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# Brood desertion by great tits *Parus major* caught at the nest

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900 catchings of great tits on their nests on the Vistula Spit (MW) and in Szwalewo Forest (SZ) in northern Poland were analysed. Males did not desert the nest after having been caught. Incubating females caught did abandon their nests in 14% (SZ) and 29% (MW) of cases, twice as often at the start of incubation as at the end, and more frequently after 17°° hrs (43%) than between 12°° and 17°° (21%) and before 12°° hrs (SZ 0%; MW 8%). Replacement clutches were deserted more often (55%) than not replaced ones (22%). Females touched but not caught in order to read their ring numbers did not desert the nest. Brooding females caught on small nestlings (up to 6 days old, with a wing length of up to 12 mm) deserted the nest on average in 22% of cases (before 12°° – 6%, after 12°° – 28%); if the nestlings were larger, in 2–3% of cases. The means of releasing the female had no effect on the frequency of nest desertion. The influence of the air temperature, length of catching time and previous catching of a female on the nest desertion frequency was analysed Provisional tables for calculating nestling age from feather development stage (taking probabilities into account) and wing length are given.

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Покидание кладок и выводков большой синицей *Parus major* вследствие отлова на гнезде

Проанализировали 900 случаев отловов большой синицы на гнезде, произведенных на Вислинской косе (MW) и в Швалевских лесах (SZ) в северной Польше. Самцы не покидали гнезда после того, что были словлены. Самки отловленные во времия насиживания покидали гнездо в 14% случаев (SZ) и в 29% случаев (MW); в начальной стадии насиживания в два раза чаще, чем под конец; чаще после 17°° (43%), чем между 12°° и 17°° (21%) и до 12°° (SZ 0%; MW 8%); чаще в случае повторных кладок (55%), чем регулярных (22%). Самки, к которым прикасались с целью идентификации кольца, но не словленные, не бросали гнезда. Самки отловленные на гнезде с маленькими птенцами (до 6 для жизни, с крылом до 12 мм) бросали гнезда в среднем в 22% случаев (до 12°° – в 6%, после 12°° – в 28%); когда птенцы были старше – в 2–3% случаев. Не обнаружили влияния способа выпущения самки на частоту покидания гнезда. Проанализировали зависимость частоты покидания гнезд от температуры воздуха, продолжительности манипулирования возле гнезда, прежнего отлова самки. Представили предварительные таблицы для вычисления возраста птенцов на основании стадий развития оперения (с принятием во внимание вероятностей) и длины крыла.

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## INTRODUCTION

In many ethological and ecological investigations there is a need to catch the owners' of a particular nest. However, catching these birds may lead to their abandoning the nest. It is well known that the frequency of nest desertion varies in different species and depends on the stage of development that eggs or nestlings have reached, on the weather, the researcher's conduct and other circumstances. Nevertheless, there is little definite information on this problem in the literature. The researcher thus has no alternative but to gain experience by himself, by trial and error. And errors here signify the abandonment of eggs or nestlings by the parents. I believe that people who have acquired knowledge at such a cost have a moral duty to share it with others.

In this paper, I would like to present my experiences with the great tit, gained during investigations carried on this frequently caught species.

## MATERIAL

The data were obtained during catching adult great tits in the day time on their nests in nestboxes. The boxes were hung up in woods on the Vistula Spit (54°22′N, 19°21′E, *c.* 550 nestboxes) and in Szwalewo Forest (Szwalewo forestry district in the Iława Lakeland, 53°43′N, 19°32′E, almost 500 nestboxes), in northern Poland. The boxes were fixed $3\frac{1}{2}$ m above the ground, every 50–60 m, most often along forest paths. Usually they were checked every 2 weeks.

I have analysed some 900 catchings on the Vistula Spit in 1979–84 and in Szwalewo Forest in 1979–83 (Table 1) carried out by myself (78% of catchings), Hanna SZARAFIŃSKA (10%), Wojciech JANKOWSKI (5%), Tomasz COFTA (4%) and six other people (3%). To compare the frequency of nest desertion by females variously released after being ringed, I have made use of a further 23 catchings, which I did myself on the Vistula Spit in 1986.

## METHODS

Great tits were caught either by hand when they were found on the nest during nestbox checks, or with traps when the adults were feeding their young.

During the routine inspections of nestboxes, incubating or brooding females were taken, and in some cases, both the female and the male, which had just entered the box with food and had decided to stay put on hearing the ladder being placed against the tree. On approaching the nestbox, we did not keep particularly quiet. On the contrary, we tried not to take the incubating birds by surprise. In 1981–84 we avoided catching incubating females and females with small nestlings, especially on cool days and in the afternoon. We did, however, try to see whether a bird was ringed, and if it was, to read the number without handling the bird. After slowly raising the front of the nestbox, the edge of the nest was depressed with the fingers to reveal the leg of the incubating bird, in some cases gently pulling the leg out from under the bird and rotating the ring. Sometimes the bird did not react, sometimes it jumped away to the rear of the box. Even then it was occasionally possible to rotate the ring sufficiently far for the number to be legible. If the bird attempted to fly out of the nestbox, which is what happened most often, it was not impeded.

Great tits of both sexes feeding the young were caught mostly with traps which made it impossible for birds to fly out of the nestboxes once they had entered. Two kinds of traps were used, both being placed at the entrance, inside the box: 1) a flap made from X-ray film, *i.e.* celluloid with black emulsion, or from blackened cardboard, supported by a stick; 2) 2–3 thin metal wires pivoting into the box only, to whose presence at the entrance the birds had earlier been accustomed by similar wires hung loosely over the entrance and freely movable within the box. The nestlings were ringed and measured usually after the parents had been caught and placed for the time being in cretonne bags. If the nestlings were fairly big, some of them were sometimes taken out of the nestboxes when the traps were being fitted, so that they could be measured and ringed while the parents were being awaited.

The caught great tits were treated in two ways. In 1979–81, they were ringed near the nestbox, after which they were carefully replaced on the nest, the hand containing the birds being moved under the raised front of the box. On some occasions, the birds then left the nest immediately, on others, they stayed. In 1982–84 and 1986, the recommendations of GRACZYK (1975) were followed. The caught bird's eyes were, if possible, covered. Then it was put in a bag, taken about 100 m from the nest (GRACZYK suggested 30 m), ringed there and released.

In this analysis I have included nests which were checked after a parent had been caught, usually two weeks later. I regarded nests as having been deserted owing to catching if: 1) the eggs had been abandoned, with no sign of predation; 2) all the nestlings were dead and had remained at the same stage of development they were in at the moment the parents had been caught (sometimes the stage of development in the decaying nestlings could be assessed only approximately). Of course, the reason for nest desertion could always have been unconnected with the catching – the parent could have been killed by a predator. But the probability of this happening, greatest in the case of nests regarded as deserted owing to criterion "1", was always small. This is discussed in greater detail on p. 84.

If a bird was caught several times, I have considered only the first catching on

each nest. Second and further catchings of the same birds on different nests in the same year have been treated differently for males and females (see the appropiate sections).

When catching adult great tits, we recorded the hour, and in some cases the time between the trap's fitting and its removal. Furthermore, the stage of feather development (KANIA 1983) in the most advanced sibling was noted, and usually the length of the folded wing of the largest sibling as well. These data were either used to assess the nestlings' age (see Appendix) and to calculate the hatching date, or used directly as an index of the nestlings' growth. If, on the day the parents were caught, the nestlings were not measured and described, the requisite data was calculated from measurements obtained before or after on the basis of the tables given in the Appendix.

The age of adult great tits was determined according to BUSSE (1984). I have described tits, completing their 1st and starting their 2nd year of life, *i. e.* in their 2nd calendar year, as "young", and birds at least one year older, *i. e.* older then the 2nd calendar year, as "old". A few great tits whose age was not determined (but which were after their 1st calendar year) have been taken into account only where the analysis refers to old and young birds together.

Air temperatures come from the Institute of Meteorology and Water Management's station at Świbno (25 km to the west of the western edge of the study area on the Vistula Spit) and from Prabuty (20 km west of Szwalewo Forest). Temperatures for individual catchings were interpolated from temperatures accurate to 0.1°C read at 8°°, 14°° and 20°° hours, assuming that they changed linearly. The use of temperatures measured at places some distance away from the catching points precludes our attributing these cases of nest desertion to particular air temperatures, but it does allow the general trends to be analysed.

I have calculated the significance of differences in the frequency of nest desertion by means of the proportional difference significance test, FISHER's exact test or the chi-squared test with YATES's correction (BLALOCK 1977). Wherever the name of the test is not given, I have used the first mentioned. 0.05 was adopted as the significance level of a difference.

## CATCHING OF MALES

Males were caught while feeding nestlings, usually by means of traps (179 by traps versus 3 by hand). In all, 199 males were caught on 213 nests (Table 1) – 7% of the catchings refer to males caught on more than one nest.

Of the 110 nests on which the male was caught without the female, only 2 were abandoned afterwards (Table 2). This happened on 10th June 1982, on the coolest of all the catching days in Szwalewo Forest in 1979–83. The air temperatures in the morning, at noon and in the evening were 8, 12 and 10°C respectively; it had also been cool the previous day. The person who caught both these males was rather

Table 1. Catching adult great tits and reading ring numbers in 1979–84

Taken into consideration are only those nests whose further fate was known, and the first catching in each nest. MW – Vistula Spit, SZ – Szwalewo Forest

Tabela 1. Schwytania dorosłych bogatek i odczyty numerów ich obrączek, dokonane w latach 1979–84

Uwzględniono tylko gniazda, których dalszy los był znany, oraz pierwsze schwytania na każdym gnieździe. MW – Mierzeja Wiślana, SZ – Lasy Szwalewskie

| Year / Rok | Site / Miejsce | ♂♂ | | | | ♀♀ | | |
|---|---|---|---|---|---|---|---|---|
| | | Only ♂ Tylko ♂ | ♂ & ♀ | | Total Razem | Readings** Odczytania** | Caught on Schwytane na | |
| | | | separately* oddzielnie* | together* razem* | | | eggs jajach | nestlings pisklętach |
| 1979 | MW | 1 | – | 1 | 2 | | 38 | 37 |
| | SZ | 1 | 1 | 2 | 4 | | 10 | 15 |
| 1980 | MW | 2 | 5 | 2 | 9 | | 75 | 48 |
| | SZ | 1 | – | – | 1 | | 35 | 23 |
| 1981 | MW | 11 | – | 5 | 16 | 11 | 5 | 72 |
| | SZ | 7 | 3 | 7 | 17 | 2 | 2 | 49 |
| 1982 | MW | 6 | 2 | 18 | 26 | 3 | 7 | 52 |
| | SZ | 6 | – | 11 | 17 | | 1 | 30 |
| 1983 | MW | 7 | 15 | 19 | 41 | 1 | 1 | 67 |
| | SZ | 8 | 6 | 9 | 23 | | 1 | 29 |
| 1984 | MW | 9 | 19 | 29 | 57 | 2 | 2 | 74 |
| Total Razem | MW | 36 | 41 | 74 | 151 | 17 | 128 | 350 |
| | SZ | 23 | 10 | 29 | 62 | 2 | 49 | 146 |
| | MW & SZ | 59 | 51 | 103 | 213 | 19 | 177 | 496 |

* Catchings together are regarded as those done in one operation lasting 2 hours at the most. Separate catchings almost always took place on different days.

* Za „schwytania razem" uznano te, których dokonano w jednej operacji, trwającej najwyżej 2 godziny. Schwytania oddzielnie prawie zawsze miały miejsce w różne dni.

** The ring number was read off without the bird being caught.

** Odczytania numeru obrączki bez schwytania ptaka.

inexperienced, and ringing and measuring these birds and their nestlings (12 in each nest) probably took a long time, which led to excessive temperature loss by the nestlings. It seems, therefore, that these two cases were exceptional.

The frequency of desertion after catching male and female in a single operation (6%, Table 2) does not differ significantly from the frequency of desertion after females alone had been caught using traps while they were feeding their young (8% for 64 nests), *i. e.* in the same conditions under which males were caught. It thus seems that catching the male does not increase the probability of nest desertion by the caught female. The conviction of this conclusion is weakened by the fact that rather few of the analysed catchings were in nests with the smallest and therefore most sensitive nestlings (Table 2). Nonetheless, I have considered simultaneous catchings of male and female together with catchings of females only.

Table 2. Desertion of nests on which feeding males were caught, with respect to the stage of nestling development

Tabela 2. Porzucanie gniazd, na których schwytano karmiące samce, w zależności od stopnia rozwoju piskląt

| The most advanced nestling in the nest Najbardziej rozwinięte pisklę w gnieździe | | Catching of ♂♂ Schwytania ♂♂ | | Nest desertion after catching Porzucenia gniazd po schwytaniach | |
|---|---|---|---|---|---|
| Stage of development* Stadium rozwoju* | Most probable age** Najbardziej prawdopodobny wiek** | separately from ♀*** oddzielnie od ♀*** | together with ♀*** razem z ♀*** | separately from ♀*** oddzielnie od ♀*** | together with ♀*** razem z ♀*** |
| A–C, ⩽ 12 | 1–6 | 8 | 5 | – | 2 |
| C, > 12 | 6–9 | 18 | 16 | – | 1 |
| D | 9–12 | 10 | 14 | 2 | 1 |
| E–F | 10–16 | 31 | 30 | – | 2 |
| G | 13–19 | 43 | 38 | – | – |
| Total – Razem | | 110 | 103 | 2 | 6 |

* The feather development stage (KANIA 1983) of the most advanced sibiling and the wing length (mm) of the largest sibling are given. For the criterion of dividing the nestlings into categories, see pp. 92, 93.

Podano stadium rozwoju upierzenia (KANIA 1983) pisklęcia najbardziej rozwiniętego i długość skrzydła (mm) pisklęcia największego spośród rodzeństwa. Uzasadnienie podziału piskląt na kategorie – zob. str. 92, 93.

** In days, counting the hatching day as the 1st day of life

** W dniach, licząc dzień klucia jako 1. dzień życia.

*** See note under Table 1.

*** Zob. odnośnik pod tab. 1.

## MULTIPE CATCHINGS OF FEMALES

Some females were caught on 2 or 3 different nests, in the same year or in different years. Analysis of catchings of females incubating eggs or brooding small nestlings (wing ⩽ 12 mm), *i.e.* in the period when they desert the nest fairly often (see pp. 88 and 94), did not show that a previous catching increased the probability of the nest being abandoned after the next catching (Table 3). On the other hand, it turned out that females behaved in the same way after the second catching as after the first more often than would simply happen by chance (Table 4, $p = 0.048$, FISHER's test) though the connection between the frequencies of nest desertion after the first and second catching is a weak one ($\Phi = 0.32$). In order to retain the independence of the data used to define the significance of differences, I have no longer taken second

Table 3. Nest desertion by females caught a second time in the same year on a different nest
This table covers catchings on eggs and nestlings with wing length ⩽ 12 mm on the Vistula Spit in 1979–81
Tabela 3. Porzucanie gniazda przez samice chwytane powtórnie w danym roku na innym gnieździe
Uwzględniono schwytania na jajach i pisklętach o skrzydle ⩽ 12 mm, na Mierzei Wiślanej w latach 1979–81

| Catchings – Schwytania | | Desertions Porzucenia | | Significance of difference ($p$)* Istotność różnicy ($p$)* |
|---|---|---|---|---|
| consecutive no. – nr kolejny | $N$ | $N$ | % | |
| First – Pierwsze | 157 | 38 | 24 | 0.13 |
| Second** – Drugie** | 26 | 9 | 35 | |

* One-sided test
* Test jednostronny
** See Table 4
** Por. tab 4

Table 4. Nest desertion by females caught a second time with respect to the fate of the nest after the first catching
Data from Table 3 taken into account
Tabela 4. Porzucanie gniazda przez samice chwytane powtórnie w zależności od losu gniazda po pierwszym schwytaniu
Uwzględniono dane z tabeli 3

| Catching Schwytanie | | Second – Drugie | | |
|---|---|---|---|---|
| | Nests Gniazda | not deserted nie porzucone | deserted porzucone | total razem |
| First – Pierwsze | not deserted nie porzucone | 11 | 2 | 13 |
| | deserted porzucone | 6 | 7 | 13 |
| | total razem | 17 | 9 | 26 |

catchings into consideration if these catchings were on nests with eggs/nestlings at the same class of development. To define this class, a four-point scale was used: 1) eggs; 2) small nestlings (wing length ⩽ 12 mm); 3) medium and large nestlings (wing length > 12 mm), but whose feather had reached development stage F at the most (this class includes the second and third nestling age group from p. 92); 4) fledglings, in feather development stage G.

## CATCHING OF INCUBATING FEMALES

Incubating females were caught mainly in 1979–80 (Table 1). Among the nests which I regarded as having been deserted owing to the catching of the female, there could have been some which were abandoned for other reasons. But as the analysis of nest desertion by females not caught on the nest shows (Table 5), this hardly happened at all.

Table 5. Desertion of nests containing eggs* on which females were not caught
Data from the Vistula Spit
Tabela 5. Porzucanie gniazd z jajami*, na których nie schwytano samic
Dane z Mierzei Wiślanej

| Year – Rok | | | 1979 | 1980 |
|---|---|---|---|---|
| Number of nests Liczba gniazd | checked<br>w których dokonywano przeglądu | | 88 | 204 |
| | deserted at the egg stage with no sign of nest destruction or of the female having been killed by a predator | *n* | 0 | 4 |
| | porzuconych w stadium jaj bez oznak zniszczenia gniazda lub zabicia samicy przez drapieżnika | % | 0 | 2 |

* This refers to nests with at least 6 eggs, and disregards the few with incomplete 1- and 3-egg clutches, since the females could not have been caught before incubation began.

* Uwzględniono gniazda z przynajmniej 6 jajami, pomijając kilka z niepełnymi 1 i 3 jajowymi zniesieniami, bowiem samice nie miały szans być schwytanymi przed rozpoczęciem wysiadywania.

**The effect of the advancement of incubation.** It is not known at which stage of the incubation the eggs were abandoned. But the dependence of the egg desertion rate on the advancement of the incubation can be inferred indirectly from the relationship between the number of nests which were not deserted by caught females and the time that elapsed between catching and hatching.

In my analysis I have used the index $A_d$:

$$A_d = \sum_e \frac{B_{de}}{(N_{de} : \sum_{d=1}^{14} N_{de}) \cdot 100},$$

where: the subscript $d$ stands for the number of days before hatching; the hatching day itself is 0; the subscript $e$ is the date when the incubating female was caught; $A_d$ is the rate of the non-desertion of nests by females caught on their eggs on day $d$; $B_{de}$ is the absolute number of nests which, $d$ days before hatching, were not abandoned by the females caught on day $e$;

$N_{de}$ is the total number of nests in the population investigated (including the

nests on which females were not caught) on day $e$, which were $d$ days before hatching. This number in the present analysis does not include nests destroyed or deserted at the egg stage, because in these cases it was not possible to determine how far incubation had advanced (*i.e.* the number of days left before hatching). However, in view of the relatively small number of such nests, disregarding them should not significantly affect the value of $A_d$; $\sum_{d=1}^{14} N_{de}$ (abbreviated to $\sum N_{de}$) is the total number of clutches being incubated on day $e$, *i. e.*, which on this day were 14, 13, ... , 2, 1 days before hatching (assuming that the incubation period in the great tit is 14 days).

I derived the above formula from the following reasoning: The nests with eggs on which females were caught on day $e$ were a random sample of nests containing incubated eggs (catching of females laying eggs was unlikely and can be ignored) on day $e$. These nests were at various stages of incubation ($d$). The number of nests at particular stages differed. Therefore $B_{de}$ depends not only on the number of females which did abandon their nests but also on the number of nests at stage $d$ present in the investigated population on day $e$.

In order to eliminate the influence of this last number, $B_{de}$ has to be divided by a suitable weight. This weight is the percentage represented by $N_{de}$ in relation to $\sum N_{de}$.

To obtain each of the values of $A_d$ ($A_1$, $A_2$, ... $A_{14}$ in the case of the great tit), the above calculations have to be repeated for each day of catching ($e$) when incubating females at stage $d$ were caught.

Not knowing the exact dates of hatching, I took the most probable hatching dates which I calculated from the age of the nestlings determined from their wing lengths (Appendix). For the same reason, I could not determine the number of nests which were at a given stage of incubation, *i. e.* $N_{de}$ and $\sum N_{de}$, either. I therefore replaced these numbers with the appropriate sums of the probabilities that given nests were at a particurlar stage of incubation, which I calculated from the age of the nestlings determined from their feather development stage (Appendix).

As an example, I shall show how I calculated $A_d$ for the eighth day prior to hatching, *i. e.* $A_8$ (Fig. 1). There were 4 nests not deserted by their females which had been caught on the 8th day before hatching (assuming the hatching dates to be the most probable ones calculated from the nestlings' wing length). 3 females were caught on 1 July 1980 on the Vistula Spit, the fourth one on 26 June 1980 in Szwalewo Forest. The hatching of this first three females' nestlings probably commenced on 9 July 1980. The sum of the probabilities of hatching on 9 July 1980, that is $N_{de}$ (where $d = 8$, $e = 1$ July) was 7.2% of $\sum N_{de}$, that is, of the sum of probabilities of hatching on 2 – 15 July 1980 – the first 14 days after the catching date. Dividing $B_{de}$ (here $B_{8,\ 1\ \mathrm{July}}$) = 3 by 7.2, I got 0.42. To this value I added 0.10, similarly calculated[1] for the fourth female, and obtained 0.52 (Fig. 1).

[1] For $\sum N_{de}$ calculated for the period 27 June – 10 July 1980 for the data from Szwalewo Forest.

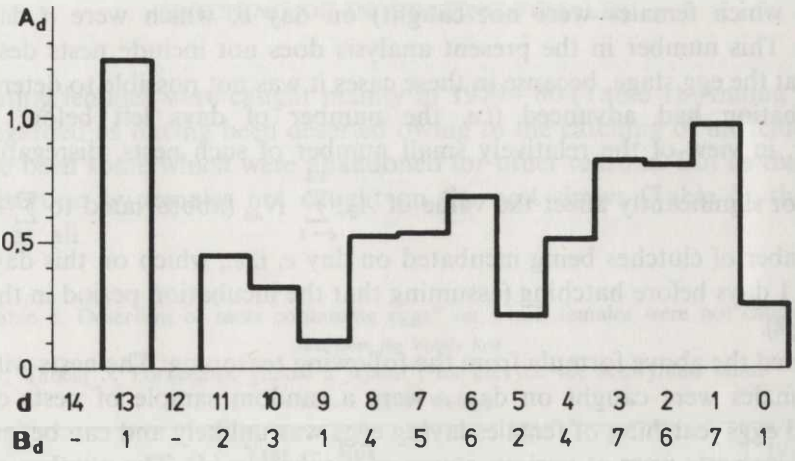


Fig. 1. Relative numbers of second clutch nests not deserted after catching the female (explanations in the text)

Data from the Vistula Spit and Szwalewo Forest in 1980.
d – days before hatching, $B_d$ – absolute number of nests

Ryc. 1. Względna liczebność gniazd drugiego lęgu, nie porzuconych po schwytaniu samicy (objaśnienia w tekście)

Dane z Mierzei Wiślanej i Lasów Szwalewskich z 1980 r.
d – dni przed kluciem, $B_d$ – bezwzględna liczba gniazd

However, in order to calculate $A_d$ in this way we can use only the catchings made on the days when nests in all stages of incubation were present in the population. This condition was satisfied by the catchings on second-clutch nests from 30 June to 2 July 1980 on the Vistula Spit (Fig. 2) and from 23 to 27 June 1980 in Szwalewo Forest.

The picture thus obtained (Fig. 1) shows that the probability of nest desertion following the catching of the incubating female decreases as the hatching date approaches. This probability is about twice as high at the start of incubation as at the end.

There were two cases in which (young) females did not desert their nests on being after laying the second egg (the complete clutches comprised 10 and 9 eggs), at 14°° and 19°° hours, in both cases about 15 days before hatching started.

**The effect of the means of releasing the female.** To compare the frequency of nest desertion by females replaced on the nest after ringing and by those released 100 m from the nest, I have used only catchings done on the Vistula Spit between 7°° and 16°° hours, because the females released 100 m from the nest had been caught on their clutches only in this place and at these times. The difference was not significant (Table 6). Even so, in the further analysis I have used only data on females replaced on the nest after being ringed, because the number of females released 100 m away from their nests was rather small (less than 20% of the data from 1979–84).

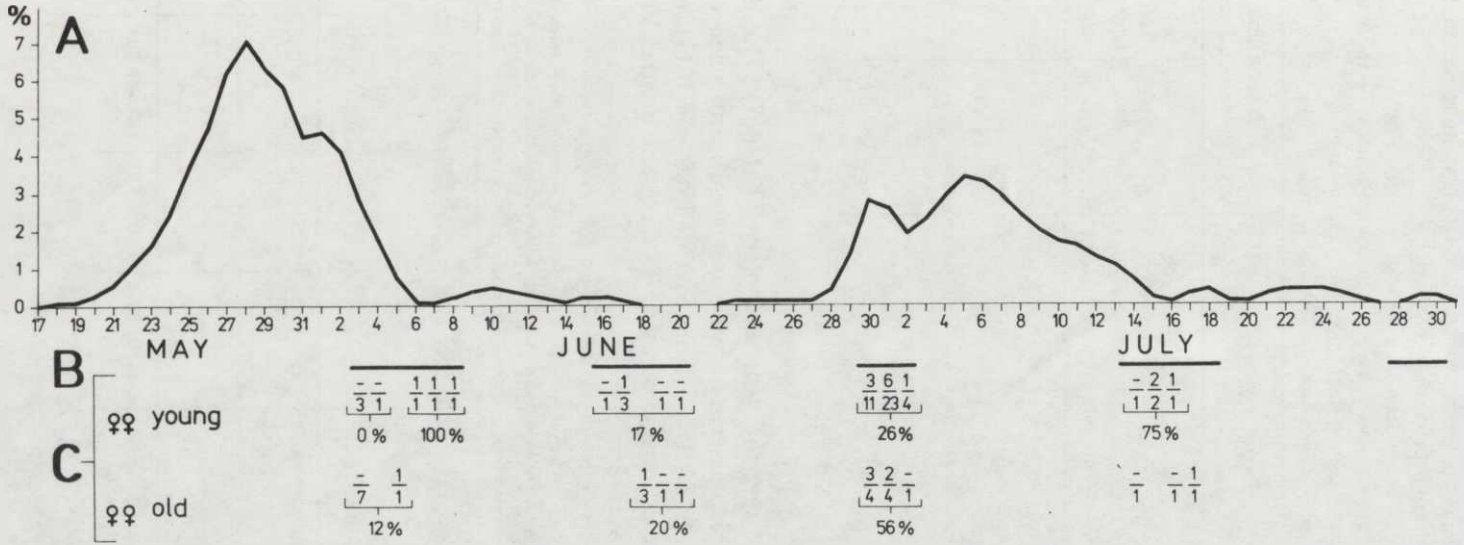


Fig. 2. Nest desertion frequency after catching incubating females with respect to the breeding period phase, on the Vistula Spit in 1980

A – probability distribution of hatching on particular days for 254 nests, calculated using the conversion of feather development stage to age (Appendix); B – nest check days; C – ratio of the number of nests deserted following catching of the incubating female to the number of all catchings of incubating females, separately for females of different ages, and % of desertions

Ryc. 2. Częstość porzucania gniazda po schwytaniu samicy na jajach, w zależności od fazy okresu lęgowego, na Mierzei Wiślanej w 1980 r.

A – rozkład prawdopodobieństw klucia w poszczególne dni dla 254 gniazd, obliczony z wykorzystaniem przeliczania stadiów rozwoju upierzenia piskląt na wiek (Dodatek); B – dni przeglądów gniazd; C – stosunek liczb gniazd porzuconych w wyniku schwytania wysiadującej samicy do liczb wszystkich schwytań samic na jajach, oddzielnie dla samic różnego wieku, oraz % porzuceń

Table 6. Nest desertion by females caught on eggs between 7°° and 16°° hrs with respect to the method of releasing the female after ringing

Data from the Vistula Spit. Explanation of symbols – see Table 7

Tabela 6. Porzucanie gniazda przez samice, schwytane na jajach w godzinach 7–16, w zależności od sposobu wypuszczenia samicy po zaobrączkowaniu

Dane z Mierzei Wiślanej. Objaśnienia symboli – zob. tab. 7

| Female age<br>Wiek samic | | Young – Młode | | Young and old<br>Młode i stare | |
|---|---|---|---|---|---|
| Method of release<br>Sposób wypuszczania | Years<br>Lata | $N_C$ $N_D$ % | Significance of difference<br>Istotność różnicy<br>($p$) | $N_C$ $N_D$ % | Significance of difference<br>Istotność różnicy<br>($p$) |
| Replacement on nest<br>Położenie na gnieździe | 1979–81 | 54 9 17 | 0.36 | 72 14 19 | 0.30 |
| Release 100 m from nest<br>Wypuszczenie 100 m od gniazda | 1982–84<br>&<br>1986 | 23 2 9 | | 28 3 11 | |

**The effect of the female's age, the year and place** (Table 7). The differences between the proportions of nest desertions were not significant when comparing either young and old birds (*e. g.* for the Vistula Spit in 1980, $p = 0.11$), or the two years. On the other hand, desertions were twice as frequent on the Vistula Spit

Table 7. Nest desertion by females caught on eggs

MW – Vistula Spit, SZ – Szwalewo Forest, $N_C$ – number of catchings, $N_D$ – number of desertions, % – percentage of desertions

Tabela 7. Porzucanie gniazda przez samice schwytane na jajach

MW – Mierzeja Wiślana, SZ – Lasy Szwalewskie, $N_C$ – liczba schwytań, $N_D$ – liczba porzuceń, % – procent porzuceń

| Female age<br>Wiek samic | | Young – Młode | | Old – Stare | | Total – Razem | |
|---|---|---|---|---|---|---|---|
| Year<br>Rok | Site<br>Miejsce | $N_C$ $N_D$ % | $N_C$ $N_D$ % | $N_C$ $N_D$ % | $N_C$ $N_D$ | $N_C$ $N_D$ % | $N_C$ $N_D$ % |
| 1979 | MW | 27 7 26 | | 9 2 22 | | 36 9 25 | |
| | SZ | | 9 1 11 | | 1 – | | 10 1 10 |
| 1980 | MW | 50 13 26 | | 17 8 47 | | 67 21 31 | |
| | SZ | | 28 5 18 | | 5 – | | 33 5 15 |
| Total<br>Razem | MW | 77 20 26 | | 26 10 38 | | 103 30 29* | |
| | SZ | | 37 6 16 | | 6 – | | 43 6 14* |

* $p = 0.03$.

(29%) as in Szwalewo Forest (14%). The incubation stage when birds were caught in these two places was the same.

**The effect of temperature.** Nest desertion after catching the female was significantly more frequent when the temperature was between 20 and 22°C then at lower temperatures (Table 8).

Table 8. Nest desertion by females caught on eggs with respect to air temperature
Data from 1979–81. Explanation of symbols – see Table 7
Tabela 8. Porzucanie gniazda przez samice, schwytane na jajach, w zależności od temperatury powietrza
Dane z lat 1979–81. Objaśnienia symboli – zob. tab. 7

| Female age<br>Wiek samicy | Young – Młode | | | Old – Stare | | | Total – Razem | | |
|---|---|---|---|---|---|---|---|---|---|
| Temperature (°C)<br>Temperatura (°C) | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % |
| 10.1–12.0 | 4 | – | – | 2 | 1 | – | 6 | 1 | 17 |
| 12.1–14.0 | 22 | 6 | 27 | 8 | 3 | – | 30 | 9 | 30 |
| 14.1–16.0 | 30 | 5 | 17 | 5 | 1 | – | 35 | 6 | 17 |
| 16.1–18.0 | 34 | 6 | 18 | 10 | 3 | – | 44 | 9 | 20 |
| 18.1–20.0 | 8 | 2 | 25 | 2 | – | – | 10 | 2 | 20 |
| 20.1–22.0 | 9 | 5 | 56* | 4 | 2 | – | 13 | 7 | 54** |
| 22.1–24.0 | 4 | – | | 3 | – | – | 7 | – | |
| 24.1–26.0 | 3 | 2 | 29 | – | – | – | 3 | 2 | 18 |
| 26.1–28.0 | – | – | | 1 | – | – | 1 | – | |
| 10.1–20.0 | 98 | 19 | 19* | 27 | 8 | 30 | 125 | 27 | 22** |
| Total – Razem | 114 | 26 | 23 | 35 | 10 | 29 | 149 | 36 | 24 |

* $p = 0.04$; chi-squared = 4.29; df = 1.
** $p = 0.02$; chi-squared = 5.37; df = 1.

**The effect of time of day.** The probability of nest desertion after the female has been caught increases as the day progresses (Table 9, Fig. 3). The frequencies of desertion by females on the Vistula Spit and in Szwalewo Forest are similar in the afternoon (after 15°° hrs), but different in earlier hours (Table 9, $p = 0.04$, FISHER's test).

**The effect of a replacement clutch.** Desertion of nests containing replacement clutches is far more frequent than the abandonment of nests containing first-time clutches (Table 10, $p = 0.05$, chi-squared = 3.8, df = 1). The significance of the difference is even 0.002 (chi-squared = 10.3) if the catchings on the Vistula Spit on the 3 and 4 July 1980 (Fig. 2) are rejected, assuming that they were done at the late first-time nests.

Table 9. Nest desertion by females caught on eggs with respect to time of day

Data from 1979–81. Explanation of symbols – see Table 7

Tabela 9. Porzucanie gniazda przez samice schwytane na jajach, w zależności od pory dnia

Dane z lat 1979–81. Objaśnienia symboli – zob. tab. 7

| Female age<br>Wiek samic | Young – Młode | | | | | | | | | Old – Stare | | | Young and old<br>Młode i stare | | | Significance of difference<br>Istotność różnicy<br>($p$) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site<br>Miejsce | MW | | | SZ | | | total<br>razem | | | MW & SZ | | | MW & SZ | | | |
| Hour of catching<br>Godzina schwytania | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | |
| 7 | – | – | – | 1 | – | – | 1 | – | – | – | – | – | 1 | – | – | |
| 8 | 1 | – | – | 2 | – | – | 3 | – | – | 1 | – | – | 4 | – | – | |
| 9 | 9 | 1 | 11 | 4 | – | – | 13 | 1 | 8 | 3 | 1 | – | 16 | 2 | 12 | |
| 10 | 9 | 1 | 11 | 5 | – | – | 14 | 1 | 7 | 1 | – | – | 15 | 1 | 7 | |
| 11 | 5 | – | – | 3 | – | – | 8 | – | – | 2 | – | – | 10 | – | – | |
| 12 | 9 | 2 | 22 | 3 | – | – | 12 | 2 | 17 | 2 | 1 | – | 14 | 3 | 21 | |
| 13 | 6 | 1 | 17 | 2 | – | – | 8 | 1 | 12 | 5 | 1 | – | 13 | 2 | 15 | |
| 14 | 4 | 2 | 50 | 3 | – | – | 7 | 2 | 29 | 3 | 1 | – | 10 | 3 | 30 | |
| 15 | 7 | 1 | 14 | 3 | 1 | 25 | 10 | 2 | 20 | 3 | – | – | 13 | 2 | 15 | |
| 16 | 4 | 1 | 25 | 5 | 1 | | 9 | 2 | 22 | 3 | 1 | – | 12 | 3 | 25 | |
| 17 | 8 | 4 | 50 | 1 | 1 | | 9 | 5 | 56 | 4 | 1 | – | 13 | 6 | 46 | |
| 18 | 9 | 5 | 56 | 5 | 2 | 44 | 14 | 7 | 50 | 1 | 1 | – | 15 | 8 | 53 | |
| 19 | 7 | 1 | | 3 | 1 | | 10 | 2 | | 4 | 2 | – | 14 | 4 | 29 | |
| 20 | 1 | – | 22 | – | – | – | 6 | – | 25 | 2 | 1 | – | 3 | 1 | 40 | |
| 21 | 1 | 1 | | – | – | – | 1 | 1 | | 1 | – | – | 2 | 1 | | |
| 7–11 | 24 | 2 | 8 | 15 | – | – | 39 | 2 | 5 | 7 | 1 | 14 | 46 | 3 | 7 | 0.02 |
| 12–16 | 30 | 7 | 23 | 16 | 2 | 12 | 46 | 9 | 20 | 16 | 4 | 25 | 62 | 13 | 21 | 0.02 |
| 17–21 | 26 | 11 | 42 | 9 | 4 | 44 | 35 | 15 | 43 | 12 | 5 | 42 | 47 | 20 | 43 | |
| Total<br>Razem | 80 | 20 | 25 | 40 | 6 | 15 | 120 | 26 | 22 | 35 | 10 | 29 | 155 | 36 | 23 | |

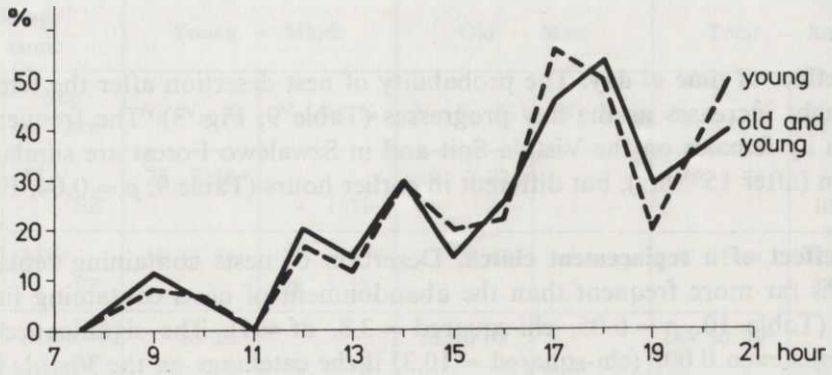


Fig. 3. Percentage of nests abandoned by young and old females caught on eggs at different times of the day

Combined data from the Vistula Spit and Szwalewo Forest, from Table 9

Ryc. 3. Procent gniazd porzuconych przez samice młode i stare, schwytane na jajach w różnych godzinach

Połączone dane z Mierzei Wiślanej i Lasów Szwalewskich, z tab. 9

Table 10. Nest desertion by young females, caught on eggs, with respect to the breeding period phase
Explanation of symbols – see Table 7
Tabela 10. Porzucanie gniazda przez samice młode, schwytane na jajach, w zależności od fazy okresu lęgowego
Objaśnienia symboli – zob. tab. 7

| Clutch<br>Lęg | Site<br>Miejsce | Period<br>Okres | $N_C$ | $N_D$ | % |
|---|---|---|---|---|---|
| 1. | MW | 28 May – 1 June 1979 | 21 | 4 | 19 |
| 2. | MW | 16–20 June &<br>30 June – 2 July<br>1980** | 44 | 11 | 25 |
| 2. | SZ | 11 & 23–27 June 1980 | 25 | 5 | 20 |
| total 1. and 2.<br>razem | | | 90 | 20 | 22 |
| replaced*<br>powtarzane* | MW | 3–8 June &<br>14–16 July 1980** | 11 | 6 | 55 |

* Clutches were regarded as replacement clutches if hatching occurred after the completion of the main wave of hatchings of 1st and 2nd clutches.
* Za zniesienia powtarzane uznano zniesienia, w których klucie nastąpiło po zakończeniu głównej fali kluć 1. i 2. lęgu.
** See Fig. 2.
** Zob. ryc. 2.

**The effect of the presence of predators.** It appears that the large-scale destruction of nests by the pine marten *Martes martes* or the squirrel *Sciurus vulgaris* in the area does not increase the tendency for female great tits caught by humans to abandon their clutches, so long as they had not lost a clutch earlier on (Table 11).

**Reading rings without catching females.** None of the 19 incubating females, whose ring numbers were read off without the birds being handled, abandoned their nests.

## CATCHING OF BROODING FEMALES

Apart from those nests which, on the basis of the criteria outlined in the methods section, I regarded as deserted or not deserted as a result of catching the female, there were 13 nests (Table 12) which I have omitted from further consideration. In four of them, the nestlings were developing abnormally or were famished (some I found dead). Their chances of survival were small, regardless of the female's reaction to being caught. In 9 cases the nests were destroyed by a predator which could has been attracted by the particularly shrill voices of the nestlings, famished after the break in feeding caused by catching. It seems, however, that the omission of these 13 catchings would tend to lower the number of nests not deserted after the female had been caught rather than the number of nests abandoned for that reason.

Table 11. Nest desertion following catching of great tit females with respect to intensity of predation by pine marten and/or squirrel on the Vistula Spit in 1980
Tabela 11. Porzucanie gniazda po schwytaniu samicy bogatki w zależności od natężenia drapieżnictwa kuny i/lub wiewiórki na Mierzei Wiślanej w 1980 r.

| Number<br>Liczba | Area intensively hunted by predators<br>Obszar intensywnej penetracji drapieżnika | Area not or only sporadically hunted by predators<br>Obszar bez lub ze słabą penetracją drapieżnika |
|---|---|---|
| nestboxes<br>skrzynek lęgowych | 99 | 470 |
| nests destroyed by the pine marten or squirrel*<br>gniazd zniszczonych przez kunę lub wiewiórkę* | 20 | 2 |
| nests on which great tit females were caught<br>gniazd, na których schwytano ♀♀ bogatki | 13 | 110 |
| nests deserted after great tit females had been caught<br>gniazd porzuconych po schwytaniu ♀♀ bogatki | 3 = 23% | 27 = 25% |

* Nests destroyed by the pine marten or squirrel were regarded as those which had been overturned, with nesting material pulled up towards the box entrance and often pulled right outside. Here, the nests of all bird species have been taken into account, mainly those of tits and of the pied flycatcher.

* Za gniazda zniszczone przez kunę lub wiewiórkę uznano te, które były wywrócone, z materiałem podciągniętym ku otworowi skrzynki lęgowej, często przezeń wyciągniętym na zewnątrz. Uwzględniono tu gniazda wszystkich gatunków ptaków, głównie sikor i muchołówek żałobnych.

On the other hand, of those nests, I regarded as deserted owing to the female having been caught, the nestlings in three of them (in Szwalewo Forest in 1982) could have perished for a different reason. In two nests there were 7- and 11-day old nestlings which had been kept out of the nest for far longer than normal, while in the third, the 11-day old nestlings were somewhat underweight. In some cases I have treated them separately, using the term "desertion uncertain".

**The effect of nestling age.** I have divided the nests with nestlings on which females were caught into 4 groups (Table 13):

1. nests with biggest sibling naked, requiring intensive brooding by the female, in feather development stages form A to C, having a wing length of up to 12 mm, 1–6 days old. Such nestlings I later called "small" ones;

2. nests with biggest sibling still not covered with feathers and requiring brooding, in stage C, with a wing length longer than 12 mm, 6–9 days old;

3. nests with biggest sibling feathered and not really needing to be warmed by the female any more, but not capable of flight either, in stages D to F, 9–16 days old;

Table 12. Desertion of nests where females were caught on nestlings
Tabela 12. Porzucanie gniazd, na których schwytano samicę na pisklętach

| Year Rok | Site Miejsce | Number of catchings Liczba schwytań | | Nest desertions – Porzucenia gniazd | | | |
|---|---|---|---|---|---|---|---|
| | | | | because of catching z powodu schwytania | | probably for other reasons prawdopodobnie z innych powodów | |
| 1979 | MW | 37 | | 6 | | | |
| | SZ | | 15 | | 2 | | |
| 1980 | MW | 45 | | 4 | | | |
| | SZ | | 22 | | 3 | | 3 |
| 1981 | MW | 67 | | 5 | | | |
| | SZ | | 46 | | 3 | | 3 |
| 1982 | MW | 49 | | 5 | | 1 | |
| | SZ | | 29 | | 8* | | |
| 1983 | MW | 64 | | 2 | | 1 | |
| | SZ | | 27 | | 3 | | 2 |
| 1984 | MW | 67 | | 3 | | 3 | |
| Total Razem | MW & SZ | 329 | 139 | 25 | 19 | 5 | 8 |
| | | 468 | | 44 | | 13 | |

* Including 3 "uncertain" desertions.
* W tym 3 porzucenia „niepewne"

4. nests with biggest sibling generally capable of horizontal or upward flight, in stage G, 13–19 days old.

The two first groups I differentiated by taking into consideration the fact that the nests with nestlings whose wing lengths had not yet reached 13 mm were often abandoned (every fifth nest), whereas nests with bigger nestlings were rarely deserted (1 in 33, or even 45 nests, if we reject the three "uncertain" cases, Table 13). The borderline between groups 1 and 2 is a clear-cut one. Of 9 nests in which at female catching the wing length of the largest nestlings was 12 mm, 3 were abandoned, whereas not one of the 8 in which the largest nestlings had a wing length of 13 mm.

Within none of these 4 groups was it possible to determine any difference in the frequency of desertion dependent on wing length. On the other hand, the nests in group 1 were deserted significantly more often than nests containing larger nestlings (for both young and old females $p < 0.0001$).

Table 13. Nest desertion by females caught on nestlings with respect to the stage of nestling development and the duration of catching

Explanation of symbols – see Table 7

Tabela 13. Porzucanie gniazda przez samice schwytane na pisklętach w zależności od stopnia rozwoju piskląt i długości czasu chwytania

Objaśnienia symboli – zob. tab. 7

| Female age<br>Wiek samic | | Young – Młode | | | | | | | | | Old – Stare | | | | | | Young and old<br>Młode i stare | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Catching duration<br>Czas chwytania | | ⩽ 15′ | | | > 15′ | | | total***<br>razem*** | | | ⩽ 15′ | | | > 15′ | | total***<br>razem*** | ⩽ 15′ | | | > 15′ | | | total***<br>razem*** | | |
| Stage of nestling development**<br>Stadium rozwoju piskląt** | Age (days)<br>Wiek (dni) | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | $N_C$ $N_D$ % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % |
| A – C, ⩽ 12 | 1 – 6 | 49 | 10 | 20 | 8 | 5 | 62 | 117 | 25 | 21 | 14 | 4 | 29 | 6 | – | 34 7 21 | 65 | 15 | 23 | 15 | 6 | 40 | 157 | 34 | 22 |
| C, > 12 | 6 – 9 | 8 | – | – | 19 | 2* | 11 | 60 | 2 | 3 | 9 | – | – | 10 | – | 24 – – | 18 | – | – | 33 | 3 | 9 | 90 | 3 | 3 |
| D – F | 9 – 16 | 16 | 1* | 6 | 45 | 3* | 7 | 85 | 5 | 6 | 5 | – | – | 24 | – | 32 – – | 21 | 1 | 5 | 71 | 3 | 4 | 120 | 5 | 4 |
| G | 13 – 19 | 7 | – | – | 45 | 1 | 2 | 61 | 1 | 2 | 2 | – | – | 15 | – | 18 – – | 9 | – | – | 63 | 1 | 2 | 83 | 1 | 1 |
| Total<br>Razem | | 80 | 11 | | 117 | 11 | | 323 | 33 | | 30 | 4 | | 55 | | 108 7 | 113 | 16 | | 182 | 13 | | 450 | 43 | |

* Including one "uncertain" desertion (see p. 92).

* W tym jedno porzucenie „niepewne" (zob. str. 92).

** See note under Table 2.

** Zob. odnośnik pod tabelą 2.

*** This includes catchings where the method (by hand or with a trap) was not noted.

*** Uwzględniono tu także schwytania, przy których nie zanotowano, czy zostały dokonane ręką, czy za pomocą pułapki.

**The effect of the means of releasing the female.** I did not discover any significant difference between the frequencies of nest desertion by females variously released after being caught (Table 14). So in my further analysis, I have treated the catchings of females replaced on the nest after being ringed and of those released some distance away from it as a single group (unlike the case of catchings on eggs, as similar treatment would lead to the omission of too much data).

Table 14. Nest desertion by females caught on nestlings having a wing length of $\leqslant 12$ mm with respect to the method of releasing the female after ringing

Explanation of symbols – see Table 7

Tabela 14. Porzucanie gniazda przez samice, schwytane na pisklętach o skrzydle $\leqslant 12$ mm, w zależności od sposobu wypuszczenia samicy po zaobrączkowaniu

Objaśnienia symboli – zob. tab. 7

| Site – Miejsce | | MW | | | SZ | | | Total – Razem | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Method of release<br>Sposób wypuszczania | Years<br>Lata | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | Significance of difference<br>Istotność różnicy ($p$) |
| Replacement on nest<br>Położenie na gnieździe | 1979–81 | 77 | 13 | 17 | 28 | 6 | 21 | 105 | 19 | 18 | 0.16 |
| Release 100 m from nest<br>Wypuszczenie 100 m od gniazda | 1982–84 & 1986 | 24 | 6 | 25 | 10 | 4 | 40 | 34 | 10 | 29 | |

**The effect of catching duration.** I have divided catching times into $\leqslant 15$ minutes and $> 15$ minutes (Table 13). The first group included females caught by hand surprised in the nestbox during routine checks, and those caught by a trap, so long as no more than 15 minutes elapsed from the installation of the trap to its removal (12 cases). The second group contained all other trappings, even those where the trapping time was not noted (in 16% cases this time may have been less than 15 minutes, assuming the data in Fig. 4b to be representative). In young females brooding small nestlings (wing length $\leqslant 12$ mm), where trapping lasted over 15 minutes (*i. e.* together with ringing and measuring the nestlings and their parents – over *c.* 30 minutes), the frequency of desertion was significantly greater than in catching of shorter duration (Table 13, $p = 0.02$, FISHER's test). The difference was not significant where old females were involved ($p = 0.21$, FISHER's test), neither was it significant when females brooding nestlings with wing lengths exceeding 12 mm were caught.

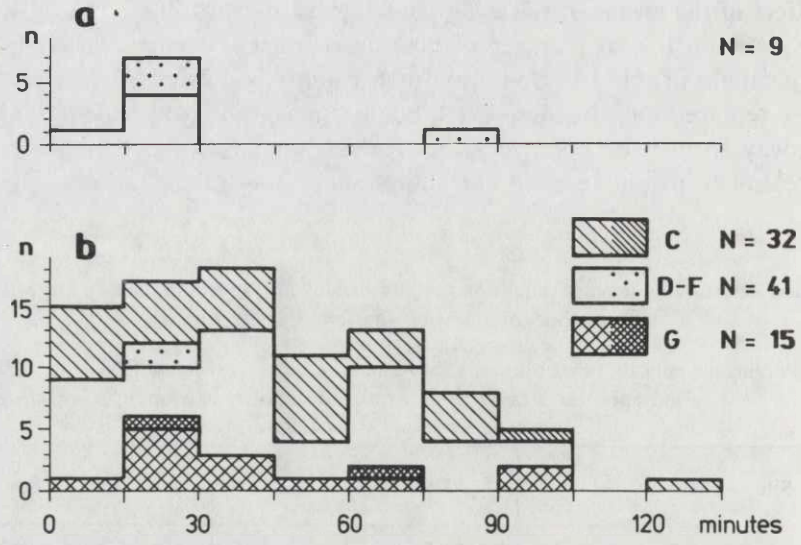


Fig. 4. Trapping time (from installing to removing the trap) of brooding females

a – nests with nestlings having a wing length of up to 12 mm (1–6 days old); b – nests containing nestlings with wing lengths over 12 mm, in plumage development stages C, D-F and G (6–9, 9–16 and 13–19 days old); N – number of trappings. The thicker dashes or dots indicate nests deserted after the female had been trapped

Ryc. 4. Czas chwytania (od założenia do zdjęcia pułapki) samic na gniazdach z pisklętami

a – gniazda z pisklętami o długości skrzydła do 12 mm (1–6 dniowymi); b – gniazda z pisklętami o długości skrzydła ponad 12 mm, w stadiach rozwoju upierzenia C, D–F i G (6–9, 9–16 i 13–19 dniowymi); N – liczba schwytań. Gęstszym kreskowaniem lub kropkami zaznaczono gniazda porzucone w wyniku schwytania samicy

Of 97 trappings whose durations I measured, there were many which, though taking rather long, did not lead to the abandonment of the nestlings (Fig 4).

**The effect of the female's age.** With catching on small nestlings lasting 15 minutes or less, I did not find any significant difference in the nest desertion rate between young and old females. But when catching took longer, the old females did not abandon their nestlings, whereas the young females did so frequently (Table 13). Although the number of such catchings was low, the difference was significant at the 0.03 level (FISHER's test).

Old females caught on nestlings whose wing length exceeded 12 mm, did not desert a single nest, whereas the young ones did do so occasionally. Nevertheless, the difference between the two age groups is significant only if the three "uncertain" desertions are included (for catchings on nestlings in groups C > 12 and D-F, together – $p = 0.05$; for catchings on nestlings from all three groups – $p = 0.04$; omitting these 3 nests, $p = 0.10$ and $p = 0.09$ respectively).

**The effect of place and year.** The frequency of nest desertion on the Vistula Spit and in Szwalewo Forest (Table 15), if we leave out the 3 "uncertain" desertions, did not differ significantly either in the particular years or in all the years taken together; likewise, there was no difference between years. By contrast, if we do take those three nests into account, the desertion frequency of nests with nestlings of wing

Table 15. Nest desertion by females caught on nestlings, in different sites and in different years

Explanation of symbols – see Table 7

Tabela 15. Porzucanie gniazda przez samice, schwytane na pisklętach, w różnych miejscach i w różnych latach

Objaśnienie symboli – zob. tab. 7

| Stage of nestling development** Stadium rozwoju piskląt** | A–C, ⩽ 12 mm | | | | | | C–G, > 12 mm | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Site – Miejsce | MW | | | SZ | | | MW | | | SZ | | |
| Year – Rok | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | % |
| 1979 | 28 | 6 | 21 | 7 | 2 | 29 | 9 | – | – | 8 | – | – |
| 1980 | 22 | 4 | 18 | 6 | 2 | 33 | 23 | – | – | 12 | – | – |
| 1981 | 37 | 5 | 14 | 16 | 3 | 19 | 30 | – | – | 27 | – | – |
| 1982 | 12 | 4 | 33 | 8 | 2 | 25 | 36 | 1 | 3 | 21 | 6* | 29 |
| 1983 | 11 | 2 | 18 | 5 | 2 | 40 | 52 | – | – | 20 | 1 | 5 |
| 1984 | 5 | 2 | 40 | – | – | – | 59 | 1 | 2 | – | – | – |
| Total – Razem | 115 | 23 | 20 | 42 | 11 | 26 | 209 | 2 | 1 | 88 | 7 | 8 |

* Including 3 "uncertain" desertions (see p. 92).
* W tym 3 porzucenia „niepewne" (zob. str. 92).
** See note under Table 2.
** Zob. odnośnik pod tab. 2.

lengths > 12 mm is relatively high in Szwalewo Forest in 1982, significantly higher than on the Vistula Spit in the same year ($p = 0.01$, FISHER's test) and than in the same place in 1981 ($p = 0.005$, FISHER's test).

**The effect of air temperature.** The frequency of nest desertion by females caught on nestlings was independent of air temperature if the nestlings were small (Table 16; data for old females are too scarce for analysis). Desertions at very high temperatures did occur as well (*e.g.* at 26 and 29°C by old females).

Desertions of larger nestlings took place only at temperatures below 20°C. Both desertions at temperatures above 16°C concerned 6–7 day old nestlings not yet feathered (in stage C, wing length 15 and 19 mm) and included one "uncertain" one. Females brooding larger nestlings deserted the nest significantly more often when the ambient temperature was below 12°C compared with desertions at higher temperatures (for comparison with desertions at temperatures between 12 and 16°C, excluding "uncertain" ones, $p = 0.02$, FISHER's test).

**The effect of time of day.** Females caught on small nestlings in the morning abandoned their nests much less often than if they were caught at 12°° hrs or later (Table 17, $p = 0.002$, one-sided test).

Table 16. Nest desertion by young females caught on nestlings, with respect to air temperature

Explanation of symbols – see Table 7

Tabela 16. Porzucanie gniazda przez młode samice schwytane na pisklętach w zależności od temperatury powietrza

Objaśnienia symboli – zob. tab. 7

| Stage of nestling development* Stadium rozwoju piskląt* | A – C, ⩽ 12 mm | | | | | C – F, > 12 mm | | | | | G | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Duration of catching Czas chwytania | ⩽ 15′ | | total razem | | | > 15′*** | | total razem | | | total razem | |
| Temperature (C°) Temperatura (C°) | $N_C$ | $N_D$ | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ | $N_C$ | $N_D$ | % | $N_C$ | $N_D$ |
| 8.1 – 12.0 | – | – | 11 | 2 | 18 | 5 | 1 | 16 | 3 | 19 | 11 | 1 |
| 12.1 – 14.0 | 8 | 3 | 16 | 4 | 25 | 5 | – | 21 | 1** | 5 | 15 | – |
| 14.1 – 16.0 | 6 | 1 | 14 | 4 | 29 | 3 | 2** | 22 | 2** | 9 | 8 | – |
| 16.1 – 18.0 | 3 | – | 17 | 3 | 18 | 3 | 1** | 23 | 1** | 4 | 10 | – |
| 18.1 – 20.0 | 7 | 1 | 24 | 7 | 29 | 8 | – | 30 | 1 | 3 | 8 | – |
| 20.1 – 22.0 | 7 | 1 | 13 | 1 | 8 | 10 | – | 17 | – | – | 1 | – |
| 22.1 – 24.0 | 8 | 2 | 12 | 3 | 25 | 2 | – | 9 | – | – | 2 | – |
| 24.1 – 30.0 | 4 | – | 8 | – | – | – | – | 5 | – | – | – | – |
| Total ÷ Razem | 43 | 8 | 115 | 24 | 21 | 36 | 4 | 143 | 8 | 6 | 55 | 1 |

* See the note under Table 2.
* Zob. odnośnik pod tab. 2.
** Including 1 "uncertain" desertion (see p. 92).
** W tym 1 porzucenie „niepewne" (zob. str. 92).
*** Catchings of shorter duration were few; in most cases the duration was not noted.
*** Chwytań trwających krócej było niewiele; w większości przypadków czas chwytania nie był notowany.

Table 17. Nest desertion by females caught on nestlings with a wing length ⩽ 12 mm, with respect to the time of day

Explanation of symbols – see Table 7

Tabela 17. Porzucanie gniazda przez samice, schwytane na pisklętach o skrzydle ⩽ 12 mm, w zależności od pory dnia

Objaśnienia symboli – zob. tab. 7

| Hours Godziny | 8 | 9 | 10 | 11 | Total Razem 8 – 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | Total Razem 12 – 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of catchings Liczba schwytań | 4 | 16 | 16 | 10 | 46 | 14 | 12 | 20 | 16 | 13 | 8 | 8 | 8 | 6 | 2 | 107 |
| Desertions *N* | – | 2 | – | 1 | 3 | 4 | 2 | 9 | 4 | 4 | 2 | 2 | 2 | 1 | 1 | 31 |
| Porzucenia % | | | | | 7 | | | | | | | | | | | 29 |

## DISCUSSION

**Brood stage.** On the Vistula Spit and in Szwalewo Forest, one quarter of the incubating females caught and one fifth of those caught on small nestlings deserted their nests. The frequency of desertion dropped sharply when the largest sibling had exceeded a size characterized by a wing length of 12 mm. The nestling is then in its 5th or 6th day of life. It is not even covered by quills and the female broods it intensively. This continues for the next day or two at least. The decreased tendency to desert the nest is therefore not connected with the change in the nestlings' brooding requirements.

Similarly, females caught on the nest at night do not abandon it if their nestlings are at least a week old, but frequently do so if they are younger (BERNDT 1974).

The decreased tendency for birds to desert their broods as these proceed is widely known. But there is no explanation why in great tits this change is so abrupt when the nestlings' wing length increases from 12 to 13 mm. It could be that at this point, the ratio of the nestling's body weight to its suface area crosses a threshold value, above which heat loss to a lethal level does not take place before the caught female resumes brooding.

**Regional differences.** The conviction that female great tits caught on their eggs or nestlings often desert them is quite widespread (*e. g.* BERNDT 1974). But I have also come across ringers who say that great tits do this only exceptionally. However, these opinions were not supported by actual figures, so it is hard to say to what extent they reflect catching methods (*e. g.* catching restricted to the morning when nest desertion is least frequent). Neither is it known whether the conviction that nest desertion is rare stemmed from a lack of findings of abandoned nests caused by lack of nest checkings in the days following catching. Nonetheless, these opinions may well be based on the actual rarity of nest desertion in some areas.

That the nest desertion rate in consequence of the female being caught can vary in different places is demonstrated by the fact that significantly fewer nests with eggs (but not nests with nestlings) were deserted before noon in Szwalewo Forest than on the Vistula Spit (Tables 6 and 9). The existence of this difference cannot be put down to any of the factors examined in this paper, except, perhaps, for predator density.

M. GROMADZKI (pers. comm.) found that in the starling *Sturnus vulgaris* (a species more sensitive to disturbance at the nest than the great tit) nest desertion after the parents had been caught was more frequent where they were often disturbed by the presence of humans nearby. In the great tit, anxiety brought about by earlier catching on the nest (Table 3) or the hunting activities of predators in the area (Table 11) does not lead to a significant increase in the desertion rate by the female on being caught. It does appear, however, that if the nest is destroyed by a predator, the tendency for a female to abandon her replacement clutch is rather high (Table 10). Thus nest desertion by female great tits caught by humans could be a comparatively rare occurrence in places where there are few predators destroying nests.

**Method of releasing the female.** GRACZYK (1975) states that "a bird forms and retains an association of danger with the place it was scared away from" and that to eliminate nest desertion by hole-nesters (including the great tit) caught on their eggs, it suffices to cover their eyes to prevent them from seeing the nearest neighbourhood of the nest just after being caught, and to release the birds 30 m from the nest. However, the figures in Tables 6 and 14 show that GRACZYK's recommendations (changed by increasing the distance between the nest and the place of release to 100 m) had no significant influence on the desertion rate of eggs or small nestlings in the case of the great tit.

**Age of the female.** Significant differences in the nest desertion rate on catching females of various ages were noted only when catching lasted for more than 15 minutes and the females were brooding small nestlings (Table 13). In such cases, young females desert their nests very frequently, significantly more often than when catching is of shorter duration. The desertion rate in old females in short and long catchings is not significantly different. So either all the young females caught stay away from the nest longer than the old ones, or more young females than old ones stay away from the nest for a time exceeding the period during which unbrooded nestlings can remain alive.

**Air temperature.** The high egg desertion rate at air temperatures of 20–22°C as compared with the relatively low frequency when it is cooler could be the result of a stronger drive to incubate the eggs in the second case. The birds thus return faster to the nest, more than making up for the increased cooling rate of the eggs.

The independence of the frequency of desertion of small nestlings on the air temperature could be due to the great rapidity with which such nestlings lose heat, even at quite high ambient temperatures, and/or to a greater tendency to abandon a brood on which less effort has been expended.

The desertion of larger nestlings, some of which were no longer being brooded by the female, was more frequent at low temperatures than at high ones, at least in young females. The nestlings then require more energy to heat their bodies. At the same time, the availability of the necessary insect food diminishes, which may severely hit the feeding efficiency of young parents, which according to PERRINS and MOSS (1974) are less adept at finding food. An additional break in feeding caused by the catching of the female can make it impossible for the nestlings to maintain the body temperature required to stay alive.

## CONCLUSIONS

1. Males caught while feeding nestlings do not desert nests.
2. Caught incubating females deserted their nests:
   a) in 29% of cases on the Vistula Spit and in 14% of cases in Szwalewo Forest;
   b) on average twice as often at the start of incubation as at the end of it;
   c) more often at air temperatures of 20–22°C than at lower temperatures;

d) more often after 17°° hrs (43%) and between 12°° and 17°° hrs (21%) than before noon (mean 7%); before 12°° hrs, young females on the Vistula Spit deserted 8% of nests, but in Szwalewo Forest none at all;

e) more often in the case of replacement clutches (55%) than not replacement ones (22%).

3. Incubating females touched (but not caught) in order to read their rings did not abandon their nests.

4. Caught brooding females deserted their nests:

a) if the nestlings were small (*i. e.* the largest sibling had a wing length of up to 12 mm and was 6 days old at the most) – on average in 22% of cases;

b) if the nestlings were larger – in 2–3% of cases; the nestlings size borderline below which nests were frequently abandoned was a sharp one.

5. The tendency to desert a nest may be different in various females.

6. The catching of a female not leading to nest abandonment does not increase the tendency for her to desert a second nest after she has been caught there.

7. In the case of young females caught on small nestlings, the desertion rate was higher if the catching duration (together with handling nestlings and adults) exceeded $^1/_2$ hour than if it was shorter. The frequency of desertion in young females caught on larger nestlings and in old females was unaffected by the duration of catching (up to $1^3/_4$ hour).

8. When catching and handling females on small nestlings took longer than $^1/_2$ hour, young females deserted the nest more often than old ones did. On the other hand, there was no difference between females of various ages when catching and handling took less time.

9. No difference was found between the Vistula Spit and Szwalewo Forest in the frequency of desertion by females caught on nestlings (see conclusion 2a).

10. The frequency of nest desertion after catching the female did not depend on the air temperature if the nestlings were small. But nests containing larger nestlings were deserted at temperatures below 16°C, exceptionally between 16 and 20°C. Desertions at temperatures below 12°C were significantly more frequent than ones at temperatures above 12°C.

11. Females caught on small nestlings after 12°° hrs deserted their nests more often (29% of cases) than if they were caught earlier (7%).

12. There was no difference in the frequency of desertion nests with eggs or nestlings by females which, after catching, were blindfolded and released 100 m from the nest in comparison with females which were replaced directly on the nest.

## NOTES FOR RESEARCHERS CATCHING GREAT TITS AT THE NEST

Catching a great tit on its nest hardly ever caused desertion if the nestlings had a wing length greater than 12 mm, that is, they were at least 5–6 days old, and the air temperature was higher than 12°C. As long as catching and handling the

nestlings and their parents on small nestlings took no longer than half an hour and was done before noon it caused desertion in no more than a few per cent of cases. Nests with eggs were deserted, on average, in less than 10% of cases when the females were caught before 15°° hrs, but desertion was twice as frequent at the start of incubation as at the end. The frequency with which caught females abandon nests may differ in different places and probably in different years, especially when they are caught on eggs.

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STRESZCZENIE

[Porzucanie lęgów przez bogatki *Parus major* chwytane na gniazdach]

Przeanalizowano około 900 schwytań bogatek na gniazdach, zbudowanych w skrzynkach lęgowych na Mierzei Wiślanej i w Lasach Szwalewskich, w północnej Polsce, w latach 1979–84 i 1986. Na jajach chwytano samice ręką. Na pisklętach chwytano bogatki obu płci, na ogół za pomocą pułapek zakładanych po wewnętrznej stronie otworu wlotowego.

Przedstawiono ocenę zależności częstości porzucania gniazd przez samice schwytane na jajach od zaawansowania wysiadywania, na podstawie analizy liczby gniazd nie porzuconych.

Schwytanie samca prowadziło do porzucenia gniazda wyjątkowo.

Samice schwytane na jajach porzucały je na Mierzei Wiślanej w 29%, w Lasach Szwalewskich – w 14% przypadków, przy czym istotna różnica między tymi terenami występowała przed południem (8 i 0%). Porzucenia były dwukrotnie częstsze na początku wysiadywania niż przy jego końcu. Porzucenia piskląt były jednakowo częste na obu terenach. Samice schwytane na małych pisklętach (o skrzydle $\leqslant$ 12 mm, w wieku do 6 dni) porzucały gniazdo w 22% przypadków, a schwytane na pisklętach większych – w 2–3% przypadków. Częstość porzucania gniazd gwałtownie się zmniejszała, gdy długość skrzydła pisklęcia największego w gnieździe przekraczała 12 mm. Żadna samica dotykana i przesuwana na gnieździe celem odczytu numeru obrączki, ale nie chwytana, nie porzuciła jaj. Schwytanie samicy na gnieździe nie powodowało zwiększenia skłonności do porzucenia gniazda przy następnym schwytaniu. Nie stwierdzono różnicy w częstości porzucania gniazda między samicami, po schwytaniu kładzionymi na gnieździe i tymi, które z zasłoniętymi oczami odnoszono na odległość 100 m.

Większa wrażliwość samic na Mierzei Wiślanej mogła być spowodowana częstszym niszczeniem tu gniazd przez drapieżniki. Stwierdzono, że porzucanie jaj z lęgów powtarzanych, czyli lęgów samic, których pierwsze gniazdo zostało zniszczone przez drapieżnika, było istotnie częstsze (55%) niż porzucenie gniazd pierwszego lub drugiego lęgu (22%). Jaja były częściej porzucane przy temperaturach powietrza 20–22°C niż przy niższych. Częstość porzucenia małych piskląt nie zależała od temperatury, podczas gdy pisklęta większe porzucane były głównie wtedy, gdy było chłodno. Częstość porzucania jaj zwiększała się w ciągu dnia, od średnio 7% przed południem, poprzez 21% w godz. 12°°–17°°, do 43% później. Porzucenia małych piskląt, na których samice schwytano przed południem, zdarzały się w 6% wypadków, przy schwytaniach późniejszych – w 28% wypadków. Samice młode, schwytane na pisklętach małych, porzucały gniazdo około 3 razy częściej, gdy czas chwytania przekraczał 15 minut (tj. 30 minut wraz z mierzeniem i obrączkowaniem ptaków). Nie stwierdzono istotnej różnicy pod tym względem w przypadku ptaków starych, a także i starych i młodych, gdy pisklęta były większe (przy chwytaniach trwających do $1^3/_4$ godziny). Przy chwytaniu (wraz z mierzeniem i obrączkowaniem) samic na pisklętach małych dłużej niż przez pół godziny, samice młode porzucały gniazda częściej niż stare. Natomiast nie stwierdzono różnicy między samicami różnego wieku przy chwytaniu trwającym krócej.

Wnioski o znaczeniu praktycznym, wynikające ze streszczonych wyżej badań: chwytanie bogatek na gnieździe prawie nigdy nie powodowało jego porzucenia, jeśli pisklęta miały skrzydło długości ponad 12 mm, czyli były w wieku przynajmniej 5–6 dni, a temperatura powietrza przekraczała 12°C. Chwytanie bogatek na pisklętach mniejszych, jeśli wraz z obrączkowaniem i mierzeniem piskląt i rodziców nie trwało dłużej niż pół godziny i odbywało się przed południem, powodowało porzucenie gniazda w kilku procentach przypadków, a chwytanie na jajach przed godziną 15 – w poniżej 10% przypadków, przy czym dwukrotnie częściej na początku okresu wysiadywania niż przy jego końcu. Częstość porzuceń gniazd przez schwytane samice może być różna w różnych miejscowościach i prawdopodobnie w różnych latach, zwłaszcza przy chwytaniu samic na jajach.

## APPENDIX

### Table A. The age of great tit nestlings in various stages of feather development

Definitions of stages see KANIA 1983. The probability of a nestling belonging to each one-day age class is given. These probabilities were established for the most advanced nestlings in comparison with their siblings on the basis of daily checks of 19 nests in Gdańsk in 1979–81 and 1983

### Tabela A. Wiek piskląt bogatki, będących w różnych stadiach rozwoju upierzenia

Definicje stadiów zob. KANIA 1983. Podano prawdopodobieństwo należenia pisklęcia do każdej jednodniowej klasy wieku. Prawdopodobieństwa ustalono dla piskląt najbardziej rozwiniętych w gnieździe, na podstawie wyników codziennych przeglądów 19 gniazd w Gdańsku, w latach 1979–81 i 1983

| Stage Stadium | Day of life – Dzień życia | | | | | | | | | | | | Total Razem | Number of nests checked Liczba zbadanych gniazd |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | | |
| A | .59 | .41 | | | | | | | | | | | 1.00 | 17 |
| B | | .15 | .47 | .35 | .03 | | | | | | | | 1.00 | 16 |
| C | | | | .06 | .17 | .21 | .21 | .21 | .11 | .03 | | | 1.00 | 15 |
| D | | | | | | | | | .25 | .37 | .25 | .13 | 1.00 | 12 |

| Stage Stadium | Day of life – Dzień życia | | | | | | | | | | | | Total Razem | Number of nests checked Liczba zbadanych gniazd |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | | |
| E | .17 | .30 | .30 | .13 | .09 | | | | | | | | .99 | 15 |
| F | | .06 | .15 | .20 | .23 | .17 | .13 | .06 | | | | | 1.01 | 12 |
| G | | | .02 | .05 | .15 | .15 | .20 | .18 | .15 | .07 | .02 | .02 | 1.01 | 14 |

The age was determined on the basis of daily measurements of the largest sibling, in 10 nests in Gdańsk in 1971–81 and 1983, and 1 or 2 measurements in 42 nests in the Vistula Spit and Szwalewo Forest in 1979–84

## Tabela B. Wiek piskląt bogatki o różnej długości skrzydła

Wiek określono na podstawie codziennych pomiarów piskląt, największych spośród rodzeństwa, w 10 gniazdach w Gdańsku, w latach 1978–81 i 1983 oraz 1 lub 2 krotnych pomiarów w 42 gniazdach na Mierzei Wiślanej i w Lasach Szwalewskich w latach 1979–84

| Wing length Długość skrzydła (mm) | Day of life Dzień życia | | No. of nests in which nestlings were measured Liczba gniazd, w których mierzono pisklęta | | Wing length Długość skrzydła (mm) | Day of life Dzień życia | | No. of nests in which nestlings were measured Liczba gniazd, w których mierzono pisklęta | |
|---|---|---|---|---|---|---|---|---|---|
| | possible możliwy | most probable najbardziej prawdopodobny | daily co dzień | 1 or 2 times 1 lub 2 razy | | possible możliwości | most probable najbardziej prawdopodobny | daily co dzień | 1 or 2 times 1 lub 2 razy |
| 5 | 1 | 1 | 7 | 0 | 34–35 | 9–12 | 11 | 10 | 3 |
| 6 | 1–2 | 1 | 7 | 0 | 36 | 11–12 | 11 | 10 | 2 |
| 7 | 2–3 | 2 | 7 | 0 | 37–38 | 11–13 | 12 | 10 | 2,1 |
| 8 | 3–4 | 3 | 7 | 0 | 39 | 12–13 | 12 | 10 | 2 |
| 9 | 3–4 | 4 | 7 | 0 | 40–41 | 12–14 | 12 | 10 | 2,1 |
| 10–11 | 4–5 | 5 | 10 | 1 | 42 | 12–14 | 13 | 10 | 1 |
| 12 | 5–6 | 6 | 10 | 0 | 43 | 12–14 | 14 | 10 | 3 |
| 13–14 | 5–7 | 6 | 10 | 2 | 44 | 12–15 | 14 | 10 | 3 |
| 15 | 6–7 | 6 | 10 | 1 | 45–46 | 13–15 | 14 | 10 | 3,4 |
| 16–17 | 6–7 | 7 | 10 | 0 | 47 | 13–16 | 15 | 10 | 5 |
| 18 | 6–8 | 7 | 10 | 0 | 48–49 | 14–16 | 15 | 10 | 7,8 |
| 19 | 7–8 | 7 | 10 | 0 | 50–51 | 14–17 | 15 | 8 | 6,7 |
| 20–21 | 7–8 | 8 | 10 | 0 | 52 | 15–17 | 15 | 8 | 9 |
| 22 | 8–9 | 8 | 10 | 0 | 53–54 | 15–18 | 15 | 5,4 | 8,6 |
| 23–24 | 8–9 | 9 | 10 | 0,1 | 55 | 15–16 | 16 | 3 | 5 |
| 25–27 | 9–10 | 9 | 10 | 2–3 | 56 | 15–17 | 16 | 3 | 6 |
| 28–29 | 9–11 | 10 | 10 | 1,2 | 57 | 16–17 | 16 | 3 | 7 |
| 30 | 10–11 | 10 | 10 | 0 | 58–59 | 16–18 | 17 | 2 | 7,5 |
| 31 | 9–11 | 10 | 10 | 1 | 60 | 16–17 | 17 | 0 | 2 |
| 32 | 9–12 | 10 | 10 | 1 | 61 | 17–18 | 18 | 0 | 2 |
| 33 | 9–12 | 11 | 10 | 2 | 62 | 18 | 18 | 0 | 1 |

Since Table B is based on measurements from rather a small number of nests, the most probable day of life could in fact differ by 1 from the one quoted, especially in the case of nestlings with minimum and maximum wing lengths for the given most probable day of life. For the same reason the range of possible days of life of nestlings with a certain wing length must in fact be greater than is given here, particularly for medium-sized and large nestlings. I think, however, that at least for nestlings with wing lengths of up to 54 mm, the ages in the table do not differ from the actual ages to an extent significant in most analyses.

Ponieważ tabela B oparta jest na pomiarach ze stosunkowo niewielu gniazd, najbardziej prawdopodobny dzień życia może być w rzeczywistości o 1 różny od podanego, zwłaszcza w przypadku piskląt o długości skrzydła minimalnej i maksymalnej dla danego, najbardziej prawdopodobnego dnia życia. Z tego samego powodu zakres możliwych dni życia piskląt o danej długości skrzydła w rzeczywistości musi być większy, niż podany, zwłaszcza dla piskląt średnich i dużych. Sądzę jednak, że przynajmniej dla piskląt o skrzydle do 54 mm długości podany w tabeli wiek nie różni się od rzeczywistego w stopniu istotnym dla większości rozważań.