Factors affecting fledgling output of great tits, *Parus major*, in the long term

S. Rodríguez, E. Álvarez & E. Barba

Abstract

Factors affecting fledgling output of great tits, Parus major*, in the long term.*— Fledgling production has often been used as an estimator of avian reproductive success, and it is conditioned by factors affecting offspring development and/or survival during the nesting period. We aimed to determine which predictors influenced fledgling output among a set of basic breeding parameters and local temperature data collected over 25 years in a Mediterranean great tit, *Parus major,* population, using an information–theoretic approach for model selection. Of the studied variables, the number of hatchlings per nest was the single–most important predictor influencing fledgling production, with larger broods eventually yielding more fledglings, although mass prior to fledging may have been compromised. This result suggests an overall good adjustment between brood size and resource availability in the studied population.

Key words: Fledgling production, Nestling survival, Brood size, Long–term study

Resumen

Factores que afectan a la producción de volantones en el carbonero común, Parus major*, a largo plazo.*— La producción de volantones ha sido frecuentemente utilizada para estimar el éxito reproductor de las aves y está condicionada por factores que afectan al desarrollo de los pollos, a la supervivencia o a ambos durante su estancia en el nido. Nuestro objetivo en este trabajo fue determinar los factores predictores que influyen en la producción de volantones a partir de un conjunto de parámetros reproductivos básicos y temperaturas locales recopilados durante 25 años en una población mediterránea de carbonero común, *Parus major*, haciendo uso de criterios de información para la selección de modelos. De las variables estudiadas, el número de huevos eclosionados por nido resultó ser el factor predictor con mayor influencia en la producción de volantones, de tal forma que las puestas más grandes originaron más volantones, si bien el peso de los pollos antes de abandonar el nido podría haberse visto comprometido. Este resultado sugiere que hay un buen ajuste general entre el tamaño de puesta y la disponibilidad de recursos en la población estudiada.

Palabras clave: Producción de volantones, Supervivencia en el nido, Tamaño de puesta, Estudio a largo plazo

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Introduction

Avian reproductive success is a recurrent topic in ornithological research. It depends on the number of breeding attempts, with predation being the main cause of complete nest failure (see Martin, 1995), and on the number of individuals surviving to become breeding adults per successful attempt. Among successful nests (*i.e.*, those with at least one young fledged), the number of fledglings has often been used as a reliable estimator of the number of re-cruited young (Weatherhead & Dufour, 2000; Wiens & Reynolds, 2005) and is conditioned by factors influencing offspring development and/or survival during the nesting period.

Among the factors potentially affecting fledgling output, breeding date has proven to influence offspring fitness, with nestlings raised earlier in the season usually benefitting from higher resource availability (Catry et al., 1998), although in certain years, breeding too early could also be disadvantageous (Monrós et al., 2002). In this sense, hatching date could be a more accurate parameter than laying date when analyzing the optimal timing of reproduction in birds (Tomás, 2015). Egg size, in turn, may affect nestling immune function and/or growth (Williams, 1994; Hipfner, 2000), as larger eggs provide the embryo access to higher quantities of energy (Birkhead & Nettleship, 1982). The aforementioned factors (*i.e.,* egg size and bird phenology), together with clutch size, may be indicators of the quality of the parents and their ability to raise the brood, which would have direct consequences on chick survival to fledging (Pettifor et al., 2001). Moreover, if parents optimize their clutch size based on resource availability (Cresswell & Mc-Cleery, 2003; Naef–Daenzer et al., 2004), and some of these eggs fail to hatch, the remaining young may receive greater care and thus improve their survival prospects. As a result, not only the absolute number of hatchlings, but also the number of unhatched eggs could affect fledgling production.

Temperature is one of the main abiotic factors influencing nesting conditions and eventual fledgling production. Nestlings have limited thermoregulatory abilities during their first days of life, which makes them especially vulnerable to suboptimal thermal conditions (Murphy, 1985; McCarty & Winkler, 1999; Takagi, 2001; Bradbury et al., 2003). When exposed to high tempe-ratures, nestlings lose appetite, and their growth rate and musculature decrease (Belda et al., 1995; Geraert et al., 1996). On the other hand, low temperatures also limit nestling condition (Krijgsveld et al., 2003), as colder nest microclimates require a higher investment in thermoregulation, at the expense of processes such as growth or development of the immune system (Dawson et al., 2005; Rodríguez & Barba, in press).

Although many factors have been shown to affect fledgling production, they have seldom been studied simultaneously to determine their relative importance (Coulter & Bryan, 1995; Martín–Vivaldi et al., 1999; Knight & Rogers, 2004; Gullet et al., 2015; Herman & Colwell, 2015). Moreover, their relative weight may vary from year to year, so that long–time series are needed to elucidate each factor's net effect on long temporal scales. Using reproductive and local tempe-rature data collected over 25 years in a Mediterranean great tit, *Parus major*, population, we here aimed to determine the predictors with the greatest influence on the number of fledglings. We also assessed the relationships between the relevant predictors and condition at fledging (*i.e.,* mass and size at fledging).

Material and methods

Fieldwork

Data used for the present study were obtained during a long–term research project on a Mediterranean great tit population breeding near Sagunto (Valen-cia, eastern Spain 39º 42' N, 0º 15' W, 30 m a.s.l.). The study area was located within a homogeneous, extensive orange plantation (Andreu & Barba, 2006). We used reproductive and thermal data collected from 1986 to 2010. Mean laying date of the first egg (given as April dates) for the studied population during this period was 15.92 ± 5.20.

Each year, we placed wooden nest boxes (see Lambrechts et al., 2010, for dimensions) by the end of February. They were removed after each breeding season. Nest boxes were visited with the periodicity necessary (daily at some stages) to accurately de-termine the following reproductive parameters: clutch size, hatching date (date of hatching of the first egg), number of hatchlings and number of fledglings (*e.g.,* Greño et al., 2008). We measured the length and width of every egg of most clutches once it was considered to be complete (at least three days without the appea-rance of new eggs), using a caliper (± 0.1 mm). We determined the volume of each egg using the equation:

$$V = (0.4673 \times L \times B^2) + 0.042$$

V being the egg volume in mm^3, 0.4673 the shape parameter, *L* the egg length in mm and *B* the egg width in mm (Ojanen et al., 1978). When nestlings were 15 days old, they were ringed with individually numbered metal rings and weighed (digital balance, ± 0.01 g), and their tarsus length was measured (ca-liper, ± 0.01 mm). We visited the nest boxes at least five days later to determine the number of fledglings.

Within–nest mean egg volume, mean nestling body mass and mean nestling tarsus length were used in analyses to avoid pseudoreplication (Hurlbert, 1984). We only have data of nestling biometry since 1993. We used data from first clutches, of non–manipulated nests. As we were only interested in successful nests, we also excluded those nests where no nestlings fledged, and those for which data from any of the recorded reproductive parameters was missing. This led us to eventually discard data from three years (*i.e.,* 1989, 2004 and 2005), either because of absence of a reasonable number of successful nests (*i.e.,* less than five nests in 2004), or absence of data on egg size (1989 and 2005). Overall, we used data from 644 successful nests in the analyses.

Daily ambient temperatures were obtained from the Meteorological Station 'El Pontazgo', close to the study area. For each nest, we calculated average mean ambient temperatures during the first five and 15 days after hatching. We chose these periods so as to (1) encompass a period of high vulnerability to changes in ambient temperature (during their first five days of age, great tit nestlings lack the capacity to regulate their internal body temperature; see experiments in Shilov 1973), and (2) to account for overall temperatures experienced during nestling development.

Statistical analyses

We conducted Generalized Linear Models (GLMs) with a Poisson error distribution and log link function to determine which factors explained nestling survival, taking an information–theoretic approach to model selection (Johnson & Omland, 2004; Whittingham et al., 2006). As dependent variable, we considered the absolute number of fledglings. As explanatory variables, we considered mean egg size, clutch size, hatching date, number of hatchlings, number of unhatched eggs (i.e., the difference between clutch size and the number of hatchlings), and mean ambient temperatures during the first five and 15 days after hatching. To simplify interpretation and limit the set of models considered, we did not include interaction terms. We also analyzed the relationship between the number of fledglings per nest and the number of hatchlings (see results for explanation) by fitting different regression curves and choosing the simplest model from among the significant ones. Additionally, we performed simple linear regressions to examine the relationship between the number of hatchlings per nest (see results for explanation) and mean nestling mass, and mean nestling tarsus length.

We assessed the relevance of incorporating the year as a factor by performing a Likelihood Ratio Test with the fully–parameterized model. As its addition did not result in a statistically significant improvement in model fit (χ^2 = 18.903, P = 0.5914) we rejected its inclusion in the models. We tested the validity of this general model by visually inspecting its residuals. Previous studies have shown that all of the analyzed predictors can affect nestling survival when considered individually, so we had no reason to select certain combinations of variables over others. Therefore, we generated 128 models considering all possible non–redundant combinations of predictive variables, ranking them using the small sample sizes' corrected Akaike Information Criterion (AICc, Burnham & Anderson, 1998). We relied on model averaging to obtain a weighted average of predictor estimates from a subset of equally–plausible models (i.e., models with AICc value differing less than two units from the higher–ranked model), and determined each predictor's relative importance in this subset by adding the Akaike weights of those models where it appeared. To further contrast the influence of each parameter in the model subset, we examined their model–averaged weighted effect sizes or β estimates. When the 95% confidence intervals (CIs) of a model–averaged β estimate for a particular parameter overlapped zero, we considered it unlikely that the parameter had much influence on the response variable. Analyses were performed using the lmtest, MuMIn, and glmulti packages in R (R Development Core Team, 2010; Zeileis & Hothorn, 2002; Barton, 2013; Calcagno, 2013), as well as SPSS v. 22.

Results

We found that 89% of the eggs laid in the 644 nests included in this study produced live hatchlings, and 86% of these hatchlings eventually fledged. Moreover, in 48% of the nests, all the hatchlings eventually fledged and among the remaining nests (i.e., with at least one nestling lost prior to fledging), an average of 73% of the hatchlings left the nest. Mean annual number of fledglings per nest during the study period was 6.14 ± 0.88 (mean of yearly means; range: 4.25–7.71; n = 22 years).

Considering the initial model set (128 models), two predictor variables showed a higher probability of inclusion in the best approximating model of the number of fledglings, as given by the sum of Akaike weights of the models in which they appear: number of hatchlings (ΣW_i = 0.784) and clutch size (ΣW_i = 0.648). Egg size (ΣW_i = 0.545) had intermediate importance, whereas number of unhatched eggs (ΣW_i = 0.432), hatching date (ΣW_i = 0.320), and mean ambient temperatures during the first 15 days after hatching (ΣW_i = 0.278) and during the first five days after hatching (ΣW_i = 0.273) had lower importance.

Four models fitted the data equally well, as given by their AICc scores. This set of best–fitting models included clutch size, egg size, number of hatchlings and number of unhatched eggs as explanatory variables (table 1, models 1, 2, 3, and 4). Overall, a total of 22 additional models had AICc values within two units of the best–ranked models. They generally explained 46–48% of the deviance of the null model. The combined Akaike weight of this subset of best–fitting models was 0.625. According to the model–averaged coefficients of the predictor variables (table 2), the number of fledglings decreased with hatching date and number of unhatched eggs, and increased with egg size, number of hatchlings, temperatures during the first five and 15 days after hatching. The relative importance of the predictor variables in the model–averaged subset, calculated by the sum of the Akaike weights over all the models in which they appear, was high for number of hatchlings (ΣW_i = 0.77), clutch size (ΣW_i = 0.69), number of unhatched eggs (ΣW_i = 0.69), and egg size (ΣW_i = 0.63). Of these parameters, only the number of hatchlings had a strong effect size (i.e., β estimate), with CIs ranging from 0.105 to 0.184, whereas clutch size, number of unhatched eggs and egg size had CIs overlapping zero (table 2). The remaining variables were of low importance and their 95% CIs overlapped zero (table 2): hatching date (ΣW_i = 0.22), mean ambient temperatures during the first five and 15 days after hatching (both ΣW_i = 0.10). The simplest best–fitting

Table 1. Top–ranked models (*i.e.*, with ΔAICc < 2) and last ranked model used to test the effect of temperature and reproductive parameters on the number of fledglings: CS. Clutch size; ES. Egg size; NH. Number of hatchlings; NUE. Number of unhatched eggs; T5. Mean ambient temperatures during the first five days after hatching; T15. Mean ambient temperatures during the first 15 days after hatching; AICc. Corrected Akaike Information Criterion for small sample sizes; ΔAICc. Difference in AICc values in relation to model 1.

Tabla 1. Los modelos mejor puntuados (es decir, con ΔAICc < 2) y el último modelo empleados para analizar el efecto de la temperatura y los parámetros reproductivos en el número de volantones: CS. Tamaño de puesta; ES. Tamaño de huevo; NH. Número de huevos eclosionados; NUE. Número de huevos sin eclosionar; T5. Promedio de la temperatura ambiental durante los primeros cinco días después de la eclosión; T15. Promedio de la temperatura ambiental durante los primeros 15 días después de la eclosión; AICc. Criterio de Información de Akaike corregido para muestras pequeñas; ΔAICc. Diferencia de los valores de AICc en relación con el modelo 1.

Model	Parameters included	AICc	ΔAICc	Akaike weight
1	CS, ES, NH	2562.307	0	0.04166
2	CS, ES, NUE	2562.307	0	0.04166
3	ES, NH, NUE	2562.307	0	0.04166
4	CS, ES, NH, NUE	2562.307	0	0.04166
5	NH, NUE	2562.543	0.236	0.03702
6	CS, NH	2562.543	0.236	0.03702
7	CS, NUE	2562.543	0.236	0.03702
8	CS, NH, NUE	2562.543	0.236	0.03702
9	ES, NH	2563.106	0.799	0.02794
10	NH	2563.867	1.560	0.01770
11	CS, HD, ES, NH	2563.969	1.662	0.01814
12	CS, HD, ES, NUE	2563.969	1.662	0.01814
13	HD, ES, NH, NUE	2563.969	1.662	0.01814
14	CS, HD, ES, NH, NUE	2563.969	1.662	0.01814
15	CS, HD, NH	2564.200	1.893	0.01617
16	CS, HD, NUE	2564.200	1.893	0.01617
17	HD, NH, NUE	2564.200	1.893	0.01617
18	CS, HD, NH, NUE	2564.200	1.893	0.01617
19	T5, CS, ES, NH	2564.236	1.929	0.01588
20	T5, ES, NH, NUE	2564.236	1.929	0.01588
21	T5, CS, ES, NH, NUE	2564.236	1.929	0.01588
22	T5, CS, ES, NUE	2564.236	1.929	0.01588
23	T15, CS, ES, NH	2564.259	1.952	0.01569
24	T15, CS, ES, NUE	2564.259	1.952	0.01569
25	T15, ES, NH, NUE	2564.259	1.952	0.01569
26	T15, CS, ES, NH, NUE	2564.259	1.952	0.01569
128	T5, HD	2776.394	214.1	1.3527E–48

function explaining the relationship between the number of fledglings (NF) and the number of hatchlings (NH) was linear (NF = 0.8891 NH – 0.1359, r = 0.983, P < 0.001; fig. 1).

There was a significant, negative relationship between mean nestling mass (M) and the number of hatchlings (NH) per nest (M = –0.2318 NH + 18.349, r = 0.282, P < 0.001; fig. 2). We also found

Table 2. Model–averaged coefficients of the predictor variables from the subset of best–fitting models. (For abbreviations, see table 1.)

Tabla 2. Coeficientes promediados de los factores predictores incluidos en el subconjunto de modelos con mejor ajuste. (Para las abreviaturas, véase la tabla 1.)

Parameter	Estimate	SE	Adjusted SE	95% CI Lower	95% CI Upper	Z value	$P(>|Z|)$
T15	0.003135	0.01118	0.01120	–0.01882	0.02509	0.280	0.780
HD	–0.001254	0.002065	0.002069	–0.005309	0.002802	0.606	0.545
ES	0.0002104	0.0001381	0.0001384	–0.00006084	0.0004816	1.520	0.128
NH	0.1448	0.02010	0.02012	0.1054	0.1843	7.197	<2E–16
T5	0.002941	0.009218	0.009235	–0.01516	0.02104	0.319	0.750
CS	0.02048	0.07555	0.07556	–0.1276	0.1686	0.271	0.786
NUE	–0.09400	0.06468	0.06469	–0.2208	0.03279	1.453	0.146

a non–significant trend for mean nestling tarsus length (T) to decrease with the number of nestlings (T = –0.0269 NH + 19.582, r = 0.074, P = 0.077).

Discussion

The number of hatchlings had a significant, positive effect on fledgling production, so that larger broods eventually yielded more fledglings. In this long–term approach, we did not find other significant predictors of the number of fledglings produced per nest in the studied population, although other predictors are likely relevant in certain years, depending on environmental conditions.

Several studies have analyzed the importance of brood size for nestling growth and survival (Groves, 1984; Coulson & Porter, 1985; Burness et al., 2000; Benharzallah et al., 2015), although its effect, either positive or negative, is dependent on parental quality and resource availability (Gebhardt–Henrich & Richner, 1998). Taking care of large broods is energetically demanding, forcing parents to adjust clutch sizes based on their ability to rear the resulting chicks
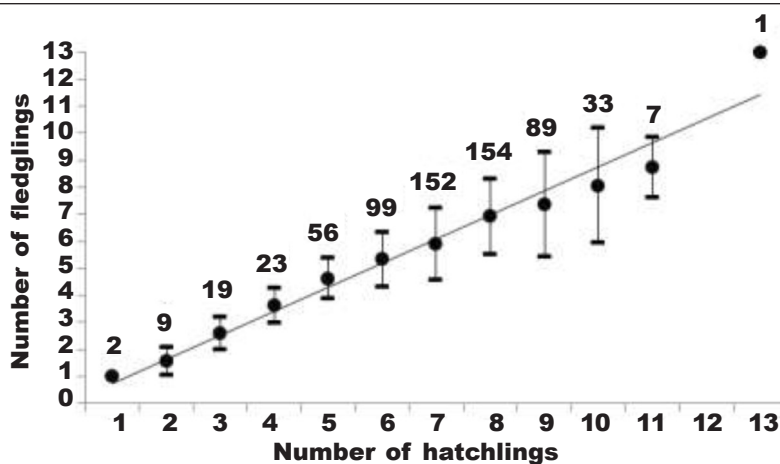

Fig. 1. Average number of fledglings (± SE) produced per nest in relation to the number of hatchlings. Sample sizes above error bars refer to the number of nests.

Fig. 1. Promedio de volantones producido por nido (± EE) en relación con el número de eclosiones. Los tamaños muestrales indicados sobre las barras de error se refieren al número de nidos.
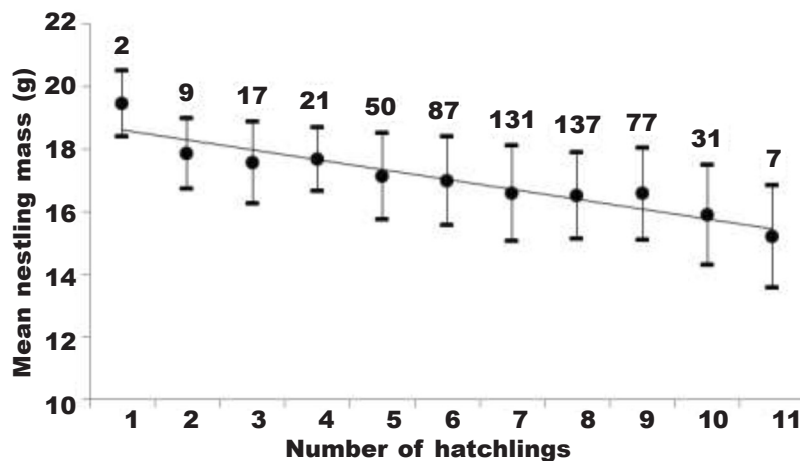
Fig. 2. Relationship between mean nestling mass at day 15 (± SE) and the number of hatchlings per nest. Sample sizes above error bars refer to the number of nests.

Fig. 2. Relación entre el peso medio de los pollos en el día 15 (± EE) y el número de eclosiones por nido. Los tamaños muestrales indicados sobre las barras de error se refieren al número de nidos.

efficiently (Lack, 1947; Murphy & Haukioja, 1986; Wellicome et al., 2013). Parental age has been positively correlated with chick growth, either as a result of increased experience (Coulson & Porter, 1985) or reproductive effort (Pugesek, 1995). Moreover, parental breeding performance is necessarily linked to the ability to provide food to the developing chicks, so that limitations in food supply under resource–poor scenarios may carry over restrictions in nestling growth and/or survival inside the nest (Gebhardt–Henrich & Richner, 1998; Wellicome et al., 2013). In our study, most chicks hatched per nest survived to leave the nest, suggesting a good adjustment between brood size and resource availability in the studied population in the long term. In addition, the mean annual number of fledglings was comparable to that of other areas within the same latitudinal range (Sanz, 2002; Atiénzar et al., 2012).

The demands of raising large broods may have limited nestling growth, as revealed by the negative relationship between number of hatchlings and mean mass at fledging. In this study, nestling quality appeared to be compromised by nestling quantity. This result agrees with previous observational studies, where mean nestling mass has been shown to decline with increasing brood size (Perrins, 1965 reviewed in Klomp, 1970). Moreover, experimentally–enlarged broods produced lighter fledglings in several manipulative experiments (Smith et al., 1989; Tinbergen & Daan, 1990; Pettifor et al., 2001; Hõrak, 2003). In this population, previous studies revealed that adults reduced the number of feeding visits per nestling as brood size increased (Barba et al., 2009), and nestling growth rate decreased as clutch size increased (Barba et al., 1993).

None of the other predictors considered in this study had a significant effect on the number of fledglings

in the long term. Therefore, nestling survival during the analyzed period seems to have been determined by brood size, regardless of the importance that, to a greater or lesser extent, other factors may have during certain years depending on particular environmental conditions. Adverse weather events prior to incubation, for instance, may negatively affect egg volume and clutch size, or bring about delays in hatching dates (Monrós et al., 1998). These breeding alterations may eventually affect nestling development and/or survival to fledging (Monrós et al., 1998; Krist, 2011; Etezadifar & Barati, 2015). Additionally, suboptimal nest temperatures during the nestling stage as a result of episodic hot or cold spells may directly handicap chick fitness and ultimately increase mortality (Belda et al., 1995; Takagi, 2001). Based on our results, the weak predictive power of these factors could be explained by the annual variability in the intensity of their effects on fledging production.

In conclusion, brood size emerged as the best predictor of the number of fledglings produced per nest in our Mediterranean great tit population. Larger broods produced more fledglings, although mass prior to fledging may have been compromised. The relatively weak effect sizes of the remaining potential predictors of fledging output could be a consequence, at least in part, of their dependence on environmental variation between years.

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