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Is the small clutch size of a Corsican blue tit population optimal?

Abstract In an attempt to test predictions of the optimisation hypothesis of life history traits in birds, we estimated fitness consequences of brood size manipulations. Experiments were carried out over a period of 4 years in a Mediterranean population of blue tits *Parus caeruleus* which is confronted with a particular set of environmental constraints. Effects of brood size manipulation were investigated in relation to year-to-year variation in environmental conditions, especially caterpillar abundance. There was a strong variation in the effects of brood size manipulation depending on year. Most effects were on offspring quality (fledging mass, tarsus length). The absolute number of recruits did not significantly differ among categories (reduced, control, enlarged broods) but varied considerably among years. Females recruited from enlarged broods were of lower quality, started to breed later and laid fewer eggs than those recruited from control and reduced broods. Neither parental survival nor reproductive performances of adults in year $n + 1$ was affected by brood size manipulation in year n. Thus there was no evidence for a cost of reproduction in this population. Since the number of recruits did not depend on brood size manipulation (recruitment rates were higher in reduced broods), but recruits from reduced broods were of better quality compared with other groups, we conclude that adults lay a clutch that is larger than that which is predicted by the optimisation hypothesis. Producing more young could incur some penalties because offspring from large broods are of lower quality and less likely to recruit in the population. Two possible reasons why decision rules in this population seem to be suboptimal are discussed.

Introduction

A central tenet in evolutionary ecology is that animals optimise life history traits to maximise fitness (Maynard-Smith 1978). This implies trade-offs between different fitness related traits, among which two major trade-offs (Lessells 1991) are those between current and future reproduction of the adults (i.e. the cost of reproduction, Williams 1966), and those between the number and quality of offspring. The individual optimisation hypothesis (Drent and Daan 1980; Högstedt 1980; Pettifor et al. 1988) predicts that birds adjust their reproductive behaviour or 'decision rules', e.g. laying date and clutch size, according to environmental variation and phenotypic quality. Individual optimisation should result in phenotypic variation in clutch size reflecting differences in the ability of individuals to successfully raise offspring. To disentangle individual components of phenotypic variation from environmental confounding variables, one has to manipulate reproductive variables and measure the fitness consequences of manipulation. About half of the manipulation studies so far carried out in birds have shown that experimentally increased reproductive effort results in a decrease in the survival and future reproduction of the parents and/or offspring fitness components (reviews in Linden and Møller 1989; Nur 1990; Lessells 1991). Therefore results of experimentally increased brood sizes are often contradictory. For example, from manipulation studies on blue tits, Nur (1984a, b, 1988) concluded that increased reproductive effort results in penalties on the young and significant costs for the parents, especially the females. However, reanalysing Nur's data, and adding his own, Pettifor (1993a, b) found no strong evidence for a cost of reproduction, expressed either as an increase in mortality or a decrease in fecundity the year(s) after manipulation.

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One explanation for these contradictions is that negative effects of increased reproductive effort on adult survival or offspring quality do not occur every year and are more likely to occur under stressful circumstances (e.g. in 'bad years') than under particularly favourable conditions where they might be masked (De Steven 1980; Bell and Koufopanou 1986). A relatively low level of reproduction could incur high penalties in an environment where resources are limited, while a high level of investment could incur little or no penalties at all when resources are abundant (Tuomi et al. 1983).

Trade-offs are ultimately mediated by a number of factors including predators, parasites and the abundance of food available for the different stages of the breeding process (egg-laying, incubation, raising of the young). For many passerines including tits, the most important food is leaf-eating caterpillars. The year-to-year variation in both the timing and the duration of the period of caterpillar abundance, as well as the amount of caterpillars available to birds, may be large. Few studies have examined the consequences of manipulation of reproductive variables under different environmental conditions, especially the seasonal and year-to-year variation in the food supply.

The environment of tits in the Mediterranean region differs greatly from that in mid-Europe where most tit studies have been carried out. Within the Mediterranean region, there is enormous among-population variation in life-history traits and this variation has been shown to mostly depend on whether the dominant tree species in the habitat is deciduous summergreen (e.g. downy oak *Quercus pubescens*) where food is available early in spring, or sclerophyllous evergreen (e.g. holm oak *Q. ilex*) where food is available 4 weeks later (see Blondel et al. 1993 for details). A population of blue tits *Parus caeruleus* living in a sclerophyllous habitat on Corsica is characterised by the latest onset of breeding (12 May $\pm$ SD $= 6.7$ days, $n = 780$) and the lowest clutch-size (6.45 eggs $\pm$ 1.16, $n = 780$) so far recorded in Europe (see Blondel et al. 1993). Compared with populations living in summergreen oak habitats on the nearby mainland and at higher latitudes, this population is confronted with three environmental constraints: (1) trophic constraints because the food abundance is low, albeit diverse (Zandt et al. 1990; Blondel et al. 1991; Banbura et al. 1994), (2) thermal and water constraints because ambient temperatures are high in June when tits raise their young with water-poor food items (Nager and Wiersma 1996); and (3) parasitic constraints with exceptionally high parasitic loads of the blood-sucking larvae of *Protocalliphora* spp. blowflies (Hurtrez-Boussès et al. 1997).

The aim of this study was to examine whether the exceptionally low clutch size in this population is an adaptation to the set of constraints cited above. For that purpose, we conducted brood size manipulation experiments and made two predictions. (1) If clutch size is optimal, any experimental change in brood size is expected to result in a negative association between ma-nipulation and offspring fitness, e.g. an enhanced fitness in reduced broods and a reduced fitness in enlarged broods. (2) According to several previous studies on the cost of reproduction (e.g. Pettifor 1993b and references herein), we expected no significant effect of brood size manipulation on the residual reproductive value of the parents, i.e. their reproductive performances the year(s) after the experiment. In addition we examined whether fitness consequences of brood size manipulation varied among years as a result of the yearly variation in food availability. Because caterpillar availability is lower and more variable in sclerophyllous evergreen oaks of the Mediterranean region than in broad-leaved deciduous oaks at higher latitudes in Europe (Zandt et al. 1990), we predicted that the effects of brood size manipulation in relation to the variation in caterpillar abundance should be more variable, i.e year effects should be higher than those reported in other populations, e.g. that of Wytham, south England (Pettifor 1993a, b). We test these predictions using a 4-year experiment of brood size manipulation. We analyse the impact of brood size manipulation in relation to year on: (1) current reproductive success of the tits, (2) breeding parameters of offspring recruited from manipulated and control broods, and (3) future reproduction of the adults in the year following the manipulation (year $n + 1$). We measured fitness components of the broods as the number of recruits and the laying date and clutch size of both adults and recruits the year after brood size manipulation.

Study area and methods

Field work was carried out during the breeding seasons 1990–1993 in a mature sclerophyllous forest on the island of Corsica, France, at an altitude of 120–360 m, near Calvi (42°34′N/08°44′E) where blue tits have been studied since 1975. Holm oak is the dominant tree species (see Blondel 1985 for a detailed description of the habitat). Within the study area (ca. 70 ha), 137 nestboxes were evenly distributed at a density of approximately 2 nestboxes ha^{-1}. Nearly all blue tits breed in the nestboxes (ca. 60 breeding pairs annually) and produce only one brood per year.

The study area is situated on silicaceous soil poor in nutrients and the densities of leaf-eating caterpillars in the evergreen holm oaks are low in comparison with those of deciduous forests. Food abundance (foliage-eating caterpillars) was measured throughout the breeding season in five plots using 0.25 m^2 trays (3 trays per plot) that collected the frass of caterpillars (see Zandt et al. 1990 for details on the method). Frass was collected twice a week and sorted under a microscope. Food abundance was expressed as mg frass/m^2/day. The caterpillar peak-date of each year was defined as the sampling day with the highest median value of caterpillar abundance for the 15 samples. There was a huge variation in the caterpillar peak-date and caterpillar abundance among the 4 study years (Table 1). Since the interval between the caterpillar peak-date and hatching date of tits is known to have strong effects on the reproductive success, we examined the yearly interval between these two events. Tits fairly well synchronized their breeding time to year-to-year variation in the timing of caterpillar availability since hatching date consistently occurred between 1 day and 6 days after the caterpillar peak-date (Table 1). Caterpillar growth is dependent on ambient temperatures so that frass production may be a biased estimator of caterpillar abundance if there is a large year-to-year variation in ambient temperatures. However mean ambient tem-

Table 1 The yearly variation in caterpillar peak-date (*CPD*), frass weight at CPD (mg/m²/day), average frass weight from 10 days before to 10 days after the peak-date (*AFW*), hatching date (*HD*), and number of days between CPD and HD. CPD and AFW differed significantly among years (Kruskall-Wallis test, H = 15.71, $P = 0.001$, and H = 13.65, $P = 0.003$, respectively)

Year	CPD	Frass weight at CPD (mg/m²/day)	AFW (SD) (mg/m²)	Hatching date (SD)	No. of days between CPD and HD (days)
1990	3 June	82.6	51.8 (17.4)	29 May (5.6)	5
1991	12 June	164.2	108.0 (54.9)	6 June (5.0)	6
1992	31 May	338.7	207.8 (115.4)	26 May (4.0)	5
1993	5 June	188.5	145.3 (39.9)	4 June (4.9)	1

peratures during the 'window' of caterpillar growth (estimated from 10 days before to 10 days after the caterpillar peak-date) varied between 19.3°C in 1992 and 20.1°C in 1993. Because this variation was rather low, we assumed that frass weight was a reasonable estimator of the year-to-year variation of food availability for the tits.

Breeding pairs were randomly assigned to three groups (sample sizes in Table 2) with the sole constraint that manipulated and control broods having the same hatching date. Broods with the same hatching date were treated in pairs. Two randomly chosen 2-day-old chicks were moved from a sample of broods, whatever the initial size of the latter, (reduced) and moved to another sample (enlarged). One third of the broods were left with their natural brood size with random exchanges of two chicks among them (control). Such small scale manipulations (i.e. within the range of normal brood size) has the disadvantage that large sample sizes are needed to detect any effects, but they have the advantage that the resulting brood-size variation is of the same order of magnitude as the natural variation, which is crucial if alternatives to the birds' decision rules are to be estimated realistically (Linden and Møller 1989; Gustafsson et al. 1994). Laying date, clutch size, hatching date, and number of hatchlings were recorded through almost daily inspection of the nestboxes. Nestboxes were subsequently visited to catch the adults and count and measure the nestlings. The average yearly laying date varied widely from 6 May ± SD = 4.1 days in the earliest year (1992) to 16 May ± 6.0 days for the latest year (1991) with intermediate values of 11 May ± 6.0 days in 1990 and 15 May ± 4.8 days in 1993 ($F_{3,226} = 45.5$, $P < 0.001$). The average clutch size was 6.58 ± 1.18 eggs ($n = 229$) and varied between 6.43 ± 1.15 ($n = 51$) in 1990 and 6.88 ± 1.13 in 1992 ($n = 59$) ($F_{3,226} = 1.87$, $P = 0.134$). Brood sizes (just after manipulation) ranged from 3.63 ± 1.07 chicks for reduced broods ($n = 68$) to 8.28 ± 1.24 chicks for enlarged broods ($n = 68$) (Table 2). Hatching date did not significantly differ among the experimental groups ($F_{2,223} = 0.79$, $P = 0.45$). As a measure of breeding success we counted the number of fledglings from each nest. Nestlings were individually ringed at day 5. They were weighed to the nearest 0.1 g at day 15 ('fledging mass') using a pesola spring balance. Tarsometatarsus (hereafter called tarsus) length was measured to the nearest 0.1 mm when young were 15 days old (except in 1991). To identify parents, we trapped them in the nestbox when feeding 9 to 12-day-old young and marked them with individually numbered rings, and also weighed and measured (wing, tarsus, culmen) them. Each adult was aged according to Perrins (1979) as either about 1-year-old (yearling) or older. Adult survival and the number of offspring recruited in the breeding population were determined by catching the breeding birds within the study area in subsequent years. Nearly all successful breeders were caught but capture rates of birds that failed to fledge any young were lower. For nests with at least one fledgling we identified 97% of the females and 89% of the males. The experimental manipulation had no significant adverse influence on nest failure rates: total nest failure amounted to 14% in non-manipulated broods, 16% in enlarged broods and 15% in reduced broods. However, we kept the nests with total failure in the analyses.

In some analyses, to be able to compare laying dates and clutch sizes between the different years, we standardised values by subtracting the yearly mean values from the measured values and dividing the result by the standard deviation for each year and trait. Statistical analyses were carried out using GLIM (NAG 1986) with stepwise backward deletion of variables with non-significant effects. We used a normal error distribution for most variables, a Poisson error distribution for the number of fledglings or recruits, and a binomial error distribution for fledging rate, recruitment rate, and survival rate of adults. Adjustment of the scale parameters was used to correct for overdispersion in some models as suggested by Aitkin et al. (1989). *F*-values were calculated following Crawley (1993). Unless specified otherwise, all statistical tests are two-tailed. To avoid pseudoreplication, we analysed the mean values for each brood as a dependent variable so that all sample sizes refer to number of broods.

Results

Effects of treatment and year on offspring numbers and quality

The values of various reproductive traits in relation to treatment and year are presented in Table 2 and Figs. 1 and 2, and the statistical analyses in Table 3. Although manipulation of the chicks has been made randomly with the sole constraint that hatching date of broods treated as dyads occurred on the same date, natural clutch sizes were slightly but significantly higher in enlarged broods than in the two other groups as shown by a significant effect of the interaction between year and treatment on clutch size (Table 3). However, adding clutch size as an explanatory variable in the models did not change the effects of the experiments on fitness components of the young ($\chi^2 = 0.05$, $P = 0.82$, and $\chi^2 = 0.69$, $P = 0.41$ for fledging success and recruitment rates, respectively). Therefore, we did not introduce clutch size as an explanatory variable in the subsequent analyses. The consequences of brood size manipulation on the number of fledglings and on fledging success (number of fledglings/brood size after manipulation) depended on the interaction between year and treatment (Fig. 1, Table 3). Except in 1990, enlarged broods produced significantly more fledglings than control and reduced broods (number of fledglings = 3.4, 5.2 and 6.9 in reduced, control and enlarged broods, respectively, ANOVA, $F_{2,190} = 34.17$, $P = 0.000$, see Fig. 1A) but fledging success was highest in reduced broods in 3 of the 4 years (Fig. 1B). Fledging mass and tarsus length of the offspring were significantly higher in reduced than in control and enlarged broods and the values of these variables differed significantly

Table 2 Average values of various reproductive traits of blue tits in relation to year (Y) and treatment (T, two chicks removed from or added to natural broods). Values are given with sample sizes (in parentheses) and SD

	1990			1991			1992			1993			Stats[b]
	-2	0	+2	-2	0	+2	-2	0	+2	-2	0	+2	
Laying date (in «Marchdate ≫)[a]	72.6 (16) 4.9	70.0 (19) 7.6	72.4 (16) 4.6	77.7 (15) 5.2	77.2 (22) 7.5	76.9 (15) 4.4	68.1 (16) 3.2	67.3 (27) 5.2	66.7 (16) 2.8	75.6 (21) 3.8	78.0 (26) 5.2	75.3 (21) 4.8	Y
Clutch size	6.7 (16) 1.06	6.5 (19) 1.12	6.1 (16) 1.23	6.3 (15) 0.88	6.5 (22) 1.14	6.9 (15) 1.03	6.3 (16) 0.68	6.8 (27) 1.24	7.6 (16) 0.88	6.2 (21) 0.87	6.5 (26) 1.81	6.7 (21) 0.97	T*Y
Number of hatchlings	6.3 (16) 1.19	5.9 (19) 1.29	5.7 (16) 1.30	5.3 (15) 1.11	5.5 (22) 1.44	6.4 (15) 0.83	5.6 (16) 0.62	6.3 (27) 1.51	7.0 (16) 1.41	5.3 (21) 1.06	5.5 (26) 1.75	6.1 (21) 1.09	NS
Fledging mass (g)	10.0 (12) 0.76	9.7 (14) 0.84	9.1 (12) 1.27	11.8 (14) 0.73	10.8 (17) 0.84	10.7 (13) 1.03	10.5 (16) 0.46	9.8 (21) 0.65	9.6 (15) 0.65	10.5 (14) 0.87	9.5 (20) 0.87	9.8 (19) 0.69	T,Y
Tarsus length of the fledglings (mm)	15.81(5) 0.44	16.00 (16) 0.46	15.40 (14) 0.61	—	—	—	16.35 (5) 0.42	16.14 (18) 0.35	15.85 (19) 0.43	16.17 (8) 0.54	15.81 (14) 0.61	16.4 (19) 0.37	T,Y
Number of recruits	0.44 (16) 0.63	0.26 (19) 0.56	0.25 (16) 0.58	0.27 (15) 0.46	0.27 (22) 0.55	0.47 (15) 0.64	0.44 (16) 0.63	0.48 (27) 0.80	0.19 (16) 0.40	0.00 (21) 0.00	0.09 (26) 0.21	0.19 (21) 0.40	Y

[a] March 31 = 31, April 1 = 32
[b] Significant effects of Y = year; T = treatment; T*Y = interaction between year and treatment

among years (Tables 2, 3). On average, the heavier the fledglings, the longer their tarsi ($r = 0.49$, $P < 0.001$, $n = 118$).

We estimated the number of recruits by capturing locally breeding birds in subsequent years. From the 939 young fledged in the 4 years, 64 birds (21 females and 43 males, sex bias in the sample, $\chi_1^2 = 6.41$, $P < 0.01$) were recovered locally as breeding birds the year(s) after their birth (16, 19, 23 and 6 from young born in 1990, 1991, 1992, and 1993, respectively). The number of recruits per brood varied among years but did not significantly de-
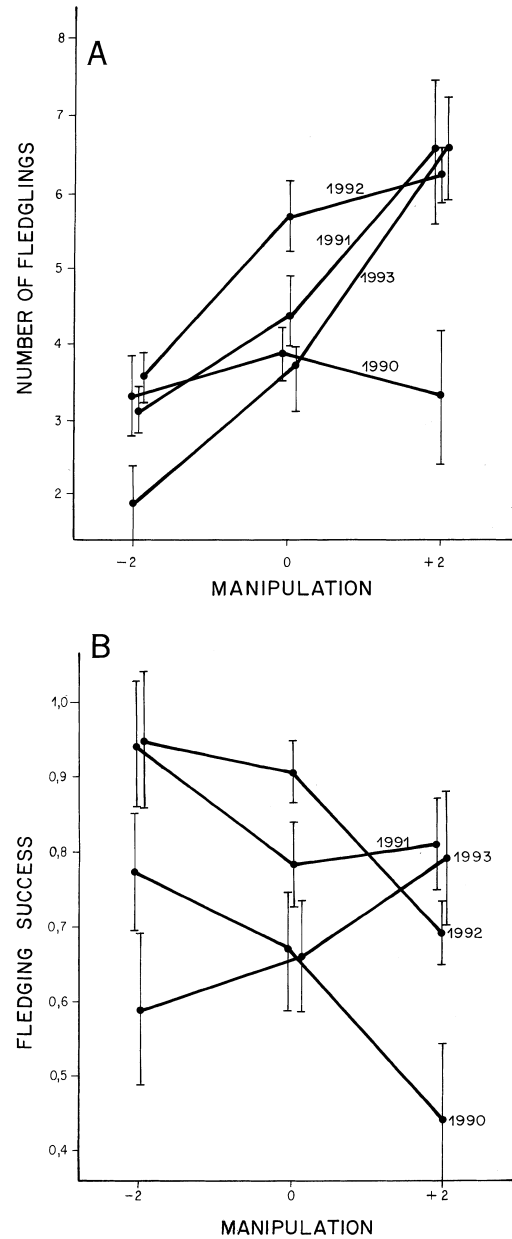
Fig. 1 Number of fledglings (**A**) and fledging success defined as the proportion of nestlings that fledged (**B**) according to year and treatment (lines are the fitted values from logistic regression, the *vertical bars* are 1 SE)

Table 3 Main effects of treatment (*T*), year (*Y*) and of their interaction term ($T \times Y$) on various reproductive traits of blue tits using stepwise backward models (GLIM, see Methods). Models with Poisson error for numbers of fledglings, numbers of hatchlings and numbers of recruits ($\Delta D = \chi^2$ values, see Crawley 1993). Factors with non significant effects were removed from the model. Factors with significant effects were reintroduced (* means correction for overdispersion)
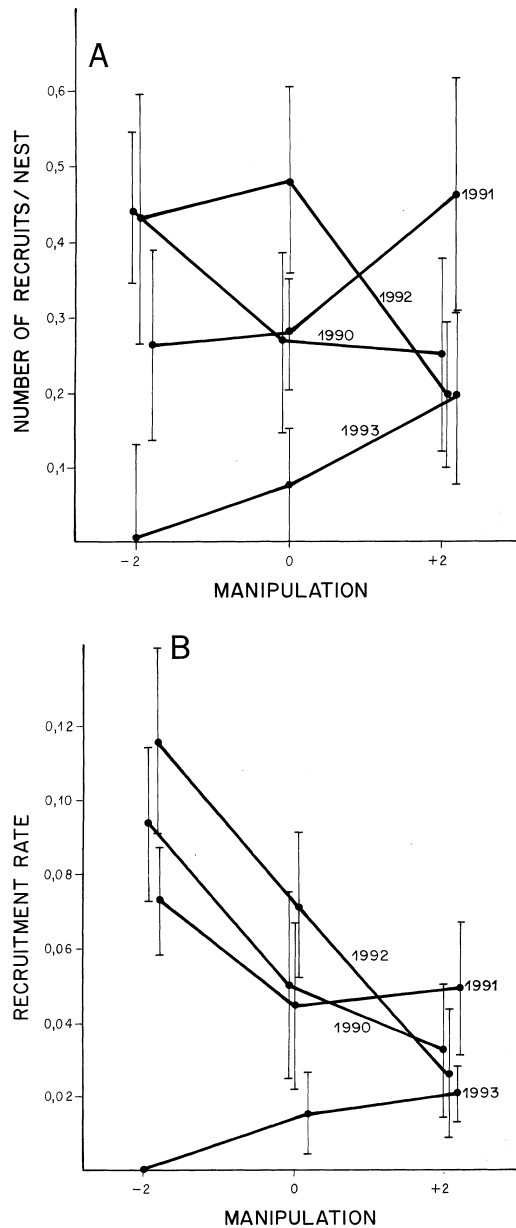
	Deviance (df)	ΔD (Δdf)		*P*
Laying date				
Null model	9858 (229)			
Full model	5952 (218)			
– $T \times Y$		180.6 (6)	$F_{6,218} = 0.01$	0.999
– T		13.9 (2)	$F_{2,224} = 0.25$	0.776
– Y		3712 (3)	$F_{3,226} = 45.53$	0.000
Clutch size				
Null model	324.24 (229)			
Full model	291.19 (218)			
– $T \times Y$		18.0 (6)	$F_{6,218} = 2.25$	0.039
Hatching date				
Null model	9541 (228)			
Full model	5165 (217)			
– $T \times Y$		190.2 (6)	$F_{6,217} = 1.33$	0.243
– T		38.3 (2)	$F_{2,223} = 0.79$	0.451
– Y		4147 (3)	$F_{3,225} = 57.66$	0.000
Number of hatchlings				
Null model	236.61 (229)			
Full model	323.31 (218)			
– $T \times Y$		2.5 (6)		0.868
– T		3.6 (2)		0.165
– Y		7.2 (3)		0.066
Number of fledglings*				
Null model	391.79 (229)			
Full model	306.85 (218)			
– $T \times Y$		20.7 (6)		0.002
Fledging mass				
Null model	205.93 (186)			
Full model	115.19 (175)			
– $T \times Y$		4.7 (6)	$F_{6,175} = 1.20$	0.308
– T		26.4 (2)	$F_{2,181} = 19.92$	0.001
– Y		57.9 (3)	$F_{3,181} = 29.17$	0.001
Tarsus length of the fledglings				
Null model	31.12 (117)			
Full model	24.45 (109)			
– $T \times Y$		2.1 (4)	$F_{4,109} = 2.33$	0.060
– T		2.0 (2)	$F_{2,113} = 4.30$	0.016
– Y		2.2 (2)	$F_{2,113} = 4.72$	0.011
Number of recruits				
Null model	191.33 (229)			
Full model	165.77 (218)			
– $T \times Y$		10.6 (6)		0.103
– T		0.0 (2)		
– Y		15.0 (3)		0.002

pend on treatment (Fig. 2A, Table 3). Concomitantly, nestling recruitment rate (proportion of nestlings recruited as breeding birds in the population) decreased from reduced to enlarged broods except in 1993 when very few of the offspring produced have been subsequently recruited (Fig. 2B, Table 3). One important variable affecting the probability that a fledgling would recruit to the population was its fledging mass. The mean fledging mass of broods that recruited at least one offspring has been 10.2 g ± 0.66 (SD) (*n* = 56) against 9.8 g ± 0.63 (*n* = 127) for those that did not (ANOVA, $F_{1,182} = 4.33$, *P* = 0.039). There was a tendency for the mean tarsus of broods that recruited at least one offspring to be higher than that of those that did not, but the difference was not significant [recruits:

16.12 mm ± 0.49 (*n* = 31); no recruits: 15.97 mm ± 0.50 (*n* = 84); ANOVA, $F_{1,114} = 2.07$, *P* = 0.152].

Breeding performance of the recruits in relation to treatment of their nest of origin

Next, we examined the breeding performances of recruits in year *n* + 1 in relation to the manipulative treatment of the brood in which they were raised (Table 4). Females that were raised in enlarged broods laid significantly later and produced significantly smaller clutches than those raised in reduced and control broods. These lower performances were associated with a lower quality of the birds in terms of morphology.

15.95 ± 0.43 mm and 16.30 ± 0.19 mm in enlarged, control and reduced broods, respectively, $F_{2,16} = 6.38$, $P = 0.0092$). Females recruited from reduced broods started to lay slightly earlier than those recruited from control broods but the difference is not significant (Table 4). There was no effect of treatment on any breeding traits of male recruits from experimental nests and none of their morphological traits significantly differed among treatment categories although there was a trend of shorter wing and tarsus in recruits from enlarged broods.

Effects of treatment on adults

To avoid pseudoreplication we estimated survival of adult blue tits from their recapture rate considering only the first event of return for those individuals that bred more than 2 consecutive years during the study period. For females, recapture rates depended on year (Table 5), with females that bred in 1993 having a lower probability of returning as breeders in 1994 (0.37) than females that bred in the other years (0.50 in 1990, 0.73 in 1991 and 0.59 in 1992). For males, none of the variables affected return rates although the interaction between treatment and year was close to significance (Table 5).

Finally we examined whether brood size manipulation in year n had effects on the breeding performance of adults in year $n + 1$. Several factors are known to influence laying date, including the age of the female (Perrins and McCleery 1985; Dhondt 1989) and site fidelity (Nager and van Noordwijk 1995). On average, females older than 1 year started to lay 2 days earlier than yearlings ($F_{1,221} = 4.88$, $P = 0.028$) and resident females which had already bred in the study area started to lay on average 4 days earlier than immigrant females of the same age class ($F_{1,179} = 12.47$, $P = 0.0005$). Therefore we controlled for age and immigrant status to examine the effects of brood size manipulation in year n on clutch size in year $n + 1$. Analysing intra-individual differences in laying date and clutch size as a response to treatment in year n, females that laid earlier in year n were also those that laid earlier in year $n + 1$ and clutch size was similar whatever the brood size they were assigned in year n (Table 5). In females, there was no effect of treatment in year n on the number of fledglings in year $n + 1$. In all traits examined there was a slight tendency for a negative effect of treatment but none was significant. Manipulation had no effect on laying date and the number of fledglings in year $n + 1$ for males, but there

Fig. 2 Number of recruits (**A**) and recruitment rates defined as the proportion of fledglings that were recruited as breeding birds (**B**) according to year and treatment (lines are the fitted values from logistic regression, the *vertical bars* are 1 SE)

Females recruited from enlarged broods had a shorter wing and a shorter tarsus than those recruited from the two other categories but only the difference in tarsus length was significant (tarsus length: 15.58 ± 0.39 mm,

Table 4 Laying date and clutch size (standardised values) of yearling females in relation to the manipulation treatment of the brood in which they were raised

	Manipulation			F (P)
	−2	0	+2	
Laying date	−0.383 ± 0.343 (n = 7)	−0.251 ± 0.321 (n = 8)	0.940 ± 0.407 (n = 5)	3.60 (0.050)
Clutch size	0.347 ± 0.328 (n = 7)	0.346 ± 0.307 (n = 8)	−1.038 ± 0.388 (n = 5)	4.77 (0.023)

Table 5 Effects of treatment (*T*) and year (*Y*) in year *n* on return rate and breeding performances (laying date, clutch size and number of fledglings in year *n* + 1) of adult blue tits. Models fitted with binomial error for return rates and Poisson error for number of fledglings ($\Delta D = \chi^2$ values, * means correction for over-dispersion). Standardised values for laying date and clutch size. The models for laying date and clutch size controlled for age and immigrant status of the birds

	Deviance (df)	ΔD(Δdf)	F	P
Females				
Return rates				
Null model	309.65 (223)			
Residual	288.86 (212)			
− T × Y		2.9 (6)		0.821
− T		1.8 (2)		0.406
− Y		16.1 (3)		0.011
Laying date				
Null model	107.56 (117)			
Residual	102.32 (105)			
− T × Y		3.5 (6)	$F_{6,105} = 0.60$	0.732
− T		0.3 (2)	$F_{2,111} = 0.18$	0.835
− Y		1.2 (3)	$F_{3,113} = 0.44$	0.728
Clutch size				
Null model	98.54 (117)			
Residual	90.06 (106)			
− T × Y		4.7 (6)	$F_{6,106} = 0.93$	0.478
− T		1.7 (2)	$F_{2,112} = 1.00$	0.373
− Y		2.0 (3)	$F_{3,114} = 0.81$	0.493
Number of fledglings*				
Null model	144.36 (117)			
Residual	135.75 (106)			
− T × Y		2.9 (6)		0.826
− T		0.3 (2)		0.839
− Y		5.4 (3)		0.145
Males				
Return rates				
Null model	179.45 (129)			
Residual	160.67 (118)			
− T × Y		12.0 (6)		0.061
− T		2.3 (2)		0.318
− Y		4.4 (3)		0.217
Laying date				
Null model	890.94 (98)			
Residual	803.82 (86)			
− T × Y		33.4 (6)	$F_{6,98} = 0.60$	0.732
− T		15.2 (2)	$F_{2,92} = 0.83$	0.442
− Y		33.1 (3)	$F_{3,94} = 1.22$	0.306
Clutch size				
Null model	181.41 (98)			
Residual	151.77 (86)			
− T × Y		10.9 (6)	$F_{6,86} = 1.03$	0.412
− T		13.7 (2)	$F_{2,92} = 3.60$	0.031
− Y		3.5 (3)	$F_{3,92} = 0.66$	0.582
Number of fledglings*				
Null model	119.03 (98)			
Residual	109.92 (87)			
− T × Y		1.5 (6)		0.957
− T		0.2 (2)		0.886
− Y		7.3 (3)		0.062

was a significant effect of treatment on clutch size with larger clutch size in control broods (7.3 eggs) than in reduced (6.4) and enlarged (6.8) broods (Table 5).

Discussion

Our basic prediction was that blue tits would not experience stronger effects of brood size manipulation in the extreme and variable environment of Corsica than in more favourable environments where many similar studies have been conducted (e.g. Pettifor 1993a, b) if the low clutch size were adapted to the local constraints cited in the Introduction (low and variable food supply, thermo-hydric constraints, parasitic loads). We also expected a large year-to-year variation in the effects of manipulation on breeding performances of the tits because of the large yearly variation of both the peak-date and abundance of caterpillars (Table 1).

Results partly support these predictions. There were clear effects of brood size manipulation on the quality of the young produced in the year of the experiment and these effects also reflected in the quality of recruits. There were also year effects independently of treatment (no interaction between year and treatment). A surprising result was the absence of any significant effect of brood size manipulation on the absolute number of recruits. This could be due to the fact that offspring survival after fledging depends on many factors we do not control (climate, predation etc.) or to the fact that manipulation (which involved only two chicks) was relatively small in comparison to other studies. It could be also that effects of treatment have been masked by large year effects which were significant in all the traits examined, either as a main factor or in interaction with treatment. These large year effects may be due to the large yearly variation in the food supply which reflected the large variation of the proportion of caterpillars brought to nestlings by the parents (Blondel et al. 1991; Banbura et al. 1994). The worst year in terms of caterpillar abundance (1990) was also the year with the strongest effects of treatment on fledgling numbers and fledgling quality, but not on the number of recruits (Table 2). In such a variable environment, a detailed analysis of the effects of brood size manipulation in relation to caterpillar availability would need very large sample sizes spread over many years.

Although enlarged broods resulted in more young fledged, these were lighter and smaller and less likely to recruit in the breeding population. Others have also found a relationship between offspring survival and fledging mass (Perrins 1965; Garnett 1981; Tinbergen and Boerlijst 1990; Verhulst and Tinbergen 1991).

One interesting outcome of this 4-year experiment is that female recruits which were raised in enlarged broods had a shorter tarsus, started to breed later in life and had smaller clutches than those which were raised in reduced or control broods. This result, which is similar to those of Gustafsson and Sutherland (1988) and Gustafsson et al. (1994) on the collared flycatcher *Ficedula albicollis*, suggests that an important effect of experimental increase in parental effort is on the next generation, both on recruitment rates and future reproductive performance of the recruits. Recruits from enlarged broods could be penalised because of lower quality at fledging and lower quality of the territory where they will settle. Indeed, Verhulst et al. (1997) demonstrated in the great tit *Parus major* that conditions during early development, e.g. fledging mass, have effects on the quality of the environment where recruits subsequently settle.

On the other hand, there was hardly any observable effect of brood size manipulation on adults. These results differ from those of some manipulation experiments that revealed costs either in survival of adults, or reproductive potential in the following year (Askenmo 1979; Röskaft 1985; Lessells 1986; Gustafsson and Sutherland 1988; Nur 1988, 1990; Gustafsson et al.

1994), but they agree with the conclusions of Pettifor et al. (1988) on the great tit and Pettifor (1993b) on the blue tit where brood size manipulation in year *n* did not negatively influence any component of breeding success in year *n* + 1. The absence of any effect of brood size manipulation on adults supports the idea that brood size-dependent mortality rates or any other detrimental effects on future reproductive prospects for parents probably play a minor selective role in shaping life histories in short-lived species such as tits (De Steven 1980) compared to effects on offspring (Linden and Møller 1989). In fact, as Alerstam and Högstedt (1984) pointed out, few manipulative studies have shown differential mortality of reproductive adults with experimentally enlarged clutch size (but see Dijkstra et al. 1990; Daan and Tinbergen 1997) and the general picture is that trade-offs between reproductive investment and parental survival are far less common than trade-offs between clutch size and offspring performance.

Despite the fact that the total number of recruits did not significantly differ among the three groups, reduced broods produced young of better quality (higher fledging mass and longer tarsus), which is also expressed in reproductive traits in the next generation. It is known that males with longer tarsus attract more females (Kempenaers et al. 1992), which may play a role in social interactions for limiting resources because young that fledge earlier have higher chances to establish a territory. A similar number of recruits of better quality in reduced broods compared to control broods suggests that blue tits in this population lay more eggs than the number required to optimise fitness. This result differs from that of Pettifor (1993b) who found that parent blue tits at Wytham recruited more offspring from broods of the natural size than from reduced or enlarged broods, which was an argument supporting the Individual Optimisation Hypothesis (Pettifor et al. 1988).

Two non mutually exclusive explanations may account for a clutch size that is larger than optimal in this Corsican population. The first explanation, which is consistent with the huge year-to-year variation in both caterpillar abundance and fitness components of young produced in this habitat, is that the best clutch size varies according to year. In some years large clutch sizes have a higher fitness than smaller ones, whereas the opposite may be true in other years, as suggested by the large year effects in the numbers of fledglings and recruits. In this variable environment a bet-hedging strategy may be an insurance provided that this does not incur any additional cost for the adults (O'Connor 1978), which seems to be the case in this population. Second, the suboptimal decision rules evolved in this population, resulting in birds laying too many eggs, may be due to gene flow from better habitats in the mosaic of highly diverse habitats that characterise Mediterranean landscapes, including on Corsica (Lambrechts et al. 1997). The gene flow hypothesis has been proposed by Dhondt et al. (1990) for a population of blue tits in Belgium and by Verhulst (1995) for the population of

great tits on Vlieland, the Netherlands. In addition, exceptionally high parasite loads by blood sucking larvae of *Protocalliphora* blowflies may explain why clutch size is not optimal. More than 90% of the nests are infested and parasite intensities can reach 100 larvae per nest with a high among year variation in intensity (Hurtrez-Boussès et al. 1997). This is not an artefact due to the utilisation of nestboxes because inspection of blue tit nests in natural cavities indicate similar prevalences and intensities of parasites (personal observation). The presence of parasites represents a transfer of energy from nestlings to blowflies which corresponds to approximately two chicks (Hurtrez-Boussès et al., unpublished data). Since *Protocalliphora* larvae attack nests with different clutch sizes randomly and parasite intensities vary strongly from year to year, selection pressures are not always in the same direction so that the parasitic constraint may represent a local 'artefact' against which tits have not been selected for.

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