

DETERMINATION OF CLUTCH SIZE IN THE BLUE TIT *PARUS CAERULEUS* IN CENTRAL SPAIN: FIELD EXPERIMENTS

Juan MORENO*, Luis M. CARRASCAL*, Juan A. FARGALLO*
and Eduardo SOTO-LARGO**

SUMMARY.—*Determination of clutch size in the Blue Tit (Parus caeruleus) in Central Spain: field experiments.* Two field experiments were performed in a Central Spanish population of Blue Tit (*Parus caeruleus*) breeding in nestboxes in order to elucidate if food availability at laying constrains clutch size (experiment 1), or if clutch size affects nestling growth and survival (experiment 2). In the first, mealworms were offered at the nestboxes of certain pairs during the laying days. No effect of food supplementation on clutch size and egg mass was detected. There was a significant advancement of the onset of incubation in the supplemented group, with the consequent advancement of hatching date. Females used only the extra food to combine laying and incubation earlier. In the second experiment, two chicks were added or removed soon after hatching, and fledging success, fledging mass and size and starvation mortality compared between the reduced, control and enlarged broods. Chicks in enlarged broods suffered a higher starvation mortality and fledged with lower masses than in control and reduced broods, while there were no effects of the brood manipulation on parental condition. Clutch size in the study population is not constrained by food availability at laying, and affects nestling fitness presumably through the feeding capacity of individual breeding pairs.

Key words: brood manipulation, Central Spain, clutch size, egg mass, fledging mass, food supplementation, nestling mortality, *Parus caeruleus*.

RESUMEN.—*Determinación del tamaño de puesta del Herrerillo (Parus caeruleus) en España central: experimentos de campo.* Se realizaron dos experimentos de campo en una población de Herrerillo (*Parus caeruleus*) de España central que se reproduce en nidos artificiales, para dilucidar si la disponibilidad de alimento durante la puesta limita el tamaño de puesta (experimento 1), o si el tamaño de puesta está determinado por la capacidad de cebar pollos de cada pareja (experimento 2). En el primero, ofrecimos gusanos de harina en el nidal de ciertas parejas durante los días de la puesta. No se detectó ningún efecto del alimento suplementario sobre el tamaño de puesta o el peso de los huevos. Si hubo un anticipo del inicio de la incubación en el grupo experimental, con el consiguiente anticipo de la fecha de eclosión. Las hembras sólo utilizaron el alimento suplementario para compaginar antes puesta e incubación. En el segundo experimento, añadimos o quitamos dos pollos inmediatamente después de la eclosión en ciertos nidos, y comparamos el éxito de nidada, el peso y tamaño de los volantones y la mortalidad por hambre entre nidadas reducidas, control y aumentadas. Los pollos de nidadas aumentadas sufrieron una mayor mortalidad por hambre y volaron con menos peso que en nidadas control y reducidas, mientras no hubo efecto de la manipulación de nidada sobre la condición parental. El tamaño de puesta en la población de estudio no está limitado por la disponibilidad de alimento durante la puesta, sino que está ajustado a la capacidad de cebar pollos de las distintas parejas reproductoras.

Palabras clave: alimento suplementario, España central, manipulación de nidada, mortalidad de pollos, *Parus caeruleus*, peso de huevos, peso de volantones, tamaño de puesta.

INTRODUCTION

The determination of clutch size in altricial birds has attracted a great deal of attention since Lack's (1947; 1954) pioneering work. Both proximate and ultimate factors have been proposed as regulating clutch size

(Klomp, 1970; Murphy & Haukioja, 1986; Martin, 1987). Thus, clutch size has been shown to be proximately constrained at the time of laying by some factor (energy, specific nutrients): laying is terminated when particular body reserves fall to a threshold level (Jones & Ward, 1976; Fogden & Fogden, 1979;

* Museo Nacional de Ciencias Naturales-CSIC, José Gutiérrez Abascal, 2. E-28006 Madrid.

** Plaza Mariano de Cavia, 1. E-28007 Madrid.

Pinowska, 1979). On the other hand, Lack (1947; 1954) originally proposed that clutch size in altricial birds is adjusted to the future requirements of dependent young (Lack, 1947; 1954; Slagsvold & Lifjeld, 1988; Simons & Martin, 1990). Later reformulations of Lack's hypothesis have incorporated reproductive costs (Williams, 1966; Charnov & Krebs, 1974), or are based on a seasonal decline of the reproductive value of eggs (Daan *et al.*, 1988; Daan *et al.*, 1990; Tinbergen & Daan, 1990) or consider the interaction of food availability and the risks of predation (Lima, 1987; Martin, 1992). The first hypothesis is based on mechanistic constraints, while the second hypothesis is based on tactical decisions at the time of laying, involving the reproductive costs while feeding nestlings.

The most common approach for determining the importance of food availability at laying in the context of clutch size determination, has been to provide supplemental food before and during laying (Martin, 1987; Daan *et al.*, 1988). Food supplementations initiated before laying have frequently led to an advancement of laying, and more infrequently to an increase in clutch size (Daan *et al.*, 1988). Given the common pattern of a tight relationship between laying date and clutch size (Klomp 1970), it becomes necessary to separate the effects of date and food supplementation on clutch size. One way to do this, is to supply food only after females have started to lay (Nilsson, 1991; Nilsson & Svensson, 1993). At that stage, the decision to begin laying is fixed and cannot be altered by the experiment. An effect on clutch size can only be ascribed to the effect of the food itself. Experiments with this design have rendered conflicting results. While the Marsh Tit *Parus palustris* increased clutch size in response to food provisioning (Nilsson, 1991), the related Blue Tit *Parus caeruleus* did not (Nilsson & Svensson, 1993). However, females may respond to increased food availability by improving egg quality instead of its number (Nilsson & Svensson, 1993). Large eggs produce large hatchlings (Bryant, 1978; O'Connor, 1979), and hatchling size may affect its subsequent development (Williams, 1994). Also, by advancing the onset of incubation with respect to the laying of the last egg, parents may induce an earlier hatching

of the first-laid eggs (Nilsson, 1993). An early hatching date has been shown to improve the survival prospects of fledged young (Daan *et al.*, 1988). It is necessary to note that showing that clutch size is affected by food supplementation at laying, does not disprove that birds are adjusting their clutch size to the situation when young are in the nest. The extra food supply at laying could reduce the reproductive costs imposed by nestling feeding and thus affect the optimal clutch size. However, finding no effect of supplementary food at laying, would negate the proximate constraint hypothesis.

If clutch size is not constrained at laying, but adjusted to the number of feedable nestlings, we would expect a decrease in offspring fitness in experimentally enlarged broods with respect to controls (Hegner & Wingfield, 1987; Wiggins, 1990; Török & Toth, 1990; Källander & Smith, 1990). Alternatively, parents would suffer condition losses (Nur, 1984a; Smith *et al.*, 1988), with possible negative repercussions on subsequent survival (Reyer, 1984; Reyer & Westerterp, 1985; Dijkstra *et al.*, 1990; Bryant, 1991). To ascertain if clutch size is optimal with respect to parental fitness, one would have to quantify the fitness consequences of different clutch sizes for both the parents and the nestlings in terms of survival and subsequent reproduction (Gustafsson & Sutherland, 1988; Tinbergen & Daan, 1990). However, showing that nestlings in enlarged broods suffer costs in terms of reduced growth and survival indicates that the trade-off function involving parental survival costs and benefits in terms of nestling production has been altered by the experiment. This, in turn, suggests that clutch size determines this trade-off function.

In the present study in central Spain, we have used field experiments with a well-studied species such as the Blue Tit, to determine which of the two main hypotheses better explains clutch size determination. Although the Blue Tit has received a great deal of attention in this context in Scandinavian and British populations (Nur, 1988; Nilsson & Svensson, 1993; Pettifor, 1993a, 1993b), Mediterranean populations of the Blue Tit differ in several reproductive parameters from more Northern populations (Blondel *et al.*, 1993; Gil-Delgado *et al.*, 1992). Also, it is widely

recognized that experiments in behavioural ecology are too rarely repeated. Whilst exact duplication is scientifically useful to confirm the repeatability of results, the repetition of an experimental study by other researchers can also be valuable because of new insights into experimental methods, different interpretations of the same experimental results, and intriguing inferences about the validity of earlier work (Smith & Montgomerie, 1991). Experiments and observations replicated in different populations are equally important because they may indicate the generality of previous findings (e.g. studies by Tinbergen, 1987; Smith *et al.*, 1987; Lindén, 1988).

In the first experiment, we have used Nilsson's (1991) design by commencing food supplementation at the initiation of laying. We predicted that if clutch size is not constrained by food availability at laying, food-supplemented females would not lay more and/or larger eggs than controls, and would not initiate incubation earlier with respect to cessation of laying (Nilsson & Svensson, 1993). In the second experiment, we have added or removed two chicks at hatching, following Gustafsson & Sutherland (1988) and Pettifor (1993a, 1993b). We predicted that if clutch size is determined by the trade-off between nestling production and parental reproductive costs involved in raising young, nestlings in enlarged broods would be lighter and smaller than in control and reduced broods, and/or parents caring for enlarged broods would become lighter at the end of the nestling period, suggesting possible survival costs due to lower parental condition.

STUDY AREA AND METHODS

The study was conducted in a deciduous forest of Pyrenean oak *Quercus pyrenaica* at 1200 m a.s.l. in the vicinity of La Granja, Segovia province, Central Spain (40° 48' N, 4° 01' W). In 1991, 200 nestboxes were erected in a grid with 50 m between adjacent boxes. Every year, the nestboxes are checked for occupation by blue tits, and the dates of clutch initiation, clutch size and number of fledged young are determined. The two field experiments were carried out during the breeding seasons of 1993 and 1994.

Experiment 1: Food supplementation during laying

In 1993, small feeding trays were placed on the front of boxes occupied by blue tits, and immediately below the entrance hole. Supplementation at some nests was begun on the day when the first egg was found. We assigned nests to the supplemented and control categories randomly, but pairing nests with respect to laying date. In this way, 13 pairs of nests were created. The first day, 10 g of live mealworms (larvae of *Tenebrio molitor*) were placed in the trays. On subsequent days, the remaining mealworms were weighed and new ones were added up to a weight of 10 g. We frequently observed the nest owners consuming the mealworms, while we never observed other birds at the trays. Feeding was discontinued on the day after cessation of laying. Eggs were weighed on the day of laying on an electronic field balance with a precision of 0.01 g. The onset of incubation was taken to be the first day when the female was observed sitting on the eggs, or the first day when the eggs in a nestbox were uncovered and warm. The chicks resulting from experimental and control clutches were banded with standard metal bands at the age of approximately 13 days. Due to losses, the number of nests included in the analysis of reproductive success differs from the original 13 pairs.

Experiment 2: Brood manipulation

In 1994, 52 broods were randomly assigned to one of 3 experimental categories. In 17 broods we removed two nestlings on the day after hatching (reduced broods) and added them to 17 other broods hatched on the same day (enlarged broods). The 18 remaining broods were left as controls. The chicks were transferred in a warm box, and transport time never exceeded 15 min. Two of the enlarged broods were deserted for unknown reasons and have been excluded from all analyses. When the nestlings were 13 days, the parents were captured at the nest with traps while feeding their young. At this age, the nestlings were banded, weighed with a Pesola spring balance to the nearest 0.1 g

TABLE 1

Effects of experimental food supplementation during laying on clutch size, mean egg mass and the number of eggs laid before and after the onset of incubation in the study population of Blue tits. Results of paired *t*-tests are also presented. SD in brackets.

[Efectos de la adición experimental de alimento durante la puesta sobre el tamaño de puesta, el peso medio de los huevos y sobre el número de huevos puestos antes y después del inicio de la incubación en la población de herrerillos estudiada. Se presentan también los tests de la *t* pareados. Desviación típica entre paréntesis.]

	Control [Control]	Supplemented [Alimento suplementario]	<i>t</i> ₁₂	P
Clutch size	10.38 (0.87)	9.69 (1.03)	1.81	0.095
[Tamaño de puesta]				
Egg mass (g)	1.19 (0.09)	1.15 (0.08)	1.22	0.246
[Masa del huevo]				
Eggs laid before onset of incubation	8.85 (1.52)	8.00 (1.15)	2.17	0.050
[Huevos puestos antes del inicio de la incubación]				
Eggs laid after onset	1.54 (1.56)	1.69 (0.95)	0.52	0.613
[Huevos puestos después del inicio de la incubación]				

and measured (wing length to the nearest 0.5 mm). Fledging success was estimated as the percentage of hatchlings that fledged.

Means of egg and chick measurements per clutch/brood have been used in statistical analyses. Means are presented with SD.

RESULTS

Experiment 1: Food supplementation during laying

Supplemented pairs consumed on average 41.6 ± 15.9 g during the laying period (range = 10.5–66 g). There was no significant difference in the number of eggs laid by supplemented and control females (Table 1). Egg weight was also unaffected by experimental treatment (Table 1). However, there was a significant difference between treatments in the number of eggs laid at the onset of incubation, with experimental females beginning incubation with one egg less than control females (Table 1). There was no difference in the number of eggs laid after the onset of incubation (Table 1). The number of fledged young in the two groups of nests did not differ significantly (paired *t*-test: $t_7 = 0.11$, $P = 0.91$).

Experiment 2: Brood manipulation

As expected from the experimental design, there were no significant differences between treatments with respect to laying date ($F_{2,48} = 0.40$, $P = 0.95$), clutch size ($F_{2,48} = 0.78$, $P = 0.46$) and hatching success ($F_{2,48} = 1.04$, $P = 0.34$). The number of chicks fledged differed significantly between treatments (Table 2), with the enlarged broods producing significantly more fledglings than the control broods, which in turn produced more fledglings than the reduced broods (Table 2). Enlarged broods suffered the highest mortality, although the fledging success did not differ significantly between treatments (Table 2). The mean fledgling mass was negatively related with the number of previously starved chicks ($F_{2,44} = 5.70$, $P = 0.006$), with broods having lost two chicks having significantly smaller masses than those having lost none or one chick (Tukey test, Fig. 1). There were significant differences in fledgling mass (Table 2), with fledglings from enlarged broods being significantly lighter than those from reduced and control broods (Tukey's tests, $P < 0.05$). The mean fledgling weight decreased significantly with the number of chicks fledging (Figure 2). There were no significant differences in the weights of parents (Table 2).

TABLE 2

Comparison between experimental treatments of different measures of reproductive success and female and male mass at a chick age of 13 days. Values under the same continuous line are not significantly different (Tukey's tests, $P < 0.05$; n : sample size). SD in brackets.

[Comparación entre tratamientos experimentales de diferentes medidas de éxito reproductivo y de peso de hembras y machos cuando los pollos tienen 13 días. Los valores bajo la misma línea continua no son significativamente diferentes (tests de Tukey, $P < 0.05$); n : tamaño de muestra. Desviación típica entre paréntesis.]

	Reduced [Reducida]	Control [Control]	Enlarged [Aumentada]	F	P
No. of fledglings	6.3 (1.5)	7.4 (1.5)	9.1 (1.2)	14.82	0.000
<i>n</i>	16	18	15		
[Núm. de pollos]					
No. of starved chicks	0.3 (0.6)	0.2 (0.4)	0.9 (0.8)	6.48	0.003
<i>n</i>	17	18	15		
[Núm. de pollos muertos por hambre]					
Fledgling success (%)	94.9 (9.8)	96.8 (6.2)	92.9 (7.4)	1.47	0.238
<i>n</i>	16	18	15		
[Supervivencia de pollos]					
Fledgling mass (g)	10.6 (0.7)	10.6 (0.7)	9.3 (1.3)	8.16	0.000
<i>n</i>	16	18	14		
[Peso de pollos]					
Fledgling wing length (mm)	31.9 (4.7)	34.9 (4.2)	31.2 (6.1)	2.14	0.128
<i>n</i>	16	18	16		
[Longitud de ala de pollos]					
Female mass (g)	10.4 (0.4)	10.4 (0.5)	10.1 (0.5)	2.05	0.137
<i>n</i>	16	18	13		
[Peso de la hembra]					
Male mass (g)	10.7 (0.5)	10.7 (0.4)	10.8 (0.5)	0.22	0.800
<i>n</i>	16	18	11		
[Peso del macho]					

DISCUSSION

The results of the first experiment confirm the absence of any effect of food supplementation during laying on clutch size and egg size found in a Scandinavian population of Blue Tit (Nilsson & Svensson, 1993). These authors argued that the increase in food availability might not have been enough to affect clutch size due to the experimental set-up, as the extra food was apparently available to other birds (Nilsson & Svensson, 1993). This was highly unlikely in our case as food was offered on the nestbox itself, and not < 10 m away as in the Swedish study. Nilsson and Svensson (1993) also mentioned as an explanation for the lack of effects, that the experi-

ment was performed in a year of high breeding density of different tit species in their study area. The high breeding density may have been a more important cue of present and future food availability than the supplement itself. In our study area, the density of blue tits is 1.4 pairs/ha, which is the breeding density in optimal habitats (1.2-1.5 pairs/ha, Dhondt *et al.* 1982). An alternative explanation is that food resources at laying in this population have a limited predictive value for the availability of food for dependent nestlings. Females may follow other cues than food availability while laying, like some index of future caterpillar availability or temperature (Perrins, 1970; Perrins & McCleery, 1989; Haywood, 1993).

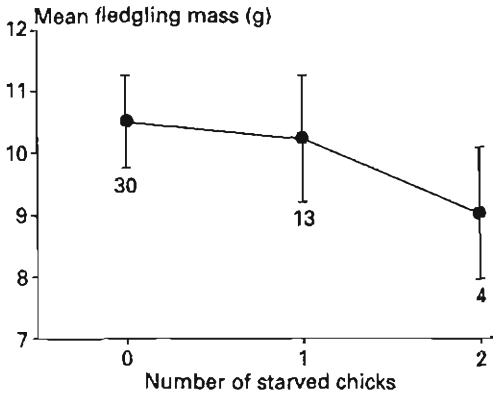


FIG. 1.—Mean fledgling mass in relation to the number of previously starved chicks. Means are presented with SD.

[Peso medio de pollos volantones en relación con el número de pollos muertos de hambre previamente. Se representa la media con la DE.]

In the Swedish study, supplemented females started incubating earlier in the laying sequence, thus advancing the initiation of hatching (Nilsson & Svensson, 1993). This advancement would promote the survival (Perrins, 1979; Newton & Marquiss, 1984; Daan *et al.*, 1988) and establishment prospects of some young of the brood (Nilsson, 1989, 1990; Nilsson & Smith, 1988), with the concomitant costs of a longer hatching spread (Nilsson, 1993). In our study, this advancement in the onset of incubation was also detected. Thus, supplemented females in our study population used the extra food resources available to advance one day the hatching date of part of their brood. Incubating while producing eggs may be energetically costly (Mertens, 1980), but would be promoted in conditions of high food availability (Nilsson, 1993). Given that there was no difference between treatments in the number of eggs laid after the onset of incubation, we should not expect a greater hatching spread in the experimental broods. The results of the food supplementation experiment indicate that clutch size is not directly constrained by food availability for laying females.

Our second experiment shows that pairs caring for experimentally enlarged broods are not able to care for them as well as con-

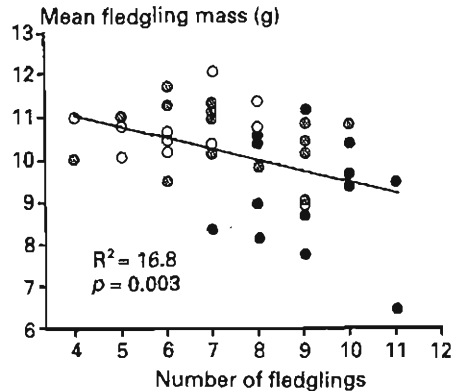


FIG. 2.—Mean fledgling mass as a function of the number of fledglings. The coefficient of determination and the significance of the regression line are presented. Open dots represent reduced broods, hatched dots represent control broods and filled dots are enlarged broods.

[Peso medio de pollos volantones en función del número de volantones en el nido. Se presenta el coeficiente de determinación y la significación de la regresión. Los símbolos blancos representan nidadas reducidas, los símbolos rayados nidadas control y los símbolos negros nidadas aumentadas.]

trol pairs. Food limitation was indicated by starvation and reduced fledgling masses in enlarged broods, by the reduction in fledgling mass with the number of fledglings and by the association of previous chick mortality with reduced fledgling mass. This result is in accordance with the results of other brood manipulation experiments showing that, on average, individual females lay a clutch that corresponds to the highest number of offspring they can recruit (Högstedt, 1980; Gustafsson & Sutherland, 1988; Pettifor *et al.*, 1988; Alatalo & Lundberg, 1989; Daan *et al.*, 1990; Tinbergen & Daan, 1990; Robinson & Rotenberry, 1991; Pettifor, 1993a). We assume that fledgling mass has a significant effect on recruitment probability, as shown in other species (Nur, 1984b; Tinbergen & Boerlijst, 1990; Magrath, 1991; Lundberg & Alatalo, 1992). Like in other brood manipulation experiments, parents caring for enlarged broods do not suffer condition losses (Lindén & Möller, 1989; Dijkstra *et al.*, 1990; Lessells, 1991). Also, as frequently reported in this type of studies, it is the chicks in enlarged

broods that fare worse than those in control broods (Hegner & Wingfield, 1987; Wiggins, 1990; Török & Toth, 1990; Källander & Smith, 1990).

To conclude, the two experiments indicate that clutch size determination in our population of Blue Tit is not constrained by food availability at laying, and that parents are not able to care properly for broods larger than the clutch size laid.

ACKNOWLEDGEMENTS.—The study was funded by project PB91-0084-C03-01 (DGICYT, MEC), and is a contribution from the field station «El Ventorrillo», Museo Nacional de Ciencias Naturales. We are grateful to R. Johnston for initiating the Blue Tit study in 1991, to J. J. Sanz for helping to put up the nestboxes, to B. Torres for making wirecages to protect nestboxes from woodpeckers, to G. Blanco for helping with field-work and to L. García Sancho for lending us his electronic balance. J. A. Nilsson and J. M. Tinbergen offered valuable comments. Nestboxes were donated by ICONA-Madrid and ICONA-Valladolid. The director of ICONA-Valsain, J. Donés, kindly allowed us to work in the Valsain forest.

BIBLIOGRAPHY

- ALATALO, R. V. & LUNDBERGER, A. 1989. Clutch-size of the Pied Flycatcher, *Ficedula hypoleuca*: an experiment. *Ornis Fennica*, 66: 15-23.
- BLONDEL, J., DIAS, P. C., MAISTRE, M. & PERRET, P. 1993. Habitat heterogeneity and life-history variation of Mediterranean Blue tits (*Parus caeruleus*). *Auk*, 110: 511-520.
- BRYANT, D. M. 1978. Establishment of weight hierarchies in the broods of House Martins *Delichon urbica*. *Ibis*, 120: 16-26.
- 1991. Constraints on energy expenditure by birds. *Acta XX Congressus Internationalis Ornithologici*: 1989-2001.
- CHARNOV, E. L., & KREBS, J. R. 1974. On clutch-size and fitness. *Ibis*, 116: 217-219.
- DAAN, S., DIJSTRA, C., DRENT, R. H., & MEIJER, T. 1988. Food supply and the annual timing of avian reproduction. *Acta XIX Congressus Internationalis Ornithologici*: 392-407.
- , — & TINBERGEN, J. M. 1990. Family planning in the Kestrel (*Falco tinnunculus*): the ultimate control of covariation of laying date and clutch size. *Behaviour*, 114: 83-116.
- DHONDT, A. A., SCHILLEMANS, J. & DE LAET, J. 1982. Blue Tit territories at different density levels. *Ardea*, 70: 185-188.
- DIJSTRA, C., BULT, A., BIJLSMA, S., DAAN, S., MEIJER, T., & ZIJLSTRA, M. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): effects on offspring and parent survival. *Journal of Animal Ecology*, 59: 269-285.
- FOGDEN, M. P. L. & FOGDEN, P. M. 1979. The role of fat and protein reserves in the annual cycle of the Grey-backed Camaroptera in Uganda (Aves: Sylviidae). *Journal of Zoology (Lond.)*, 189: 233-258.
- GIL-DELGADO, J. A., LÓPEZ, G. & BARBA, E. 1992. Breeding ecology of the Blue Tit *Parus caeruleus* in eastern Spain: a comparison with other localities with special reference to Corsica. *Ornis Scandinavica*, 23: 444-450.
- GUSTAFSSON, L. & SUTHERLAND, W. J. 1988. The costs of reproduction in the Collared flycatcher *Ficedula albicollis*. *Nature*, 335: 813-817.
- HAYWOOD, S. 1993. Role of extrinsic factors in the control of clutch-size in the Blue Tit *Parus caeruleus*. *Ibis*, 135: 79-84.
- HEGNER, R. E. & WINGFIELD, J. C. 1987. Effects of brood size manipulations on parental investment, breeding success, and reproductive endocrinology of house sparrows. *Auk*, 104: 470-480.
- HÖGSTEDT, G. 1980. Evolution of clutch-size in birds: adaptive variation in relation to territory quality. *Science*, 210: 1148-1150.
- JONES, P. J. & WARD, P. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the Red-billed Quelea *Quelea quelea*. *Ibis*, 118: 547-574.
- KÄLLANDER, H. & SMITH, H. G. 1990. Manipulation of the brood size of Pied Flycatchers. In: J. Blondel, A. Gosler, J. D. Lebreton & R. McCleery (Eds.): *Population Biology of Passerine Birds*, pp. 257-268. Springer Verlag, Berlin.
- KLOMP, H. 1970. The determination of clutch-size in birds. A review. *Ardea*, 58: 1-124.
- LACK, D. 1947. The significance of clutch size in birds. Parts I and II. *Ibis*, 89: 302-352.
- 1954. *The natural regulation of animal numbers*. Clarendon, Oxford.
- LESSELLS, C. M. 1991. The evolution of life histories. In: J. R. Krebs & N. B. Davies (Eds.): *Behavioural Ecology*, pp. 32-68. Blackwell Sci Publ. Oxford.
- LIMA, S. L. 1987. Clutch size in birds: a predation perspective. *Ecology*, 68: 1062-1070.
- LINDÉN, M. 1988. Reproductive trade-off between first and second clutches in the great tit *Parus major*: an experimental study. *Oikos*, 51: 285-290.
- & MÖLLER, A. P. 1989. Cost of reproduction and covariation of life history traits in birds. *Trends in Ecology and Evolution*, 4: 367-371.
- LUNDBERGER, A. & ALATALO, R. V. 1992. *The Pied Flycatcher*. Poyser, London.

- MAGRATH, R. D. 1991. Nestling weight and juvenile survival in the Blackbird, *Turdus merula*. *Journal of Animal Ecology*, 60: 335-351.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review in Ecology and Systematics*, 18: 453-487.
- 1992. Interaction of nest predation and food limitation in reproductive strategies. In, D. M. Power (Ed.): *Current Ornithology*, Vol. 9, pp. 163-198. Plenum Press. New York.
- MERTENS, J. A. L. 1980. The energy requirements for incubation in great tits and other bird species. *Ardea*, 68: 185-192.
- MURPHY, E. C. & HAUKIOJA, E. 1986. Clutch size in nidicolous birds. In, R. F. Johnston (Ed.): *Current Ornithology*, Vol. 4, pp. 141-180. Plenum Press. New York.
- NEWTON, I. & MARQUISS, M. 1984. Seasonal trends in the breeding performance of Sparrowhawks. *Journal of Animal Ecology*, 53: 809-829.
- NILSSON, J. A. 1989. Causes and consequences of natal dispersal in the Marsh Tit *Parus palustris*. *Journal of Animal Ecology*, 58: 619-636.
- 1990. Establishment success of experimentally delayed juvenile Marsh Tits *Parus palustris*. *Ethology*, 85: 73-79.
- 1991. Clutch size determination in the Marsh Tit *Parus palustris*. *Ecology*, 72: 1757-1762.
- 1993. Energetic constraints on hatching asynchrony. *American Naturalist*, 141: 158-166.
- & SMITH, H. G. 1988. Effects of dispersal date on winter flock establishment and social dominance in Marsh Tits *Parus palustris*. *Journal of Animal Ecology*, 57: 917-928.
- & SVENSSON, E. 1993. Energy constraints and ultimate decision during egg-laying in the Blue Tit. *Ecology*, 74: 244-251.
- NUR, N. 1984a. Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. *Oecologia*, 65: 125-137.
- 1984b. The consequences of brood size for breeding blue tits. II. Nestling weight, offspring survival and optimal brood size. *Journal of Animal Ecology*, 53: 497-517.
- 1988. The consequences of brood-size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity and differential dispersal. *Evolution*, 42: 351-362.
- O'CONNOR, R. J. 1979. Egg weights and brood reduction in the European Swift (*Apus apus*). *Condor*, 81: 133-145.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis*, 112: 242-255.
- 1979. British tits. Collins, London.
- & McCleery, R. H. 1989. Laying dates and clutch-size in the Great Tit. *Wilson Bulletin*, 101: 236-253.
- PETTIFOR, R. A. 1993a. Brood-manipulation experiments. I. The number of offspring surviving per nest in blue tits (*Parus caeruleus*). *Journal of Animal Ecology*, 62: 131-144.
- 1993b. Brood-manipulation experiments. II. A cost of reproduction in blue tits (*Parus caeruleus*)? *Journal of Animal Ecology*, 62: 145-159.
- , PERRINS, C. M. & MCCLEERY, R. H. 1988. Variation in clutch-size in Great Tits: evidence for the individual optimisation hypothesis. *Nature*, 336: 160-162.
- PINOWSKA, B. 1979. The effect of energy and building resources of females on the production of House Sparrows *Passer domesticus* L. populations. *Ekologia Polska*, 27: 363-393.
- REYER, H. U. 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, 32: 1163-1178.
- & WESTERTERP, K. R. 1985. Parental energy expenditure: a proximate cause of helper recruitment in the pied kingfisher (*Ceryle rudis*). *Behavioral Ecology and Sociobiology*, 17: 363-369.
- ROBINSON, K. D. & ROTENBERRY, J. T. 1991. Clutch size and reproductive success of house wrens rearing natural and manipulated broods. *Auk*, 108: 277-284.
- SIMONS, L. S. & MARTIN, T. E. 1990. Food limitation of avian reproduction: an experiment with the Cactus Wren. *Ecology*, 71: 869-876.
- SLAGSVOLD, T. & LIFJELD, J. T. 1988. Ultimate adjustment of clutch size to parental feeding capacity in a passerine bird. *Ecology*, 69: 1918-1922.
- SMITH, H. G. & MONTGOMERIE, R. 1991. sexual selection and the tail ornaments of North American barn swallows. *Behavioral Ecology and Sociobiology*, 28: 195-201.
- , KÄLLANDER, H. & NILSSON, J. A. 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. *Auk*, 104: 700-706.
- , —, FONTELL, K. & LJUNGSTRÖM, M. 1988. Feeding frequency and parental division of labour in the double-brooded great tit *Parus major*. *Behavioral Ecology and Sociobiology*, 22: 447-453.
- TINBERGEN, J. M. 1987. Cost of reproduction in the great tit: intraseasonal costs associated with brood size. *Ardea*, 75: 111-122.
- & BOERLIJST, M. C. 1990. Nestling weight and survival in individual Great tits (*Parus major*). *Journal of Animal Ecology*, 59: 1113-1127.
- & DAAN, S. 1990. Family planning in the Great tit (*Parus major*): optimal clutch size as integration of parent and offspring fitness. *Behaviour*, 114: 161-190.

- TÖRÖK, J. & TOTH, L. 1990. Costs and benefits of reproduction of the Collared flycatcher, *Ficedula albicollis*. In, J. Blondel, A. Gosler, J. D. Lebreton & R. McCleery (Eds.): *Population Biology of Passerine Birds*, pp. 307-319. Springer Verlag. Berlin.
- WIGGINS, D. A. 1990. Clutch size, offspring quality, and female survival in tree swallows - an experiment. *Condor*, 92: 534-537.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist*, 100: 687-690.
- WILLIAMS, T.D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews*, 68: 35-59.

[Recibido: 22.3.95]
[Aceptado: 14.8.95]