Date of laying, clutch size and second brood percentage in Great Tit *Parus major* and Blue Tit *Parus caeruleus* in the Natural Reserve "Monte Rufeno" (VT, Central Italy)

MASSIMO BELLAVITA* e ALBERTO SORACE**

* Riserva naturale "Monte Rufeno"

c/o Comune di Acquapendente, 01021 Acquapendente (VT) ** Stazione Romana per l'Osservazione e la Protezione degli Uccelli (S.R.O.P.U.) c/o Oasi Naturale WWF ''Bosco di Palo'', Via di Palo Laziale, 2 00055 Ladispoli (Roma).

Abstract — The breeding biology of Great Tit and Blue Tit has been studied in the natural reserve "Monte Rufeno". For both species, compared to other European areas, an earlier laying date, a smaller clutch size and a higher percentage of second clutches were observed. These results are discussed.

Introduction

Pioneers studies on the breeding biology of Blue Tit *Parus caeruleus* and Great Tit *Parus major* (e.g., Lack 1947, 1948, 1955, 1958, 1964, Gibb 1950, Kluyver 1951, 1963 Perrins 1965) aimed at understanding the factors affecting breeding parameters such as the date of laying, clutch size, laying a second clutch; since then many other investigations have been carried out.

The length of day produces basic physiological changes in birds during their breeding season (Immelmann 1971, Perrins 1979) but the laying date should vary regularly if affected by day-length only. Many authors have noted that high temperatures in spring and late winter induce early laying dates (e.g. Kluyver 1951, Slagvold 1976, Michelland 1980, Schmidt 1984). This is probabily due to the positive correlation between temperature and speed of trees leafing that, in turn, causes the appearance of caterpillars (Lack 1954, Perrins 1965, Leclerg 1977). The onset of Great and Blue Tit breeding season is also related to the latitude (Slagsvlod 1975, Perrins 1979), genetic traits of breeders (van Noordwijk et al. 1980, 1981, Blondel et al. 1990), enviroment (Dhondt et al. 1984, Blondel 1985, Blondel et al. 1987), female age (Perrins 1965), kind of nest box (Dhondt and Eyckerman 1979). Furthermore the Blue Tit's laying date is earlier than that of the Great Tit (Winkel 1975, Dunn 1976).

Lack (1954) suggested that the clutch size

corresponds to the largest number of offspring that parent birds can successfully nourish; after this and other works by the English author (1947, 1948), the evolutionary significance of this reproductive parameter has drawn many researchers' attention (for review, see Ricklefs 1983, Murphy and Haukioja 1986). Clutch size is influenced by inherited factors (Perrins and Jones 1974, van Noordwijk et al. 1981), the date of laying (e.g. Kluyver 1951, Lack 1955, Perrins 1965, Balat 1970), the altitude (Pikula 1975, Slagsvold 1982, Zang 1982), breeders density (e.g. Kluyver 1951, Perrins 1965, Lack 1966), the environment (e.g. Perrins 1965, Lack 1966, van Balen 1973), age of the female (Perrins 1965), nest box size (see Cianchi and Sorace in press), the latitude (Lack 1966, Ojanen et al. 1978, Perrins 1979). The decrease in clutch size as a function of the latitude (toward the south) may be related to the shorter spring day in the south allowing the parents less time to feed their young (Lack 1966). On the other hand, Ashmole (in Ricklefs 1980) stated that clutch size should increase in direct proportion to the seasonal availability of food supplies. Finally the clutch size latitudinal decrease toward the south could be correlated with the increasing risk of brood hyperthermia in the south (van Balen and Cavè 1970), a hypothesis that finds little favour. Some authors (Neub 1977, Slagvold 1982, Blondel et al. 1987) deny the latitudinal decline in clutch size and add that the main factor for the geographical

variation of clutch size seems to be the quality of the habitat.

Kluyver (1951) noted that the main factors promoting the laying of a second clutch are the poor success obtained with the first clutch, a low breeding density and an early date of laying, in fact there is a relatively fixed date after which no second broods are started (Kluyver 1963, Tinbergen and van Balen 1988).

Moreover there are marked differences between habitats in the percentage of second clutches: birds in pine woods (Berndt 1938, Kluyver 1951, Lack 1966, Winkel 1975) and in mediterranean scrub (Cramm 1982, Isenmann 1983 b) have a higher percentage of second clutches than those living in deciduos wood. Some authors (van Balen 1973, Perrins 1979, Isenmann 1983 b) stated that a large part of these observations as well as others, e.g. more common occurence of a second clutch in the European Continent compared to England, are related to food supply that is more abundant in the Continent and spread over a longer period in pine wood and in mediterranean scrub. On the other hand, Den Boer (1979) found that extra food does not increase the likelihood of starting a second brood, but reduces the interval between the first and the second clutch. In other studies a negative relationship was observed between both the probability of laying a second clutch and the 'clutch interval' and the number of fledging in the first brood (Tinbergen and Albers 1984, Tinbergen 1987, Smith et al. 1987).

The studies quoted above were mostly carried out in northern and central Europe localities. Therefore it is interesting to observe the influence of latitudinal conditions of a central Italy area on the laying date, the clutch size and the laying of a second clutch.

Study area and methods

This investigation was carried out in the main enviroments of "Monte Rufeno" Natural Reserve (Acquapendente, VT): a) 25-30 year-old deciduous wood (prevailing species *Quercus cerris*); b) pine wood with *Pinus halepensis* (20-25 year-old) and *P.pinaster* e *P.nigra* (15 year old); c) mediterranean scrub with *Quercus ilex, Phyllirea latifolia, Viburnum tinus, Arbutus unedo* ecc. (see Calvario *et al.* 1989 in Bellavita *et al.* 1990). Average altitude of study area is 490 m.

In autumn 1988, thirty nest-boxes were placed in the deciduos wood, twenty in the pine wood and twenty in the mediterranean scrub. In autumn 1989 ten other boxes were placed in the deciduos wood. The nest boxes (14 cm x 14 cm x 22 cm, entrance hole

3.7 cm) were placed at c. 3.5 m above the ground, spaced about 100 m apart.

During the 1989 and 1990 breeding seasons, the boxes were checked weekly. The date of laying was calculated assuming that females lay one egg for day (Kluijver 1951, Lack 1955). For every clutch the following parameters were considered: clutch size, hatching success (chicks number/eggs number x 100); fledging success (fledged young/eggs hatched x 100); breeding success (fledged young/eggs number x 100); fledged young. Mean values of the last parameter were obtained from the clutches with at least one hatched egg.

Clutches after May 12 for the Great Tit and after May 14 for the Blue Tit were considered as second clutches on these dates, for the first time in the season, clutches that one may regard as second (Perrins 1979, Smith *et al.* 1987) were laid: in fact they were laid in the same box where young had already fledged successfully. Second clutch percentage is the ratio between number of females that lay a second clutch and number of females that effect a first clutch (e.g. Kluijver 1951, Perrins 1979).

Results

Blue Tit Parus caeruleus has a higher nest-box occupation percentage in the deciduous wood than Great Tit Parus major, that conversely prevails in the other two environments considered. Comparative data on Blue Tit occupation percentages show a statistical significance (I Year: deciduos wood-pine wood-mediterranean scrub $\chi^2 = 9.5$ p<0.01; deciduos wood-mediterranean scrub $\chi^2 = 8.7$ p<0.01; II Year: deciduos wood-pine woodmediterranean scrub $\chi^2 = 12.3$ p<0.01; deciduos wood-pine wood $\chi^2 = 6.7$ p<0.01; deciduos woodmediterranean scrub $\chi^2 = 8.8 \text{ p} < 0.01 \text{ (Tab. 1)}.$ Great Tit laying date in deciduos wood is delayed compared to pine wood (Mann-Whitney U-test, $n_1 = 11$, $n_2 = 14$, U = 38.5 p<0.05) and to the Blue Tit's laying date in deciduos wood (Mann-Whitney U-test, $n_1 = 14$, $n_2 = 35$, z = 2.6 p<0.02) (Tab. 2). Great Tit laying date, considering the data relating to all three enviroments, is in advance in the first year studied (april 14.5) with respect to the second (april 15.3) (Mann-Whitney U-test $n_1 = 13$, $n_2 = 17$, U = 98 N.S.); on the contrary, Blue Tit's laying dates are respectively april 11.4 and april 10.7 (Mann-Whitney U-test, $n_1 = 24$, $n_2 = 26$, z = 0.32, N.S.). Great Tit second clutch percentages are higher than

in Blue Tit (Tab. 3), but the differences were not statistically significant (e.g. three environments altogether, $\chi^2 = 2.8$, N.S.). Maximum occurrence of second clutches is observed for both species in the

·	occupation percentage						
	Deciduous wood	Pine wood	Mediterranean scrub	Total			
l year:							
Great Tit	23.3	35.0	30.0	28.6			
Blue Tit	56.7	30.0	15.0	37.1			
Boxes number	30	20	20	70			

37.5

55.0

40

Table 1 - Nest-boxes occupation percentages of the two studied species.

Table 2 - Average laying date (days number since 1 april) of the two studied species. In parentheses number of clutches.

45.0

20.0

20

30.0

15.0

20

37.5

35.0

80

		date of	laying (1 = apr	ril 1°)			
	Deciduo x	ous wood S.D.	Pine x	wood S.D.	Medite <i>x</i>	r. scrub S.D.	To x	tal S.D.
Great Tit (n)		11.1 4)	9.2	8.3 1)	13.4	1.5 5)		10.4 0)
Blue Tit (n)		8.7 (5)	13.9 (1	10.5 0)		3.9 5)	11.6 (5	8.9 0)

Table 3 - Second clutch percentage of two studied species and number of first clutches.

II clutch percentage							
	Deciduous wood	Pine wood	Mediterranean scrub	Total			
Great Tit	66.7	50.0	25.0	50.0			
I clutch (n)	12	10	8	30			
Blue Tit	37.5	10.0	_	28.3			
I clutch (n)	32	10		42			

deciduous wood, the minimum in the mediterranean scrub (Tab. 3), however the differences in second clutch percentage for a single species in different enviroments were not significant (e.g. Great Tit, three enviroments $\chi^2 = 3.3$, N.S.; Blue Tit, deciduous woodpine wood $\chi^2 = 1.6$, N.S.). Great Tit second clutch percentage, considering all the data for all three enviroments, turned out to be in the first year 63.6% and in the second year 42.1% ($\chi^2 = 0.6$ N.S.); the data for Blue Tit were 33.3% and 23.1% respectively ($\chi^2 = 0.3$ N.S.).

II year: Great Tit

Blue Tit

Boxes number

Clutch size decreases from the first to the second clutch for both the species in all the environments (Tab. 4). Differences in clutch size between Great and Blue Tit were not statistically significant (three enviroments altogether, Mann-Whitney U-test, I clutch: $n_1 = 46$, $n_2 = 26$, z = 0.42, N.S; II clutch: $n_1 = 18$, $n_2 = 15$, U = 120.5, N.S).

Breeding success is better in the second than in the first clutch (Tab. 5): this was related to the hatching failure of the whole clutch in the first part of the breeding season, probably due to bad weather; predation events or nest desertion due to other species invading occupied nests were not observed (Tab. 5).

In the area being considered, 46.2% of Great Tit and 69.2% of Blue Tit lay a second clutch in a previously used nest for a successfull first brood. The main results quoted in the work as concerns the laying date, second clutch percentage, clutch size and

			clu	itch size					
	Deciduous wood		Pine wood		Mediter. scrub		Total		
	x	S.D.	ñ	S.D.	x	S.D.	x	S.D.	
Great Tit:									
I clutch	7.8	1.2	7.8	1.4	8.3	0.5	8.0	1.2	
(n)	(12)		(10)		(4)		(26)		
H clutch	6.5	2.0	7.0	1.8	6.5	0.5	6.7	1.8	
(n)	(10)		(6)		(2)		(18)		
Blue Tit:									
I clutch	8.2	1.3	8.2	1.3	8.3	0.9	8.2	1.3	
(n)	(32)		(10)		(4)		(46)		
II clutch	6.6	1.0	6.0	0.0			6.5	1.0	
(n)	()	(14)		(1)		—		(15)	

Table 4 - Average clutch-size of Great Tit and Blue Tit. In parentheses number of clutches.

Table 5 - Average values of breeding success parameters of the two studied species. In parentheses number of clutches.

	C	Great Tit		
	fledged young	hatching success	fledging success	breeding success
deciduous wood:				
I clutch	6.9 ± 1.4	72.8	95.6	70.1
(n)	(10)	(12)	(10)	(12)
II clutch	5.4 ± 1.8	93.2	90.6	84.9
(n)	(10)	(10)	(10)	(10)
pine wood:				
I clutch	7.5 ± 1.6	56.1	95.6	53.6
(n)	(6)	(10)	(6)	(10)
11 clutch	5.8 ± 2.4	87.5	92.5	80.6
(n)	(6)	(6)	(6)	(6)
mediter. scrub:				
I clutch	4.7 ± 2.2	63.0	54.1	43.5
(n)	(6)	(6)	(6)	(6)
II clutch	3.5 ± 2.5	57.1	100.0	57.1
(n)	(2)	(2)	(2)	(2)
	J	Blue Tit		
	fledged	hatching	fledging	breeding
	young	success	success	success
deciduous wood:				
I clutch	7.1 ± 1.8	84.9	96.6	82.0
(n)	(30)	(32)	(30)	(32)
II clutch	5.9 ± 1.4	95.5	93.1	88.9
(n)	(14)	(14)	(14)	(14)
pine wood:				
I clutch	7.6 ± 1.0	85.6	98.8	84.7
(n)	(10)	(10)	(10)	(10)
II covata	6.0 ± 0.0	100.0	100.0	100.0
(n)	(1)	(1)	(1)	(1)
mediter. scrub:				
I covata	7.0 ± 0.0	63.0	93.7	59.3
(n)	(3)	(4)	(3)	(3)

breeding success were also observed by considering only the pairs of data formed by a first and a second clutch laid in the same nest, with the exception of Blue Tit breeding success, wich, in this case, was lightly higher in first clutch.

Discussion

Great and Blue Tit date of laying in "Monte Rufeno" was earlier than observed in other European areas, also considering only studies in deciduos wood (see Sorace 1985). This result was expected because of the colder temperatures and delayed spring season at higher latitudes. On the other hand, there are some observations in southern areas (Kiziroglu 1982, Blondel 1985, Potti et al. 1988) that seem to conflict with this statement; in fact, Great and Blue Tit laying dates in these studies are very delayed. Island effect in Corsica (Blondel et al. 1980, Blondel 1985) and cold weather on the Ayllón massif (1300-1400 m) in Spain (Potti et al. 1988) and the Anatoly plateau in Turkey (Kiziroglu 1982) have been probably decisive for these results. Moreover, the relationship latitude-laying date may be complicated by numerous factors related with the onset of the breeding.

In spite of an earlier date of laying, that generally yields a larger clutch size, the average clutch size in "Monte Rufeno" is lower compared to other European regions located at higher latitudes, for both Great Tit (see Ojanen et al. 1978, Cramm 1982, Sorace 1985) and Blue Tit (see Cramm 1982, Fraticelli et al. in Sorace 1985, Isenmann 1987). This statement seems true also considering the studies performed in deciduos wood only (see Sorace 1985) for Great Tit and Cramm 1982 for Blue Tit). Furthermore, clutch size for both species was higher in comparison with places located at lower latitude (Isenmann et al. 1982, Sorace 1985, Potti et al. 1988, Ruvolo et al. in press). These results could be related to the clutch size latitudinal gradient (Lack 1966); on the other hand, it is difficult to prove this gradient since many factors influence clutch size (see introduction). Careful analyses of geographical variations in Blue Tit (Isenmann 1987) and Great Tit (Orell and Ojanen 1983) clutch size, however, do not emphasize the latitudinal decline. The sharp drop in tits' clutch size toward the south of Europe could be related to the fact that the mediterranean area is the southern fringe of their breeding range (Isenmann 1987), in agreement with Järvinen (1986) who described an analogue clutch size drop for some passerines at the northern fringe of their breeding range.

Second clutch percentages for Great and Blue Tit

in "Monte Rufeno" Natural Reserve were high compared to the results of other European studies (see Perrins 1979, Sorace 1985). These results could be related, in agreement with Kluijver (1963), to the earlier laying date (see above), to the scarce density of Tits in the area (which is smaller than in other nearby areas, Bellavita et al. 1990), and to the poor reproductive success in first clutch. On the other hand, yearly and enviromental variations in second clutch percentage and date of laying do not show evident relations, in agreement with den Boer (in Tinbergen and van Balen 1988). Moreover the highest second brood percentage in Tits is observed in deciduos wood in spite of the fact that their density in Monte Rufeno mediterranean scrub was seen to be lower, with a very high significance, than in other two environments considered (Bellavita et al. 1990) and in disagreement with Kluijver (1951) Dhondt (1971) and van Balen (1973) since the availability of caterpillars in deciduous wood displays a high peak and then declines (Perrins 1965, Leclerg 1977, Sorace 1985). Finally, scarce reproductive success in the first clutch is not related to chicks fledging failure, in disagreement with Isenmann (1982), and high second brood percentage was observed in areas with greater reproductive success in the first clutch (Fraticelli *et al.* in press, Sorace 1985, De Laet and Dhondt 1989, see also results for Blue Tit). Therefore a high second clutch percentage in mediterranean enviroments might possibly be related to a low first clutch size; it has generally been observed that the Blue Tit does not usually lay a second clutch but presents, in sympatry with the Great Tit, a greater clutch size than the other species (Kluyver 1963, Perrins 1979, Isenmann 1983 b, De Laet and Dhondt 1989): this has not been observed in this study.

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Riassunto — Nelle stagioni riproduttive 1989 e 1990 è stata studiata la biologia riproduttiva della Cinciallegra e della Cinciarella in tre ambienti della Riserva Naturale di Monte Rufeno (Acquapendente, VT). La Cinciarella ha occupato le cassette nido del bosco misto in misura maggiore rispetto alla Cinciallegra, mentre in pineta e in macchia mediterranea predomina quest'ultima specie. La data media di deposizione per entrambe le specie è anticipata in confronto ad altre località europee più settentrionali. La dimensione media della covata è inferiore per entrambe le specie a quella di altre stazioni europee situate a latitudini più settentrionali. Questo risultato è discusso alla luce delle principali teorie sulla variazione geografica della covata nelle cince. La percentuale di seconda covata è risultata alta sia per la Cinciallegra che per la Cinciarella. In accordo con Kluyver (1963) questo risultato può essere attribuito alla data di deposizione anticipata, al successo riproduttivo più alto in seconda covata e alla densità non elevata delle cince nell'area studiata inferiore a quella di altre stazioni del Lazio. D'altra parte le variazioni annuali e ambientali della data di deposizione non sembrano influenzare le variazioni analoghe della percentuale di seconda covata. Inoltre, in disaccordo con Kluyver (1963) la percentuale di seconda covata per entrambe le specie è risultata più alta nel bosco misto rispetto agli altri due ambienti. Questi risultati e le osservazioni di un'alta percentuale di seconde deposizioni in località dove il successo riproduttivo è stato più alto in prima covata fanno supporre che in ambiente mediterraneo un' alta percentuale di seconde deposizioni sia causata anche dalla dimensione non elevata della prima covata.

References

- Balat F. 1970. Clutch size in the Great Tit, *Parus major*, in Pine Forest of Southern Moravia. *Zool.Listy* 19: 321-331.
- Balen J.H. van 1973. A comparative study of the breeding biology of the Great Tit *Parus major* in different habitats. *Ardea* 61: 1-93.
- Balen J.H. van and Cavé, A.J. 1970. Survival and weight loss of nestling Great Tit, *Parus major*, in relation to brood size and air temperature. *Neth. J.Zool.* 20: 464-474.
- Bellavita M., Leandri E. and Sorace A. 1990. Aspetti della biologia riproduttiva di Cinciallegra Parus major e di Cinciarella Parus caeruleus nella riserva naturale "Monte Rufeno" (VT). Picus 16: 7-15.
- Berndt R. 1938. Ueber die Anzahl der Jahresbruten bei Meisen und ihre Abhängigkeit vorm Lebensraum, mit Angaben über Gelegestärke und Brutzeit. *Deutsche Vogelwelt* 63: 140-151 e 174-181.
- Blondel J. 1985. Breeding strategies of the Blue tit and Coal tit (*Parus*) in mainland and island mediterranean habitats: a comparison. J. Anim. Ecol. 54: 531-556.
- Blondel J., Isenmann P., Michelland D. 1980. Insularité et démographie chez la Mésange bleue Parus caeruleus et la Mésange noire Parus ater en Corse. Ois. Rev. fr. Orn. 50: 299-305.
- Blondel J., Clamens A., Cramm P., Gaubert H., Isenmann P. 1987. Population studies on tits in the mediterranean region. Ardea 75: 21-34.
- Blondel J., Perret P., Maistre M. 1990. On the genetical basis of the laying-date in an island population of blue tits. *J. evol. Biol.* 3: 469-475.
- Cianchi F. and Sorace A. in press. Nidificazione di Cinciallegra *Parus major* in cassette nido di notevoli dimensioni. *Picus*.
- Cramm P. 1982. La reproduction des mésanges dans une chênaie verte du Languedoc. Ois. Rev. fr. Orn. 52: 347-360.
- De Laet J.F. and Dhondt A.A. 1989. Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits *Parus major* and Blue Tits *P. caeruleus. Ibis* 131: 281-289.
- Den Boer-Hazenwinkel J. 1979. De productie van tweede broedsels door koolmezen. Jaarverslag 1979.
- Dhondt A. A. 1971. The regulation of numbers in Belgian populations of Great Tits. In: Den Boer P.J. e Gradwell G.R. (eds.). Dynamics of Populations: Proceedings of the Advanced Study Institute on 'Dynamics of Number in Populations', Oosterbeek, the Netharlands, 7-18 September 1970. pp. 532-547. Wageningen: Pudoc.

- Dhondt A.A. and Eyckerman R. 1979. Temperature and date of laying by Tits *Parus spp. Ibis* 121: 329-331.
- Dhondt A.A., Eyckerman R., Moermans R. and Hublé J. 1984. Habitat and laying date of Great and Blue Tit *Parus major* and *Parus caeruleus*. *Ibis* 126: 388-397.
- Dunn E. K. 1976. Laying dates of four species of tits in Wytham Wood, Oxfordshire. *Brit. Birds* 69: 45-50.
- Gibb J.A. 1950. The breeding biology of Great and Blue Titmice. *Ibis* 92: 507-539.
- Gwinner H., Gwinner E. and Dittami J. 1987. Effects of nestboxes on I.H, testosterone, testicular size, and the reproductive behaviour of male European Starlings in spring. *Behaviour* 103: 68-83.
- Haftorn S. and Reinertsen R.E. 1985. The effect of temperature and clutch size on the energetic cost of incubation in a free living Blue Tit (*Parus caeruleus*). Auk 102: 470-478.
- Immelmann K. 1971. Ecological aspects of periodic reproduction. In: Farner D.S. and King J.R. (eds.). Avian biology. Vol.1. Acad. Press, New York, pp. 342-389.
- Isenmann P. 1983 a. Zur Brutbiologie einer Blaumeisen-Population (*Parus caeruleus*) in Süd-Frankreich. *Die Vogelwelt*, 104: 142-148.
- Insenmann P. 1983 b. A case of higher clutch-size in second broods of Great Tit *Parus major* breeding in a mediterranean evergreen habitat. *Gerfaut* 73: 123-126.
- Isenmann P. 1987. Geographical variation in clutch-size: the example of the Blue Tit (*Parus caeruleus*) in the Mediterranean area. *Vogelwarte* 34: 93-99.
- Isenmann P., Dubray D., Baouab R., Thevenot M. 1982. First results on clutch-size and breeding time of Blue Tit (*Parus caeruleus*) in Morocco. *Vogelwarte* 31: 461-463.
- Järvinen A. 1986. Clutch size of passerines in harsh environments. *Oikos* 46: 365-371.
- Kiziroglu I. 1982. Investigations of the breeding biology of four Parus species near Ankara. J.Ornithol. 123: 409-423.
- Kluijver H.V. 1951. The population ecology of Great Tit (*Parus major*). Ardea 39: 1-135.
- Kluijver H.V. 1963. The determination of reproductive rates in *Paridae*. *Proc. 13 Int.Orn.Cong.*: 706-716.
- Lack D. 1947. The significance of clutch size. Ibis 89: 302-352.
- Lack D. 1948. The significance of clutch size. III. Some interspecific comparisons. *Ibis* 90: 25-45.
- Lack D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford.
- Lack D. 1955. British Tits (*Parus ssp.*) in nesting boxes. Ardea 43: 50-84.
- Lack D. 1958. A quantitative breeding study of British Tits. Ardea 46: 50-84.
- Lack D. 1964. A long-term study of the great tit *Parus major*. J. Anim. Ecol. 33: 159-173.
- Lack D. 1966. Population Studies of Birds. Clarendon Press, Oxford.
- Leclerq B. 1977. Etude phénologique des parametres liés à la reproduction des mésanges en futaie de chenes. *Terre Vie* 31: 599-619.
- Michelland D. 1980. La reproduction des mésanges dans la cédraie du Mont-Ventoux (Vaucluse) en 1976-1979. *Alauda* 113-129.
- Murphy E.C. and Haukioja E. 1986. Clutch size in nidicolous birds. *Current Ornith* 4: 141-180.
- Neub M. 1977. Evolutionsökologische Aspekte zur Brutbiologie von Kohlmeise Parus major und Blaumeise P.caeruleus. Thesis, Univ. Freiburg.
- Noordwijk A.J. van, Balen J.H. van, Scharloo W. 1980. Heritability of ecologically important traits in the Great Tit *Parus major. Ardea* 68: 193-203.

- Noordwijk A.J. van, Balen J.H. van, Scharloo W. 1981. Genetic variation in the timing of reproduction in the Great Tit. *Oecologia* 49: 158-166.
- Ojanen M., Orell M., Väisänen R.A. 1978. Egg and clutch sizes in four passerine species in northern Finland. Ornis Fennica 55: 60-68.
- Orell M. and Ojanen M. 1983. Effect of habitat, date of laying and density on clutch size of the Great Tit (*Parus major*) in northern Finland. *Holarct Ecol.* 6: 413-423.
- Perrins C. 1965. Population fluctuations and clutch-size in the great tit. J. Anim. Ecol. 34: 601-647.
- Perrins C. 1979. British Tits. Collins, London.
- Perrins C. and Jones P.J. 1974. The inheritance of clutchsize in the Great Tits (*Parus major*). Condor 76: 225-229.
- Pikula J. 1975. Gelegegrösse und Brutbeginn bei Parus major und Parus ater im Bergmassiv Belanské Tatry. Zool. Listy 24: 273-284.
- Potti J., Montalvo S., Sanchez-Aguado F.J., Blanco D. 1988. La reproducción del Herrerillo comun (*Parus caeruleus*) en un robledal del centro de España. Ardeola 35: 31-43.
- Ricklefs R.E. 1980. Geographical variation in clutch size among passerine birds. Ashmole hypothesis. *Auk* 97: 38-49.
- Ricklefs, R.E. 1983. Comparative avian demography. Current Ornith 1: 1-32.
- Ruvolo U., Sarrocco S., Sorace A. in press. Dati preliminari sulla biologia riproduttiva della Cinciallegra e della Cinciarella nella Riserva regionale "Lago di Vico". Atti V Conv. ital. Orn., Bracciano 1989.
- Schmidt K.H. 1984. Frühjahrstemperaturen und Legebeginn bei Meisen (Parus). J.Orn. 125: 321-331.
- Slagsvold T. 1975. Breeding time of birds in relation to latitude. Norw. J. Zool. 23: 213-218.

- Slagsvold T. 1976. Annual and geographical variation in the time of breeding of the Great and Pied Flycatcher in relation to environmental phenology and spring temperature. *Ornis Scand.* 7: 127-145.
- Slagsvold T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159-169.
- Smith H.G., Källander H., Nilsson J. 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. Auk 104: 700-706.
- Snow D.W. 1956. The annual mortality of the Blue Tit in different parts of its range. *Brit. Birds* 49: 174-177.
- Sorace A. 1985. La biologia riproduttiva della Cinciallegra e della Cinciarella in un bosco mediterraneo. Tesi di laurea, Univ. "*La Sapienza*", Roma.
- Tinbergen J.M. 1987. Cost of reproduction in Great Tits (*Parus major*): intraseasonal costs associated with brood size. *Ardea* 75: 111-122.
- Tinbergen J.M. and Albers K. 1984. Parental effort and future reproductive output in the Great Tit *Parus major*. Pp. 8-11 in Institutes of the Royal Netherlands Academy of Arts and Sciences, Progress Report 1983.
- Tinbergen J.M. and Balen J.H. van 1988. Food and Multiple Breeding. Proc. Int. Ornithol. Congr. 19: 380-391.
- Winkel W. 1975. Vergleichend-brutbiologischeUntersuschungen an 5 Meisen-Arten in einem Aufforstungsgebiet mit Larix leptolepis. Vogelwelt 96: 41-63 e 104-114.
- Zang H. 1982. Der Einflub der Höhenlage auf Alterszusammensetzung und Brutbiologie bei Kohl- und Blaumeise (*Parus major, P.caeruleus*) im Hartz. J. Orn. 123: 145-154.