Ornis Fennica 75:177–183. 1998

Timing of breeding, clutch size and double-broodedness in Barn Swallows *Hirundo rustica*

Jerzy Bańbura & Piotr Zieliński

Bańbura, J., Department of Ecology and Vertebrate Zoology, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland. E-mail: jbanb@biol.uni.lodz.pl
Zieliński , P., Department of Ecology and Vertebrate Zoology, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland. E-mail: pziel@biol.uni.lodz.pl

Received 30 March 1998, accepted 13 May 1998

In a population of Barn Swallows (*Hirundo rustica*) in central Poland studied in 1994-1997, the mean onset of egg laying ranged from 18 to 30 May and mean clutch sizes were 4.86 ± 1.02 (SD) for first clutches, 4.47 ± 0.75 (SD) for second clutches and 4.26 ± 0.98 (SD) for repeat clutches. Clutch sizes were negatively correlated with laying dates and varied between the brood categories, i.e. first, second and repeat broods, but not between years. The frequencies of single-brooded and double-brooded females differed between years. Yearling or immigrant females started breeding later, produced smaller clutches and tended to be single-brooded more often than older ones. Consequently, multi-broodedness may be considered to be an age-related characteristic in Barn Swallows. The seasonal decline in clutch size may also be, at least in part, explained by a relation to female age. The observation for Barn Swallows that clutch sizes consistently decrease during the course of the breeding season does not fit the hypothesis for multi-brooded bird species. In this hypothesis, clutch sizes initially increase with the date of laying and only after reaching a peak do they decrease.

1. Introduction

It has been commonly believed that birds have to time their reproduction to match the nestling stage of their offspring to the period when food is most abundant (Lack 1950; Perrins 1970; Drent & Daan 1980; Martin 1987; Svensson 1995; Bańbura 1997). The capability of producing two or more broods per breeding season is limited by the time period when enough food is available (Lack 1954; Tinbergen & van Balen 1988; Svensson 1995). As a result, species dependent on food which is available only for a short time are single-brooded, as is the case for Blue and Great Tits (*Parus caeruleus* and *P. major*) which live in deciduous woodlands and feed nestlings mostly with caterpillars (Perrins 1965, 1991; Blondel 1985; Bańbura et al. 1994; Lambrechts et al. 1997). Although aerial insects, almost the exclusive food of Barn Swallows *Hirundo rustica*, undergo phenological changes in species composition within the breeding season, they seem relatively numerous from April to September (Bryant 1975; Karg 1980). Consequently, Barn Swallows can raise two broods in most of their habitats in the European area (Møller 1984). On the other hand, breeding late in the season is likely to increase the danger of brood failure due to both reverse weather spells and unrelated juvenile Swallows invading the nest during bad weather (Zieliński & Bańbura 1995).

The abundance and distribution of food over time constitute the ultimate and proximate factors determining the timing of reproduction, clutch size and other life-history traits of birds (Lack 1950, 1954). The way in which food influences avian life history is still not clear, as shown by the results of experimental studies re-analysed by Svensson (1995). Although for many species, individuals supplied with additional food started breeding earlier than control ones, they usually did not lay more eggs (Svensson 1995 for review). In general, a highly consistent link has been described between the time of breeding and clutch size, a negative correlation between these variables being reported for many bird species (Perrins 1970). Klomp (1970) has suggested that seasonal trends in reproductive success may take different forms in double-brooded species (populations) and single-brooded ones. Crick et al. (1993) have recently put forward specific hypotheses concerning this differentiation and have tested them using comparative data on British birds. They have proposed that females in multi-brooded species undergo selection to commence breeding before the time when the environmental and trophic conditions are most favourable and their optimal clutch size is largest. They predicted that multi-brooded species should first increase and then decrease their clutch size during the course of the breeding season.

The aim of this paper is to provide some descriptive data on the timing of breeding, clutch size and the number of broods in the Barn Swallow. The breeding season of this species is long enough to enable breeding pairs to raise two or even more clutches (Cramp 1988). An attempt is made to find a reason, perhaps not an exclusive one, why not all pairs raise two broods. It is assumed that this may be connected with female age. The relation between clutch size and the timing of Swallow breeding was also analysed to check if it fits the above hypothesis of Crick et al. (1993).

2. Material and methods

The study was carried out at a big farm at Goślub, central Poland (52°05´N; 19°28´E) in 1994–1997. All potentially suitable nesting sites were checked for Swallow nests before the laying of eggs started, all nests were marked and then monitored throughout the breeding season. All active nests were checked at regular intervals to quantify broods, clutch sizes and laying dates. Laying dates were recorded directly or estimated by assuming that females produced one egg a day and that incubation of eggs took fourteen days after laying the final egg.

Adult Swallows were trapped in mist nets at nesting sites and ringed. As almost all females breeding in 1994–1996 were ringed, in 1995–1996 it was possible to distinguish between females that had been ringed earlier and the immigrant females that were caught for the first time. For this study, the former group were classified as at least two-year-old females and the latter group as immigrants, composed most probably of yearling females who had just reached breeding age. Adult Barn Swallows are known to be very faithful to a breeding site, while one-year-old individuals, showing dispersal from their natal sites (Cramp 1988, Turner 1994 for review), are likely to create a group of newcomers at a study site.

As a result of monitoring breeding pairs and their nests, we were able to classify females as single-brooded or double-brooded. The single-brooded females produced one clutch of eggs and some of them produced a replacement clutch in case of a first clutch failure. The double-brooded females produced a true second clutch after raising a first clutch or a repeat first clutch.

Standard statistical methods were used to describe and analyse the data (Sokal & Rohlf 1981). Calculations were conducted using the SPSS for Windows package.

3. Results

At the Goślub study site, Barn Swallows started breeding during the first two weeks of May; the onset of egg laying in the earliest nests of the first brood was recorded on 3 May 1994, 8 May 1995, 7 May 1996 and 10 May 1997. Mean dates of the onset of laying, ranging from 18 May in 1996 to 30 May in 1994, are shown in Figure 1. Laying onset varied slightly between years in the first brood, but was not significantly differentiated in the second brood.

The number of broods initiated by females ranged from 1 to 3, and the number of eggs pro-

duced within a season from 2 to 15. Mean clutch sizes within first, second and repeat broods were relatively stable during the four-year study period (Table 1). The differences in clutch size between broods (i.e. first, second and repeat broods) and years were tested applying ANCOVA, because clutch size is a time correlated variable, negative correlation being consistently observed within breeding seasons (Table 2, Fig. 2). The ANCOVA for clutch size with brood categories (i.e. first, second and repeat broods) and years as factors and the laying date as the covariate showed that clutch sizes differed between the brood categories ($F = 4.428$; $df = 2, 143$; $P = 0.014$) but not between years ($F = 0.076$; $df = 3, 143$; $P = 0.973$)(Table 1). The interaction between years and broods was insignificant ($F = 0.819$; $df = 6, 144$; $P = 0.557$). The Scheffe test showed that first broods had larger clutches than second broods ($P = 0.023$) and repeat broods ($P = 0.031$), whereas no difference was found between second and repeat broods ($P = 0.920$). The frequency of single-brooded and double-brooded females varied between the years (Table 3).

In 1995–1996 it was possible to analyse breeding characteristics in relation to female age/immigration status. The prediction that the younger females which immigrated to the study site should start breeding later during the season and lay smaller clutches than the older resident females, turned out to be true (Table 4). Moreover, while none of the at least 2-year-old resident females were single-brooded, a half of the immigrants were single-brooded (Table 5).

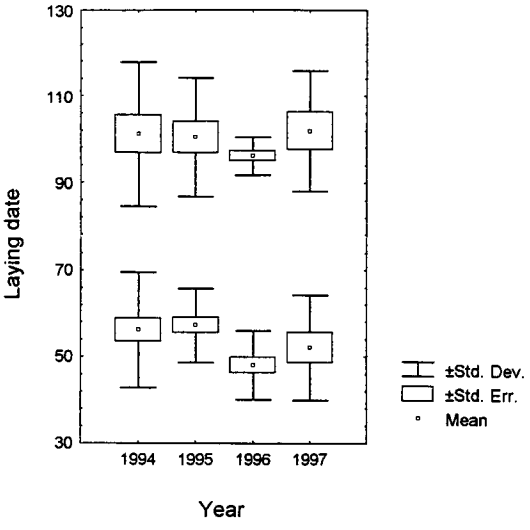

Figure 1. Mean date (SE and SD) of the onset of laying first and second clutches in 1994-1995. First broods (N = 76) slightly differ in laying dates (one-way ANOVA: $F = 2.87$; $df = 3, 71$; $P = 0.043$). Second broods (N = 52) do not differ between years ($F = 0.529$; $df = 3, 48$; $P = 0.665$). Laying dates are given as April dates (1 April = 1).

4. Discussion

The timing of breeding is obviously linked to latitude, so that Barn Swallows start producing first clutches in March in southern Spain, in mid-May in Britain and at the end of May in Scandinavia (Cramp 1988). In the Polish population, as analysed in this paper, the earliest females commence laying in the first week of May but mean laying dates, differing a little from year to year, are usually in the second half of May, which fits the general European pattern and data for two other Polish populations (Nitecki 1964; Kuźniak 1967).

Møller (1984) suggested that Barn Swallows tend to produce more second clutches of fewer eggs with decreasing latitudes; thus the number of eggs produced by females per breeding season is inversely related to latitude. With about 70% of females starting second broods, the studied popu-

Table 1. Mean clutch sizes ± SD (n) in first, second and repeat broods of Barn Swallows in 1994–1997.

Year	First brood	Second brood	Repeat brood
1994	4.80 ± 1.04 (25)	4.21 ± 1.05 (14)	4.46 ± 1.13 (13)
1995	4.74 ± 0.86 (23)	4.57 ± 0.65 (14)	3.71 ± 0.76 (7)
1996	4.83 ± 1.29 (18)	4.79 ± 0.43 (14)	4.33 ± 0.82 (6)
1997	5.17 ± 0.83 (12)	4.30 ± 0.67 (10)	5.00 (1)
Pooled	4.86 ± 1.02 (78)	4.47 ± 0.75 (52)	4.26 ± 0.98 (27)

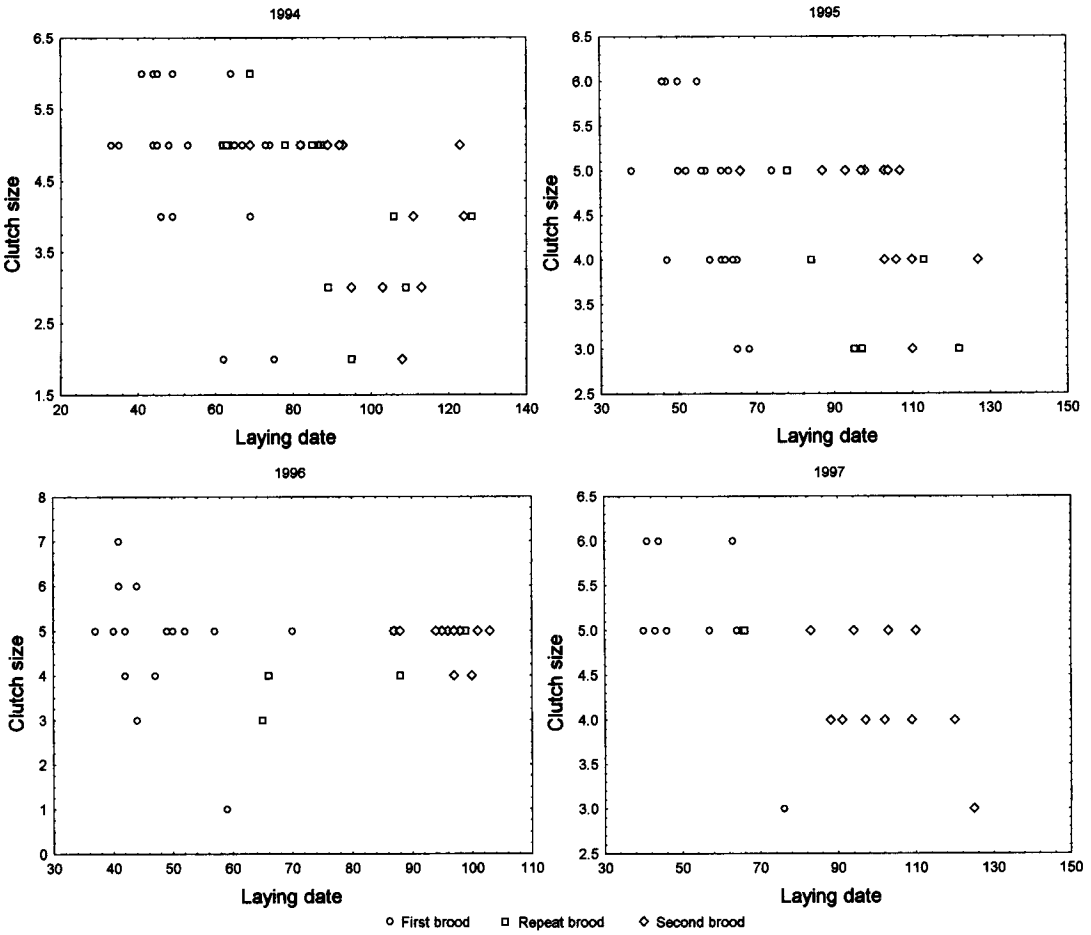

Figure 2. The relationships between clutch size and the onset of egg laying in first, second and repeat broods in 1994–1997. Laying dates are given as April dates (1 April = 1).

lation is close to those described by Nitecki (1964) and Kuźniak (1967). However, the proportion of double-brooded females may vary between breeding seasons. So the data on geographical variation in the frequency of second broods should be considered with caution. This appears to be supported by the data from different parts of the Swallow range reviewed by Møller (1984), where some very close locations are characterised by completely different estimates of the frequency.

Table 2. Searman rank correlations between clutch size and the laying onset date during breeding seasons (broods pooled) 1994-1997.

Year	r	n	p
1994	– 0.50	52	0.000
1995	– 0.46	44	0.002
1996	– 0.20	38	ns
1997	– 0.67	23	0.003

The mean second clutch size 4.47, is close to that predicted from the latitude-related trend postulated by Møller (1984). Kuźniak (1967) reported the exceptionally low value of 4.06 egg per clutch in his study population. The size of first clutches does not seem to form any clear pattern related to geographical co-ordinates (Møller 1984), but there still can exist a more complicated geographical pattern as it is clear that relatively close locations show little differentiation in this variable. In agreement with this, the overall mean first clutch size of the present study 4.86, is similar to the values of Nitecki's (1964) and Kuźniak's (1967) study

populations in Poland (4.79 and 4.83, respectively).

A consistent decline in clutch size during the course of the breeding season was recorded, which also seems to be characteristic for other European Barn Swallow populations (e.g. Lohrl & Gustscher 1973, McGinn & Clark 1978, Kondelka 1985, Loske 1989). A similar negative correlation is clear from Kuźniak's (1967) data, with a recalculated value of r = -0.55 (N = 139; P < 0.0001). Such a declining trend is consistent both within first, second and repeat broods treated separately and over the entire breeding season. The proportion of pairs producing two clutches has been negatively related to the onset date of the pair's first clutch (Møller 1994). It has usually been suggested that a consistent seasonal decline in clutch size is specific for single-brooded birds (Klomp 1970; Crick et al. 1993). An initial increase followed by a decrease in clutch size during the course of the breeding season would be expected in multi-brooded species. This would result from an assumption that multi-brooded birds have to commence first broods as early as possible to be able to produce subsequent clutches and, consequently, they start earlier than would be optimal from the viewpoint of conditions for raising nestlings (Crick et al. 1993). Thus, it could be concluded that Barn Swallows do not fit this model. The case of Barn Swallows supports another version of the model, modified for migrant multi-brooded species, where the time of arrival prevents them from starting breeding as early as do resident multi-brooded species (Crick et al. 1993).

One of the factors contributing to both the frequency of double-broodedness and the seasonal decline in clutch size may be the age of females. Because of the juvenile dispersal from the natal site, it is not possible to determine the exact age of adult Swallows. On the other hand, adult Barn Swallows show high site fidelity and it is mostly yearling birds which are newcomers to established breeding colonies (Cramp 1988, Loske 1989, Turner 1994). Accordingly, it seems reasonable to assume that most immigrants are one-year-old individuals. It was found that all the resident females produced two clutches, while some 50% of newcomers did so (see Table 5). Furthermore, it

Table 3. Per cent of female Swallows initiating first clutches who eventually also raised second clutches (some of them also had repeat clutches) in 1994–1997. The alternative category was composed of females who started only first broods and a repeat brood in case of a first brood failure. G test for interyear differences in the proportion of double-brooded females: G = 13.77; df = 3; p = 0.0032

Year	% double-brooded females	n
1994	66.6	24
1995	65.0	20
1996	80.0	20
1997	83.0	12

Table 5. Relation between female age and raising one brood (or replacement clutch in case of a failure of the first brood) or two broods (plus repeat clutch in some cases). The values given are the numbers of females.

Broods	Females	
	Immigrants	At least 2-year-old
One brood	4	0
Two broods	5	11
Fisher's exact test:	p = 0.0260	

Table 4. Age-related differences in laying dates and clutch sizes in first broods. Specific hypotheses that in immigrant one-year-old females the mean laying dates are higher and mean clutch sizes lower than in the females who are at least two years old were tested by the one-tailed t-test. Note that laying dates were log-transformed before testing but mean values given in the table are untransformed April dates (i.e. 1 April = 1).

Variable	Mean values ± SD for females		t (df)	p (1-tailed)
	Immigrants	At least 2-year-old		
Laying date	57.00 ± 9.94	45.72 ± 4.47	3.42 (18)	0.0015
Clutch size	4.22 ± 1.39	5.30 ± 1.16	− 1.84 (17)	0.0417

was also evident that the immigrants started laying later and laid smaller clutches than the older females. These findings suggest that there was an age-related pattern in the study population.

Age-related patterns of reproductive performance, including clutch size and its seasonal trends, have been reported for many species, for example in the Hirundinidae, the basically single-brooded Tree Swallow *Tachycineta bicolor* (De Steven 1978; Stutchbury & Robertson 1988; Winkler & Allen 1996). The positive influence of female age on clutch size and the ability to produce multiple broods has been reported in Rock Pipits *Anthus petrosus* (e.g. Askenmo & Unger 1986; Hario 1997) and Black Wheatears *Oenanthe leucura* (Soler et al. 1995). We suggest that the relation with age may be an important factor explaining great short-distance spatial and year-to-year variation in the proportion of single-brooded and double-brooded pairs of Barn Swallows observed by some authors (e.g. Nitecki 1964, Kuźniak 1967, Møller 1984, Loske 1989, this study).

Acknowledgements. We are grateful to Mr. H. Warszawski, Director of the Stadnina Koni Walewice Ltd. and Mr. and Mrs. Jaros, for their permission to study swallows at the Goślub farm. We thank S. R. Reddy, M. Mönkkönen, J. Sundberg and an anonymous referee for their criticism and helpful comments on the MS. The study was supported by the grant PB 6/P04F/037/09 from the KBN.

Selostus: **Haarapääskyn pesinnän ajoitus, pesyekoko ja monipesyeisyys puolalaisessa populaatiossa**

Kirjoittajat tutkivat haarapääskyn pesintää vuosina 1994–1997 Keski-Puolassa. Muninnan aloitus tapahtui 18 ja 30 toukokuuta välisenä aikana. Pesyekoko oli suurempi ensimmäisissä pesyeissä kuin toisissa ja uusintapesyeissä (Taulukko 1). Yleinen suuntaus oli, että myöhään munituissa pesyessä oli vähemmän munia kuin aikaisin munituissa pesyeissä (Taulukko 2, Kuva 2), mutta vuosien välillä ei ollut eroa pesyekoossa. Kaksi pesyettä munivien naaraiden osuus vaihteli 65 ja 83%:n välillä eri vuosina ja vuosien väliset erot olivat merkitseviä (Taulukko 3). Nuoret (koloniaan kyseisenä vuotena rekrytoituneet) naaraat munivat myöhemmin ja pienempiä pesyeitä kuin vanhat (+2kv) naaraat (Taulukko 4). Kirjoittajat päättelevät, että myöhemmin munittujen pesyeiden pienempi koko johtui ainakin osittain siitä, että nuoret naaraat aloittavat pesinnän vanhoja myöhemmin. Vanhat naaraat munivat useammin toisen pesyeen kuin nuoret naaraat (Taulukko 5), joten myös tämä ominaisuus on ikään kytkeytynyt. Keskipuolalaisesta haarapääskypopulaatiosta tehdyt havainnot eivät tue Crickin ym. (1993) hypoteesiä. Tämän hypoteesin mukaan pääosin kaksipesyeisillä lajeilla pesyekoko ensin kasvaa munintakauden alusta lähtien pienentyen sitten kohti myöhäisempiä pesyeitä, mutta haarapääskyllä ei tällaista havaittu.

References

Askenmo, C. & Unger, U. 1986: How to be double-brooded: Trends and timing of breeding performance in the Rock Pipit. — Ornis Scand. 17: 237–244.

Bańbura, J. 1997: Variation in blue tit breeding timetables: what factors trigger reproduction? — TREE 12: 293–294.

Bańbura, J., Blondel, J., de Wilde-Lambrechts, H., Galan, M.-J. & Maistre, M. 1994: Nestling diet variation in an insular Mediterranean population of Blue Tits Parus caeruleus: effects of years, territories and individuals. — Oecologia 100: 413–420.

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.

Bryant, D. M. 1975: Breeding biology of house martins Delichon urbica (L.) in relation to aerial insect abundance. — Ibis 117: 180–216.

Cramp, S. (Ed.) 1988: Handbook of Birds of Europe, the Middle East and North Africa. Vol. V. — Oxford University Press, Oxford.

Crick, H. O. P., Gibbons, D. W. & Magrath, R. D. 1993: Seasonal changes in clutch size in British birds. — J. Anim. Ecol. 62: 263–273.

De Steven, D. 1978: The influence of age on the breeding biology of the Tree Swallow Iridoprocne bicolor. — Ibis 120: 516–523.

Drent, R. H. & Daan, S. 1980: The prudent parent: energetic adjustments in avian breeding. — Ardea 68: 225–252.

Hario, M. 1997: Survival prospects of single-brooded and double-brooded Rock Pipits Anthus petrosus. — Ornis Fennica 74: 99–104.

Karg, J. 1980: Density and variation of aeroentomofauna in agricultural landscape. — Pol. Ecol. Stud. 6: 329–340.

Klomp, H. 1970: The determination of clutch size in birds. A review. — Ardea 58: 1–124.

Kondelka, D. 1985: Gelegegrosse und Brutverluste der Rauchschwalbe (Hirundo rustica) im nordmahrischen

Kreis (CSSR). — Folia Zool. 34: 149–158.
Kuźniak, S. 1967: Observations on the breeding biology of Swallow, Hirundo rustica L. — Acta Ornith. 10: 177–211. (In Polish with English summary).
Lack, D. 1950: The breeding seasons of European birds. — Ibis 92: 288–316.
Lack, D. 1954: The Natural Regulation of Animal Numbers. — Clarendon Press, Oxford.
Lambrechts, M. M., Blondel, J., Hurtez-Bousses, S., Maistre, M. & Perret, P. 1997: Adaptive inter-population differentiation in Blue Tit life-history traits on Corsica. — Evol. Ecol. 11: 599–612.
Lohrl, H. & Gustscher, H. 1973: Zur Brutokologie der Rauchschwalbe in einem sudwestdeutschen Dorf. — J. Orn. 114: 399–416.
Loske, K.-H. 1989: Zur Brutbiologie der Rauchschwalbe (Hirundo rustica) in Mittelwestfalen. — Vogelwelt 110: 59–82.
Martin, T. E. 1987: Food as a limit on breeding birds: a life-history perspective. — Ann. Rev. Ecol. Syst. 18: 453–487.
McGinn, D. B. & Clark, H. 1978: Some measurements of Swallow breeding biology in lowland Scotland. — Bird Study 25: 109–118.
Møller, A. P. 1984: Geographical trends in breeding parameters of Swallows Hirundo rustica and House Martins Delichon urbica. — Ornis Scand. 15: 43–54.
Møller, A. P. 1994: Sexual Selection and the Barn Swallow. — Oxford University Press, Oxford.
Nitecki, C. 1964: Observations of the breeding of the Barn Swallow (Hirundo rustica L.). — Zeszyty Naukowe Uniwersytetu Mikołaja Kopernika w Turuniu, Biologia 8: 65–90. (In Polish with English summary).
Perrins, C. M. 1965: Population fluctuations and clutch-size in the great tit, Parus major L. — J. Anim. Ecol. 34: 601–647.
Perrins, C. M. 1970: The timing of birds' breeding season. — Ibis 112: 242–255.
Perrins, C. .M. 1991: Tits and their caterpillar food supply. — Ibis 133 (Suppl. I):49–54.
Sokal, R. R. and Rohlf, F. J. 1981. Biometry. — New York: Freeman.
Soler, M., Moreno, J., Moller, A. P., Linden, M. & Soler, J. J. 1995: Determinants of reproductive success in a Mediterranean multi-brooded passerine: the Black Wheatear Oenanthe leucura. — J. Orn. 136: 17–27.
Stutchbury, B. J. & Robertson, R. J. 1988: Within-season and age-related patterns of reproductive performance in female tree swallows (Tachycineta bicolor). — Can. J. Zool. 66: 827–834.
Svensson, E. 1995: Avian reproductive timing: when should parents be prudent? — Anim. Behav. 49: 1569–1575.
Tinbergen, J. M. & van Balen, J. H. 1988: Food and multiple breeding. — Proc. Int. Ornithol. Congr. XIX: 380–391.
Turner, A. K. 1994: The Swallow. — Hamlyn, London.
Winkler, D. W. & Allen, P. E. 1996: The seasonal decline in tree swallow clutch size: Physiological constraint or strategic adjustment? — Ecology 77: 922–932.
Zieliński, P. & Bańbura, J. 1995: Selfish behaviour of juvenile Barn Swallows (Hirundo rustica) intruding in active nests. — Ornis Fennica 72: 89–90