Experimental evidence for density dependence of reproduction in great tits

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Summary

1. Density dependence of avian reproduction has often been analysed using correlations between annual mean reproductive output and population density. Experiments are necessary to prove that density is the cause of the observed patterns, but so far, three out of four experimental studies do not support a direct causal effect of density on reproduction.

2. This paper presents experimental evidence that reproductive decisions in great tits, *Parus major* L., are causally affected by breeding density. The breeding density of great tits was manipulated by providing nest-boxes at different densities in an ecologically homogeneous area.

3. Within years the densities in the high and low density plots differed approximately 8-fold. During the 11 years of the experiment, clutch size, nestling mass and the proportion of birds starting a second brood were all lower in the high density plot. In 5 years with equal breeding densities in both parts, clutch size did not differ between the plots. The patterns found were consistent with the density effects as predicted from the non-experimental data.

Key-words: clutch size, density dependence, density manipulation, *Parus major*, reproduction.

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Introduction

Density-dependent reproduction or survival are important in regulating population numbers. Several studies on birds have shown that annual mean clutch size declines with increasing density (e.g. Kluyver 1951; Lack 1958; Perrins 1965; Van Balen 1973; Ekman 1984; Arcese & Smith 1988; Möller 1989) although density-dependent clutch size was not detected in all studies (e.g. Tompa 1967; Alatalo & Lundberg 1984; Orell & Ojanen 1984; Virolainen 1984; Stenning, Harvey & Campbell 1988; Van Balen & Potting 1990; Dhondt, Kempenaers & Adriaensen 1992). Other aspects of avian reproduction are also correlated with density (for review see Sinclair 1989). Most of these studies are descriptive and are based on between year differences in density. They therefore suffer from the problem that the observed correlation may not be due to a direct causal relationship, but may result from both density and reproduction being affected by a third unknown factor. For instance, in

some bird species breeding density is determined by variation in winter survival (Perrins 1965; Van Balen 1980; Arcese & Smith 1988). High densities therefore might be associated with a higher percentage of low quality individuals in the population, which might lay smaller clutches (Haywood & Perrins 1992). Few experiments on density dependence of reproduction in birds have been performed, so it is still unclear whether variation in breeding density causes the correlations observed using natural variation in density.

Four studies exist in which density dependence of avian reproduction was investigated experimentally. Tompa (1967) manipulated pied flycatcher *Ficedula hypoleuca* Pall. densities by manipulating the density of nest-boxes. In his study no effect of the experimental density on any aspect of reproduction could be established. Alatalo & Lundberg (1984) also manipulated pied flycatcher densities by manipulating nest-box density. In two experimental years they found only that nestling survival and growth were slightly higher in the low density area. The effect was strongest in the year with unfavourable conditions. Török & Tóth (1988) performed a similar experiment in the closely related collared flycatcher, *F. albicollis* Temm. No effects were found on clutch size, hatching

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success and fledgling mass, but nestling survival was better in the low density area. Dhondt, Kempenaers & Adriaensen (1992) manipulated blue tit, *Parus caeruleus* L., densities by altering the competition for nest-boxes with great tits. Their experiment is based on between-year differences, and here an effect of density on clutch size was found. Dhondt, Kempenaers & Adriaensen (1992) showed that this effect was mainly due to more low quality territories being occupied in high density years, in which smaller clutches were laid. Thus only one of these four studies has demonstrated a direct causal effect of density on clutch size. Nestling growth and survival were both affected in some of the flycatcher studies.

There is some support for the theory that food competition is the underlying mechanism resulting in density dependence of reproduction. Arcese & Smith (1988) found a negative correlation between the annual mean clutch size and the annual density in a song sparrow, *Melospiza melodia* Wilson, population. In this population, food was supplemented in a breeding season with a high density, and it was found that the average clutch size was larger than expected from the high density, but was comparable with years with a low density. Arcese & Smith's study strongly suggests that food competition has an effect on reproductive decisions. It also illustrates how difficult studies on competition in a natural environment can be: during periods with high food availability, competition might be absent, and density-dependent effects are not very likely to be found. Therefore studies on density-dependent effects should be continued over a longer period, in order to investigate the density effect over the natural variation in food supply that occurs across years.

In this paper experimental data on density dependence of reproduction in great tits are presented. In his influential study on the population ecology of great tits, Kluiver (1951) observed that several reproductive variables were associated with density. Kluiver initiated the experimental study reported here in 1955 with the aim of investigating whether local competition was the cause of these density-dependent patterns. This paper uses data from the resulting 40 year study, first to examine which reproductive variables are correlated with annual density, and second to test whether density is indeed the cause of any correlations found across years.

Methods

The study was carried out between 1955 and 1995 in the Liesbos area, southern Netherlands. The study area can be regarded as optimal habitat for great tits, with oak, *Quercus robur* L., as the predominant tree species. The area was subdivided into two parts, in which nest-boxes were provided at different densities. The part with the high nest-box density contained about 100 nest-boxes over 19 ha (about 5 boxes per

ha). The low density part had about 30 nest-boxes over 76.5 ha (about 0.4 boxes per ha). The study was started in 1955, and the high nest-box density area is still studied, while observations of the low density area were made until 1968, excluding 1960–62. Data are thus available for 40 years for the high density area, and for 11 years for the low density area. Nest-boxes were checked at least once a week. Nestlings were ringed at about 7 days after hatching, and the breeding adults were caught at the same time for ringing. In 1968 no attempts were made to catch the breeding adults. For more details about the standard procedure see Van Balen (1973).

The rationale behind the two densities of nest-boxes was to manipulate the density of breeding great tits. The drawback of this experimental procedure is that the breeding density of tits in the low density area is underestimated because tits that cannot occupy a nest-box might breed in a natural cavity. Furthermore only the better quality individuals might be able to occupy a nest-box (which is the preferred nest site) in the low density area. However, if tits in the low density area bred more often in natural cavities, their recapture rate in nest-boxes in the next breeding season would be lower, because they would not be caught in a natural cavity, or they apparently 'skip' breeding more often. However, recapture rates did not differ between the areas (see results), and adults did not skip breeding one year more often in the low than in the high density area (observed percentages of parents skipping breeding one year: males 3% in high density, 2% in low density, $\chi^2_1 = 0.24$, NS; females 2% in high density, 3% in low density, $\chi^2_1 = 0.19$, NS; see also results for other treatment of capture probabilities). These data suggest no difference in the proportion of great tits breeding in natural cavities between the two density plots, suggesting that the observed differences in density based on tits breeding in nest-boxes represent a real difference in density between the two parts of the study area.

Another problem is that the study area was divided throughout the study into the same two parts with different densities of nest-boxes. Any difference in reproduction between the plots could result from habitat quality differences, despite the area appearing homogeneous in human eyes. However, in 5 years (1960–63 and 1965) an 18 ha part of the low density plot was supplied with the same nest-box density as the high density plot, resulting in comparable breeding densities in both plots (paired *t*-test for density per year, $t_4 = -0.30$, NS). Clutch size was equal in both plots when the densities were comparable (Table 1; mean clutch size was 0.016 (SE = 0.16) larger in the original high density plot; year effect: $F_{4,346} = 6.11$, $P = 0.014$, area effect $F_{1,346} = 0.0091$, $P = 0.92$, interaction $F_{4,342} = 0.50$, $P = 0.74$) while laying date differed slightly between the two plots (Table 1; mean laying date being 1.1 (SE = 0.45) days later in the original high density plot; year effect: $F_{3,250} = 6.57$,

Table 1. Density, mean clutch size and mean laying date for the two plots in the 5 years that nest-box densities were similar. In 1965 no data were available for laying dates. For statistics see text

Year	Density		Mean clutch size		Mean laying date	
	High	Low	High	Low	High	Low
1960	0.84	0.67	9.69 (0.30)	9.83 (0.52)	17.9 (1.02)	19.3 (1.33)
1961	3.55	3.06	9.71 (0.22)	9.44 (0.24)	13.0 (0.50)	11.8 (0.34)
1962	1.32	2.44	8.64 (0.38)	8.77 (0.24)	31.1 (1.00)	28.5 (0.53)
1963	1.63	1.17	10.1 (0.17)	9.90 (0.31)	25.2 (0.42)	24.7 (0.47)
1965	2.47	2.39	9.36 (0.20)	9.63 (0.20)	—	—

$P < 0.001$, area effect $F_{1,250} = 6.57$, $P = 0.011$, interaction $F_{3,247} = 2.33$, $P = 0.074$). Although the lack of a significant result does not imply that no difference in clutch size exists between the plots at equal densities, the difference is very small, and if anything, the tits in the low density plot are at least not laying larger clutches when the densities are similar. With respect to clutch size this comparison strongly suggests that the two plots are of equal quality to the tits.

Clutches were regarded as first clutches if they were started within 30 days of first clutch in a given year. Repeat clutches of females whose first clutch had failed were excluded. Second clutches were the clutches of identified females, who had already successfully raised a first clutch. Reproduction was separated into different components. 'Clutch size' was the number of eggs a female laid. Only clutches where a female started incubating were included in the analyses. 'Clutch success' is the probability of a nest producing at least one hatchling, and 'brood success' is the chance of a nest producing at least one fledgling. 'Nestling survival' is the ratio of the number of fledglings to the number of hatched chicks, only for the nests that produced at least one fledgling. The reason for separating brood success and nestling survival is that two different processes might be involved: nest predation or predation of parents on the one hand, and food shortage or parasite infections on the other. The nestlings in some nests were weighed between 15 and 19 days after hatching of the first chick in the nest (mean 16.5, $SD = 0.97$) in two of the experimental years. At this age nestlings have reached their asymptotic fledging mass. 'Recruitment rate' is the ratio of locally recruited offspring to the number of fledglings per nest. Because differences might exist in the probability of a bird being caught alive, the recruitment rate was analysed while taking capture probability into account using the program SURPH (Smith *et al.* 1994). In this analysis each fledgling was treated as a data point, and the effects of area, year and the interaction were first fitted on the chance of a bird not being caught while known to be alive (which will be referred to as the capture probability). Using a back-

wards procedure a capture model was constructed, and this capture model was used when analysing the local survival. For parental survival the same procedure was used, using the captures of adults in the next year's breeding seasons.

Two series of analyses were made on the effect of density. First, the annual means of reproductive parameters were correlated with the annual density, using 40 years of data from the high density plot. Second, reproductive parameters were compared within years between the high and low density plots, using the 11 years for which data are available (1955–68, excluding 1960–1962). The first analyses were performed using average values per year, and ignoring within year variation. As a result this analysis has relatively few degrees of freedom, and can be regarded as conservative. In the comparison of the low and high density plots each nest was used as an independent data point. Year was included in these models because there are probably marked differences between years in food availability, weather conditions and other environmental variables. If the effect of year is included in the models, the effect of the experimental plot is investigated within years. The effect of density is only analysed as the difference between the high and low density plots, instead of using the measured densities in both plots. Scaling the experimental density effect with the annual densities in the time-series could not be carried out because of the bimodal nature of the resulting density data; the densities in the high density area were always considerably higher than in the low density plot. Binomial data are analysed using logistic regression, and the Williams correction has been performed when appropriate (Crawley 1993). Logistic regression could not be performed on all proportional data, because the deviance was too small to fit an appropriate model. In these cases, year effects were not analysed, and the experimental effect was analysed using the Wilcoxon matched pair test on the annual proportions per plot. Analysis of the annual means of the low and high density plots have mostly used non-parametric statistics because of the small sample sizes. All the significance tests were two-tailed. Multiple

regression analysis was performed using a backwards procedure. Interaction terms presented in tables are not mentioned in the text if they were not significant. To investigate non-linearity in regressions on density, the quadratic term was included in the models. This never gave a better fit of the model and is not mentioned in the results.

Results

DESCRIPTIVE DATA

In the high density area the annual mean clutch size decreased with population density ($F_{1,38} = 4.2$, $P = 0.047$). There was no effect of density on the clutch success (logistic regression, $F_{1,38} = 0.13$, NS), hatching success (logistic regression, $F_{1,38} = 1.4$, NS), brood success (logistic regression $F_{1,38} = 1.7$, NS), or the nestling survival (logistic regression $F_{1,38} = 0.95$, NS). The recruitment rates were analysed using the number of recruits from a given year, divided by the number of fledglings. The analysis is based on a similar analysis of Perdeck and co-workers (unpublished) in which a more extensive treatment of the subject is given. The capture probability of first year birds was not affected by the density ($\chi^2_1 = 0.12$, NS, for 24 years). After correcting for annual differences in capture probability, recruitment rates of first brood fledglings were negatively correlated with density (logistic regression, $F_{1,19} = 7.244$, $P = 0.005$). Effects of the annual beech crop and the winter temperature on recruitment rates were not found in this population (analysis taken from Perdeck, Visser, Verboren & van Balen, unpublished). The annual proportion of birds starting a second brood after a successful first brood was negatively correlated with the density (logistic regression, $F_{1,33} = 11.9$, $P < 0.005$), but no correlation was found between mean clutch size of second broods and density ($F_{1,29} = 0.64$, NS).

EXPERIMENTAL DATA

The density experiment resulted in an 8-fold difference in the density of great tits breeding in nest-boxes (experimental effect $F_{1,20} = 110.4$, $P < 0.001$). This difference is smaller than the 13-fold difference in nest-box density between the experimental plots, due to the higher nest-box occupancy in the low density plot (logistic regression, $\chi^2_1 = 110.2$, $P < 0.001$, $N = 22$). In all the years the density was higher in the high than in the low density plot. Density in the low and the high density plots was not correlated within years (Spearman rank, $r = 0.12$, $n = 11$, NS), perhaps because nest-boxes were limited in the low density plot to the extent that all the nest-boxes were occupied in most years. The proportion of first year female breeders did not differ between the experimental plots (logistic regression, year: $\chi^2_8 = 16.4$, $P = 0.037$; area: $\chi^2_1 = 0.8$, $P = 0.37$; interaction: $\chi^2_8 = 10.3$, $P = 0.24$,

$N = 281$), so female age was not corrected for in the analyses. Laying date was 0.9 days earlier in the low density area (year effect $F_{10,582} = 79.6$, $P < 0.001$, $F_{1,582} = 0.583$, $P < 0.05$). Because reproduction in great tits is often related to laying date (see e.g. Kluyver 1951; Perrins 1965; Perrins & McCleery 1989; Verhulst & Tinbergen 1992), the effects of year, laying date and treatment were analysed simultaneously in an ANCOVA.

Clutch size in the high density plot was on average about 0.6 eggs smaller than in the low density plot (Fig. 1, Table 2). This effect was not due to all nests being treated as independent data points, because the annual mean clutch size also differed between the areas (paired t -test, $t_{10} = -3.01$, $P = 0.013$). In an ANCOVA where laying date is included, neither the three-way, nor the two-way interaction terms explained a significant part of the variation in clutch size. From the main effects, year and treatment again explained a significant part of the variation, while no effect of laying date was found on clutch size variation in this population (year: $F_{10,581} = 14.89$, $P < 0.0001$; plot: $F_{1,581} = 16.09$, $P < 0.0001$; laying date: $F_{1,581} = 3.01$, NS). The annual mean clutch size correlated positively between the areas (Spearman rank correlation, $r = 0.71$, $N = 11$, $P = 0.014$). The clutch success was similar for both areas (Table 2). Nests failing to fledge any offspring were rare (high density: 4.6%, low density: 4.3%). The experimental effect was not significant (Table 2). Nestling survival for those nests that managed to produce fledglings was high (high density: 98.4%; low density: 98.4%), and no experimental effect was found (Table 2). The mean fledgling mass per nest was 0.6 g higher in the low density area ($F_{1,36} = 4.2$, $P = 0.049$). No differences existed between the 2 years for which these data were collected ($F_{1,36} = 1.4$, $P = 0.24$). Thus both the number and the quality of young were higher in the low density area.

Fig. 1. The effect of experimental density manipulation on the average clutch size per year ($\pm$ SD). Solid bars are the high density area, open bars are the low density area. For statistics see Table 1.

Table 2. Analyses of variance of the effect of density manipulation and year on reproduction in great tits. Percentages have been analysed using logistic regression or the Wilcoxon matched pair test. The latter was used if the variance in the data was too small to analyse the year effect in a logistic regression

	Density manipulation	Year	Interaction
Clutch size (1st clutch)	$F_{1,582} = 17.6^{***}$	$F_{10,582} = 15.0^{***}$	$F_{10,572} = 1.9^*$
Clutch success	$\chi^2_1 = 0.7$	$\chi^2_{10} = 15.7$	$\chi^2_1 = 7.0$
Brood success	$Z = 1.36$	—	—
Nestling survival	$Z = 0.98$	—	—
Recruitment	$\chi^2_1 = 0.14$	$\chi^2_9 = 68.2^{***}$	$\chi^2_9 = 14.1$
Probability 2nd clutch	$\chi^2_1 = 4.0^*$	$\chi^2_9 = 41.2^{***}$	$\chi^2_9 = 25.1^{**}$
Clutch size 2nd clutch	$F_{1,93} = 4.4^*$	$F_{9,93} = 4.3^{***}$	$F_{7,85} = 3.3^{**}$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The proportion of birds starting a second brood was affected by density, but the effect differed between years (Table 2, Fig. 2); there were two years in which none of the females in the high density area produced a second brood, while in the low density area some second broods were always produced. The annual proportion of second broods was not correlated between the low and the high density area (Spearman rank correlation, $r = 0.46$, $N = 10$, $P = 0.21$). The variation in annual proportion of second broods is smaller for the low density area than for the high density area ($F_{9,9} = 3.2$, $P = 0.049$). Second clutches were about 0.5 eggs larger in the low density area (Table 2).

Recruitment rates measured as the number of recruits divided by the number of fledglings per brood were not affected by the experiment (Table 2). The recruitment rate was also analysed taking each fledgling as a data point and including the capture probability using SURPH. Capture probability did not differ between the years and the two plots (year: $\chi^2_7 = 10.09$, NS; plot: $\chi^2_1 = 1.305$, NS; interaction $\chi^2_7 = 3.47$, NS). In the recruitment rate analysis the

null model for capture rate was therefore used. Recruitment rate differed between the years, but not between the plots (year: $\chi^2_7 = 30.98$, $P < 0.001$; plot: $\chi^2_1 = 0.44$, NS; interaction: $\chi^2_7 = 9.64$, NS). Adult males differed in capture rate between the years, but not between the plots (year: $\chi^2_7 = 14.76$, $P < 0.039$; plot: $\chi^2_1 = 0.82$, NS; interaction: $\chi^2_7 = 0.00$, NS). Using the capture model including year, the survival did not differ between years or plots (year: $\chi^2_7 = 8.33$, NS; plot: $\chi^2_1 = 0.98$, NS; interaction: $\chi^2_7 = 4.94$, NS). Female capture rates were equal across years and between plots (year: $\chi^2_7 = 3.68$, NS; plot: $\chi^2_1 = 2.25$, NS; interaction: $\chi^2_7 = 2.79$, NS). Female survival differed between the years, but not between the plots (year: $\chi^2_7 = 29.81$, $P = 0.0001$; plot: $\chi^2_1 = 1.79$, NS; interaction: $\chi^2_7 = 10.89$, NS).

Discussion

Clutch size, fledgling mass and the proportion of great tits starting a second brood were all lower in the high density than in the low density treatment. This difference was not due to habitat differences, because clutch size was equal at equal densities. Clutch size was also found to be negatively correlated with natural variation in density in the long-term study. The annual mean clutch size correlated between the high and the low density plots, suggesting that environmental factors acting on a larger spatial scale, such as annual differences in food availability, also affected clutch size. The annual proportion of second broods was not correlated between the two density treatments.

The experiment shows that great tit reproduction is causally related to the density. This suggests that the frequently found negative correlation between reproduction and natural density is indeed caused by variation in density (e.g. Kluyver 1951; Perrins 1965; Krebs 1970; Van Balen 1973). This is the first experimental study to demonstrate an effect of density on clutch size within years. All three experimental studies on flycatchers (Tompa 1967; Alatalo & Lundberg 1984; Török & Tóth 1988) found no effect on clutch

Fig. 2. The effect of experimental density manipulation on the proportion of birds starting a second clutch. Solid bars are the high density area, open bars are the low density area. For statistics see Table 1.

size, which was clearly affected in the present study. It is notable that a negative correlation between clutch size and density between years has been found far more often in great tits than in flycatchers (12 out of 17 studies for great tits, 0 out of 6 studies for pied flycatchers, no effect in a single study on collared flycatchers, unpublished data, Kluyver 1951; Perrins 1965; Van Balen 1973; Alatalo & Lundberg 1984; Orell & Ojanen 1984; Virolainen 1984; Sasvari, Török & Tóth 1987; Stenning, Harvey & Campbell 1988; Dhondt, Kempenaers & Adriaensen 1992). Pied flycatchers might normally occur at breeding densities at which competition does not act, which might be a consequence of the migratory habit of the species. For flycatchers interspecific competition might also be more severe, because they start breeding later in the season than the tit species, *Parus spp.*, which are important food competitors (Gustafsson 1987). Although no effects were found on clutch size, density seems to have a slight effect on nestling growth in flycatchers. In these species females may be unable to adjust their clutch size to final breeding density, because females are still arriving while many females are laying. The effect of experimental density on clutch size in blue tits (Dhondt, Kempenaers & Adriaensen 1992) was found between years with different densities. This effect might also be confounded by effects of interspecific competition with great tits (see Dhondt 1977; Minot 1981), because they manipulated blue tit density by changing the competition for nest-boxes with great tits, so that they possibly not only increased the density of blue tits, but also decreased the great tit density. Kluyver (1951) also reported the results of an experimental manipulation of great tit density, without analysing the effect of experimental density. The experiment consisted of 4 years with a low nest-box density and 5 succeeding years with a high nest-box density. In the low density years both the clutch size of first and second broods, and the proportion of second broods were higher than in the high density years (see Table 3). These data confirm the presented experimental results, and suggest that density-dependent reproduction is a general phenomenon in great tits (see also Both 1998).

Clutch size in great tits has been shown to be individually optimized (Perrins & Moss 1975; Pettifor, Perrins & McCleery 1988; Tinbergen & Daan 1990). Density dependent clutch size therefore should also be considered as an adaptive decision, and full understanding of the pattern will only be possible if the selection pressures associated with the density are identified. Competition for food during laying might cause females to lay smaller clutches in high density years. Perrins & McCleery (1996) showed that great tits do not only reduce clutch size with increasing density, but also have reduced egg mass, which suggests that competition during egg laying is indeed important. However, food supplementation studies have hardly shown any increase in clutch size (Daan

et al. 1988; Boutin 1990; Nager, Rieger & Van Noordwijk 1997), which would have been expected if competition for food is an important cause of the density-dependent clutch size. Furthermore, when the amount of time fighting with conspecifics was experimentally increased during the egg laying period, there was no decrease in clutch size in great tits (Kempenaers & Dhondt 1992). Krebs (1970) found that larger great tit clutches were more often predated by weasels in high density years, suggesting that nest predation rates are an important selection pressure. In the present study nest predation was rare, and can therefore be neglected. Lack (1947) suggested that clutch size is adjusted to the number of nestlings that parents can feed, and food competition during chick feeding might therefore be an important selection pressure explaining why birds reduce clutch size with increasing densities. The observation that not only clutch size, but also fledgling mass is reduced, suggests that chicks received less food in the high density treatment. This, together with an increase in fledgling mass while supplementing food during the nestling period (J.M. Tinbergen, unpublished results), suggests that one of the important factors causing the density-dependent clutch size is food competition during chick feeding. The lower fledgling mass in the high density part disagrees with the suggestion of Krebs & Perrins (1978) that females reduce clutch size to produce better quality offspring in more competitive environments. Although the alternative explanation for the difference in clutch size would be that parents choose to work less hard when the density is high, there is no experimental evidence in great tits that the costs of reproduction extend beyond the present breeding season (Pettifor *et al.* 1988; Tinbergen & Daan 1990). The data therefore suggest that the selection pressure causing the density-dependent clutch size is the competition for food during the nestling phase.

Great tits started a second brood more often in the low density plot. No correlation was found between the annual proportion of second broods in both areas, which is probably due to the small number of years. The value of a second brood is dependent on the timing of the tits relative to the peak in food availability, and the competition second brood fledglings face from first brood fledglings (Kluyver 1951; Tinbergen, Van Balen & Van Eck 1985; Verhulst 1992). Both the factors affecting timing and the density of first brood fledglings probably act on a larger spatial scale than the scale of the experiment, suggesting that great tits should adjust the decision whether to continue with a second brood or not on more than only the local density. It seems unlikely that the breeding density has an overriding effect in the decision to start a second brood, because otherwise it would have been expected that the proportion of birds starting a second brood would have been higher in the low density area in all years.

Recruitment rates were not affected by differences

Table 3. Data on annual mean clutch size and proportion of great tits starting a second clutch in an experimental density study carried out by Tjittes and mentioned in Kluyver (1951). The first 4 years had a low nest-box density, which resulted in a low breeding density, while the succeeding 5 years had a high breeding density due to a high nest-box density. The last row gives the results of Mann–Whitney *U*-tests, testing differences between the two density treatments. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Year	Mean clutch size Density	Mean clutch size 1st clutch (SD)	Percentage 2nd clutch (SD)	2nd clutches
1926	5	9.8 (1.7)	8.0 (0.0)	80
1927	6	9.7 (3.4)	7.8 (0.8)	83
1928	8	10.4 (1.5)	6.7 (2.3)	38
1929	8	9.6 (1.5)	8.8 (2.0)	50
1930	24	8.6 (1.5)	6.8 (0.8)	21
1931	23	8.5 (1.5)	6.0 (0.0)	9
1932	24	8.0 (1.4)	6.0 (0.0)	8
1933	19	8.0 (2.1)	6.7 (1.2)	31
1934	23	7.2 (1.7)	5.5 (0.7)	9
U-statistic	20**	20**	18.5*	20**

in density between the plots, although there was a strong negative correlation with the natural variation of density in the long-term study (as was found by Tinbergen *et al.* 1985; Verhulst 1992). This difference might be partly due to between year differences in other factors that affect recruitment rates, which might play an important role in the correlational study, but not in the experimental study in which the year effects were controlled for in the analysis. Because of dispersal of young it is also likely that local differences in breeding density do not reflect the strength of competition that independent offspring face.

The consequences of density-dependent reproduction for population dynamics of great tits are as yet unclear. Lack (1966) considered it as having a minor effect on population dynamics, while Krebs (1970) found that clutch size was one of the key factors regulating the great tit population at Oxford. In the present study the difference in great tit breeding density between the low and the high density part was huge (on average 8-fold), but, compared to this, the resulting decline in the total number of great tits fledged per year due to density was small; on average the number of fledged young per hectare was still 7 times higher for the high density area. In contrast, in a mixed forest, which is probably a poorer quality breeding habitat for great tits, Kluyver (1951) increased the breeding density by a factor of 3.4, but found that the increase in number of fledglings only increased by a factor of 2.2. Thus although density-dependent reproduction in Liesbos seems to have only a minor effect on the population dynamics, it might have a more significant effect in other populations (see also Krebs 1970). These differences might be attributed to between area differences in food availability per pair during the breeding season. Although the effect of density-dependent reproduction on population dynamics seems to be small in the Liesbos population, individuals clearly gain from breeding in the low density area.

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