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Unpredictable food supply modifies costs of reproduction and hampers individual optimization

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Abstract Investment into the current reproductive attempt is thought to be at the expense of survival and/or future reproduction. Individuals are therefore expected to adjust their decisions to their physiological state and predictable aspects of environmental quality. The main predictions of the individual optimization hypothesis for bird clutch sizes are: (1) an increase in the number of recruits with an increasing number of eggs in natural broods, with no corresponding impairment of parental survival or future reproduction, and (2) a decrease in the fitness of parents in response to both negative and positive brood size manipulation, as a result of a low number of recruits, poor future reproduction of parents, or both. We analysed environmental influences on costs and optimization of reproduction on 6 years of natural and experimentally manipulated broods in a Central European population of the collared flycatcher. Based on dramatic differences in caterpillar availability, we classified breeding seasons as average and rich food years. The categorization was substantiated by the majority of present and future fitness components of adults and offspring. Neither observational nor experimental data supported the individual optimization hypothesis, in contrast to a Scandinavian population of the species. The quality of fledglings deteriorated, and the number of recruits did not increase with natural clutch size. Manipulation revealed significant costs of reproduction to female parents in terms of future reproductive potential. However, the influence of manipulation on recruitment was linear, with no significant polynomial

effect. The number of recruits increased with manipulation in rich food years and tended to decrease in average years, so control broods did not recruit more young than manipulated broods in any of the year types. This indicates that females did not optimize their clutch size, and that they generally laid fewer eggs than optimal in rich food years. Mean yearly clutch size did not follow food availability, which suggests that females cannot predict food supply of the brood-rearing period at the beginning of the season. This lack of information on future food conditions seems to prevent them from accurately estimating their optimal clutch size for each season. Our results suggest that individual optimization may not be a general pattern even within a species, and alternative mechanisms are needed to explain clutch size variation.

Keywords Brood size manipulation · Caterpillar availability · Clutch size · *Ficedula albicollis* · Year effect

Introduction

The cost of reproduction is a decrease in prospects for survival and future reproduction as a result of increased investment in the current reproductive attempt (Williams 1966). Individual optimization refers to a fine-tuning of reproductive investment to the state of the individual and that of its environment (Perrins and Moss 1975). The individual optimization hypothesis makes distinct predictions at the population level. First, no association between present reproductive investment and future prospects, and a positive relationship between reproductive investment and present success (Price and Liou 1989; Robinson and Rotenberry 1991; Brown and Brown 1999). Second, a negative response in terms of fitness to both experimental increase and decrease of investment (Gustafsson and Sutherland 1988; Pettifor et al. 1988).

There are two main measures of the response to clutch or brood size manipulation: the number of sexually mature offspring produced, and the residual reproductive value (RRV; survival and future reproduction) of the parents. Let

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us, for example, examine the case of brood size alteration. First, if recruitment increases, but RRV remains the same with increasing manipulation, different numbers of offspring are produced at an indistinguishable cost. This implies that either brood rearing does not adequately represent costs of reproduction, or that costs of reproduction, and consequently, optimization, are not important. Second, if increasing manipulation results in the same number of recruits at an increasing future cost, the experimentally reduced broods produce the most offspring per unit effort, which again does not support optimization. There are two types of result consistent with individual optimization. First, if both recruitment and the future reproduction of females are reduced in manipulated broods relative to controls. Second, if the fitness increase due to more recruits from enlarged broods is more than balanced by the impaired future reproduction of females.

It was proposed already very early on that costs of reproduction may only be manifested in unpredictably bad conditions (Tuomi et al. 1983; Reznick 1985). It is also accepted that food abundance may seriously affect the costs of reproduction (Tinbergen and Dietz 1994; Blondel et al. 1998). The fact that the optimal value of clutch size in birds may vary with environmental quality has been widely suggested by variation of selection differentials across seasons (van Noordwijk et al. 1981; Gibbs 1988) and significant year effects on reproductive success in long-term studies (Pettifor 1993; Orell et al. 1996; Blondel et al. 1998; Pettifor et al. 2001).

Year effect is not only a confounding factor that should be allowed for in multi-season databases. Unpredictable environmental fluctuations may both preclude the individual optimization of clutch size (McNamara 1998) and provide an alternative explanation for the maintenance of its variability (Meyers and Bull 2002). Few studies have addressed optimization of reproduction to specific environmental factors that could be linked to between-year variation in success (Both et al. 2000). Here we assess the effect of yearly variability in food supply on the optimization of clutch size in a Central European population of the collared flycatcher (*Ficedula albicollis* Temm.). We perform a three-step analysis on a 6-year set of natural and experimentally manipulated broods. First, we statistically categorize years based on food conditions as an environmental factor that might have affected reproduction. Second, we ask whether the patterns of success and/or survival fit the categorization. Third, we analyse reproductive success and future prospects of parents and offspring in relation to natural clutch size, brood size manipulation and year category.

Materials and methods

The collared flycatcher is a socially monogamous, hole-nesting, long-distance migratory passerine. The readiness of this species to occupy nestbox plots in relatively high densities makes it a suitable subject for life history research (e.g. Gustafsson and Sutherland 1988; Gustafsson

1989; Gustafsson et al. 1995). A long-term study of population dynamics has been conducted at Pilis Field Station, in Pilis Mountains, near Budapest (47°10'N, 19°09'E), since 1982 (Török and Tóth 1988, 1990). In this paper, we used observational and experimental data collected in 1988–1993 in three study plots covering parts of a single continuous oak woodland where >600 nest-boxes were placed in a grid system. Modal clutch size in our population is six, with a range of four to eight. The few atypical clutches with three or nine eggs were excluded from all analyses.

During the 6 years, a total of 318 nests were manipulated. Experimental nest pairs were randomly chosen among clutches with the same hatching date and clutch size. Two or four young were transferred between these nests when nestlings were 2 days old. The range was thus larger than in the classic study of Gustafsson and Sutherland (1988). Only nests with a clutch size of five to seven were manipulated, as there were too few synchronous nest pairs with a common clutch size of four or eight. The nestling transport took <10 min, so there is no reason to suspect that it increased mortality among foster nestlings. The few (ten out of 318) manipulated broods that had died within 4 days after swapping (probably deserted) were omitted from all analyses. These had been exposed to the experimental treatment for a very short period, and therefore do not provide information on either costs or optimization. Numbers of data for each year and treatment category are given in Table 1. Degree of manipulation did not depend on original clutch size or laying date in this dataset (multiple regression; clutch size $\beta \pm \text{SE} = -0.014 \pm 0.036$, $t_{896} = -0.392$, $P = 0.695$; laying date $\beta = 0.004 \pm 0.036$, $t_{896} = 0.010$, $P = 0.921$).

Tarsus length (to nearest 0.1 mm measured with callipers) and body mass (to nearest 0.1 g measured with a Pesola spring balance) of nestlings were measured at the age of 13 days. Fledgling body condition was assessed in an analysis of covariance (ANCOVA) of body mass while entering tarsus length as a covariate. The use of tarsus length as an index of body size has been validated in previous studies of this species (e.g. Pärt 1990; Qvarnström 1999). Fledging success was defined as the number of young fledged divided by the number of young at 2 days of age (in control broods) or the number of young after manipulation (in manipulated broods). We arcsine square-root transformed fledging success before analyses.

Table 1 Number of manipulated and non-manipulated broods used in our analyses for each year

	Brood adjustment				
	-4	-2	0	+2	+4
1988	10	10	109	10	10
1989	15	9	166	8	15
1990	15	29	174	28	15
1991	6	18	100	14	8
1992	12	13	100	14	12
1993	8	11	125	10	8
Total	66	90	774	84	68

In this paper we estimate the detailed responses to manipulation in female parents only, for several reasons. First, there is no clutch size optimization in males, so the number of eggs laid can be adjusted to male quality only indirectly by females (e.g. Petrie and Williams 1993), and the consequences of this process on males are poorly known. Quantifying costs of reproduction is also difficult in males. There is a potentially important role for condition-dependent sexual signals (Gustafsson et al. 1995; Griffith 2000; Török et al. 2003), which we did not measure in the study period. Finally, male fitness in most socially monogamous birds, including our study species, is hard to determine without extensive paternity tests (Sheldon and Ellegren 1999).

It is possible that no consequence of manipulation can be detected on future life history variables of females. These negative results can be interpreted only if it is known that they did adjust their feeding activity in relation to manipulation (Mauck and Grubb 1995; Moreno et al. 1995; Allander 1997). We therefore examined body mass changes of females measured repeatedly during the offspring-rearing period in relation to brood size manipulation. As the contribution of males to brood rearing may influence fitness effects on both females and young, we also assessed male body mass changes in response to natural clutch sizes and brood size manipulation. Effects on body mass changes were tested in ANCOVAs while correcting for tarsus length, original mass, laying date, age of nestlings at the first measurement, and the number of days elapsed between the two measurements.

All fledglings and >90% of parents were individually marked with a standard numbered aluminium ring. A female was assumed to have died if it ceased to return during the three seasons following the focal year. Owing to the high site fidelity of the species (Pärt 1991; Hegyi et al. 2002) and the high capture effort, this probably reflects true survival (also see Török et al. 2003). We assessed the number of young returned based on the following three seasons, referred to as long-term recruitment.

The availability of lepidopteran larvae, an important component of the nestling diet of collared flycatchers (Török 1986, 1993), was estimated each year. Fifteen frass collectors, each with a surface area of 0.25 m², distributed randomly under the canopy of trees in the study area (Schwerdtfeger 1931; Török and Tóth 1988; Perrins 1991; Dias and Blondel 1996; Blondel et al. 1998), were emptied on every third day. Rains and other accidents resulted in a varying number of samples per collection period. Year type characterization was based on the daily averages of the 3 days with the highest frass mass in each year (caterpillar peak period). Frass data were log(10) transformed before analyses.

We analysed clutch size and manipulation effects on all fitness components using a single model for each dependent variable and all available data. In these models, effects of natural clutch size can be detected while controlling for manipulation, and vice versa. However, “effects” of natural clutch size on first-year offspring reproduction and the next-year success of female parents

are likely to be positive, due to the genetic background of life history traits (Merilä and Sheldon 2000). We therefore focused on manipulation when interpreting these analyses. To correct for its possible confounding effect, we included laying date as a covariate in all analyses. This was necessary since late broods were not manipulated in any season. We also corrected for the number of unhatched eggs in the analyses, because hatching failure was significantly affected by food supply (but not by original clutch size, data not shown) and may have thus contributed to any year type difference in success, and/or in the relationships between clutch size or manipulation and success. Therefore, all analyses included year type (see results) as a factor, and clutch size, hatching failure, laying date, and the linear and second-order effects of manipulation as covariates. In the case of the next-year clutch size of female parents, to take within-individual repeatability into account, we included clutch size from the year of manipulation, and laying date from both the year of manipulation and the year of recapture. Likewise, next-year laying date was analysed with clutch size and laying date in the year of manipulation as covariates. Analyses of the first-year clutch size in female recruits also included laying date in the respective year. The shortage of data on the reproduction of recruits forced us to categorize manipulation as reduced, control or enlarged in this case. We also did not use second-order terms in the analyses of offspring reproduction. Effects on laying date, clutch size and hatchling number were assessed for female recruits only. The number of fledglings and fledging success were considered for both male and female recruits with sex as a factor, because the mechanisms involved are partly identical.

Continuous dependent variables were assessed in ANCOVAs. Female survival and the long-term recruitment of young, as well as binary reproductive success were analysed in generalized linear models (GLM) with binomial error and logit link (female survival and binary success) or Poisson error and log link (recruitment). In GLMs we employed a stepwise backward model selection procedure. We started with the most general model and first deleted non-significant interactions one by one in increasing order of *P*, until only significant interactions remained. We then repeated the sequential deletion for the individual explanatory variables, and retained only those with significant main effect and/or at least one significant interaction. For factors/interactions in the final model, we report Wald statistics from this model. For a factor/interaction deleted during model selection, the reported statistics refer to the addition of this factor/interaction to the final model. All analyses were done in Statistica 5.5.

Results

Year type categories

Daily mean frass masses of the collection period with the highest values were significantly different among years

(ANOVA, $F_{5,70}=62.205$, $P<0.0001$). Only one of the post hoc comparisons (LSD tests) was significant ($P=0.028$, 1989 and 1991) within two groups of years (1988–1991 with low and 1992–1993 with very high values), whereas all possible comparisons were highly significant between these groups (all $P<0.0001$). These two periods will hereafter be termed “average” and “rich food (or good) years”, respectively (Fig. 1). To show if females can predict future caterpillar availability from that of the current season, we used yearly peak frass masses from 1988 to 2002. Values of two consecutive seasons were not significantly correlated ($r=0.461$, $F_{1,12}=3.236$, $P=0.097$). There was apparently no adjustment of clutch size to food supply, as we found a significant relationship between year type and natural clutch size (four to eight) in a direction opposite to that predicted: females laid less eggs in rich than in average food years (ANCOVA with all broods pooled irrespective of subsequent manipulation, laying date as a covariate; year type $F_{1,1150}=22.463$, $P<0.001$; mean±SE for rich food years 6.263 ± 0.052 , for average food years 6.357 ± 0.029).

Body mass changes of parents

Males lost a similar amount of body reserves in average and rich food years, but their mass loss increased with manipulation (Table 2). There was a significant interaction between manipulation and year type: the relationship between male mass loss and manipulation was only apparent in rich food years ($\beta=-0.234$, $t_{92}=-2.749$, $P=0.007$) but not in average years ($\beta=-0.049$, $t_{96}=-0.535$, $P=0.594$). Male mass loss was not related to either the second-order term of manipulation, or its interaction with year type. Male mass change showed no effect of natural clutch size, or interaction between clutch size and year type.

There was no year type effect on female residual body mass change, but a negative effect of increasing manip-

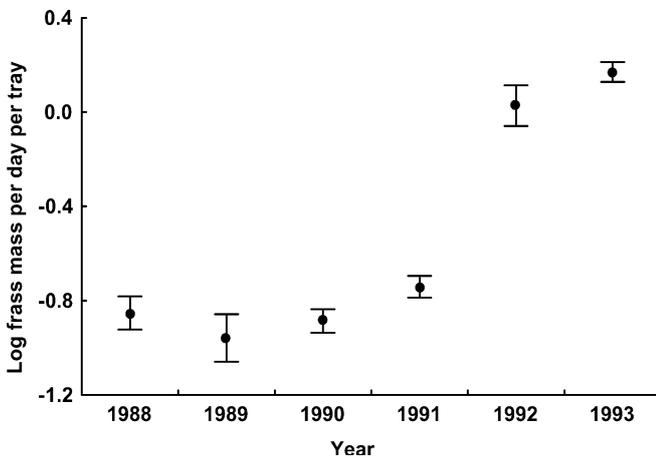


Fig. 1 Quantification of yearly food supply for breeding collared flycatchers in the study years: daily mean (±SE) frass masses (log 10 transformed) of the 3-day collection period showing the highest value in each year

Table 2 Analysis of covariance (ANCOVA) for body mass changes of males and the continuous fitness components of females. Columns list the independent variables and relevant interactions. F-values are reported for year type and its interactions with covariates, and t-values for individual covariates. NA Not applicable

	Number of cases	Year type	Clutch size	Manipulation	Square of manipulation	Year type × manipulation	Year type × clutch size	Year type × manipulation × clutch size	Laying date	Hatching failure	Days between measurements	Mass at first measurement	Tarsus length	Nesting age at first measurement	Next-year laying date	Next-year clutch size
Male mass change	208	1.511	0.538	-2.282*	1.361	0.380	4.216*	0.191	0.118	0.103	-1.503	-7.249***	-0.074	-0.397	NA	NA
Female mass change	313	0.382	0.238	-4.764***	1.115	0.081	0.004	0.463	-0.066	-1.256	-9.284***	-12.208	1.690	-2.109*	NA	NA
Number of fledglings	1,082	97.153***	4.284***	5.908***	-3.587***	1.469	27.492***	11.486***	-2.644**	5.835***	NA	NA	NA	NA	NA	NA
Fledging success	1,082	82.606***	-1.698	-6.146***	-1.200	0.966	2.064	3.377	-3.151**	-2.376*	NA	NA	NA	NA	NA	NA
Next-year laying date	387	3.134	-1.781	1.076	-0.592	3.333	1.700	0.001	-1.147	-0.699	NA	NA	NA	NA	NA	NA
Next-year clutch size	386	2.054	5.828***	1.135	-0.460	2.504	0.636	1.641	3.377***	-0.367	NA	NA	NA	NA	NA	NA
Next-year fledging number	386	0.664	0.243	-0.920	-1.144	1.158	1.153	1.509	-0.690	0.429	NA	NA	NA	-11.651***	NA	NA
Next-year fledging number	269	7.679***	-0.163	-0.928	-2.514*	2.863	3.814	1.145	-0.855	-0.598	NA	NA	NA	-2.306*	6.888***	1.593
Next-year fledging no. excluding zeros	193	14.046***	-0.884	0.403	1.134	1.262	1.987	0.403	1.051	-2.141*	NA	NA	NA	-1.718	5.371***	NA

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

ulation (Table 2). There was no interaction between year type and manipulation. There was neither a second-order effect of manipulation, nor interaction between the second-order effect and year type. After correcting for manipulation, female body mass change did not correlate with natural clutch size, irrespective of year type. In sum, females apparently adjusted their feeding activity in response to manipulation, but males did so only in rich food conditions.

Nestling development

The year type effect on tarsus length of fledglings was significant, but there was no effect of clutch size or interaction (Table 3). The effect of brood size manipulation on tarsus length of fledglings was significantly negative. Better food conditions led to larger fledglings, but there was no interaction between year type and manipulation. There was no significant second-order effect of manipulation on tarsus length or interaction between the quadratic effect and year type. Fledgling condition was significantly influenced by year type: better food conditions resulted in young of better condition (Table 3). Body condition of offspring was overall negatively related to clutch size, but the interaction with year type was also significant (Fig. 2a). The relationship was significantly negative in average years ($\beta=-0.205$, $t_{420}=-5.055$, $P<0.0001$), but not significant in good years ($\beta=-0.056$, $t_{213}=-0.834$, $P=0.405$). Body condition of fledglings was significantly negatively affected by manipulation. The interaction between manipulation and year type was also significant. The treatment effect was more pronounced in average ($\beta=-0.260$, $t_{420}=-6.759$, $P<0.0001$) than in good years ($\beta=-0.195$, $t_{213}=-3.188$, $P=0.002$). Nestling body condition was unaffected by the second-order term of manipulation or its interaction with year type.

Fledgling number and fledging success

The number of offspring leaving the nest was significantly related to both clutch size and year type, but not their interaction (Table 2). Mean fledgling production increased with clutch size in both year types, but it was almost twice as much in rich as in average food seasons. Manipulation significantly affected fledgling number, but its interaction with year type was also significant. Mean number of young fledged increased with increasing manipulation in both types of year, but the relationship was much steeper in rich ($\beta=0.430$, $t_{307}=9.024$, $P<0.0001$) than in average food years ($\beta=0.069$, $t_{763}=1.973$, $P=0.049$). Moreover, the overall second-order effect of manipulation was significant, and there was also an interaction with year type. The polynomial effect was significant in average years ($\beta=-0.156$, $t_{763}=-4.417$, $P<0.0001$), but not in rich food years ($\beta=0.007$, $t_{307}=0.132$, $P=0.895$). Number of fledglings linearly increased with manipulation in rich food years, but levelled off in average years.

Table 3 ANCOVA for continuous fitness components of recruits. Columns list the independent variables and relevant interactions. *F*-values are reported for year type and its interactions with covariates, and *t*-values for individual covariates. For abbreviations, see Table 2

	Number of cases	Year type	Clutch size	Manipulation	Square of manipulation	Year type × clutch size	Year type × manipulation	Year type × square of manipulation	Laying date	Hatching failure	Tarsus of fledglings	Laying date at first breeding	Clutch size at first breeding	Recruit sex	Sex × clutch size	Sex × manipulation
Fledgling tarsus	648	50.723***	-0.163	-6.073***	-0.837	3.219	0.001	0.706	-1.793	-1.771	NA	NA	NA	NA	NA	NA
Fledgling condition	647	11.133***	-4.905***	-7.245***	1.473	7.345**	5.568*	0.940	-2.153*	-2.847**	14.394***	NA	NA	NA	NA	NA
Laying date at first breeding	100	6.769*	0.840	-1.170	NA	2.889	2.296	NA	2.536*	0.298	NA	NA	NA	NA	NA	NA
Clutch size at first breeding	100	5.466*	1.649	-0.370	NA	2.046	0.922	NA	1.382	-1.061	NA	-10.405***	NA	NA	NA	NA
Number of hatchlings at first breeding	99	0.001	1.773	-0.811	NA	2.928	0.122	NA	2.222*	0.433	NA	-2.701**	NA	NA	NA	NA
Number of fledglings at first breeding	138	9.982**	0.402	0.127	NA	0.003	2.578	NA	1.635	-0.891	NA	-3.131**	-0.646	4.843*	1.214	0.702
Fledging success at first breeding	122	15.700***	0.395	-0.415	NA	1.179	5.657*	NA	0.824	-0.912	NA	-3.503***	-2.075*	1.950	0.669	0.143

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

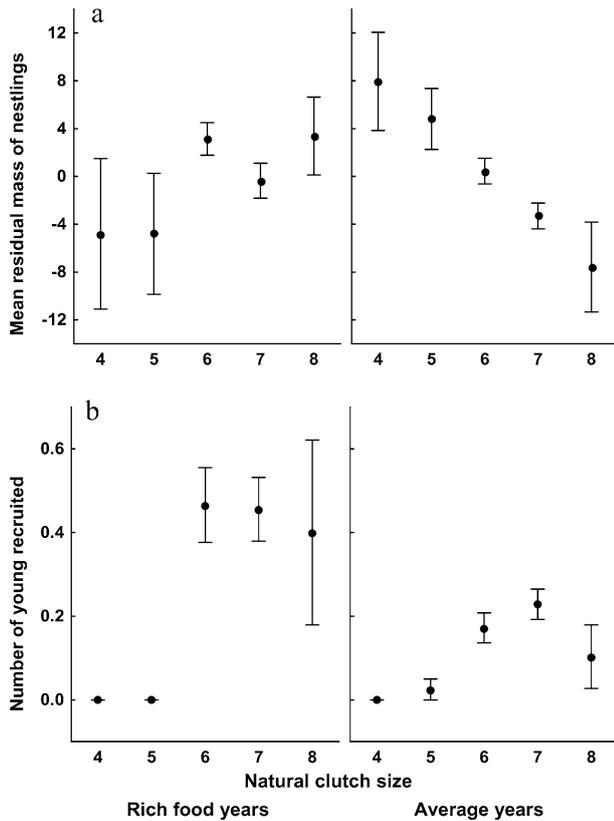


Fig. 2 The effect of natural clutch size and year quality on the body condition of fledglings (a) and on long-term recruitment (b) (means \pm SE)

There was a significant year type effect on fledging success, but no influence of natural clutch size or interaction (Table 2). Fledging success significantly decreased with manipulation; the year type-manipulation interaction was not significant. Neither the second-order effect of manipulation nor its interaction with year type was significant.

Recruitment and female survival

The number of young recruited significantly depended on year type: far more young returned from rich food years than from average years (Table 4). The effect of natural clutch size was not significant, irrespective of year type (Fig. 2b). In separate stepwise polynomial models for each year type, neither linear nor second-order polynomial effects of clutch size were significant (not shown). Manipulation did not affect recruitment but its interaction with year type was significant (Fig. 3a). There was a significant increase in rich food years (Wald=3.928, $P=0.048$), but a non-significant negative relationship in average food years (Wald=1.371, $P=0.242$). Pairwise tests of three manipulation classes (reduced, control, enlarged) showed that enlarged nests in rich food years produced more recruits than controls (Wald=6.520, $P=0.011$), but reduced nests did not differ from controls in any of the

year types. Neither the second-order effect of manipulation nor its interaction with year type was significant.

Female survival was significantly affected by year type, but not by clutch size or the interaction with year type (Table 4). More females survived after rich food seasons than after average food years. Female survival did not change in response to brood size alteration. There was no interaction between year type and manipulation. Neither the square of manipulation nor its interaction with year type explained variance in female survival.

Year type, manipulation, and next-year breeding parameters of females

Neither food supply nor the linear/quadratic terms of manipulation influenced laying date, date-residual clutch size of females or the number of young hatched in their next-year nest (Table 2). Nests manipulated in the second year were omitted from the analyses of next-year fledgling number in relation to manipulation and year (Table 2). Females fledged significantly more young after a rich food year than after an average year. There was no significant manipulation effect on next-year fledgling number. The interaction between year type and manipulation was marginally significant ($P=0.052$), but no significant

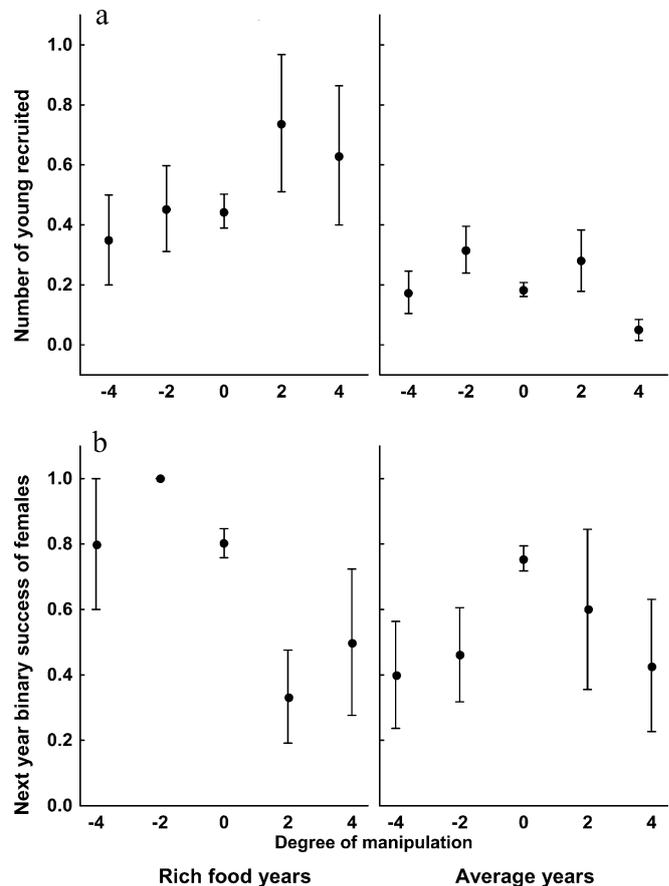


Fig. 3 The effect of brood size manipulation and year quality on the production of recruits (a) and next-year binary reproductive success of female parents (b) (means \pm SE)

Table 4 Generalized linear models for binary fitness components of females and offspring. Columns list the independent variables and relevant interactions. Wald χ^2 -values are shown

	Number of cases	Year type	Clutch size	Manipulation	Square of manipulation	Year type \times clutch size	Year type \times manipulation	Year	Year type \times square of manipulation	Laying date	Hatching failure	Next-year laying date	Next-year clutch size	First-year laying date	First-year clutch size	Recruit sex	Sex \times clutch size	Sex \times manipulation
Number of recruits	1,030	25.683***	3.064	0.277	0.168	1.739	4.885*	1.431	12.119***	4.074*	NA	NA	NA	NA	NA	NA	NA	NA
Female survival	1,030	11.400***	0.045	0.075	3.026	2.520	1.264	0.067	9.938**	0.001	NA	NA	NA	NA	NA	NA	NA	NA
Female next-year binary success	269	3.301	1.840	2.860	8.639**	4.193*	5.128*	0.436	1.265	1.332	0.398	1.065	NA	NA	NA	NA	NA	NA
Offspring first-year binary success	122	3.299	0.085	1.242	NA	1.126	3.051	NA	0.047	2.312	NA	NA	NA	0.493	4.557*	4.152*	0.356	NA

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

relationship emerged in any of the year types. The second-order manipulation effect on next-year fledgling number was significant. Females with both reduced and enlarged broods produced less fledglings in their next breeding season than controls. The year type \times squared manipulation interaction was non-significant.

Both linear and quadratic effects of manipulation became non-significant when unsuccessful nests were omitted from the analysis (Table 2). This indicates that manipulation influenced brood desertion probability in the next year. Analyses of next-year binary breeding success (successful vs. unsuccessful females, Table 4) support this hypothesis (Fig. 3b). There was no significant manipulation effect, but a significant year type \times manipulation interaction, with a negative relationship after good years (Wald=9.189, $P=0.002$), but no relationship after average years (Wald=0.322, $P=0.570$). The quadratic manipulation effect was significant, irrespective of year type. Using manipulation as a three-category factor showed that next-year binary success of females which had reared control and enlarged broods differed irrespective of year [control vs. enlarged, Wald $\chi^2=14.019$, $P < 0.001$, (year type) \times (-control vs. enlarged) Wald $\chi^2=0.800$, $P=0.371$]. However, those with reduced vs. control nests differed only if the food supply in the year of manipulation had been average [reduced vs. control, Wald $\chi^2=0.055$, $P=0.815$, (year type) \times (reduced vs. control) Wald $\chi^2=4.654$, $P=0.031$; reduced vs. control in rich food years Wald=0.920, $P=0.337$; reduced vs. control in average years Wald=8.930, $P=0.003$]. In conclusion, the cost of reproduction was manifested in the next-year brood abandonment probability of females, with a relatively higher probability to desert their next-year brood after tending an enlarged brood in a rich food year, and both a reduced or an enlarged brood in an average year.

Year type, manipulation, and first-year breeding success of recruits

Female recruits from average years started egg laying at their first breeding attempt significantly earlier than those from good years (Table 3). The effect of manipulation and the year type \times manipulation interaction on laying date of female recruits were not significant. Female recruits from average years laid significantly less eggs than those from rich food years, but there was no manipulation effect or year type \times manipulation interaction (Table 3). No significant effect or interaction was detected for the number of young hatched (Table 3). Success in raising young was analysed for both male and female recruits, but only individuals with non-manipulated broods were used (Table 3). Recruits (males and females) from rich food years raised more fledglings than those from average food years, but no manipulation effect or year type \times manipulation interaction could be detected. Fledging success of recruits showed a strong relationship with birth year type. Although the overall effect of manipulation explained a small proportion of variance in fledging success, its

interaction with year type was significant. Manipulation of their brood of origin tended to affect fledging success of recruits from average years ($\beta=-0.271$, $t_{57}=-1.666$, $P=0.101$), but not that of recruits from rich food years ($\beta=0.093$, $t_{49}=0.860$, $P=0.394$). First-year binary success of recruits did not show any effects of natural clutch size or brood size manipulation, regardless of food supply in the year of origin (Table 4).

Discussion

In this paper, we first identified two categories of year (average and rich food years) based on an environmental factor known to affect breeding success in insectivorous passerines, that is, insect food abundance as assessed by frass production at the yearly caterpillar peak period (Schwerdtfeger 1931; Zandt et al. 1990; Tinbergen and Dietz 1994; Nour et al. 1998). We then examined whether breeding success data of collared flycatchers in these years fit this categorization (Pettifor 1993). As a response to higher food supply we found an increase in the number of young fledged, fledging success, nestling size and condition, female survival and future reproductive success, as well as recruitment probability and success of first reproduction of offspring. Thus, the year quality criteria proved appropriate, so it was justified to proceed by asking how year type interacts with natural and experimentally altered investment in determining current and future reproductive performance. The power of our study is that, besides the classic correlative and experimental approaches, we could examine the effect of a considerable fluctuation in food supply, as a “pseudo experiment”, on natural and manipulated broods. The results allow us to draw a wide range of conclusions on the importance and manifestation of the cost of reproduction, and the adaptive value and individual optimization of clutch size. We note that environmental conditions at the winter quarters may be as important as the breeding environment in determining the fate of parents and offspring (Sillert et al. 2000; Saino et al. 2004). Since collared flycatchers winter in tropical Southwest Africa, winter environmental influences probably do not confound the effects of breeding conditions in this species.

The number of young fledged increased while fledging success did not change with natural clutch size. However, although fledgling size was similar across clutch sizes, the body condition of young declined with clutch size both in the whole dataset and in average years. The increasing number, but lower quality of fledglings resulted in no relationship between natural clutch size and recruitment. Neither female nor male mass loss was related to natural clutch size, and the survival of females was also unrelated to the number of eggs laid. The individual optimization hypothesis predicts no long-term effect of natural reproductive effort on the parent, but also a positive association between natural clutch size and production of recruits (Perrins and Moss 1975; Price and Liou 1989). The year-type specific deterioration of fledgling quality with natural

clutch size, and the lack of clutch size effect on recruitment do not support the hypothesis.

The significant effect of manipulation on both offspring development and female mass change implies that parental feeding activity was adjusted, but only partially, to the changed food demand of the brood, in line with many previous studies (e.g. Nur 1984; Smith et al. 1988; Tinbergen and Verhulst 2000), and also with our previous results using automatic visit recorders (Török and Tóth 1990) which showed that total feeding rate of parents levelled off with increasing manipulation pressure. Body mass change of females was significantly negatively affected by increasing manipulation. Female body mass loss in a Swedish population of collared flycatchers was found to be positively related to both feeding frequencies and daily energy expenditure (Pärt et al. 1992). Male mass change followed manipulation only in rich food years, but not in average years. It is unclear whether body mass changes generally reflect reproductive effort in male flycatchers (Sætre et al. 1995; Qvarnström 1997). If so, our data suggest that males did not generally help in rearing the additional young in manipulated nests, which contradicts results from a Swedish population (Gustafsson et al. 1995) and the sister species (Moreno et al. 1995).

The significant interactions between year type and both the linear and second-order polynomial effects of manipulation in determining the number of fledglings indicate a strong effect of food conditions on the short-term outcome of manipulation. With increasing manipulation, the number of fledglings increased in rich food years, but levelled off in average years. Their tarsus length, however, decreased with increasing manipulation in both year categories. The effect of treatment on body condition of young was similar, but the relationship was much less pronounced in rich than in average food years, which was also expressed by the significant year-manipulation interaction. Fledging success, that is, the number of young fledged relative to that after manipulation, decreased with increasing level of experimental treatment in both year types.

Recruitment was overall unrelated to manipulation. The fewer, but better quality individual fledglings from reduced broods were probably more likely to survive than those from the other groups. On the other hand, the small offspring from enlarged broods might have been disadvantaged, for example, due to their weaker fasting endurance (Merilä and Wiggins 1997) during the critical times after fledging (Weathers and Sullivan 1989; Lindén et al. 1992). We found a significant interaction between year type and manipulation. There was a significant positive linear manipulation effect on recruitment in good years, but a negative tendency in average years. A bell-shaped pattern in recruitment among experimental groups is frequently found in the case of individual optimization (e.g. Tinbergen and Daan 1990; Pettifor et al. 2001). In our case, the lack of non-linear manipulation effect indicates that manipulated groups did not produce systematically fewer recruits than controls. Moreover, enlarged broods recruited significantly more offspring than controls in rich

food years. In other words, there was no optimal clutch size in our data, in sharp contrast to a Swedish population of the species (Gustafsson and Sutherland 1988). An alternative manifestation of individual optimization would be a consistent increase in the number of recruits with increasing manipulation, balanced by a strong future cost to female parents rearing enlarged broods. Our data show a different pattern, with a significant difference in the recruitment/manipulation relationship between year types. This suggests that females generally laid more eggs than optimal in average years but tended to lay fewer than optimal numbers of eggs in rich food years, and refutes the individual optimization hypothesis.

The reproductive success of recruits showed only year quality effects, but no overall effect of manipulation, which suggests that offspring seriously handicapped by manipulation were eliminated before their first breeding attempt. Since laying date is highly repeatable in our population (G. Hegyi and J. Török, unpublished data), it has the potential to reflect individual quality (Wiggins et al. 1994). If so, the year-type effect on recruit laying dates may reflect a milder selection among nestlings from good years than among those from average years.

There was neither a linear nor quadratic manipulation effect on the survival of females, irrespective of food supply. Next-year laying date or clutch size were unaffected by both manipulation and food supply. However, in line with the mass change data, future reproductive success of females was affected by manipulation. The pattern of linear and second-order effects shows that although the effects of experimental brood reduction depended on food conditions, females rearing enlarged

broods suffered a reduced reproductive success the next year, irrespective of food supply in the year of manipulation. Thus, in spite of the asymptotic feeding/manipulation curve (Török and Tóth 1990), there was a detectable cost of brood size enlargement to females, in contrast to a recent study on great tits (Tinbergen and Verhulst 2000). Year-type effects were also significant; survival, fledgling number and fledging success were higher after a rich food year than after an average year.

Surprisingly, when we omitted unsuccessful broods from the analyses of next-year reproduction, manipulation effects disappeared. Our results, especially those for binary breeding success, suggest that the probability of brood desertion in the following year was affected by manipulation. This extends the timescale of previously demonstrated various within-season effects on brood desertion (Slagsvold 1984; Pöysä et al. 1997). Thus, our brood size manipulation experiment can be regarded as successful in showing that rearing young is costly in this population. However, in line with the observational data, it did not reveal individual optimization of clutch size. The fit of our results to the predictions of the individual optimization hypothesis is summarized in Table 5.

There was a significant relationship between natural clutch size and year category in the direction of smaller clutches in rich than in average years. This suggests that females cannot predict prospective food supply during brood rearing at the beginning of the season, in contrast to, for example, kestrels (Daan et al. 1990). This would imply that egg investment can only be reliably adjusted to individual condition, and perhaps to mate quality (Petric and Williams 1993; Cunningham and Russell 2000).

Table 5 Summary of evidence for individual optimization from a 6-year study of Central European collared flycatchers. In the case of individual optimization, no difference between year types is expected for fitness responses to natural clutch size or manipulation

	Predicted relationship for natural broods	Do our results contradict this prediction?	Does the relationship differ between year types?	Predicted relationship for manipulated broods	Do our results contradict this prediction?	Does the relationship differ between year types?
Female mass loss	NS or positive	No	No	Positive	No	No
Fledgling size	NS	No	No	Negative	No	No
Fledgling condition	NS	Yes	Yes	Negative	No	Yes
Number of fledglings	Positive	No	No	NS or positive	No	Yes
Fledging success	NS	No	No	NS or negative	No	No
Recruitment of recruits	Positive	Yes	No	Positive or quadratic	Yes	Yes
Reproduction ^{-a}	^{-a}	^{-a}	^{-a}	NS or negative	No	Yes
Female survival	NS	No	No	NS or negative	No	No
Female future success	^{-a}	^{-a}	^{-a}	NS or negative	Yes	Yes

^aCorrelations between natural clutch size and the future success components of females and offspring are confounded by genetic effects, so no clear prediction links these relationships to individual optimization

Variable selection differentials on clutch size among years have been obtained repeatedly (van Noordwijk et al. 1981; Boyce and Perrins 1987), but these were rarely linked to any environmental factor that would have explained the observed pattern (Both et al. 2000). In our population of collared flycatchers, both natural and experimental data suggest that unpredictable differences among years in food conditions greatly influence breeding success, and this stochasticity seems to prevent individual optimization.

One of the first complete pictures of costs and optimization of reproduction comes from a very similar brood size manipulation experiment in a Swedish population of collared flycatchers on the island of Gotland (Gustafsson and Sutherland 1988). In that study, even though degrees of manipulation were smaller than in our case, the recruitment/manipulation curve was bell-shaped, indicating successful individual optimization of clutch size. The observed population difference in life history may originate from climatic differences between the two study areas leading to different predictability of breeding conditions. Gotland has an oceanic climate governed by large-scale climatic fluctuations, which also affect the reproduction of local collared flycatchers (Przybylo et al. 2000). The minor importance of individual year effects was indicated by a 6-year study in which year did not significantly contribute to variation in either adult or juvenile survival (Doncaster et al. 1997). Hungary, on the other hand, is under three contrasting and fluctuating climatic influences (Atlantic, continental and sub-Mediterranean; Borhidi 1961; Zólyomi et al. 1997), which may have caused the significant differences between consecutive years, with no autocorrelation in food conditions, and effects on reproductive success and survival of both adults and offspring observed in our study.

In the last few years, evidence has accumulated that brood rearing is not the only costly period of the breeding season (e.g. Oppliger et al. 1996; Monaghan and Nager 1997; Bryan and Bryant 1999; Visser and Lessells 2001). It could be proposed, therefore, that we would have detected individual optimization, if we had manipulated more cost components associated with the number of eggs laid. However, the same method, with a narrower range of manipulation, led to a successful demonstration of individual optimization in another population of collared flycatchers (Gustafsson and Sutherland 1988). There is also multiple experimental evidence for egg-production costs in great tits (Oppliger et al. 1996; Visser and Lessells 2001), and this is nevertheless the species where optimization has been exhaustively demonstrated by brood size manipulation experiments (Pettifor et al. 1988, 2001). Another possible critique concerns the reliability of our local recruitment values as estimates of true offspring survival (e.g. Lambrechts et al. 2000). Recruitment is in fact lower in our case than in the island population of Gotland (Gustafsson and Sutherland 1988). It is hard to see, however, why the effect of food conditions on this variable was so marked, and why we detected linear manipulation effects, if recruitment does not adequately reflect survival.

In comparison to the preceding years, the last decade has seen a decrease in interest in the costs and optimization of reproduction (but see e.g. Mauck and Grubb 1995; Orell et al. 1996; Blondel et al. 1998; Both et al. 2000; Tinbergen and Verhulst 2000; Pettifor et al. 2001). This might reflect the view that if one investigates a sufficient number of life history traits, both costs and optimization will be detected (Pettifor et al. 2001). A refocusing of research on possible proximate mechanisms (Oppliger et al. 1996; Siikamäki et al. 1997; Nordling et al. 1998; Wiehn et al. 1999; Ilmonen et al. 2002) is also in line with this explanation. However, an increase in haemoparasite burden or a decrease in humoral immune responsiveness do not automatically imply a deterioration in future reproduction and/or survival, and many of these studies did not assess the long-term consequences of the detected physiological changes. Detailed evidence (including both short- and long-term components) for both costs of reproduction and individual optimization of clutch size, therefore, still comes from few species, considering the long period of time since the first complete report appeared (Gustafsson and Sutherland 1988; Tinbergen and Daan 1990; Deerenberg et al. 1996; Pettifor et al. 2001). There are also a number of negative results (e.g. Pettifor 1993; Young 1996; Blondel et al. 1998; Tinbergen and Both 1999). Explanations for these range from the lack of local adaptation (Dhondt et al. 1990) to the importance of unmanipulated components (Murphy et al. 2000). Year effects have also been invoked (e.g. Boyce and Perrins 1987; Pettifor 1993; Blondel et al. 1998; Tinbergen and Both 1999), but either their identification was based on reproductive success differences with the proximate factor behind the differences unknown, or the effects of the specified variable on the payoffs of individual decisions were not presented in detail. Year effects have been largely viewed as confounding factors that need only statistical attention, even though they may provide an alternative explanation for clutch size variation among individuals. Unpredictable environmental fluctuations seriously constrain the accuracy of individual optimization (McNamara et al. 1995; McNamara 1998). If the rate at which good and bad seasons occur is not itself predictable in the long-term (Boyce and Perrins 1987), frequency-dependent selection may maintain an adaptive variability of clutch size, with little change within individual females (Meyers and Bull 2002). Here we have identified an unpredictable environmental factor that modifies the strength of reproductive costs and may account for the lack of accurate optimization of reproductive effort. Few attempts have been made to link individual optimization and environmental predictability. In spite of the methodological problems (e.g. Liou et al. 1993), the topic deserves detailed investigation in the future.

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