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EGG SIZE VARIATION IN A MEDITERRANEAN GREAT TIT *PARUS MAJOR* POPULATION

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SUMMARY.—*Egg size variation in a Mediterranean Great Tit* Parus major *population*. Egg size variation was studied in a Great Tit *Parus major* population in eastern Spain during 13 years. Mean egg volume was 1.50 cm^3 (S.D. = 0.12, n = 521 clutches). Mean egg volume differed significantly between years, the differences being caused by a single year with an exceptionally large mean egg size. We found no relationship between mean egg volume of the year and mean air temperatures during the three months previous to the breeding season. Mean egg volume of the year was not related to mean laying date, but was positively related to mean clutch size of the year. Mean egg size was not related to laying date or clutch size in any of the 13 years. In conclusion, egg size showed a considerable constancy in the Great Tit population studied. A review of within-population trends of egg size variation in Great Tits showed that, though most studies reported no or little egg size variation with year, time of season or clutch size, all the possible trends were found in one or another population. Moreover, different trends could be found in the same population in different years. Studies lasting several years seem to be necessary to find out the potential responses of egg size to different environmental conditions.

Key words: clutch size, egg size, Great Tit, laying date, long-term studies, *Parus major*, within-population patterns.

RESUMEN.—*Variación del tamaño del huevo en una población mediterránea de Carbonero Común* Parus major. La variación en el tamaño del huevo de una población de Carbonero Común *Parus major* se ha estudiado en el Este de España durante 13 años. El volumen medio de los huevos fue de 1,50 cm^3 (D.T. = 0,12; n = 521 puestas). El volumen medio de los huevos difirió significativamente entre años, debiéndose las diferencias a un único año en el que el tamaño medio de los huevos fue excepcionalmente grande. No encontramos relación significativa entre el volumen medio anual de los huevos y la temperatura media durante los tres meses previos a la estación reproductora. El volumen medio anual de los huevos no estuvo relacionado con la fecha media de puesta, pero sí estuvo positivamente relacionado con el tamaño medio de puesta. El tamaño medio de los huevos no estuvo relacionado con la fecha de puesta ni con el tamaño de puesta en ninguno de los 13 años de estudio. En conclusión, el tamaño de los huevos mostró una considerable constancia en la población de Carbonero Común estudiada. Una revisión de las tendencias intrapoblacionales en el tamaño de los huevos del Carbonero Común mostró que, aunque la mayor parte de estudios señalan que no existen variaciones significativas entre años, a lo largo de la estación o con el tamaño de puesta, todas las posibles tendencias se encontraron en una u otra población. Más aún, se han encontrado diferentes tendencias en la misma población en años distintos. Parece que son necesarios estudios que duren varios años para revelar las respuestas potenciales del tamaño del huevo a diferentes condiciones ambientales.

Palabras clave: Carbonero Común, estudios a largo plazo, fecha de puesta, *Parus major*, patrones intrapoblacionales, tamaño de puesta, tamaño del huevo.

INTRODUCTION

Within-population trends in life history traits may differ between populations and, therefore, populations living along a gradient of environmental conditions should be studied to have a complete knowledge of the ways the studied species could respond to different selective pressures (Järvinen, 1984). The size of birds' eggs has been shown to have fitness consequences for the breeding individuals — in general, smaller eggs have lower probabilities of producing fledglings (e.g. Williams, 1994; Perrins, 1996). Therefore, selection pressures may act on egg size and its variability within populations, and the trends found could vary bet-

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ween populations depending on the main pressures acting in each place.

We will focus here on three patterns of egg-size variation detected in some populations of birds: annual variation, seasonal variation and variation with clutch size (e.g. Soler, 1988; Briskie & Sealy, 1990; Järvinen, 1991; Horak *et al*., 1995; Perrins, 1996; Cichon, 1997). Variation between years is usually attributed to variation in weather conditions and/or food availability, while variation throughout the season is attributed to changes in environmental conditions and/or in female age or condition (Soler, 1988; Briskie & Sealy, 1990; Järvinen, 1991; 1994; Horak *et al*., 1995; Cucco & Malacarne, 1996). Variation with clutch size has been interpreted differently depending on the results obtained. Negative correlations between clutch and egg size have been interpreted as a compromise of the female between laying few large or many small eggs (e.g. Briskie & Sealy, 1990; Cichon, 1997). Positive correlations have been suggested to be caused by energy limitations: large clutches of big eggs would be laid under good environmental conditions and/or by good quality females, while small clutches of small eggs would be laid if conditions are adverse and/or female quality is low (Coleman & Whittall, 1990; Järvinen, 1996). Curvilinear relationships, with larger eggs at intermediate clutch sizes, have been also found (Gibb, 1950; Winkel, 1970; Wiggins, 1990), though no explanation for this trend has been provided.

Great Tits *Parus major* are an excellent subject of study for inter-populational comparisons (e.g. Sanz, 1998) since they occupy a wide range of different habitat types along a large latitudinal gradient. The variation patterns studied here for a Mediterranean population have been previously studied in other European populations living in different habitats, which will provide a framework to discuss possible within-population trends in egg size.

STUDY AREA AND METHODS

We used data collected during a long-term study of Great Tits in an orange monoculture in Sagunto (eastern Spain 39°42′N, 0°15′W, 30 m a.s.l.). The population breeds in nestboxes (see Barba & Gil-Delgado, 1990 for details) which are regularly checked to obtain basic breeding parameters each year (Belda *et al*., 1998; Encabo *et al*., 2001). We included here data on egg size, clutch size and laying dates for 13 years (from 1986 to 1988 and from 1990 to 1999).

The mean laying date for each year was calculated as the mean date of laying of the first egg of all first clutches initiated in the population and not manipulated before laying started (Barba *et al*., 1995). Each nestbox was visited at least every five days before laying, so clutches were found with a maximum of five eggs. The date of clutch initiation was calculated by backdating, assuming the laying of one egg per day. This procedure is usually very accurate, since gaps (days without laying) are rare and gaps of more than one day very rare (Monrós *et al*., 1998).

The mean clutch size of each year was calculated as the mean number of eggs of all complete first clutches laid that year. Clutches manipulated before clutch completion were excluded. A clutch was considered complete when incubation had begun and no new eggs were laid for two days.

The length and breadth of each egg of most clutches were measured each year with a sliding calliper to the nearest 0.1 mm. All measurements were taken by the same author (EB) when each clutch was complete. Only complete clutches were used in this study. The study area, and consequently the number of nestboxes, has increased over the years to *ca.* 160 ha in the last year of study. This, and the exclusion of manipulated nests some years, are the main causes of between-year differences in sample sizes. A total of 521 clutches, including 3936 eggs, have been used in this study. The number of clutches used each year is shown in Table 1.

The volume of each individual egg was calculated from linear dimensions as $V = 0.4673\ LB^2 + 0.042$ (Ojanen *et al*., 1978), where V is egg volume (in mm^3), L is egg length and B is egg breadth (both in mm). We preferred this equation, calculated specifically for Great Tits, to the more general equation of Hoyt (1979), since specific equations usually give a better estimate of egg volume (Kern & Cowie, 1996). Mean egg volume was calculated for each clutch, and we used mean egg volumes as sample units for all the analyses.

Mean temperatures during the three months previous to the breeding season (January to

TABLE 1

Mean egg volume (in cm^3) in different years of the study. There was a significant annual variation in egg volume ($F_{12,508}$ = 2.75, P = 0.001).
[Volumen medio de los huevos (en cm^3) en los distintos años del estudio. El volumen de los huevos mostró diferencias interanuales significativas.]

Year *[Año]*	*n*	Egg volume *[Volumen del huevo]*			
		Mean *[Media]*	Standard deviation *[Desviación típica]*	Minimum *[Mínimo]*	Maximum *[Máximo]*
1986	15	1.49	0.10	1.30	1.63
1987	22	1.52	0.11	1.29	1.68
1988	26	1.53	0.12	1.25	1.71
1990	10	1.52	0.10	1.37	1.64
1991	17	1.60	0.10	1.44	1.76
1992	18	1.55	0.09	1.41	1.74
1993	36	1.51	0.10	1.32	1.71
1994	27	1.45	0.10	1.16	1.61
1995	56	1.52	0.12	1.25	1.89
1996	69	1.51	0.12	1.26	1.80
1997	79	1.50	0.11	1.19	1.76
1998	64	1.51	0.13	1.26	1.81
1999	82	1.47	0.11	1.20	1.75

March) were used as an indication of the goodness of the year for breeding (e.g. Kluijver, 1951; Van Balen, 1973). We would expect that, if there were between-year differences in mean egg size, larger eggs would be associated to warmer temperatures. Mean daily temperatures in a meteorological station (Pontazgo; *c.a.* 3 km from the study site) during the study years were obtained from the Centro Meteorológico Territorial de Valencia.

To explore the possible relationships between mean egg volume and laying date and clutch size within each year, we used nested ANCOVAs with either laying date or clutch size nested within each year. Analyses were performed using the SPSS/PC+ statistical package (SPSS Inc., 1998).

RESULTS

The mean egg breadth and length (±S.D.) of Great Tit eggs in our study area were, respectively 13.34 ± 0.37 mm (range 12.01 – 14.38) and 18.07 ± 0.73 mm (range 16.02 – 20.48). Mean egg volume was 1.50 ± 0.12 cm^3 (n = 521 clutches in all cases). Mean egg volume ranged from 1.16 to 1.89 cm^3.

There were significant differences in mean egg volume between years (Table 1). *A posteriori* multiple comparisons (Tukey tests) showed that the only year responsible for these differences was 1991, the year with the largest

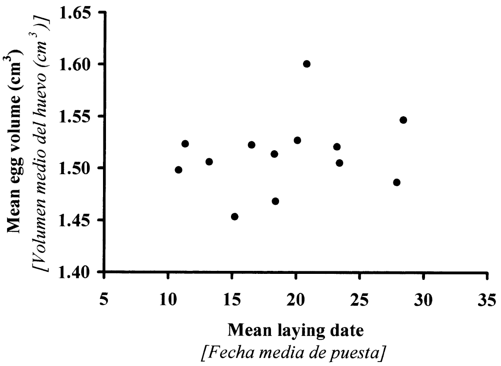

FIG. 1.—Lack of relationship between mean egg volume of each year and mean laying date (1 = 1 April) for Great Tits breeding in orange groves of eastern Spain ($F_{1,11}$ = 0.60, P = 0.454, r^2 = 0.052).
[Ausencia de relación entre el volumen medio de los huevos de cada año y la fecha media de puesta en Carboneros Comunes reproductores en los naranjales de España oriental.]

eggs, that differed significantly from three of the years with smallest eggs (1994, 1997 and 1999). We did not find any significant relationship between mean egg size and mean ambient temperature during the three months preceding laying ($F_{1,11}$ = 1.73, P = 0.22, r^2 = 0.14)

Mean egg volume in each year was not related to mean laying date (Fig. 1). Mean egg volume in each year was positively correlated with mean clutch size of the year (Fig. 2).

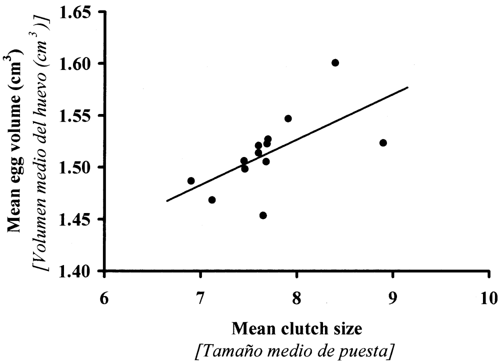

FIG. 2.—Relationship between mean egg volume of each year and mean clutch size for Great Tits breeding in orange groves of eastern Spain (Egg volume = 1.18 + 0.04 • Clutch size, $F_{1,11}$ = 6.12, P = 0.031, r^2 = 0.36).
[Relación entre el volumen medio de los huevos de cada año y el tamaño medio de puesta en Carboneros Comunes reproductores en los naranjales de España oriental (Volumen del huevo = 1,18 + 0,04 • tamaño de puesta).]

Within each year, there were no significant relationships between mean egg volume and either laying date or clutch size (Table 2).

DISCUSSION

Annual variation

Only a few studies have detected annual variation in egg size in passerines (Murphy, 1978; Soler, 1988; Briskie & Sealy, 1990; Järvinen, 1991; Hendricks, 1991; Horak *et al.*, 1995). Most of them explain this variation as a consequence of changes in environmental conditions, either food availability or weather conditions.

Significant changes in mean egg size should be exceptional. For example, Järvinen (1991), using 13 years of data from a Pied Flycatcher *Ficedula hypoleuca* population, found that only in one year was the mean egg size significantly larger, while in another year it was significantly smaller than in the others. Another long-term study, this time on Great Tits, detected a decline in egg mass during 30 years (Perrins, 1996). It was suggested that a change from wooden to concrete (predator-proof) nestboxes produced some demographic changes in the population, among them an increase in mean clutch size, that could explain the change in egg size (egg size decreased with increasing clutch size in this population). Actually, mean egg size was constant both before and after the nestbox change, steeply changing about the time when nestboxes were changed. Our long-term data

TABLE 2

Nested analyses of covariance of egg volume with laying date and clutch size within each year.
[Análisis de covarianza anidado del volumen del huevo con la fecha de puesta y el tamaño de puesta dentro de cada año.]

Source *[Variable]*	d.f. *[g.l.]*	MS *[CM]*	*F*	*P*
Year *[Año]*	12	0.0166	1.29	0.22
Laying date (Year) *[Fecha de puesta dentro del año]*	13	0.0089	0.69	0.77
Error	495	0.0129		
Year *[Año]*	12	0.0086	0.67	0.78
Clutch size (Year) *[Tamaño de puesta dentro del año]*	13	0.0102	0.79	0.67
Error	495	0.0129		

on Great Tits also showed constancy in mean egg size, with the only exception being the relatively large eggs in 1991. We did not find any significant correlation between egg volume and mean air temperatures during the three months preceding laying, a period affecting laying dates in other populations (Kluijver, 1951; Van Balen, 1973). However, Barba (1992) examined the breeding parameters of this population during six years (1986-91) and found that breeding success was higher in 1991 than in any other year, suggesting very good breeding conditions during that year.

In contrast, most short-time studies have not found annual variations in egg size (e.g. Rofstad & Sandvik, 1985; Wiggins, 1990; Suárez, 1991; Magrath, 1992; Potti, 1993; Smith *et al.*, 1993; Nager & Zandt, 1994). This suggests that egg size could vary between years, but this variation is rare and occurs only exceptionally. Therefore, long-term studies should be carried out to detect annual variation, while short-time ones only detect annual variation if they «catch» an exceptional year by chance. Given this constancy in mean egg size, some authors have suggested that the birds produce eggs of about the same size within a wide range of environmental conditions, and only in severe years mean egg size would be affected (Järvinen, 1991). Data presented here on Great Tits, and those on Pied Flycatchers (Järvinen, 1991), also indicate that the birds could respond to very good years by increasing mean egg size. This is interesting and would merit more investigation, since it suggests that the birds have the potential of producing larger eggs than those usually produced or, in other words, except in very good years, egg size is constrained. Perrins (1996) has shown that producing eggs above certain size gives no additional benefit. This would explain the production of eggs below the maximum potential size in «normal» years, but still leaves unexplained why, in good years, extra energy is allocated into increasing egg size and not into other fitness-related life history traits.

Studies on Great Tits fit perfectly into this framework. Long-term studies (Perrins, 1996; this study) detected differences in egg size between years, and in both cases exceptional causes seem to be involved. Most short-term studies, on the other hand, have failed to find annual differences (Järvinen & Pryl, 1989; Nager & Zandt, 1994; Eeva & Lehikoinen, 1995; Dufva, 1996; Riddington & Gosler, 1996). To our knowledge, the only exception is a five-year study in Estonia (Horak *et al.*, 1995), where egg size varied among years, but no explanation for this finding was given.

As found in northern Europe in two other passerines, the Pied Flycatcher and the Redstart *Phoenicurus phoenicurus* (Järvinen, 1991), the mean egg volume of the year is not related to the mean laying date in our Great Tit population. This was not very surprising, since (1) the birds probably adjust their laying date to the phenological state of the habitat, so that they are actually laying in the same phenological state each year, independently of the «calendar date»; and (2) the lack of seasonal variation means that producing eggs at different times during the breeding season does not affect egg size significantly.

A positive relationship between mean egg size and mean clutch size would have meant that, in good years, the birds produce large clutches of big eggs, while small clutches of small eggs would be produced in bad years. This positive relationship was found in our Great Tit data set. Järvinen (1991) looked for this relationship in Pied Flycatchers and Redstarts, but he did not find it. Therefore, to our knowledge, this is the first time that such a positive trend between egg and clutch size is reported for a passerine.

Seasonal variation

Most published studies on seasonal variation of egg size in passerines, including some on Great Tits, have found no significant variation throughout the season (Rofstad & Sandvik, 1985; Järvinen & Pryl, 1989; Briskie & Sealy, 1990; Järvinen, 1991; Suárez, 1991; Arnold, 1992; Nilsson & Svensson, 1993; Potti, 1993; Smith *et al.*, 1993; Nager & Zandt, 1994; Eeva & Lehikoinen, 1995; Dufva, 1996; Cichon, 1997). However, both increasing (Svensson, 1978; Magrath, 1992) and decreasing (Soler, 1988; Cucco & Malacarne, 1996) trends have been described, and both of them have been found in Great Tit populations (Haftorn, 1985; Horak *et al.*, 1995; Perrins, 1996).

It has been proposed that a seasonal increase in egg volume could be a consequence of energetic limitations early in the season (Verhulst & Tinbergen, 1991; Perrins, 1996). This seems to be more a consequence of low temperatures (Magrath, 1992) than a limitation of food, since food supplementation usually does not affect egg size in passerines (Arnold, 1992; Magrath, 1992; Nilsson & Svensson, 1993; Nager *et al*., 1997; but see Ramsey & Houston, 1997). It seems that temperatures early in the season have not been low enough to affect egg size in our study area during the 13 years of study.

The decrease of egg size in the course of the season has been detected less frequently, and has been explained as a consequence of low «quality» and/or young females breeding later (e.g. Soler, 1988; Horak *et al*., 1995; Cucco & Malacarne, 1996).

As with annual variation, all the patterns of seasonal variation of egg size could be found in Great Tits. Both Haftorn (1985) and Perrins (1996) described a seasonal increase of egg size in Norway and England, respectively. The explanation given was that egg size was limited early in the season by low food availability, but the birds traded this disadvantage for the benefits of breeding early. On the other hand, a decreasing seasonal trend of egg size has been described in an urban Great Tit population in Estonia (Horak *et al*., 1995). Apparently, poor-quality females were breeding late in the season and produced small eggs. However, again most studies reported no seasonal variation (Järvinen & Pryl, 1989; Nager & Zandt, 1994; Eeva & Lehikoinen, 1995; Horak *et al*., 1995 —rural population—; Dufva, 1996; this study), which seems to be the rule in most populations and years. Even experimental studies give different results: while Barba *et al*. (1995) showed that egg size was not affected in pairs experimentally delayed, Verhulst & Tinbergen (1991) found that egg size of experimentally-delayed pairs was larger than that of controls.

Variation with clutch size

Many studies have tried to find a trade-off between number and size of the eggs within a population, but this negative relationship has been seldom found (see e.g. Williams, 1994). The relationship between egg and clutch size has been reported to vary between species (Ojanen *et al*., 1978), between populations of the same species (e.g. Järvinen & Väisänen, 1983; Järvinen & Pryl, 1989; Horak *et al*., 1995) and even between years in the same population (Smith *et al*., 1993; Horak *et al*., 1995; Järvinen, 1996; Cichon, 1997). If resources for egg formation are not limiting, no relationship between egg and clutch size would be expected, or even a positive one could be found (Van Noordwijk & De Jong, 1986; Coleman & Whittall, 1990). A good example of this was provided by Järvinen (1996), using long-term egg and clutch size data for Pied Flycatchers. He found a positive relationship between egg and clutch size in «good» years, a negative relationship in «bad» years and no significant relationship in «normal» years. Even in Finnish Lapland, where the study was conducted, most years (12 out of 20) were «normal», and a trade-off was found only in five years. Likewise, many studies have not found any relationship between egg and clutch size (e.g. Rofstad & Sandvik, 1985; Soler, 1988; Järvinen & Pryl, 1989; Järvinen, 1991; Suárez, 1991; Dufva, 1996). Therefore, it should be more probable to find trade-offs near the limits of the area of distribution of the species studied and/or in relatively «bad» years. The lack of relationship found for Great Tits in the population studied here, in any of the 13 years, suggest that conditions for breeding are more or less stable over the years and that especially «good» or «bad» years, if they occur, should be very rare.

Once more, all the patterns described could be found in Great Tits. Egg size increases with clutch size in some populations (Busse, 1967; Ojanen *et al*., 1978), decreases with clutch size in others (Kiziroglu, 1982; Haftorn, 1985; Horak *et al*., 1995 —rural population—; Perrins, 1996), and does not vary in others (Järvinen & Pryl, 1989; Horak *et al*., 1995 - urban population-; Dufva, 1996; this study). Even a rare pattern found in Tree Swallows *Tachycineta bicolor*, namely an initial increase of egg size with clutch size, decreasing again from intermediate to large clutch sizes (Wiggins, 1990), has been described in some Great Tit populations (Gibb, 1950; Winkel, 1970). Moreover, within a population, the relationship between egg and clutch size could vary in different years (Horak *et al*., 1995).

Conclusion

Data presented here, and those compiled from the literature, show that the mean size of the eggs of a clutch is a very plastic trait. Though variation in mean egg size is not commonplace, and most of the relationships looked for in many studies over several species are not significant, almost every possible pattern of variation of egg size with the traits explored in the present study could be found. This is even more striking when all the patterns are found within a single species (studies on Great Tits and Pied Flycatchers), and many different patterns could be found within a single population in different years. We guess that many other species have the same potential, but studies including contrasting conditions, over several contrasting years, would be necessary to find them.

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