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The breeding ecology of the Greenfinch *Carduelis chloris* in urban conditions (study in Krotoszyn, W Poland)

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Abstract. Data were collected in a medium-sized town. During five years 342 nests were found. The densities of breeding pairs varied over this period between 4.5 and 5.9 p/10 ha. The distribution of breeding pairs was uneven throughout the study area. The preferred nest sites were the roadside trees, where 88.9% of the nests were built. The mean onset of egg-laying was 22 April (range 19–26 April). There was a tendency to start breeding earlier in warmer springs. The mean clutch size was 5.07 ± 0.74 . There was a positive correlation between clutch size and the date of egg-laying. These data suggest that there was a compromise between the tendency towards earlier breeding and clutch size. In the study area the Greenfinch is a double-brooded species. Unlike other studies it was noted that the average clutch size increased in the second half of the breeding season. The maximum clutch size coincides with the second or replacement clutches. Hatching, fledging and breeding success were lowest when clutch sizes were largest. The nesting success estimated with the Mayfield and the “traditional” method was approximately similar (0.40 and 0.44 respectively). Cats and mustelids were probably the cause of most breeding failures. Corvids were not responsible for nesting failures.

Key words: Greenfinch, *Carduelis chloris*, breeding biology, nest-site, timing of breeding, clutch size, breeding success, nesting success

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INTRODUCTION

The Greenfinch is widespread across most of the Western Palearctic region, breeds throughout agricultural landscapes, villages and towns (Cramp & Perrins 1994, Hagemajjer & Blair 1997). However, only a few papers present any data concerning the breeding biology of the Greenfinch in a population context (Michocki 1967, 1974, Gil-Delgado & Catala 1989). Several studies have been based on the analysis of Nest Record Cards (e.g. Monk 1954, Gnielka 1986). As stated in earlier analysis (Monk 1954, Wesolowski & Czapulak 1986) such results could be distorted by the activity of volunteers, greatest in the early part of the breeding season, as well as by difficulties involved in nest searching during summer when vegetation cover is thickest. In consequence, some aspects of the breeding biology of the Greenfinch,

especially their temporal variation (between- and within-season) are little known.

Multi-brooded species, like the Greenfinch, lay their largest clutches in the middle of the breeding season (Monk 1954, Gnielka 1986, Gil-Delgado & Catala 1989). It is known that, in multi-brooded species, seasonal reproductive success is determined not only by the productivity of each brood, but also by the number of broods raised, mainly as an effect of high rates of total failures. Thus, it was suggested that there is a very strong selection in favour of early breeding, before the date when the optimal clutch size is greatest (Perrins 1970, Crick et al. 1993).

The aim of this study was to investigate a breeding ecology of Greenfinch in specific urban conditions: abundance of the breeding population, timing of breeding, nest-site distribution and seasonal patterns of clutch size, breeding success

and nest predation. Specifically, two questions were considered:

- 1) does the spring temperature affects the timing of breeding?
- 2) how does the timing of breeding affect the clutch size?

STUDY AREA

The study was carried out in a medium-size town Krotoszyn (51°41'N, 17°26'E, 23 km², 29 000 inhabitants). The Krotoszyn region lies in a zone of temperate climate. The average annual temperature is 8.1°C. During the breeding season (April–August), the mean monthly temperature increases from 7.7°C to 17.3°C. Precipitation is relatively low and the average is over 550 mm with the maximum (84.3 mm) in July (Parysek 1995).

The detailed study area was a 44 ha plot located in an urbanised part of the town. This area represents a mosaic of variously aged housing estates and built up industrial areas (57% of the total area), tree-covered areas, e.g. taller greenery of a park-like character, alleys and street trees, small squares (30%) and barren (rural) areas (14%). There are three mature park-like patches (2.6 ha) with a predominance of lime *Tilia cordata*, as well as ash *Fraxinus excelsior*, poplars *Populus italica* and other *Populus* spp., maple *Acer platanoides* and other species. The most characteristic element of plant coverage are the street trees and alleys with hawthorn *Crataegus* sp. up to 4.5 metres in height. The total length of streets with this type of vegetation is c. 1 km. These trees are distributed evenly every 4.5 metres. The hawthorn crowns were cut off yearly in mid July, except 1998. After that crowns took on a spherical shape. The diameters of the crowns were no more than 2.5 m. The small squares are mainly covered with lawns, low bushes and coniferous trees (spruce *Picea* spp., juniper *Juniperus* spp. and thuja *Thuja* spp.). The study plot was limited or crossed by communication routes with heavy traffic and a railway line.

MATERIAL AND METHODS

Field methods

Data was collected in 1994–1998. Regular searches of the study area from mid April to the end of July resulted in the collection of data from 342 nests, from which 313 were considered as completed (since females started egg laying).

Nests which were abandoned by females before egg-laying were not included in the analysis of nesting success. The position of each nest was marked on a map, the tree species was determined, the height of the nest and exposure with respect to the direction from a tree trunk was measured. To determine hatching, fledging and breeding success nests were visited at least once a week. If the laying date of the first egg was unknown, it was calculated from the date of hatching on the basis of a 13-day incubation period and by the ageing of chicks. Adult birds were captured in mist-nets and colour-ringed in 1996–1998.

Data analysis

Cardueline finches defend a very small area around their nests and forage over wide areas away from it. In consequence, group nesting into loose colonies is frequently observed (Newton 1972), and real difficulties in estimating the numbers of a breeding population occur (Tomiałojć 1968, 1980). Hence, the maximum number of active nests during successive five-day periods was used to calculate the density of pairs.

To examine the relationship between spring temperatures and the timing of breeding, sums of mean daily temperatures >0° (“warmth-sums”) for four periods (5, 10, 15, 30 days) were calculated, according to Orell & Ojanen (1983) and Wesolowski (1998). The same fixed date ending each of the four periods was set at 17 April, i.e. five days before the average date of laying in the population (22 April), coinciding with the period of final production of egg (Kluyver 1952). First egg dates were expressed as the number of days since 1 April. For the first clutches, the relative dates were calculated as the deviations in the number of days of individual laying dates from the median date (date 0) for each season. On the basis of the phenology of the breeding season and observations of individually marked birds it was assumed that the first clutches finished on 25 May. In 83.7% (n = 118) of 141 cases, the date of first egg-laying was known. Because, there were no differences between the number of nesting attempts in both categories of data ($\chi^2 = 1.02$, ns), nests with an unknown date of laying were excluded from this analysis. Meteorological data was provided by the agrometeorological station in Smolice, situated 17 km west of Krotoszyn.

Hatching success was calculated as the number of eggs hatched from the eggs laid, fledging success as the number of free-flying young produced from nestlings hatched and breeding success as the

number of nestlings which survived to fly from the nest in relation to the number of eggs laid. All parameters were calculated from data excluding complete failures, except where indicated.

The seasonal variation of breeding parameters was described by sorting data into non-overlapping intervals — months, according to Monk (1954) and Gil-Delgado & Catala (1989). However, this method has serious disadvantages. One of which could be the improper choice of the length of interval, which makes it impossible to detect the seasonal variation of breeding parameters. In consequence, the seasonality of breeding parameters and their relationships were also estimated by calculating running-averages with 15-day overlapping intervals (Vanicsek & Ludvig 1992). The starting point of the first interval was determined so that the first interval contained at least one datum. In the case of 15-day intervals each pair of neighbouring intervals overlapped with 14 days and each 15th interval did not overlap with each other (Ludvig et al. 1995). Clutches with a known date of first egg laying and history were considered in the analysis.

Nest success was estimated by the traditional method, as a fraction of observed nests, which were successful. However, this estimator of nest success may be severely biased because unsuccessful nests are less likely to be found than successful nests. A second measure of nest success was estimated using the Mayfield method (Mayfield 1975). This method takes into account the time span of observation (exposure in nest-days) and allows calculation of the daily survival rate and the probability of survival of a nest from the start of egg laying to the fledging of young. Error terms (standard error and confidence limit) were calculated from Johnson (1979), on the basis of freeware software written by Konrad Hałupka. Daily survival rates between years were analysed with the two-tailed z-test. As the repeated use of a statistical test increases the probability of committing a type I error, the level of significance was adjusted to 0.005 using the Bonferroni method.

All statistics were performed on the basis of the statistical software package STATISTICA (StatSoft, Inc. 1997). Values reported are means \pm 1 standard deviations except otherwise stated.

RESULTS AND DISCUSSION

Nesting habitat and density of breeding pairs

The distribution of breeding pairs (nests) was uneven throughout the study area. The preferred

nest sites were the street trees, where 88.9% ($n = 304$) of the nests were built. The remaining nests were located within the squares on coniferous trees (7.6%, $n = 26$), old parks and alleys (3.5%, $n = 12$). The densities of breeding pairs varied between 4.5 and 5.9 p/10 ha (Table 1); mean 5.40 ± 0.58 p/10 ha. The mean density calculated for the greenery area was 18.32 ± 1.91 p/10 ha. The highest densities, maximum 12 nests/ca 0.5 ha, occurred in areas where street trees adjoined patches of squares and taller greenery. The breeding density found in this study was close to the highest values reported in the Wielkopolska region (Kosiński 2000a). Most of these highest densities were found in urbanised areas. In Poland the highest densities, up to ca 13 p/10 ha (data from plots > 10 ha), were recorded in villa districts, parks and cemeteries (e.g. Tomiałojć 1970, Górski & Górka 1979, Czyż & Królikowski 1990, Biaduń 1994). The same pattern was found in various countries in Europe (Cramp & Perrins 1994, Glutz & Bauer 1997).

Table 1. Numbers and densities of nests. A — nesting attempts, Max. — maximum number of active nests. Density (pairs/10 ha) was calculated for the total area (TA; 44 ha) and greenery area (GA; 13 ha).

Year	A	Max.	TA	GA
1994	85	24	5.5	18.5
1995	64	26	5.9	20.0
1996	63	20	4.5	15.4
1997	62	23	5.2	17.7
1998	68	26	5.9	20.0

Nest-site selection

Nests were built in 10 plant species; most of them were located in hawthorns (Table 2). A marked seasonal variation in the time of nesting and nest-site selection was observed (Fig. 1). Early nests were built in coniferous trees; 88% ($n = 15$) of these nests were built before the end of April. Afterwards, nests were located in broad-leaved trees. Differences in nest location within the tree-crown were also found. Before the tree leafing, nests were placed in the base or in the central part of the crown. The increase in the number of nests situated in the peripheral part of the crown was connected with the development of foliage. The preference for coniferous trees at the beginning of the season enables birds to start breeding as early as possible. Moreover, as it was stated earlier (e.g. Slagsvold & Sæther 1979, Møller 1988), nests built

Table 2. Number and percentage of nests found in different trees and shrubs.

Plant species	N	%
<i>Crataegus</i> sp.	284	83.0
<i>Acer platanoides</i>	21	6.1
<i>Picea</i> sp.	14	4.1
<i>Tilia</i> sp.	9	2.6
<i>Robinia pseudoacacia</i>	4	1.2
<i>Populus</i> sp.	3	0.9
<i>Populus italica</i>	2	0.6
<i>Juniperus</i> sp.	2	0.6
<i>Thuja</i> sp.	2	0.6
<i>Morus</i> sp.	1	0.3
Total	342	100.0

in the evergreens were less easily detected by predators in the early spring. The preference for building nests in the peripheral part of the crown could serve to evade mammalian predators.

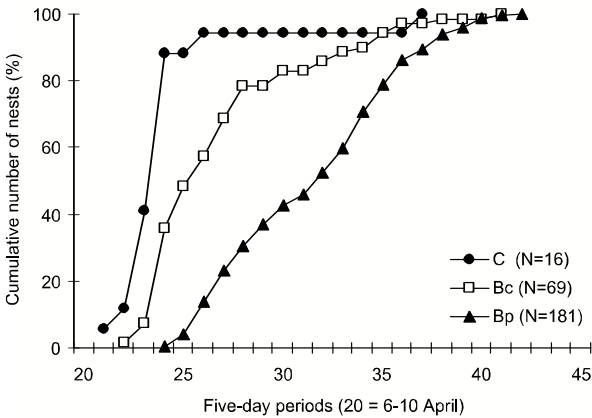


Fig. 1. The proportion and distribution of Greenfinch nests among places used for nesting according to the timing of breeding: C — coniferous trees, Bc — broad-leaved trees, nests placed in the base or in central part of the crown, Bp — broad-leaved trees, nests placed in the peripheral part of the crown.

Nests were situated 1.35–13.0 m above the ground (mean 3.08 ± 0.97 m, $n = 323$), the majority of them (94%) between 2 and 4 meters. Similar distribution patterns have been reported from other regions, e.g. Silesia (Poland) — 2.4 m (Dyrz et al. 1991), former Czechoslovakia — 2.3 m (Hudec 1983), Halle (Germany) — 2.7 m (Gnielka 1986) and Finland — 3.1 m (von Haartman 1969). In England about half the nests were placed 1–2 m above the ground (Monk 1954). There were no differences in nest-height between first and second (or replacement) broods ($t = 1.28$, ns; $n_1 = 224$, $n_2 = 99$).

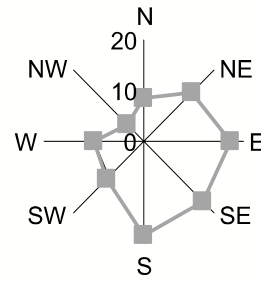


Fig. 2. Percentage distribution of nest exposure in relation to tree stem ($n = 162$, 1995–1998).

The way the nests were placed in tree crowns with respect to the direction from a tree trunk deviated significantly from the expected random distribution ($\chi^2 = 20.8$, $df = 7$, $p < 0.01$). Nests oriented from the east to south direction were more frequent than expected (Fig. 2). A similar pattern was found in the Pskov Region in Russia (Uryadova 1998). In SW Germany most nests were located according to the north-east and southern direction (von Glück 1983).

Timing of egg-laying and number of broods

The onset of egg-laying varied between 19 April and 26 April, mean 22 April. Exceptionally, the earliest, outlier data recorded for the laying of the first egg was 12 April 1998. For the first clutches, the range of the median dates of laying was 11 days, but the annual variation was not significant (Median test $\chi^2 = 8.24$, $df = 4$, ns). Laying in Krotoszyn started at the same time as reported in Silesia (Dyrz et al. 1991) and England (Monk 1954). Much earlier laying dates were found in southern latitudes (e.g. Hudec 1983, Gil-Delgado & Catalá 1989), as well as in Halle (Gnielka 1986). The climatic conditions, as well as the proportion of evergreens accessible to settle could explain a marked difference in the time of breeding. It was suggested that for the House Sparrow *Passer domesticus*, the mean time for initiating egg-laying in the season is related to the latitude (Dyer et al. 1977). The equation $Y = 2.48 + 1.94X$, where Y is calendar days from 1 January and X is latitude in decimal degrees, weekly applies to the population studied in Krotoszyn. The calculated laying date of the first egg (latitude $51^\circ 41'$) should be 12 April, ten days before the mean observed value.

The median date of laying was moderated negatively but it was not statistically significant when correlated with "warmth-sums" for 10 days before the period of rapid follicle growth

(Spearman rank correlation $r_s = -0.5$, ns). However, the distribution of relative laying dates did not deviate from the normal ($\chi^2 = 7.33$, $df = 5$, ns). In numerous studies the relationship between the spring temperatures and timing of breeding was established (e.g. Perrins 1970, Newton 1972, Slagsvold & Sæther 1979, Sokolov & Payevsky 1998, Wesolowski 1998). It was found in Krotoszyn (Kosiński 2000b) that the threshold temperature which influenced the timing of breeding varied over the years. It is possible that the onset of laying was indirectly affected by temperatures, e.g. by increasing food-supply (seeds). Sokolov & Payevsky (1998) suggested that timing of breeding probably reflect the condition of the ecosystem, especially the vegetation development. Moreover, negative correlations between the flowering time of some plants and air temperatures were found. It is likely, that food would act as a proximate, as well as an ultimate timing factor (Newton 1972).

The egg-laying period varied from 74 days in 1995 to 104 days in 1998; mean 88.2 ± 10.8 days. The young from one of the latest nests fledged on 22 August 1998. The mean value reported from NW Germany was 90 days (von Glück 1983). The number of clutches laid during successive five-day periods showed two peaks each year, in the first half of May and in the middle of June (Fig. 3 and 4). In other studies only the first peak was observed (Hudec 1983, Gnielka 1986) and if the second was found, it was not distinctly marked (Monk 1954).

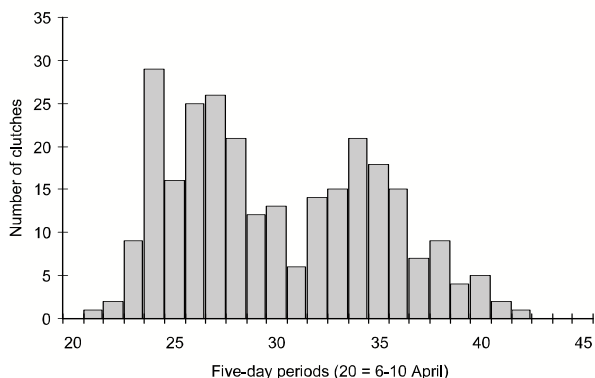


Fig. 3. The number of clutches laid during successive five-day periods ($n = 269$, 1994–1998).

The mean length of the nesting period from the date of first egg-laying to the date of last young fledging was 33.2 ± 2.7 days (range 29–39, $n = 12$). Observations of two colour-ringed

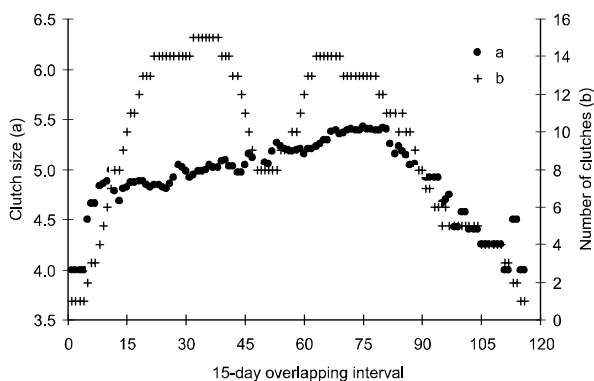


Fig. 4. The mean clutch size (a) and the number of clutches (b) in 15-day overlapping intervals since 1 April ($n = 185$, 1994–1998).

females, which nested successfully twice during the breeding season, showed that the length of their breeding period ranged from 65 and 67 days. In the first case, the female started egg-laying on 24 April (the earliest date of egg-laying in 1997) and fledglings left the nest on 26 May. Next day the same female started egg-laying for the second brood and the nestlings stayed in this nest until at least 29 June. The second female reared the first brood between c. 15 May and 18/19 June, and the next brood between 25 June and (at least) 18 July. This data suggests that the population studied is double-brooded. However, probably only few pairs breed for the full breeding season (see Stokes 1954). In captive Greenfinches, it was found that the second broods were more frequent from pairs that started early (Hinde 1954).

Clutch size

The mean clutch size was 5.07 ± 0.74 (range 3–6, $n = 215$). Most clutches (56%, $n = 121$) contained 5 eggs. Clutches of 6 were twice as common (27%, $n = 59$) as clutches of 4 (13%, $n = 27$). The clutch size varied between 4.90 ± 0.82 in 1996 to 5.30 ± 0.66 in 1995. There were no statistically significant differences in clutch size from year to year (ANOVA, $F = 1.837$, $df = 4$, ns). The mean clutch size is larger than reported for Poland (5.01, $n = 360$) on the basis data collected under the Polish Nest Record Scheme (L. Tomiałojć in Glutz & Bauer 1997). This difference could be partly explained by the activity of volunteers, greater in the early part of the breeding season when clutches are smaller (Wesolowski & Czapulak 1986) and/or by the length of a study. It was suggested that clutch size is optimized over a period above 1 year and reflects between-year variation (VanderWerf 1992). However, the relevant data (ten years) from village

park in Siemianice (SE Wielkopolska, Poland) was also lower (4.9, $n = 125$) than in Krotoszyn (Michocki 1967, 1974). It seems likely that clutch size can vary according to habitat. However, Snow & Mayer-Gross (1967) found that the clutch size of some species, e.g. Greenfinches, tends to be lower in suburban and urban than in rural habitats (see also Glutz & Bauer 1997).

Clutch size was found to increase throughout the season from 4.85 ± 0.80 in April ($n = 33$), 5.04 ± 0.72 in May ($n = 80$) to 5.29 ± 0.63 in June ($n = 73$) and then a decrease to 4.65 ± 0.88 in July ($n = 20$). Differences in clutch size between months were significant (ANOVA, $F = 5.574$, $df = 3$, $p = 0.001$), but only clutches in July were significantly smaller than clutches in June (Tukey test, $p = 0.026$). The maximum value of clutch size coincided with second or replacement clutches (Fig. 4). The data presented by Monk (1954) shows a similar pattern in England. The difference between clutch size in the first (4.99 ± 0.74) and second brood (5.20 ± 0.72) was statistically significant (Mann-Whitney test, $z = -2.05$, $p = 0.04$; $n_1 = 129$, $n_2 = 86$). The mean clutch size was found to be clearly correlated with a median date of egg-laying in first clutches ($r_s = 0.90$, $p = 0.037$). These results, as well as a tendency to lay earlier in warmer springs suggest that a trade-off between clutch size and timing of breeding occur. Greenfinches, as well as other open nesters suffer high rates of total failures. Thus, the seasonal reproductive success should be determined by the number of broods that parents could raise during the breeding season. It was suggested that, in multi-brooded species, there is a very strong selection in favour of early breeding, before the date when the optimal clutch size is greatest (Crick et al. 1993). On the other hand, when the start of breeding is "delayed" the probability of being able to raise a second brood is small. Therefore, the size of the first or subsequent (replacement) broods should be more important (larger) to the seasonal reproductive success.

Breeding success

The number of eggs hatched varied between 81% in 1998 to 97% in 1995 and the differences over the years were statistically significant (Kruskal-Wallis test $H_4 = 9.927$, $p = 0.042$, $n = 118$). Of 595 eggs laid in these clutches 525 (88.2%) hatched. Partial egg losses were higher in bigger clutches (Table 3). A similar pattern, that more eggs fail to hatch in larger clutches, was observed in different species, e.g. the House Sparrow (Murphy

Table 3. Relationship between clutch size and percentage of eggs hatched. () — the number of clutches.

Clutch	Percentage of eggs hatched					
	1	2	3	4	5	6
3	25.0 (1)	0.0	75.0 (3)	—	—	—
4	7.1 (1)	14.3 (2)	7.1 (1)	71.4 (10)	—	—
5	0.0	4.1 (3)	11.0 (8)	23.3 (17)	61.6 (45)	—
6	0.0	0.0	3.7 (1)	7.4 (2)	40.7 (11)	48.1 (13)

1978) and Blackbird (Ludvig et al. 1995). It was found that minimum hatching, fledging and breeding success coincided with maximum clutch size (Table 4, Fig. 5). These results are in opposition to the predictions of the Lack hypothesis (1966). Moreover, it was found (Kosiński 2000b) that when partial losses in five- and six-egg clutches were compared larger clutches were more productive than the modal clutch size. The hatching and breeding success was higher than that reported for village park in Siemianice — 81% and 74% respectively (Michocki 1967, 1974) but breeding success was similar when compared to rural and urban habitats in England — 89% and 90% (Snow & Mayer-Gross 1967). When broods which failed completely were included breeding success varied from 40.7% in Krotoszyn (1091 eggs laid vs. 444 fledglings) to 47.3% in eastern Germany (Blümel 1983), 52.9% in England (Monk 1954) and 54.4% in the Pskov Region (Uryadova 1998).

Table 4. Breeding success (BS) and number of fledglings during the breeding season (clutches with a known history).

Month	Nests	Eggs	Nestlings	BS	Fledglings
April	13	62	53	85.5	4.08 ± 1.19
May	34	171	152	88.9	4.47 ± 0.99
June	32	169	134	79.3	4.19 ± 1.09
July	4	19	18	94.7	4.50 ± 0.58
Total	83	421	357	84.8	4.30 ± 1.04

The number of fledglings differed significantly across years (ANOVA, $F = 2.876$, $df = 4$, $p = 0.028$) and their overall mean was 4.29 ± 1.03 ($n = 87$). The mean number of fledglings produced in 1998 (3.80 ± 1.15) was clearly lower (Tukey test, $p = 0.027$) than in 1995 (4.82 ± 1.13). There was no difference in the mean number of fledglings across the first and second brood when only the successful breeding attempts were considered (Mann-Whitney test, $z = 0.44$, ns), respectively 4.33 ± 1.08 ($n = 48$) and 4.26 ± 1.01 ($n = 35$). The mean

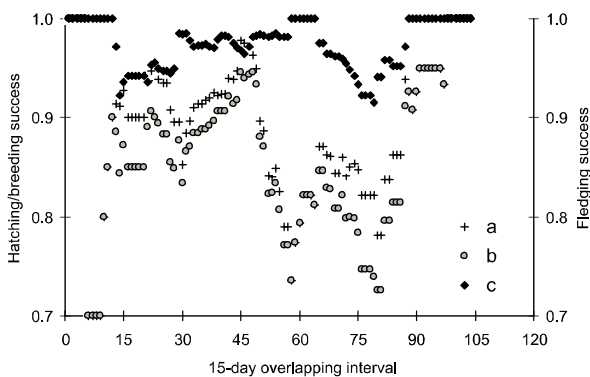


Fig. 5. The averages of hatching (a), fledging (c) and breeding success (b) per nest in 15-day overlapping intervals since 1 April ($n = 83$, 1994–1998).

number of fledglings per breeding attempt was 2.04 (standard error of the mean 0.17, $n = 183$) and did not differ between the first and second brood ($z = -0.13$, ns). The mean number of fledglings in successful nests was similar to the value observed in former Czechoslovakia — 4.26 (Hudec 1983) and eastern Germany — 4.2 (Blümel 1983). Much lower values were reported for village park in Siemianice — 3.6 (Michocki 1967, 1974) and Halle — 3.86 (Gnielka 1986). The number of fledglings per breeding attempt was by far the lowest ever reported, as a consequence of the lower value of breeding success and the higher rate of failure. In various populations this value varied between 2.21 in eastern Germany (Blümel 1983), 2.41 in village park in Siemianice (Michocki 1967, 1974) and 2.55 in England (Monk 1954).

Nest success and causes of nesting failures

In all the years, except 1997, nest success estimated using the Mayfield method was slightly less than that estimated in using the “traditional” method (Table 5). During an exposure of 4544 nest-days, 128 nests were lost (daily survival rate — 0.972603). As it was assumed that the mean length of the nesting period was 33 days, so the probability of the nest’s survival was 0.40. Independent of the method used and sample size, the nesting success was lowest in the 1994. The differences between nesting success across the years estimated using the “traditional” method were statistically significant ($\chi^2 = 19.78$, $df = 4$, $p < 0.001$). There were more unsuccessful nests than expected (56 vs. 32.6) and fewer successful nests than expected (18 vs. 32.6) in 1994. Daily survival rate in 1994 was significantly lower from the 1997 ($z = 3.489$, $p < 0.001$) and 1998 ($z = 3.940$, $p < 0.001$).

Table 5. Nesting success (probability of survival — PS) calculated from the Mayfield method and the “traditional method”. Daily survival rates (DSR (%), standard errors (SE) and 95% confidence limits (CL) are given. () — number of clutches.

Year	Mayfield method		Traditional method	
	DSR \pm SE	CL	PS	Nesting success (%)
1994	94.88 \pm 0.008 (62)	93.34–96.42	0.18	24.3 (74)
1995	97.34 \pm 0.006 (45)	96.20–98.49	0.41	45.6 (57)
1996	97.21 \pm 0.006 (55)	96.11–98.31	0.39	42.6 (61)
1997	98.03 \pm 0.005 (44)	97.08–98.98	0.52	51.9 (54)
1998	98.23 \pm 0.004 (65)	97.51–98.96	0.55	59.7 (67)
Total	97.26 \pm 0.002 (271)	96.78–97.74	0.40	44.1 (313)

< 0.001). In various habitats in the Wielkopolska region nest success varied between 76.0% (range 44%–100%) in village park in Siemianice, where most nests were situated in hornbeam hedges (Michocki 1967, 1974) to 26.7% in city park in Poznań (Mizera 1988) and 12%–24.0% in orchards (Mroczkiewicz 1974, Kwiatkowska 1989). The nest success found in this study was similar to that reported for England — 37% (Snow & Mayer-Gross 1967), Halle — 37.5% (Gnielka 1986) and the Moscow Region — 38 and 46% (Shurupov 1986, in Cramp & Perrins 1994).

Early nests were successful then nest success rapidly fell (Fig. 6). Moreover, nest success was density-dependent. The number of unsuccessful nests was positively correlated with the number of breeding attempts started each day ($r_s = 0.74$, $p < 0.001$, $n = 79$).

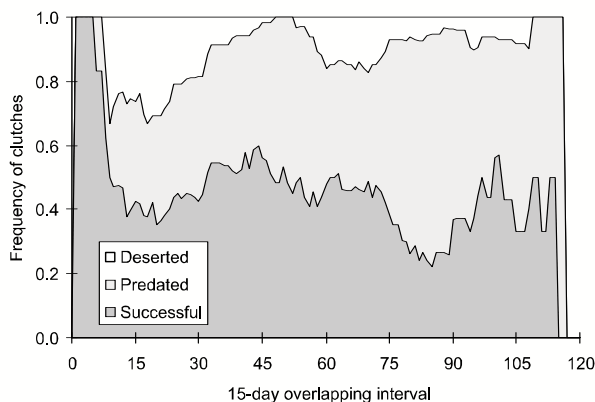


Fig. 6. The proportions of successful, predated and deserted nests in 15-day overlapping intervals since 1 April ($n = 217$, 1994–1998).

Of the 313 nests, 38.7% ($n = 121$) were destroyed by predators, 14.1% ($n = 44$) abandoned during egg laying or incubation period

and 1.3% ($n = 4$) unfertilised. In six cases (1.9%) the causes of failure were not known. Clutches were clearly more frequently destroyed than broods ($\chi^2 = 5.63$, $p = 0.018$, Table 6). There was no difference in nest success between the first and second brood ($\chi^2 = 0.07$, ns), as well as between nests placed on coniferous and deciduous trees ($\chi^2 = 0.001$, ns).

In none of the predation events were predators directly recorded. The identity of predators was inferred from nest appearance and the presence or absence of egg/nestling remains (Table 6). Most breeding failures were probably caused by cats and mustelids e.g. *Martes foina*. Cats were frequently observed within tree-crowns. It is likely that birds, especially corvids, were not responsible for the nest failures. During the study only one observation of Magpie *Pica pica* was documented. Mäck (1998) found that different densities of Magpie did not affect breeding success of 20 open-breeding species. No other potential predators were recorded. It is likely that the high rate of nest losses, especially in 1994, can be attributed to human disturbance.

Table 6. Causes of nesting (number and percentage of nests) failure.

Cause of failure	N	%
Egg stage		
Eggs missing, nest not damaged	44	36.4
Eggs partially missing, nest intact	12	9.9
Nest damaged (cat?)	14	11.6
Nest damaged by man — cut off tree crown	3	2.5
Total egg stage	73	60.4
Nestling stage		
Nestling missing, nest not damaged	32	26.4
Nest damaged (cat?)	4	3.3
Nest damaged by man — cut off tree crown	2	1.7
Total nestling stage	38	31.4
Causes not known	10	8.3
Total	121	100.0

Partial losses (Table 7) within successful nests were higher during the egg stage (12.1%) than during the nestling stage (4.5%). This could not be direct evidence of egg failure because, in most cases, unhatched eggs disappeared from the nests. Partial losses of nestlings were negligible. In most cases single young birds disappeared. In one nest, nestling starvation was observed as a result of prolonged rainfall.

Four cases of adult mortality were found. In two cases birds (males) were killed by cars on

Table 7. Partial losses during the breeding cycle for 1994–1998 (Total) and for particular years (Min–Max).

Year	Total	Min–Max.
Clutches	83	10–21
Eggs laid	421	52–105
Eggs lost (%)	12.1	3.3–21.4
Eggs hatched	370	43–95
Nestlings lost (%)	4.5	1.1–7.0
Fledglings	357	40–94
Fledglings to eggs (%)	84.8	76.9–90.1

female was tangled up in string and the other was found dead without injuries.

CONCLUSIONS

The distribution of breeding pairs was connected with habitat mosaics. Preferred nest sites were the street trees where 88.9% of the nests were located.

The densities of breeding pairs varied over the years between 4.5 and 5.9 p/10 ha; mean 5.40 ± 0.58 p/10 ha.

A marked seasonal variation in nest-site selection was found. Early nests were built in coniferous trees. Afterwards, the proportion of broad-leaved trees used for nesting increased rapidly. Before the tree leafing, nests were placed in the base or in the central part of the crown. As the development of foliage increased, most nests were situated in the peripheral part of the crown. Nests oriented from east to south direction were more frequent than expected.

The annual variation of the laying dates was not significant. However, a tendency to start breeding earlier in warmer springs was observed.

Contrary to previous studies, the number of clutches laid showed two peaks in each year. The mean length of the nesting period (33.2 ± 2.7 days), as well as the length of the breeding period of colour-ringed females suggests that the population studied is double-brooded. However, probably only a few pairs breed throughout the whole breeding season.

The clutch size (5.07 ± 0.74) was larger than reported in literature from Poland.

Clutch size was found to increase throughout the season, with a peak in June, and then a decrease. The maximum value of clutch size coincided with second or replacement clutches. The mean clutch

size was found to be positively correlated with a median date of egg-laying in the first brood.

In opposition to the predictions of the Lack hypothesis, the minimum values of hatching, fledging and breeding success coincided with the maximum clutch size.

Nest success recorded in Krotoszyn was similar to that reported for other populations. Predators, probably cats, destroyed most clutches. The nest success estimated using the Mayfield method was slightly lower than that estimated using the "traditional" method.

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STRESZCZENIE

[Ekologia lęgowa dzwońca w warunkach miejskich na przykładzie Krotoszyń]

Badania populacyjne biologii rozrodu dzwońca prowadzono w latach 1994–1998 na terenie Krotoszyń (woj. wielkopolskie). Zgromadzono dane dotyczące 342 prób lęgów dzwońca, z czego w 313 przypadkach samice rozpoczęły składanie jaj.

Powierzchnia badawcza (44 ha) obejmowała zabudowę blokową oraz przemysłową (57% powierzchni całkowitej), tereny zadrzewione (30%) oraz tereny ruderalne (14%). Charakterystycznym elementem roślinności były zadrzewienia przyuliczne utworzone z głogów *Crataegus* sp. o wysokości nie przekraczającej 4.5 m. Całkowita długość ulic z zadrzewieniami głogowymi wynosiła około 1000 m.

Preferowanym miejscem gniazdowania były zadrzewienia przyuliczne, w których stwierdzono 88,9% wszystkich gniazd ($n = 304$). Zageszcze-

nie par (równocześnie czynnych gniazd) wahało się od 4.5 do 5.9 par/10 ha (Tab. 1). Najwyższe zageszczenia, maksymalnie 12 gniazd/0.5 ha, obserwowano w miejscach gdzie zadrzewienia przyuliczne otoczone były skwerami i zadrzewieniami o charakterze parkowym. Gniazda odnotowano na dziesięciu gatunkach drzew i krzewów, przy czym najwięcej gniazd (83%) znaleziono na głogach (Tab. 2). Na początku sezonu lęgowego (przed ulistnieniem się drzew) gniazda były umieszczane na drzewach i krzewach iglastych. Następnie dzwońce rozpoczynały budowę gniazd na drzewach liściastych, przy czym przed ulistnieniem się drzew gniazda były lokowane u podstawy lub we wnętrzu korony, a po rozwoju ulistnienia na jej skraju (Fig. 1). Średnia wysokość umieszczenia gniazda wynosiła 3.08 ± 0.97 m i była zbliżona do wartości odnotowanych w innych miejscach Europy. Stwierdzono, że częściej dzwońce lokowały gniazda od wschodniej i południowej strony korony (Fig. 2).

Początek lęgów przypadał na ogół pomiędzy 19 a 26 kwietnia (średnio 22 kwietnia), wyjątkowo początek pojedynczego lęgu zanotowano 12 kwietnia 1998. Okres składania jaj trwał od 74 do 104 dni (średnio 88.2 ± 10.8). Ostatnie młode w gnieździe obserwowano 22 sierpnia 1998. Mediany dat przystępowania do pierwszych lęgów w sezonie nie różniły się istotnie. Wartości te były ujemnie, lecz statystycznie nieistotnie, zależne od sumy ciepła obliczonej dla okresu 10 dni poprzedzających okres ostatecznego kształtowania się jaja. Stwierdzono, że data przystępowania do lęgów może być zależna od stopnia rozwoju roślinności, jak to wcześniej sugerowali Newton (1972) oraz Sokolov&Payevsky (1998).

Średnia długość lęgu, od momentu złożenia pierwszego jaja w gnieździe do wylotu ostatniego młodego, wynosiła 33.2 ± 2.7 dni. Dzwońce przystępowały do dwóch lęgów w sezonie (Fig. 3 i 4). Potwierdziły to obserwacje dwóch indywidualnie oznakowanych samic, które wyprowadziły dwa zakończone sukcesem lęgi w jednym roku. Okres lęgowy wynosił u nich odpowiednio 65 i 67 dni.

Średnia wielkość zniesienia wynosiła 5.07 ± 0.74 jaja i była wyższa od wartości uzyskanych dla Polski w oparciu o dane z Kartoteki Gniazd i Lęgów (L. Tomiałojć, w Glutz & Bauer 1997). Różnice te są prawdopodobnie wynikiem większej aktywności współpracowników kartoteki na początku sezonu lęgowego, kiedy zniesienia są mniejsze. Wielkość zniesienia wzrastała wraz z upływem sezonu lęgowego osiągając wartość maksymalną w czerwcu, w okresie przystępowania

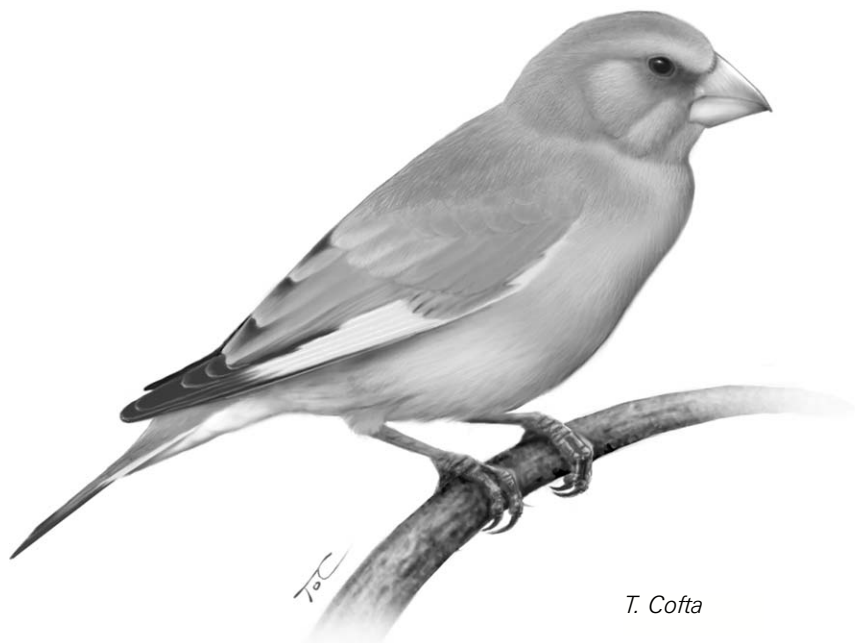
przez dzwońce do lęgów drugich i/lub powtarzanych (Fig. 4). Stwierdzono, że wielkość zniesienia była istotnie zależna od daty przystępowania do pierwszych lęgów w danym roku. W połączeniu z tendencją do wcześniejszego gnieźdzenia się w cieplejsze wiosny dane te wskazują na istnienie kompromisu pomiędzy wielkością zniesienia a czasem przystępowania do lęgów.

Sukces klucia (średnio 88.2%) zmieniał się istotnie pomiędzy latami (81–97%). Stwierdzono, że sukces klucia, sukces wylotu młodych i sukces rozrodczy były najniższe przy maksymalnej wielkości zniesienia (Tab. 3 i 4, Fig. 5). Wyniki te są sprzeczne z założeniami hipotezy Lacka (Lack 1966). Liczba piskląt zdolnych do opuszczenia gniazda (średnio 4.29 ± 1.03) różniła się istotnie pomiędzy latami (3.80–4.82).

Odsetek gniazd, z lęgami zakończonymi sukcesem, wyliczony metodą tradycyjną (0.44), był wyższy od wartości uzyskanej metodą Mayfielda

(0.40) (Tab. 5). Sukces gniazdowy był najwyższy na początku sezonu lęgowego (Fig. 6). Liczba gniazd bez sukcesu była pozytywnie zależna od liczby rozpoczynanych w danym dniu zniesień. Gniazda zawierające jaja były istotnie częściej niszczone niż gniazda z pisklętami (Tab. 6). Na podstawie wyglądu zniszczonych gniazd (Tab. 6) oraz częstości obserwowanych na badanym terenie drapieżników stwierdzono, że prawdopodobnie głównym drapieżnikiem gniazd dzwońca był kot i, w mniejszym stopniu, kuna domowa. Ptaki, szczególnie krukowate, prawdopodobnie nie były odpowiedzialne za powstawanie strat w lęgach.

Straty częściowe były wyższe w stadium jaj niż w stadium piskląt (Tab. 7). Stwierdzono cztery przypadki śmierci ptaków dorosłych spowodowane kolizjami z samochodem (2 przypadki) i zaplątaniem się (uduszenie) w sznurek polipropylenowy. W jednym przypadku przyczyna śmierci była nieznaną.



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