Density dependence of clutch size: habitat heterogeneity or individual adjustment?

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Summary

1. Two hypotheses have been proposed to explain density-dependent patterns in reproduction. The habitat heterogeneity hypothesis (HHH) explains density-dependent reproduction at the population level from poorer quality territories in heterogeneous environments only being occupied at high densities. No effect of population density is expected on reproduction within a given territory. If reproduction and territory quality are correlated, there will be a negative correlation between reproduction and density. Alternatively, density-dependent responses could be caused by variation in reproduction with population density. This will be referred to as the individual adjustment hypothesis (IAH).

2. The HHH predicts that individuals breeding on the same territory in years with different densities would show no response in reproduction to changes in population density. The response in reproduction of the population to changes in density would therefore be stronger than the within territory response. Under the IAH, the response of individuals on specific territories would be similar to the average response in the whole population.

3. This paper attempts to discriminate between these two hypotheses using data on clutch sizes of great tits *Parus major* L. from six different populations. In all populations the mean clutch size was negatively correlated with the population density. In four out of the six study populations individual females breeding on the same territory showed a negative correlation between the change in clutch size between years and the change in density. In none of the populations it was found that the response within territories was significantly smaller than the average response for the population.

4. These data suggest that density dependence of clutch size in great tits is not due to poorer quality territories being occupied more frequently at higher population densities. Within territories, individual females adjusted their clutch size to changes in density, and this was sufficient to explain the density dependence of clutch size in five of the six populations. In one population some evidence supporting the HHH was found.

Key-words: clutch size, density dependence, habitat heterogeneity, individual adjustment, *Parus major*.

Journal of Animal Ecology (1998) **67**, 659–666

Introduction

Density-dependent reproduction has been observed among many animal species (Sinclair 1989). Most of these studies are based on correlations between the annual mean reproduction and the density, without knowing whether density is the cause of the relationship, or the extent to which individuals respond to

changes in density (but see Kempenaers & Dhondt 1992). The observed density-dependent patterns in these studies could be caused either by a higher proportion of individuals occupying poor quality habitats in a heterogeneous environment at high population densities (Andrewartha & Birch 1954; referred to as the habitat heterogeneity hypothesis (HHH) by Dhondt, Kempenaers & Adriaensen (1992)), or by individuals adjusting their behaviour as a response to changing densities within the same habitat (Lack 1954). This paper evaluates the HHH as an explan-

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ation for the density dependence of clutch size in birds.

The HHH explains density dependence of clutch size by proposing that: (i) individuals settle in the best available patch, so that low quality patches are only occupied in high density years; (ii) territory quality within a patch is not affected by population density; and (iii) clutch size is affected by territory quality. The observed negative correlation between average clutch size and population density is thus due to a positive relationship between the variation in quality of occupied territories and population density, resulting in a decrease of average territory quality and hence a decrease in mean clutch size. The HHH assumes that reproductive decisions of individuals breeding in the same territory are not affected by changes in density at all (Fig. 1a). Under this hypothesis, there will be no density dependence of clutch size if there is no variation in territory quality. Differences in the amount of heterogeneity in territory quality could therefore explain why density dependence of clutch size has been found in some studies, but not in others (Perrins & McCleery 1989; Sinclair 1989; Dhondt, Kempenaers & Adriaensen 1992).

Density dependence of clutch size could also result from the response of individuals within territories to population density. If individuals on different patches are affected by density to more or less the same extent, the relationship between clutch size and density will be equally strong when measured either at the population or individual level (Fig. 1b; this will hereafter be called the Individual Adjustment Hypothesis, IAH). This prediction is different from the prediction of the HHH, and makes it possible to investigate whether the observed density dependence of clutch size is due to settlement patterns in a heterogeneous habitat, or that individuals within territories are affected by changing levels of competition. If both mechanisms occur in the same population, then individuals are

expected to adjust their clutch size to changes in density, but the density response at the level of the population will be stronger than the response at the individual level (Fig. 1c).

This paper tests the HHH and IAH in relation to the density dependence of clutch size in great tits, using data from individual female great tits that bred in more than one year.

Methods

Data are analysed for six great tit populations studied by the Netherlands Institute of Ecology. Four of these populations were followed from 1955 to 1995, while the Hoge Veluwe A (HVA) population was followed from 1955 to 1973, and the Warnsborn (W) population from 1985 to 1995. Liesbos (L) and Oosterhout (O) are mainly deciduous woods, with oak, *Quercus robur* L., as the predominant tree species. Warnsborn and Hoge Veluwe B (HVB) are mixed woods, the first on richer soil, and with higher trees than the latter. HVA and Vlieland (V) are dominated by conifers. W and HVB are the two most heterogeneous woods with respect to tree species, and probably also food availability for the tits. More detailed descriptions of the areas are given by Van Balen (1973) and, for Vlieland, by Verhulst (1995).

Nest-boxes, believed to be provided in excess, were checked at least once a week. As great tits prefer nest-boxes over natural nest-holes, the whole breeding population can be sampled. Only clutches where a female started incubating are included in the analyses of clutch size. Throughout the paper only first clutches are used, which are defined as the clutches started within 30 days of the earliest clutch in that area and year, excluding clutches of ringed females that are known to have made an earlier breeding attempt that year. Repeat clutches (after failure of the first clutch), and second clutches (after successfully raising a first brood) are thus excluded from the analyses. All nests where experimental manipulations were performed before clutch completion are excluded from the analyses. Females were caught in the nest-box approximately 7 days after the hatching of the first egg, and individually identified using aluminium rings.

Clutch size adjustment to changes in population density are investigated in individual females, not males, because females are believed to have control over clutch size (Van Noordwijk, Van Balen & Scharloo 1981). Each female that bred in two consecutive years is treated as one case in the analysis. If females bred more often, one case for each pair of consecutive years has been used. In order to exclude the effect of females moving to better or poorer quality territories, data were included only if the distance moved between the years was less than that to the second nearest neighbouring great tit nest in the first year (25–300 m depending on area). This criterion was chosen to min-

Fig. 1. Predictions of the hypotheses explaining density-dependent clutch size. In each figure both the response within territories (dashed lines), and the average response for the whole population (solid line) are given. (a) Habitat heterogeneity hypothesis (HHH): females within territories are not affected by population density changes. Territories of lower quality are occupied when density increases. The population slope (b_p) is more negative than the individual response (b_i), which equals 0 ($b_p < b_i = 0$). (b) Individual adjustment hypothesis (IAH): the population effect results from individuals adjusting their clutch size ($b_p = b_i < 0$). (c) combined effect of habitat heterogeneity and individual adjustment ($b_p < b_i < 0$).

imize the distance moved by females in the sample, without excessively reducing sample size.

Population density is the number of first clutches started in the study area, divided by its area. The population as defined here includes home-ranges of most of the tits during the breeding season, thus representing the spatial scale on which competition between individuals occurs. To scale the population density effect for the different populations, the annual population density was standardized as (population density–average population density in that area) divided by the standard deviation of the average population density. The standardized density is thus measured as units of SD from the mean population density. The annual mean clutch size for the population was calculated for all incubated first clutches excluding nests where experimental manipulations were performed before completion of egg laying. Years in which more than 25% of the clutches were manipulated are excluded from the analyses.

Results

In all populations the annual mean clutch size correlated negatively with the breeding density, but the slopes of the regressions differ markedly between the areas (Fig. 2). The mean densities ($\pm$ SD) in the areas are: HVA (0.18 ± 0.09), HVB (0.65 ± 0.19), L (2.04 ± 0.55), O (2.54 ± 1.25), V (0.29 ± 0.17) and W (1.23 ± 0.29).

The relationship between the change in clutch size between years and the change in standardized population density between years was analysed both at the population level and for individual females breeding in the same territory. In all of the populations except V the change in mean clutch size between consecutive years is significantly negatively correlated to the change in annual density (Fig. 3, Table 1). The lack of a relationship in V might be due to the gradual increase in density throughout the study, with small differences in density between consecutive years. The regression of annual differences in mean clutch size on the difference in standardized population density differs in intercept but not in slope between the six populations (ANCOVA: area effect $F_{5,161} = 21.7$, $P < 0.0001$; standardized population density effect $F_{1,161} = 57.4$, $P < 0.0001$; interaction $F_{5,156} = 0.788$, $P = 0.562$).

There is a similar negative correlation between the change in clutch size of individuals between consecutive years and the change in population density in four out of the six populations (Fig. 4, Table 1). In none of the populations were the slopes of the relationships for populations and individuals significantly different (test for equality of slopes of regression lines, $P > 0.40$ in all cases, see Fig. 5). Only for L was the difference in slopes substantial in the direction predicted by the HHH, but the difference was not significant.

Clutch size in great tits is affected by female age and laying date (Kluyver 1951; Perrins 1965; Van Balen 1973). Therefore the density dependence of clutch size might be due to annual differences in age composition of the population, or due to an effect of density on laying date. Annual mean laying date was not correlated with the population density in any of the populations (all P values > 0.05), and therefore it is not expected that the laying date will affect the density dependence of clutch size. The effect of female age was analysed for the population and the individual level. In the analysis of the age effect, age is divided into first year breeding females and older females, because the age effect is mostly due to first year breeding females laying smaller clutches (Dhondt 1989). Density dependence of clutch size on the population level might be caused by a higher proportion of first year females breeding in high density years. The annual mean clutch sizes were calculated excluding the first year females, and a regression analysis was performed on the difference in mean clutch size between years and the difference in standardized density. In HVA, HVB, O and V the slope of this regression was similar to the regression of the whole population, and in all four populations except V this slope was also significantly different from zero. In L and W the slopes were not statistically different from zero. The age effect on the individual level was analysed using multiple regression, including age as a factor with two levels (i.e. females going from first year to second year, and older females). The effect of annual changes in density on individual changes in clutch size did not differ after correcting for age in any of the populations (Table 2). However, in the HVB and W populations the older females had a weaker reaction of clutch size to changes in standardized density than first year females (slope for first to second year females HVB: -0.79 ; W: -1.25 ; slope for older females HVB: -0.30 ; W: -0.27).

Discussion

Density dependence of the annual mean clutch size was found in all six of the great tit populations investigated. There were no significant differences in the strength of density dependence at the level of the population and individual, suggesting that the observed density dependence is explained by individual adjustment rather than habitat heterogeneity. Only in L was the individual response to density not significantly different from zero, and the difference between the individual and population responses substantial (although non-significant), suggesting that the HHH might play a part in this population.

In contrast to the results of this study, Dhondt, Kempenaers & Adriaensen (1992) concluded that in blue tits, *Parus caeruleus* L., clutch size density dependence could result from habitat heterogeneity. Their evidence was that in 5 years with an experimentally

Fig. 2. Annual mean clutch size in relation to annual density for six populations of great tits. (a) HVA: $F_{1,16} = 13.85^{**}$, (b) HVB: $F_{1,36} = 17.55^{***}$, (c) L: $F_{1,30} = 5.00^*$, (d) O: $F_{1,36} = 12.27^{**}$, (e) V: $F_{1,34} = 6.82^*$, (f) W: $F_{1,9} = 7.77^*$. *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$.

high density the clutch size in high quality territories was not smaller than in the 5 preceding years with an experimentally low density. The annual mean clutch size correlated with density because in the high density treatment the low quality territories were also occupied. When density was high, the birds preferred the high quality territories in which clutch size was larger. Dhondt, Kempenaers & Adriaensen (1992) did not investigate whether females breeding in the same territories adjusted their clutch size to changes in density, which is a more straightforward test of the HHH. Although contrary to their analysis, the annual mean clutch size in the high quality territories in the high density years appears to be smaller than in the low density years (Mann–Whitney-test, $n = 10$, $P = 0.028$, instead of their nested ANOVA), which would not

be expected if habitat heterogeneity is the sole factor explaining the density dependence in their population. Furthermore density dependence tests are very sensitive to the length of the time-series analysed (Hassell, Latto & May 1989). The lack of effect of density on annual mean clutch size in three of the four populations is therefore not strong evidence for the HHH, because each of the time-series was of only 10 years duration. The fact that territory quality differs, and that individuals breeding in high quality territories are affected by density, suggests that both HHH and individual adjustment plays a role in Dhondt, Kempenaers & Adriaensen's (1992) study.

Habitat heterogeneity might have accounted for the clutch size density dependence in at most one of the populations in the current study. I have no expla-

Fig. 3. The between year change in mean clutch size in relation to between year change in standardized population density (in SD units) for six populations of great tits. (a) HVA, (b) HVB, (c) L, (d) O, (e) V, (f) W. For statistics see Table 1.

Table 1. Relationships for populations and individuals between the change in clutch size between years and the change in standardized population density between years. The columns represent slopes ($\pm$ SE and sample size) of the relationships between: (1) the change in mean clutch size between consecutive years as a function of the between year change in density; (2) the change in clutch size of individuals between consecutive years as a function of the between year change in density

Study area	Population	Individuals
	Average change between years (1)	Change within territory (2)
HVA	-0.433 ± 0.080 (17)***	-0.415 ± 0.277 (45) NS
HVB	-0.343 ± 0.128 (37)*	-0.552 ± 0.077 (603)***
L	-0.243 ± 0.088 (34)*	-0.025 ± 0.117 (112) NS
O	-0.605 ± 0.209 (36)**	-0.962 ± 0.186 (171)***
V	-0.202 ± 0.278 (35) NS	-0.524 ± 0.200 (235)**
W	-0.770 ± 0.233 (8)*	-0.944 ± 0.200 (35)***

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

Fig. 4. The between year change in clutch size of individual females breeding on the same territory, in relation to between year change in standardized population density for six populations of great tits. Per pair of years the mean change in clutch size is given ($\pm$ SE). (a) HVA, (b) HVB, (c) L, (d) O, (e) V, (f) W. For statistics see Table 1.

nation of why the effect might occur in L, especially as it is one of the most homogeneous areas in this study. The effect of habitat heterogeneity will depend on the scale of heterogeneity, the size of home ranges, and the social structure of the population, and will completely explain the density-dependent pattern only when territories are not affected in size and quality by the density of competitors. The most likely situation in which this will occur is when the habitat consists of patches each sufficient for only one pair to breed, for instance if suitable nesting sites limit breeding density, as would be the case for natural nest-holes in a managed forest. In all other cases, individual resource availability will be affected by density to some degree, and density-dependent reproduction would be due partly to individual adjustment.

Density dependence of clutch size observed in the populations was not affected by the confounding effect of laying date. Female age affected the density dependence of clutch size in HVB, L and W. In L and W the density dependence of clutch size on a population level disappeared when excluding the clutches of first year females, suggesting that the pattern might be due to more first year females breeding in high density years, rather than females adjusting clutch size to changes in density. However, for W the sample sizes were small after excluding the older females, and in this population individual females adjusted their clutch size to changes in density. In HVB and W the first year females adjusted their clutch size more strongly than older females, but this was not a general pattern. In four of the six populations the individual

Table 2. Multiple regression analysis of the effect of the individual between year change in density, age and laying date on the between year change in clutch size. The last column gives the slope of the regression line ($\pm$ SE) of the change in density on the change in clutch size taking the other variables into account. The significant interaction terms are mentioned in the text

Area	Density	Age	Interaction	Slope
HVA	$F_{1,33} = 2.72$ NS	$F_{1,33} = \beta 2.86$ NS	$F_{1,32} = 0.61$ NS	-8.51 (4.19)
HVB	$F_{1,573} = 48.77$ ***	$F_{1,573} = 7.78$ **	$F_{1,572} = 9.57$ **	-2.84 (0.41)
L	$F_{1,103} = 0.003$ NS	$F_{1,103} = 4.53$ *	$F_{1,102} = 0.05$ NS	$+0.025$ (0.22)
O	$F_{1,161} = 25.93$ ***	$F_{1,161} = 0.04$ NS	$F_{1,160} = 0.23$ NS	-0.74 (0.15)
V	$F_{1,228} = 7.24$ **	$F_{1,228} = 2.60$ NS	$F_{1,227} = 2.72$ NS	-2.99 (1.18)
W	$F_{1,31} = 22.68$ ***	$F_{1,31} = 0.35$ NS	$F_{1,30} = 4.21$ *	-3.26 (0.53)

Fig. 5. Comparison of the regression slopes ($\pm$ SE) of annual change in clutch size as a function of change in standardized population density at the level of the population and individual. The dashed line is the line where slopes are equal.

reaction to changes in density seems to be greater than the mean population response (Table 1), which would mean that females that breed only once respond less to the density than females that breed more often. Because the density effect differs between areas, this might be due to the effect of learning what the appropriate clutch size response to density is in a given area.

So far, density-dependent reproduction only could be demonstrated on a descriptive basis. Experimental studies of the effect of density on reproduction are rare, and include examples in which density does (Kempenaers & Dhondt 1992; Both 1998), or does not (Tomba 1967; Alatalo & Lundberg 1984; Török & Tóth 1988) have an effect on clutch size. Although this study was descriptive, the results imply that females adjust their clutch size in response to density. This adjustment is probably adaptive (Pettifor, Perrins & McCleery 1988; Tinbergen & Daan 1990), with competition for food during the breeding season being the main selection pressure (Both, Tinbergen & Visser, unpublished). Alternatively female condition might be lower in high density years, resulting in females not being able to produce large clutches. However, studies in which food has been supplemented during spring

rarely result in significant clutch size enlargements (e.g. Daan *et al.* 1988), suggesting that female condition in the short term is not important in explaining density dependence of clutch size. Habitat heterogeneity was not found to be an important factor in explaining the density dependence of clutch size in these great tit populations.

Acknowledgements

I am grateful to all those who collected data during the 40 years of study. Hans van Balen deserves special mention for co-ordinating the collection of data in a standardized way. Jan Visser managed the database, which can be regarded as one of the best of its kind. 'Stichting Het Nationale Park De Hoge Veluwe', 'Staatsbosbeheer', 'Stichting Het Geldersch Landschap' and Mevr. Barones van Boetzelaer van Oosterhout kindly gave permission to work on their property. Bart Kempenaers, Kate Lessells and two referees Arie van Noordwijk, Joost Tinbergen Marcel Visser provided helpful comments on earlier versions of the manuscript. This is publication 2397 of the Netherlands Institute of Ecology.

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Received 29 January 1997; revision received 7 November 1997