Reproductive rates under competition
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Abstract
Costs of reproduction are fundamental to life-history theory. However, empirical support for survival costs of increased parental effort is rare which contrasts with the idea that trading-off fitness benefits with fitness costs of reproduction maximizes fitness gain. To explain discrepancies among studies, we propose that costs of reproduction depend on the ecological context, i.e. on the level of local intraspecific competition. To test that hypothesis, we altered the social environment (nestling density and sex ratio) of 12 nest-box areas (plots) of a great tit population *Parus major* for 3 years via brood size and brood sex ratio manipulations. We expected adults with increased parental effort to pay higher reproductive costs under a high level of intraspecific competition, i.e. in high density and male biased environment. We found that costs of reproduction varied with social environment. In male biased plots, parents rearing enlarged broods had reduced survival rates compared to those in female biased plots. A similar trend was found for the probability of producing a second brood. An increase of parental effort may have affected parental competitiveness and increased their costs of reproduction especially under a high competitive regime.
INTRODUCTION

Life history theory predicts that reproductive costs generate trade-offs and that parents should produce the number of offspring that maximizes their fitness (Lessells 1991; Roff 1992). The trade-off between current and future reproduction is central to this theory. It predicts that an increase of parental effort into current reproduction reduces parental future fecundity and survival, i.e. parental residual reproductive value (Charnov & Krebs 1974; Williams 1966). Because parental reproductive effort also affects the outcome of the trade-off between number and quality of offspring (Lack 1947; Lack 1966), individual fitness should encompass both offspring and adult components of fitness.

The existence of reproductive costs has been extensively tested in avian studies using clutch size or brood size manipulations. In short-lived birds these manipulations revealed that an increase of parental effort during the current reproduction can negatively affect parental residual reproductive value in terms of reduced future fecundity in the same year (e.g. Tinbergen 1987; Smith, Källander & Nilsson 1987), in the subsequent year (e.g. Gustafsson & Sutherland 1988; Røskaft 1985) or reduced adult local survival (e.g. de Heij et al. 2006; Siefferman & Hill 2008). However empirical support for fitness costs of increased parental effort, in particular survival cost, remains limited since it is not detected in the majority of the experimental studies (see review in Parejo & Danchin 2006). To understand why costs of reproduction are detected in some studies but not in others, we propose that costs of reproduction depend on the ecological context. More specifically, we suggest that costs of reproduction depend on the level of local intra-specific competition, with individuals investing more into current reproduction loosing competitiveness and thereby fitness.

To test this hypothesis, we manipulated the level of local sex-specific competition of a great tit population Parus major by altering the social environment (local number of male and female nestlings) of different woodlots (plots). This was achieved via simultaneous brood size and brood sex ratio manipulations. We then quantified the fitness effects of the brood manipulation in relation to the altered social environment. We assumed the level of local competition to rise as the number of competitors (density) and the proportion of males (sex ratio) in a plot increase for the following reasons: In great tits, the male is the dominant (Wilson 1992; Drent 1983) and the philopatric sex (Greenwood et al. 1979) and high local densities can causally reduce breeding output through an increase of intra-specific competition for local resources (e.g. Both 1998b; but see Nicolaus et al. 2009a). Hence, high density male biased plots are expected to carry a larger number of competitors compared to low density and/or female biased plots, which should lead to a higher level of local competition.

Both rearing activity and the acquisition and defence of resources can be costly: birds may increase their workload and their energy expenditure proportionally to the number of nestlings to raise (Nilsson 2002; Sanz & Tinbergen 1999; but see Tinbergen & Verhulst 2000) and competition for resources may imply direct injuries (Piper et al. 2008), depletion of energy reserves (Heinemann 1992; Tiebout 1992) or
change in physiological status (Gill, Alfson & Hau 2007). Thus birds may have to balance their investment into reproduction with their investment into competition for resources. Presently, we predict that competition driven by the social environment will affect reproductive costs and thus will affect the outcome of the reproductive trade-off between current and future reproduction. In high competitive environment (i.e. high density and/or male biased plots) parents with increased parental effort (i.e. with enlarged brood) may allocate less energy into competition which may reduce their competitiveness and ultimately their fitness. Because males and females differ in competitive abilities (Wilson 1992) and energy requirements (Hogstad 1989), fitness effects of competition may be sex-specific. If competition between the sexes is an important factor, adult females are expected to pay a higher cost of reproduction in male biased plots, while if competition within the same sex is the important factor the minority sex is expected to enjoy reduced reproductive costs and higher fitness.

MATERIAL AND METHODS

(a) Study area and study species
The study was carried out in a great tit population in the Lauwersmeer area located in the north-east of the Netherlands (53°23’ N, 6°14’ E). Before the 2005 breeding season, we reorganised the existing study area by establishing 12 nest-box areas (plots). Each plot consisted of 50 boxes which were at a distance of 50 m apart from each other. The plots consisted of primarily young deciduous woodlots where few natural cavities were available. The majority of the breeding attempts occurred thus in the nest-boxes.

(b) Data collection
From the beginning of April on, nest-boxes were checked weekly and parameters such as laying date (back-calculated assuming that one egg was laid per day) and clutch size were monitored. Before the expected hatching date nest-boxes were checked daily to determine hatching date (day 0). At day 2, nestlings were bled and nail clipped for individual identification. Molecular sexing was performed between day 3-5 using molecular markers (Griffiths et al. 1998). At day 6, nestlings were weighed (mass ±0.1g), ringed with an aluminium ring and swapped between nests of the same age and between plots according to the experimental set-up (see below). At day 7, both parents were caught with a spring trap in the nest-box, weighted, measured and ringed for later identification if necessary. At day 14, growth measurements of the juveniles were taken. From day 19 onwards, boxes were checked every second day to determine the fledge date. Nests were emptied and checked for dead chicks. Further weekly checks gave information about the incidence of second clutches and their breeding success. We did not perform any experiment on the second broods (see definition in data selection) but the standard measurements of juveniles and adults were taken. Local adult survival probability and the number of
recruits per nest were estimated on the basis of recaptures of breeding birds in the study area the next year. Overview of the breeding parameters of the first broods of the three study years (2005-2006-2007) is presented in the appendix A.

(c) Experimental set-up
Between 2005 and 2007, we altered the social environment (number of males and females) of a great tit population in 12 study plots via simultaneous manipulations of plot nestling densities (number per plot, i.e. per 50 nest-boxes) and sex ratios (proportion of nestling males in a plot) at day 6 leaving the natural breeding densities (number of breeding pairs per plot) unchanged. That way, we created six different experimental treatments combining a manipulation of nestling density (low/high) and sex ratio (female/balanced/male). Each treatment was randomly assigned to a plot, semi-randomized between years (i.e. each plot received a different treatment in every study year) and occurred in two replicates per year. Female and male biased plots were manipulated to ca 25% or ca 75% male nestlings respectively while balanced plots were manipulated to ca 50% which reflects a natural situation (Appendix A). Low and high density plots were manipulated to ca ±13% of change in the number of nestlings in a plot (Appendix A).

Within plots, broods were manipulated such as to achieve the desired plot treatment. For the sex ratio treatment this meant that the brood treatments always were performed in the direction of the plot treatment. However, we kept variation in brood size manipulation within plot (small, intermediate and large) to be able to study the effects of the interaction between brood size (nest level) and density and plot sex ratio (plot level) on breeding output. The “small” and “large” brood size categories differed by ± 3 nestlings from the “intermediate” category (Appendices A and B). The intermediate broods were created to equal the average brood size in a given year (Appendices A and B). Consequently all broods were manipulated. For further details on the manipulation scheme and the success of the experimental changes, see Nicolaus et al. (2009b). This study was carried out under license of the Animal Experimental Committee of the University of Groningen (license DEC-4114 B).

(d) Fitness components and data selection
We analyzed the number of recruits per nest (number offspring per nest breeding in our population the next year), the probability of producing a second brood (given that the first brood was successful) and the adult local survival probability (probability to survive in our study area until the subsequent breeding season).

Our experiment was performed over 3 years (2005-2006-2007) during which we manipulated the first broods (defined as clutches started within 30 days of the earliest clutch in that year) and monitored breeding traits of the second broods (defined as broods laid by females that were known to have successfully fledged a first brood). Thus repeat clutches of known females after failure were left unmanipulated as were nests with a clutch size smaller than 3 eggs or with very high mortality rate (>50%) before manipulation because they often reflect a disturbed situation. Unmanipu-
lated brood and nests with a clutch size smaller that 3 eggs where excluded from further analysis as were broods where only one of two parents was identified.

Some adults bred repetitively in two or three of the study years (n=260 individuals). To account for inter-dependency between the measurements, we used one random breeding event for each male and female adult in the analysis (n=1013 individuals and n=506 broods). To check for the robustness of our analyses, all the models were run with different random sub-samples. The randomization did not affect the results of the adult survival analysis. Yet, the final models for the probability of producing a second brood and for the number of recruits per nest differed in their side effects (i.e. of less importance for the hypotheses tested) depending on the random selection made. Therefore, for these parameters we will present the overall model for one of the random sub-sets but detailed analyses per year can be found in the Appendices (Appendix D and E).

(e) Analyses

To account for sources of inter-dependency between measurements, we used generalized linear mixed models (MLwiN versions 2.02; Rasbash et al. 2004) distinguishing between variance on 3 or 4 levels: plot, cohort, nest, and/or individual. We defined as cohort the level corresponding to the re-samplings of a plot for every study year (e.g. different plot treatments in each year). The number of recruits per nest was analyzed using Poisson response models with a log link function. Variation in the probability of producing a second brood and the adult survival probability were studied using a binomial response model with a logit link function. Adult local survival was analyzed with mixed models rather than using mark-recapture models that control for recapture rates because mixed models can deal with hierarchical structure in the data and in our population adult recapture rate between year is high (0.90 see Tinbergen & Sanz 2004), leaving little space for experimental effects on recapture rate.

To test for the experimental effects, we used the original values of nestling density, plot sex ratio and brood size and their experimental changes calculated as the difference between the original values and the experimental values at day 6 (respectively denoted $\Delta D$, $\Delta plotSR$ and $\Delta BS$). We chose to use experimental changes and the original values rather than final experimental values because it reduces correlation between the natural and experimental variables. Laying date, parental sex, years and quadratic terms of the experimental variables as well as two- and three-way interactions among the variables were also fitted in the models. Years (2005, 2006 and 2007) and sex (female=0, male=1) were fitted as factors with respectively 2005 and female chosen as reference categories. All the other variables including the experimental effects were fitted as continuous and covariates were centred around the population mean. Model selection was based on backwards elimination of the non-significant terms in the order of their significance assessed by their Wald statistics. In addition to the best models, we reported the most relevant non-significant results retested after elimination in the best model. Means are expressed with standard error. Level of significance was set at $P=0.05$. 

Cost of reproduction and social environment
RESULTS

(a) Population breeding traits
Population breeding density (number of breeding pairs per ha) varied between years with 2006 being a low density year compared to 2005 or 2007 (Appendix A). In 2007, birds started reproduction about 4 days earlier than in the other years (Appendix A). Consistently with a negative effect of density, high density years (2005 and 2007) were associated with lower fecundity (clutch size, brood size, fledgling production, occurrence of second broods) and with lower number of recruits per nest and lower adult survival (Appendix A). In contrast to the density variation, natural plot sex ratio presented very small inter-annual variation (Appendix A), indicating that birds produced on average a balanced sex ratio that did not vary with the natural breeding densities or other annual environmental traits.

(b) Number of recruits per brood
Surprisingly, the number of recruits per nest was not affected by the experiment (Table 6.1A). Brood size manipulation had no effect on this fitness component (ΔBS: 0.031±0.023, $\chi^2_{df1} = 1.77, P=0.183$, see figure in Appendix C), also not in relation to the altered social environment (ΔDxΔBS: –0.001±0.001, $\chi^2_{df1} = 0.57, P=0.450$; ΔplotSRxΔBS: –0.179±0.107, $\chi^2_{df1} = 2.81, P=0.094$). The interaction between the plot manipulations was not significant (ΔDxΔplotSR: –0.011±0.019, $\chi^2_{df1} = 0.32, P=0.571$; ΔD: 0.011±0.004, $\chi^2_{df1} = 0.12, P=0.526$; ΔplotSR: –0.589±0.385, $\chi^2_{df1} = 2.34, P=0.126$). There was also no indication for non-linear effects of the manipulations (not shown). Pairs breeding in natural high density plots recruited less offspring, suggesting that natural high density plots may carry higher level of intra-specific competition or may be of lower “quality” (e.g. in terms of food availability or bird phenotype). We also found significant effects of the original breeding traits of the parents (original brood size and lay date) on the number of recruits per nest (Table 6.1A). Parents with natural large brood recruited more offspring, suggesting a role of parental or territory quality. Late breeders recruited less offspring in 2005 and 2006 but the opposite pattern was observed in 2007 (year x lay date, table 6.1A). Selection on lay date may thus vary between years. Patterns among different random sub-sets of the data were qualitatively all very similar to analysis shown presently (for analyses per year see Appendix D).

(c) Adult local survival probability
We found strong evidence for a survival cost of increased parental effort that varied with plot sex ratio. Pairs with enlarged broods survived worse in male biased or control plots compared to female biased plots (Table 6.1B, Fig. 6.1A-C). We found however no significant effects of the interaction between brood size manipulation and density manipulation or between the plot manipulations (ΔDxΔBS: –0.001±0.001, $\chi^2_{df1} = 1.06, P=0.304$; ΔDxΔplotSR: -0.007±0.021, $\chi^2_{df1} = 0.12, P=0.731$). Overall survival probability did not differ between the sexes (-0.149±0.149; $\chi^2_{df1} = 1.01$, Chapter 6
The experimental effects found were linear and not sex-specific (not shown).

Adult survival probability was lower in 2005 than in 2006 and 2007 (Table 6.1B and Appendix A). Adult survival probability did not related to the original plot density or plot sex ratio neither to the original breeding traits of the adults (not shown).

(d) Probability of producing a second brood
As for adult local survival probability, the effect of the brood size manipulation on the probability of producing a second brood varied with plot sex ratio; however in contrast to the survival analysis this effect differed among years (yearsx∆plotSRx∆BS, Table 6.2). Overall, parents with increased parental effort were less likely to initiate a second clutch in male biased or control plots compared to female biased plots (Fig. 6.1D-F). Birds also produced less second broods if they bred in a high density plots (natural and experimental effects, Table 6.2). The experimental change in plot density and plot sex ratio interacted significantly with each other

Table 6.1  Model summary of hierarchical models for the number of great tit recruits per nest of the 1st broods (n=506 broods) (a) and the adult local survival probability (n=1013 individuals) (b) analyzed in relation to the brood size, density and sex ratio manipulations (Δ=experimental change, D=nestling plot density; SR=nestling plot sex ratio; BS=brood size). Significant values are shown in bold.

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such that birds were less likely to produce a second brood in high density male biased plots (i.e. with expected high level of competition). We did not find significant interaction between brood size and plot density manipulations on the probability of producing a second brood ($\Delta D \times \Delta \text{plotSR}$; Table 6.2), such that birds were less likely to produce a second brood in high density male biased plots (i.e. with expected high level of competition). We did not find significant interaction between brood size and plot density manipulations on the probability of producing a second brood ($\Delta D \times \Delta \text{BS}$: $-0.003 \pm 0.003$, $\chi^2_{df1} = 0.62$, $P = 0.429$).

In contrast to the experimental effects found, natural plot sex ratio had a positive effect on the production of second broods, indicating that natural male biased environment may reflect good quality habitat or good quality breeders. Late breeders had a lower chance to produce a second clutch than early breeders (Table 6.2). Birds produced more second broods in 2006 than in 2005 and 2007 (Table 6.2 and Appendix A). Patterns among different random sub-sets of the data were qualitatively all very similar to analysis shown presently (for analyses per year see Appendix E).

**Figure 6.1** The effect of brood size manipulation on adult local survival probability (A-C) and on the probability of producing a second brood (D-F) varied with the plot sex ratio in the Lauwersmeer great tit population (see Tables 6.1B and 6.2). Averages are presented with standard errors (raw data; n=1013 individuals (A-C); n=654 broods (D-F)). For graphical purpose the broods that have been reduced or enlarged by more than 4 nestlings are pooled together.
The aim of our study was to investigate the sex-specific fitness consequences of brood size manipulation under varying competitive regimes in great tits. The experiment did not affect the number of recruits per nest, i.e. the fitness benefits of reproduction. However, consistently for the three years, survival and fecundity costs of reproduction of both sexes increased with the proportion of males in a plot, a parameter expected to affect the level of intra-specific competition. The results support our hypothesis that parents should balance the investment between energetically costly activities (reproduction vs. defence and acquisition of resources) and provide the first experimental evidence that costs of reproduction depend on the ecological context, i.e. on the level of competition. We judge it unlikely that the effect of sex ratio on brood related fitness was a brood rather than a plot effect because we could not detect any fitness effects of brood sex ratio during the nestling period (effect on nestling performance, Nicolaus et al. 2009b).

Table 6.2  Model summary of hierarchical models for the probability of producing a second brood (n=506 broods) analyzed in relation to the brood size, density and sex ratio manipulations in a great tit population (Δ=experimental change, D=nestling plot density; SR=nestling plot sex ratio; BS=brood size). Significant values are indicated in bold face.

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</table>
(a) Parental effort and number of recruits

There is experimental evidence that brood enlargement increases parental feeding activity and energy expenditure (Nilsson 2002; Sanz & Tinbergen 1999; but see Tinbergen & Verhulst 2000), indicating that reproductive effort and brood size are positively related. In our population enlarged broods fledged more young but those young were in worse condition (Nicolaus et al. 2009b; Tinbergen & Sanz 2004) and less likely to recruit (Tinbergen & Sanz 2004). We also know that brood enlargement in our population significantly increased parental visit rate to the nest (K.M. Bouwman personal communication). This suggests that parents with increased brood size must have increased their parental effort to successfully fledge extra nestlings. Yet unlike other studies (e.g. Tinbergen & Sanz 2004) this increased parental effort did not result in a higher number of recruits in our study. The lack of apparent experimental effects on the number of recruits per nest most likely is the outcome of conflicting and opposite forces: brood size enlargement increased young productivity which happened to be counter-balanced by a reduced survival of those offspring.

Altered social environment did, against our expectation, not affect the number of recruits per nest also not in interaction with brood size manipulation. This could happen if juveniles disperse and mix quickly after fledging in flocks of which composition minimizes the level of intra-specific competition. Yet, we found a negative relation between the natural plot density and the number of recruits, which suggests that juveniles may have suffered from a contest type of competition with other juveniles or adults. Although the effect of the experimental change in density scaled in the same direction we could not confirm the effect experimentally perhaps because the magnitude of the density manipulation has been too small.

(b) Costs of reproduction in an ecological context

OVERALL EFFECTS

An increase of parental effort may reduce the phenotypic quality of birds rearing enlarged broods through some physiological changes (e.g. reduced body mass, Nur 1984; reduced immune response, Pap & Markus 2003 or delayed moult, Svensson & Nilsson 1997). This change of phenotypic quality may have then drastic effects on bird competitiveness because it could set competitive asymmetries among individuals and influence the outcome of agonistic interactions (Gosler & Carruthers 1999; Lindström, Hasselquist & Wikelski 2005; van Oort et al. 2007). Therefore birds with increased parental effort may engage less competitive interactions, loose dominance and pay higher costs of reproduction especially if the level of competition for resources is high (see overview in Fig. 6.2). Consistently, our results suggested that parents with enlarged broods had to work harder and showed that those parents paid higher costs of reproduction when breeding in male biased or control plots. Male biased plots contained more of the philopatric and dominant sex implying that they were more likely to carry high numbers of competitors. This may explain why in those plots parents with enlarged broods may have lost competition and suffered from reduced fecundity and survival (Fig. 6.2). In this population we also found evi-
dence that juveniles were attracted by male biased plots which may have enhanced the negative effect of competition on the weakest parents in these areas (Nicolaus et al. unpublished). Moreover, it is known that parents with enlarged broods provide longer parental post-fledging care to the young (Smith et al. 1987). Therefore, adults may also have traded-off the duration of the post-fledging parental care of the first brood with the production of a second brood (Verhulst, Tinbergen & Daan 1997; Smith et al. 1987), resulting in a lower chance to produce a second brood for parents with enlarged broods. An overall increase of the intra-specific level of competition in male biased plots may have increased the fitness cost associated with extended parental care or with multiple breeding explaining why fewer birds initiate second broods in these areas.

The absence of sex-specific experimental effects on survival and fecundity also suggests that plot sex ratio manipulation did affect the overall level of intra-specific competition but not the level of intra- or inter-sexual competition. This may be due to the fact that in summer juveniles do not express sex-specific behaviours yet (e.g. territorial behaviour starting only after moult at the onset of autumn, Drent 1983) and thus compete with adults for non sex-specific resources (e.g. food). Their overall number may have affected the overall level of intra-specific competition and the adult sexes in a similar way.

**ADULT SURVIVAL PROBABILITY IN FEMALE BIASED PLOTS**

We predicted the negative effect of brood size enlargement on survival to increase with the proportion of males in a plot. This is what we observed in male and control plots. Nevertheless, this could not explain the positive association between brood enlargement and survival in female biased environment.

Rearing a second brood is known to bear a survival and fecundity cost (Verhulst 1998). We found that adults with reduced broods in female biased plots were more likely to produce a second brood, which could explain why these individuals suffered

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**Figure 6.2** Overview of the mechanisms underlying the costs of reproduction in an ecological context: an increase of parental effort reduces parental phenotypic quality and subsequently affects competitive abilities of the parents, resulting in a reduced fitness for those pairs especially when the level of local competition is high (i.e. high proportion of males).
from higher mortality. Nevertheless, this was not supported by the data because the production of a second brood did not associate negatively with female survival (tested but not shown). Only high phenotypic quality females may have initiated a second breeding attempt. Although we do not understand the observed pattern in female biased plots, we proposed that two other combined mechanisms linked with sex-biased dispersal in this species could underlie this pattern: It is acknowledged that dispersing individuals in birds are often females and/or individuals of lowest condition (Clobert et al. 2001). In female biased plots, most young females (i.e. 75% of the fledglings) were expected to disperse, especially those with bad condition originated from enlarged broods. In great tits, parents provide post-fledging care to their offspring during a few weeks depending on their brood size (Drent 1984; Verhulst & Hut 1996). Consequently the early disappearance of young females may relax the overall level of competition in these plots and may relieve adults with enlarged broods from post-fledgling parental care. This may then be translated into a higher survival probability for parents. Alternatively but non-exclusively, parents with enlarged female biased broods may invest less in (post-fledging) parental care because offspring females in bad condition are more likely to be outcompeted and thus have a reduced fitness prospect.

(c) Evolutionary aspects
Birds are expected to choose the strategy that maximizes their fitness, implying that a brood size manipulation often affects either investment in current or in future reproduction. Interestingly in our study both aspects were affected since brood enlargement increased parental effort and reduced future fecundity and survival. We did not calculate one fitness estimate combining adult components and recruits because dispersal rates differ strongly between these age groups and bias the fitness estimate. Yet, considering control sex ratio plots that reflect a natural situation, we found that parental future fecundity and return chance were negatively associated with brood enlargement. These findings showed thus that selection on brood size was directional towards small broods. The negative directional selection on brood size found is in contrast with earlier conclusions made in the same population where there was a positive selection on brood size (Tinbergen & Sanz 2004). The ecological settings of our population have changed over time and thereby may have modified the selective forces acting on brood size.

We hypothesized that inconsistencies among studies regarding the fitness consequences of brood size manipulations may come from differences in social context that affect costs of reproduction. Our findings confirmed that social effects are important for costs of reproduction and thus for optimal brood size. Yet, to understand population differences, full knowledge of the mechanisms underlying competition (e.g. level of resources vs. number of competitors) is needed. We thus showed that the local social environment is an important selection pressure acting on individual reproductive rates and therefore is expected to play a key-role in micro-evolutionary processes acting on fitness related traits.
ACKNOWLEDGEMENTS
This study was part of MN and SPMM PhD work. RU helped in collecting data in the field and set up the database. MvdV performed the molecular sexing of the nestlings with the help of Luc te Marvelde and Kim Meijer. Jan Komdeur (NWO-VICI grant 86503003) as well as the University of Groningen financially supported this project. CB, KMB and JMT helped in collecting data in the field and supervised the work. We are grateful to Reinder Radersma, Niels Dingemanse, Martin Keiser, Tamar Lok, Jeroen Reimerink, Kirsten Jalvingh, Alexandra Haydn, Jan Plantiga as well as to all the Animal Ecology course students between 2005 and 2008 for their help in collecting the data in the field. 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.
Appendix A. Overview of the breeding parameters and the adult survival of first broods of the Lauwersmeer great tit population. Breeding density represents the number of breeding pairs per ha. A density (“low D/high D”) and a sex ratio (“female/control/male”) treatment were assigned to every plot. The mean plot density (total number of nestlings per plot) and mean plot sex ratio (proportion of male nestlings in a plot) are presented before and after manipulation at day 6. Laying date is expressed in April date (1 = 1st of April). Means are presented with their standard deviation (SD) and their sample size for the three study years 2005, 2006 and 2007.

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Appendix B. Frequency distribution of (A) the original brood sizes before manipulation at day 6 (B) the changes in brood size at day 6 and (C) the experimental brood sizes after manipulation at day 6 of the 1st broods of the Lauwersmeer great tit population in 2005, 2006 and 2007.
Appendix C. Brood size manipulation did not significantly affect the number of recruits per first broods in the Lauwersmeer great tit population. Averages are presented with standard errors (years 2005, 2006 and 2007 combined; n=506 broods; raw data). The broods that have been reduced or enlarged by more than 4 nestlings are pooled in two groups for graphical purpose.

Appendix D. Model summary of hierarchical models for the number of recruits per brood in relation to brood size, plot density and plot sex ratio in a great tit population in the Netherlands (Δ=experimental change, D=nestling plot density; SR=nestling plot sex ratio; BS=brood size). Effects of lay date (date) and of the original brood size of the foster parents have been also tested. The final models are presented per year. Significant values are shown in bold.

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Appendix E. Model summary of hierarchical models for the probability of producing a second clutch in relation to brood size, plot density and plot sex ratio in a great tit population in the Netherlands ($\Delta$=experimental change, D=nestling plot density; SR=nestling plot sex ratio; BS=brood size). Effects of lay date (date) and of the original brood size of the parents have been also tested. The final models are presented per year. Significant values are shown in bold.

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(*) trend
OPTIMAL CLUTCH SIZE AND COMPETITION
At day 14

Photos: Romain Piault