niels Dingemanse were very valuable in discussion and in the field. We are grateful to Martin Keiser, Reinder Radersma, Tamar Lok, Jeroen Reimerink, Kirsten Jalvingh, and Alexandra Haydn as well as to all the Animal Ecology course students between 2005 and 2008 for their help in collecting the data. Finally, we thank Staatsbosbeheer and the Royal Dutch army "Koninklijke Landmacht" for their permission to work in the Lauwersmeer area and to stay in the army base.

### REFERENCES

- Alonzo SH, Sheldon BC. 2010. Population density, social behaviour and sex allocation. In: Szekely T, Komdeur J, Moore A, editors. Social behaviour: genes ecology and evolution. Cambridge: Cambridge University Press. p. 597–615.
- Arcese P, Smith JNM, Hochachka WM, Rogers CM, Ludwig D. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. *Ecology*. 73:805–822.
- Ardia DR, Bildstein KL. 1997. Sex-related differences in habitat selection in wintering American kestrels, *Falco sparverius*. *Anim Behav*. 53:1305–1311.
- Armstrong DP, Davidson RS, Perrott JK, Roygard J, Buchanan L. 2005. Density-dependent population growth in a reintroduced population of North Island saddlebacks. *J Anim Ecol*. 74:160–170.
- Beery AK, Routman DM, Zucker I. 2009. Same-sex social behavior in meadow voles: multiple and rapid formation of attachments. *Physiol Behav*. 97:52–57.
- Begon M, Harper JL, Townsend CR. 1996. Ecology: individuals, populations and communities. Oxford: Blackwell Science Ltd.
- Begon M, Mortimer M. 1981. Population ecology: a unified study of animals and plants. Oxford: Blackwell Scientific Publications.

- Benkman CW. 1997. Feeding behavior, flock-size dynamics, and variation in sexual selection in crossbills. *Auk*. 114:163–178.
- Bonenfant C, Gaillard JM, Coulson T, Festa-Bianchet M, Loison A, Garel M, Loe LE, Blanchard P, Pettorelli N, Owen-Smith N, et al. 2009. Empirical evidence of density-dependence in populations of large herbivores. *Advances in ecological research*, Vol 41. San Diego (CA): Elsevier Academic Press Inc. p. 313–357.
- Both C, Visser ME. 2000. Breeding territory size affects fitness: an experimental study on competition at the individual level. *J Anim Ecol*. 69:1021–1030.
- Breed GA, Bowen WD, McMillan JI, Leonard ML. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc R Soc Lond Ser B Biol Sci*. 273:2319–2326.
- Brouwer L, Richardson DS, Eikenaar C, Komdeur J. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. *J Anim Ecol*. 75:1321–1329.
- Caraco T, Martindale S, Pulliam HR. 1980. Avian flocking in the presence of a predator. *Nature*. 285:400–401.
- Clutton-Brock TH. 1988. *Reproductive success*. Chicago (IL): The University of Chicago Press.
- Dhondt AA. 1979. Summer dispersal and survival of juvenile great tits in southern Sweden. *Oecologia*. 42:139–157.
- Dimond WJ, Armstrong DP. 2007. Adaptive harvesting of source populations for translocation: a case study with New Zealand robins. *Conserv Biol*. 21:114–124.
- Dingemanse NJ, de Goede P. 2004. The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behav Ecol*. 15:1023–1030.
- Dreiss AN, Cote J, Richard M, Federici P, Clobert J. 2010. Age- and sex-specific response to population density and sex ratio. *Behav Ecol*. 21:356–364.
- Drent PJ. 1983. The functional ethology of territoriality in the great tit (*Parus major* L.). Groningen (The Netherlands): University of Groningen.
- Drent PJ. 1984. Mortality and dispersal in summer and its consequences for the density of great tits *Parus major* at the onset of autumn. *Ardea*. 72:127–162.
- Dunbar RIM, Crook JH. 1975. Aggression and dominance in the weaver bird, *Quelea quelea*. *Anim Behav*. 23:450–459.
- Ekman J, Cederholm G, Askenmo C. 1981. Spacing and survival in winter groups of willow tit *Parus montanus* and crested tit *P. cristatus*—a removal study. *J Anim Ecol*. 50:1–9.
- Ekman JB, Askenmo CEH. 1984. Social rank and habitat use in willow tit groups. *Anim Behav*. 32:508–514.
- Fitze PS, Le Galliard JF. 2008. Operational sex ratio, sexual conflict and the intensity of sexual selection. *Ecol Lett*. 11:432–439.
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. *Annu Rev Ecol Syst*. 31:367–393.
- Götmark F, Andersson M. 2005. Predation by sparrowhawks decreases with increased breeding density in a songbird, the great tit. *Oecologia*. 142:177–183.
- Greenwood PJ. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav*. 28:1140–1162.
- Greenwood PJ, Harvey PH, Perrins CM. 1979. The role of dispersal in the great tit (*Parus major*)—causes, consequences and heritability of natal dispersal. *J Anim Ecol*. 48:123–142.
- Griffiths R, Double MC, Orr K, Dawson RJ. 1998. A DNA test to sex most birds. *Mol Ecol*. 7:1071–1075.
- Groothuis T. 1992. The influence of social experience on the development and fixation of the form of displays in the black-headed gull. *Anim Behav*. 43:1–14.
- Groothuis T, van Mulekom L. 1991. The influence of social experience on the ontogenetic change in the relation between aggression, fear and display behavior in black-headed gulls. *Anim Behav*. 42:873–881.
- Gundersen G, Andreassen HP, Ims RA. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. *Ecol Lett*. 5:294–301.
- Gunnarsson G, Elmerg J, Sjöberg K, Pöysä H, Nummi P. 2006. Experimental evidence for density-dependent survival in mallard (*Anas platyrhynchos*) ducklings. *Oecologia*. 149:203–213.
- Hansen BT, Slagsvold T. 2004. Early learning affects social dominance: interspecifically cross-fostered tits become subdominant. *Behav Ecol*. 15:262–268.
- Hinde RA. 1952. The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour Suppl* 2:1–201.
- Hogstad O. 1989. Social-organization and dominance behavior in some *Parus* species. *Wilson Bull*. 101:254–262.
- Karels TJ, Boonstra R. 2000. Concurrent density dependence and independence in populations of arctic ground squirrels. *Nature*. 408:460–463.
- Ketterson ED. 1979. Aggressive behavior in wintering Dark-eyed Juncos—determinants of dominance and their possible relation to geographic variation in sex-ratio. *Wilson Bull*. 91:371–383.
- Klomp H. 1980. Fluctuations and stability in great tit populations. *Ardea*. 68:205–224.
- Kluyver HN. 1950. Daily routines of the great tit, *Parus major* L. *Ardea*. 38:99–135.
- Kluyver HN. 1951. The population ecology of the great tit, *Parus m. major*. *Ardea*. 39:1–135.
- Kluyver HN. 1957. Roosting habits, sexual dominance and survival in the great tit. *Cold Spring Harb Symp Quant Biol*. 22:281–285.
- Krebs JR. 1971. Territory and breeding density in great tit, *Parus major* L. *Ecology*. 52:2–22.
- Krebs JR, MacRoberts MH, Cullen JM. 1972. Flocking and feeding in great tit *Parus major*—an experimental study. *Ibis*. 114:507–781.
- Lambin X. 1994. Territory acquisition and social facilitation by litter-mate Townsends voles (*Microtus townsendii*). *Ethol Ecol Evol*. 6:213–220.
- Le Galliard JF, Cote J, Fitze PS. 2008. Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. *Ecology*. 89:56–64.
- Le Galliard J-F, Fitze PS, Ferriere R, Clobert J. 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proc Natl Acad Sci U S A*. 102:18231–18236.
- Le Galliard JF, Gundersen G, Andreassen HP, Stenseth NC. 2006. Natal dispersal, interactions among siblings and intrasexual competition. *Behav Ecol*. 17:733–740.
- Lessells CM, Mateman AC, Visser J. 1996. Great tit hatchling sex ratios. *J Avian Biol*. 27:135–142.
- Liker A, Barta Z. 2001. Male badge size predicts dominance against females in house sparrows. *Condor*. 103:151–157.
- Marra PP. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the non-breeding season. *Behav Ecol*. 11:299–308.
- Marra PP, Holmes RT. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk*. 118:92–104.
- Matthysen E, Van Overveld T, Van de Castele T, Adriaensen F. 2010. Family movements before independence influence natal dispersal in a territorial songbird. *Oecologia*. 162:591–597.
- Monros JS, Belda EJ, Barba E. 2002. Post-fledging survival of individual great tits: the effect of hatching date and fledging mass. *Oikos*. 99:481–488.
- Naef-Daenzer B. 2000. Patch time allocation and patch sampling by foraging great and blue tits. *Anim Behav*. 59:989–999.
- Naef-Daenzer B, Grüebler MU. 2008. Post-fledging range use of great tit *Parus major* families in relation to chick body condition. *Ardea*. 96:181–190.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. *J Anim Ecol*. 70:730–738.
- Neuenschwander S, Brinkhof MWG, Kölliker M, Richner H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behav Ecol*. 14:457–462.
- Newton I. 1989. *Lifetime reproduction in birds*. London: Academic Press.
- Newton I. 1998. *Population limitations in birds*. London: Academic Press.
- Newton I, Marquiss M. 1986. Population regulation in sparrowhawks. *J Anim Ecol*. 55:463–480.
- Nicolaus M. 2009. *Reproductive rates under competition*. Groningen (Netherlands): University of Groningen.
- Nicolaus M, Michler SPM, Übels R, van der Velde M, Komdeur J, Both C, Tinbergen JM. 2009. Sex-specific effects of altered competition on nestling growth and survival: an experimental manipulation of brood size and sex ratio. *J Anim Ecol*. 78:414–426.
- Nicoll MAC, Jones CG, Norris K. 2003. Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for

- non-linear density dependence and environmental stochasticity. *J Anim Ecol.* 72:917–926.
- Noske RA. 2003. Sexual differences in the foraging behaviour of Crested Shrike-tits, *Falunculus frontatus*, during winter. *Emu.* 103:271–277.
- Parish AR. 1996. Female relationships in bonobos (*Pan paniscus*)—evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Hum Nat.* 7:61–96.
- Perdeck AC, Visser ME, Van Balen JH. 2000. Great tit *Parus major* survival, and the beech-crop cycle. *Ardea.* 88:99–108.
- Perrins CM, McCleery RH. 2001. The effect of fledging mass on the lives of great tits *Parus major*. *Ardea.* 89:135–142.
- Rashbash J, Steele F, Browne WJ, Goldstein H. 2009. A user's guide to MLwiN, version 2.10. Centre for Multilevel Modelling, Bristol (UK): University of Bristol.
- Rashbash J, Steele F, Browne W, Prosser B. 2004. A user's guide to MLwiN, version 2.0. centre for Multilevel Modelling, Institute of Education, London: University of London.
- Saitou T. 1979a. Ecological study of social organization in the great tit (*Parus major*) II. Formation of the basic flock. *J Yamashina Inst Ornithol.* 11:137–148.
- Saitou T. 1979b. Ecological study of social organization in the great tit (*Parus major*) III. Home range of the basic flocks and dominance relationship of the members of basic flocks. *J Yamashina Inst Ornithol.* 11:149–171.
- Sandell M, Smith HG. 1991. Dominance, prior occupancy, and winter residency in the great tit (*Parus major*). *Behav Ecol Sociobiol.* 29:147–152.
- Smith CC. 2007. Independent effects of male and female density on sexual harassment, female fitness, and male competition for mates in the western mosquitofish *Gambusia affinis*. *Behav Ecol Sociobiol.* 61:1349–1358.
- Smith CC, Sargent RC. 2006. Female fitness declines with increasing female density but not male harassment in the western mosquitofish, *Gambusia affinis*. *Anim Behav.* 71:401–407.
- St Louis VL, Barlow JC, Sweerts J-PRA. 1989. Toenail-clipping: a simple technique for marking individual nidicolous chicks. *J Field Ornithol.* 60:211–215.
- Steer J, Burns KC. 2008. Seasonal variation in male-female competition, cooperation and selfish hoarding in a monogamous songbird. *Behav Ecol Sociobiol.* 62:1175–1183.
- Stoehr AM, McGraw KJ, Nolan PM, Hill GE. 2001. Parental care in relation to brood size in the house finch. *J Field Ornithol.* 72:412–418.
- Tinbergen JM. 2005. Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal. *J Anim Ecol.* 74:1112–1120.
- Tinbergen JM, van Balen JH, Drent PJ, Cavé AJ, Mertens JAL, Den Boer-Hazewinkel J. 1987. Population dynamics and cost-benefit analysis—an attempt to relate population dynamics via lifetime reproductive success to short-term decisions. *Neth J Zool.* 37:180–213.
- Tinbergen JM, van Balen JH, van Eck HM. 1985. Density dependent survival in an isolated great tit population: Kluvers data reanalysed. *Ardea.* 73:38–48.
- Tinbergen JM, Boerlijst MC. 1990. Nestling weight and survival in individual great tits (*Parus major*). *J Anim Ecol.* 59:1113–1127.
- Van Balen JH. 1980. Population fluctuations of the great tit and feeding conditions in winter. *Ardea.* 68:143–164.
- Vanhooff J, Vanschaik CP. 1994. Male bonds—affiliative relationships among nonhuman primate males. *Behaviour.* 130:309–337.
- de Villiers MS, Richardson PRK, van Jaarsveld AS. 2003. Patterns of coalition formation and spatial association in a social carnivore, the African wild dog (*Lycaon pictus*). *J Zool.* 260:377–389.
- Walsh PS, Metzger DA, Higuchi R. 1991. Chelex-100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *Biotechniques.* 10:506–513.
- Wauters LA, Matthysen E, Adriaensen F, Tosi G. 2004. Within-sex density dependence and population dynamics of red squirrels *Sciurus vulgaris*. *J Anim Ecol.* 73:11–25.
- White GC, Bartmann RM. 1998. Effect of density reduction on overwinter survival of free-ranging mule deer fawns. *J Wildl Manag.* 62:214–225.
- Wilson JD. 1992. Correlates of agonistic display by great tits *Parus major*. *Behaviour.* 121:168–214.
- Wolff JO, Edge WD, Wang GM. 2002. Effects of adult sex ratios on recruitment of juvenile gray-tailed voles, *Microtus canicaudus*. *J Mammal.* 83:947–956.