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Why low numbers of *Parus major* in Białowieża Forest — removal experiments

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Parus major breeds in Białowieża Forest (E Poland) in much lower densities than elsewhere in Western and Central Europe. These low densities do not result from shortage of nest sites. Removal experiments were carried out to check if breeding numbers were limited by low numbers of birds present at the onset of the breeding season or by social behaviour in the spring. Birds were removed from oak-hornbeam stands in the period of nest-building and egg-laying. In the spring of 1984 only males were removed. The plot was totally repopulated in a few days. In the spring of 1985, when numbers of the tits were much lower, both males and females were removed from another plot. New birds of both sexes settled in the experimental area but in neither case was the repopulation complete. Thus, the social behaviour had only a subsidiary, to the numbers of birds present early in the spring, effect on breeding densities in 1985. Lower than elsewhere spring numbers could be due to lower production of young and/or higher mortality in the adults. Large territories in the Białowieża *P. major* seem to be an anti-predator adaptation.

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Причины низкой плотности *Parus major* в Беловежской пуще — эксперименты с устранением птиц.

Гнездовая плотность *Parus major* в Беловежской пуще (восточная Польша) гораздо ниже чем в других регионах Центральной и Западной Европы. Не происходит это по причине недостатка мест для гнездования. С целью проверки является ли ограниченная плотность результатом низкой численности птиц, находящихся тут ранней весной, или их социального поведения в период размножения, были проведены эксперименты с устранением птиц. Птиц забирали из биотопов груда в период постройки гнезд и откладки яиц. Весной 1984 года были устранены только самцы. Через несколько дней площадь снова была полностью заселена. Весной 1985 года, когда плотность большой синицы была еще значительно ниже, с другой площади устранили как самцов, так и самок. Экспериментальная площадка была наново заселена птицами обоего пола, но их численность была гораздо ниже чем численность удаленных птиц. Таким образом, социальное поведение птиц имело только дополнительное влияние, по сравнению с небольшим количеством птиц находящихся здесь ранней весной, на гнездовую плотность в 1985 г. Более низкая, чем на других территориях, численность птиц ранней весной могла быть результатом более низкой по сравнению с другими местами продукции молодых либо более высокой смертности в послегнездовой период. Большие территории беловежских *P. major* являются, как нам кажется, приспособлением от хищников.

INTRODUCTION

In an earlier paper (TOMIAŁOJĆ *et al.* 1984) we demonstrated that the numbers of several bird species in Białowieża Forest were much lower than elsewhere in Central and Western Europe. One of the species showing this phenomenon

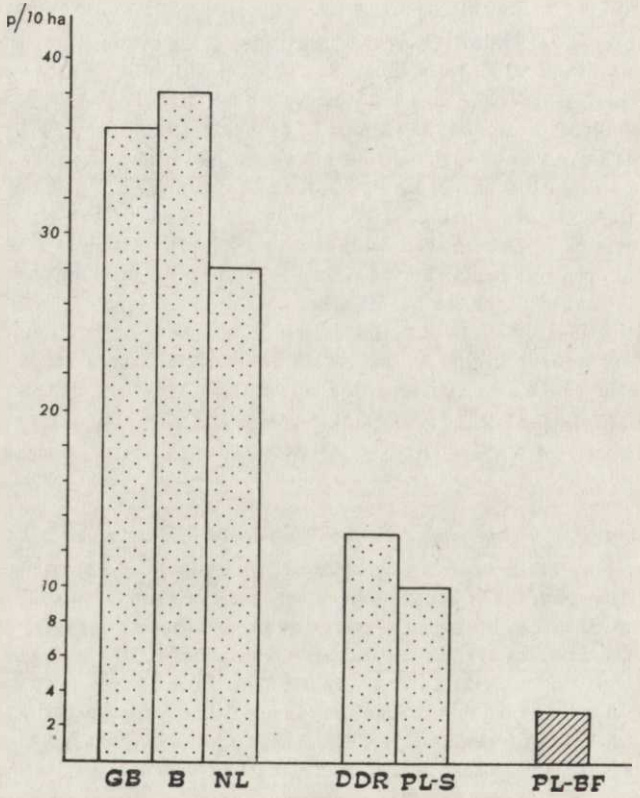

Fig. 1. Breeding densities of *Parus major* in deciduous woods in different parts of Europe

GB – Wytham Wood near Oxford, England (LACK 1966); B – vicinity of Antwerp, Belgium (DHONDT and SCHILLEMANS 1983); NL – Liesbos near Breda, Holland (VAN BALEN 1984); DDR – vicinity of Magdeburg, GDR (ULLRICH 1970); PL–S – vicinity of Wrocław, S Poland (TOMIAŁOJĆ and PROFUS 1977); PL–BF – Białowieża Forest (TOMIAŁOJĆ *et al.* 1984, unpubl.)

Ryc. 1. Zagęszczenia lęgowych bogatek *Parus major* w lasach liściastych różnych części Europy

GB – Wytham Wood koło Oksfordu, Anglia (LACK 1966); B – okolice Antwerpii, Belgia (DHONDT i SCHILLEMANS 1983); NL – Liesbos koło Bredy, Holandia (VAN BALEN 1984); DDR – okolice Magdeburga, NRD (ULLRICH 1970); PL–S – okolice Wrocławia (TOMIAŁOJĆ i PROFUS 1977); PL–BF – Puszcza Białowieska (TOMIAŁOJĆ *et al.* 1984, mat. niepubl.)

was *Parus major*. Its densities in fragmented West European woods supplemented with nest boxes often reach 35 pairs/10 ha. On the contrary a maximum recorded in the Forest was only 4.1 p/10 ha, and average densities ranged between 2 and 3.5 p/10 ha (Fig. 1 and TOMIAŁOJĆ *et al.* 1984).

It is already know that these low densities do not result from the limitation by shortage of nest sites, as it was impossible to increase the numbers of *P. major* in the Forest by providing them with nest boxes (WOŁK and WALANKIEWICZ unpubl.).

What could be the reasons for these low numbers then? A suitable approach to tackle this problem is to consider the situation occurring early in the spring, just before the onset of breeding, when the population reaches its yearly minimum. One can envisage two extreme situations (corresponding to density levels I and III in the model of BROWN 1969) then:

1. Undersaturation — breeding numbers are determined by the number of birds present early in the spring. All birds present can settle and breed; breeding habitats are not fully utilized. In this case the size of the breeding population totally results from events taking place before the breeding season, often outside the breeding grounds. Social intolerance on the breeding grounds plays no role as a limiting factor;

2. Saturation — there are more would—be settlers than places to breed, some birds are excluded from breeding by social interactions. In such a situation, territorial behaviour and other forms of social intolerance act as an important factor limiting the size of the breeding population.

Our experiments were aimed at differentiating between these two possibilities.

METHODS AND RESULTS

Study area

The Białowieża Forest complex (total area 1250 km²) is situated on the Polish-Soviet border. The Forest represents a relic remnant of vast lowland forests which once covered great parts of temperate Europe. Its present unique features result from its considerable size, great compactness and good state of preservation (FALIŃSKI 1977, TOMIAŁOJĆ *et al.* 1984). Most of the Polish part of the Forest is now under management, but a 47.5 km² block of stands preserved in primaeval state is strictly protected within the Białowieża National Park.

Mature stands remaining in the managed part are still structurally similar to the primaeval ones. They are mostly of natural origin (self-sown), and remain multi-specific and uneven-aged. However, dead and fallen trees are removed from them. Hence the main difference between the primaeval and the managed stands stems not so much from differences in the structure of the mature stands as from the much greater proportion of clearings and young tree plantations in the latter.

Experiment I

An experimental area was chosen so as to be situated far from human settlements and to be surrounded by habitats of the same type. This, to avoid the possibility of influx of birds settled earlier in other habitats into the experimentally emptied area (*cf* KREBS 1971). The experiment was carried out in 30 ha fragment of a primaeval oak-hornbeam *Tilio-Carpinetum* stand situated in the centre of the Białowieża National Park (plot MS in TOMIAŁOJĆ *et al.* 1984). This area, laid over 3.5 km away from the nearest village, was surrounded by stands of similar type. The nearest patch of coniferous stands was about 1 km away from it.

The experiment was planned so as to fall on the period just preceeding the egg-laying commencement, when one could expect that the birds present in the plot had already finished the process of spring arrival and settlement. This was important as the Białowieża birds did not spend winter in the Forest (WESOŁOWSKI unpubl.) and had to immigrate from elsewhere every spring.

During five days (26–30 April 1984) preceeding the removal, the singing males were intensively followed by one or two observers who mapped their

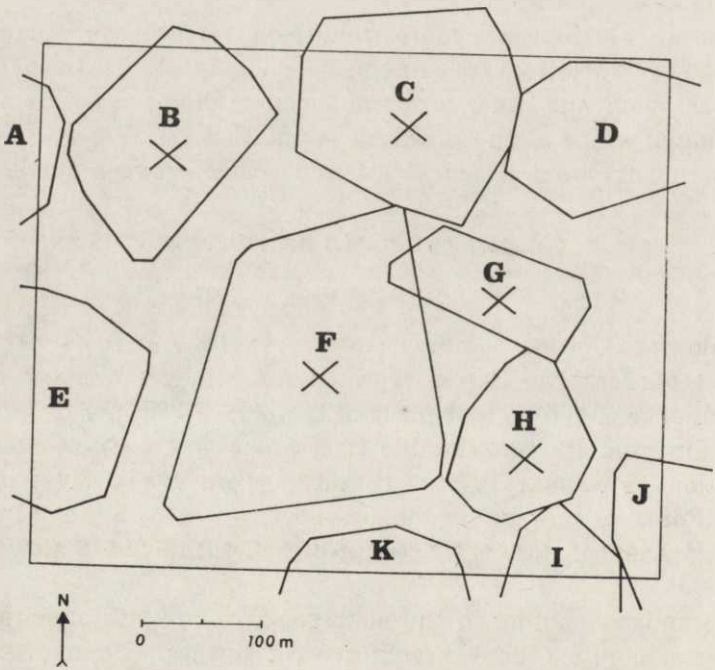

Fig. 2. Distribution of *P. major* territories in the plot MS before the removal experiment
Males were removed from territories marked with ×-signs

Ryc. 2. Rozmieszczenie terytoriów bogatek na powierzchni MS w okresie poprzedzającym eksperyment
Samce usunięto z terytoriów zaznaczonych krzyżykami

consecutive song posts in order to obtain data on the exact number and distribution of territories. The results of these observations are shown in Figure 2. The number of territories within the plot (estimated according to the rules of improved mapping — Tomiałojć 1980b) before the removal was 7.5, which corresponds to a density of 2.5 territories/10 ha.

On 1 and 2 May five males (B, C, F, G, and H) were removed from the central part of the plot. During the second day of removal some new males were already observed in areas vacated earlier and on 6 May (there were no observations between 2 and 6 May) the plot was found to have been fully repopulated, and the number of territories later on (May 10, 17, 23, June 1, 4, 7, 17) did not change (Fig. 3). Thus, no more than five days was enough for males to find the empty area and to settle there.

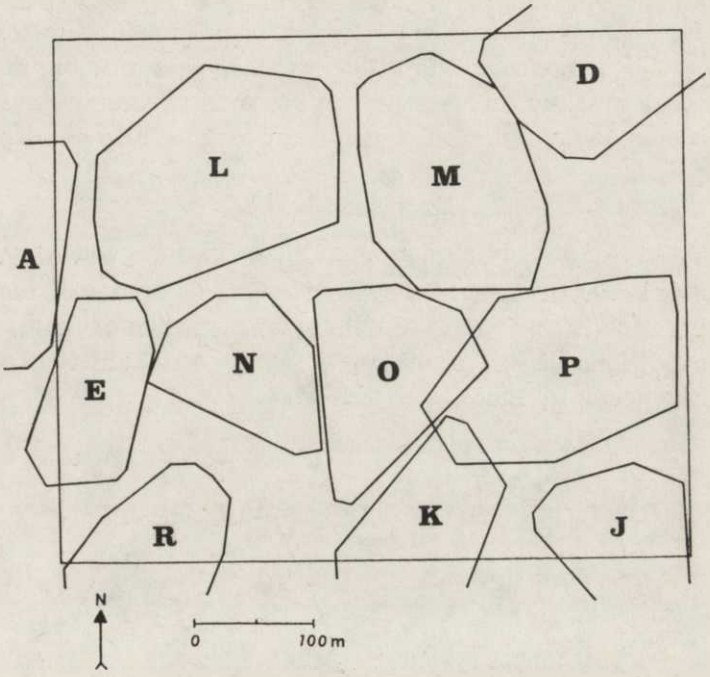

Fig. 3. Distribution of *P. major* territories in the plot MS *c.* 5 days after the removal experiment

Territories denoted by the same letters in Fig 2 and 3 are supposed to belong to the same males

Ryc. 3. Rozmieszczenie terytoriów bogatek na powierzchni MS około 5 dni po usunięciu samców

Terytoria oznaczone tymi samymi literami co na ryc. poprzedniej należą najprawdopodobniej do tych samych samców

At least five new males (L, M, N, O, and P) settled within the plot. The remaining ones were presumed to be the same birds as before, staying on their territories or expanding them into vacated land. In comparison with the pre-

removal period, the number of occupied territories increased only slightly, there were 8.5 territories, which corresponded to the density of 2.8 territories/10 ha.

These results allow one to conclude that some males were deprived of chance to establish territories due to the presence of the earlier territory owners. This, however, does not allow one to conclude that the breeding numbers in the Białowieża population were limited by social intolerance, as in *P. major* populations the males usually outnumber the females. This results from a higher mortality rate of females (*e.g.* Kluijver 1951, Bulmer and Perrins 1973, Orell and Ojanen 1979). Taking into account the monogamous breeding system of this species, it follows that due to a shortage of females, there must be a fraction of non-breeding males in a population (Perrins 1979). If, in the Białowieża population, the males also outnumbered the females, then the repopulating males could be earlier prevented from breeding not only by their inability to establish territory but also by the shortage of unmated females. Thus, we decided to carry out another, more conclusive experiment aimed at checking for a possibility of not only surplus males, but also of surplus females.

Experiment II

This was done in 1985. It happened so that the numbers of *P. major* that year were much lower than in 1984 (Fig. 4). This created still more stringent conditions for our test, as if we were able to find surplus of males and females even under conditions of low numbers we could conclude that such surplus would regularly occur in Białowieża Forest.

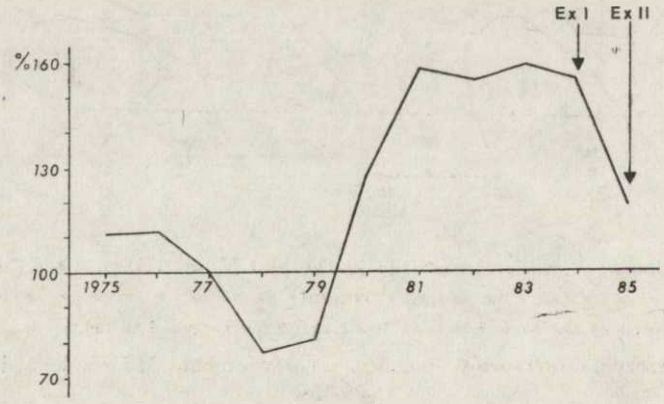

Fig. 4. Index of *P. major* numbers in the Białowieża National Park (Tomiałojć *et al.* 1984, unpubl.)

Timing of the removal experiments is denoted with Roman numerals

Ryc. 4. Indeks liczebności bogatki w Białowieskim Parku Narodowym (Tomiałojć *et al.* 1984, mat. niepubl.)

Sezony, w których przeprowadzano eksperymenty zaznaczono liczbami rzymskimi

The experimental plot was situated in the managed part of the Forest (compartment 424, part of the managed oak-hornbeam plot described in PIOTROWSKA and WESOŁOWSKI — in press), about 1.5 km away from the nearest human settlement. It was a 33.4 ha patch of an oak-hornbeam *Tilio-Carpinetum* stand surrounded on all sides by similar stands. The nearest patch of coniferous stands was about 1 km from it. The plot was covered by a fine-grained mosaic of old tree stands, young tree plantations and small clear-cut areas.

Field procedures were similar to those in the first experiment, though stimulation of birds by playing back of species specific songs was added. The birds were intensively followed in the pre-removal period (21–24 April) to obtain data on numbers and distribution of territories within the plot, as well as on the mating status of the males. There were 7.5 territories (density 2.2 p/10 ha) present (Fig. 5). The singing birds moved mostly along patches of old

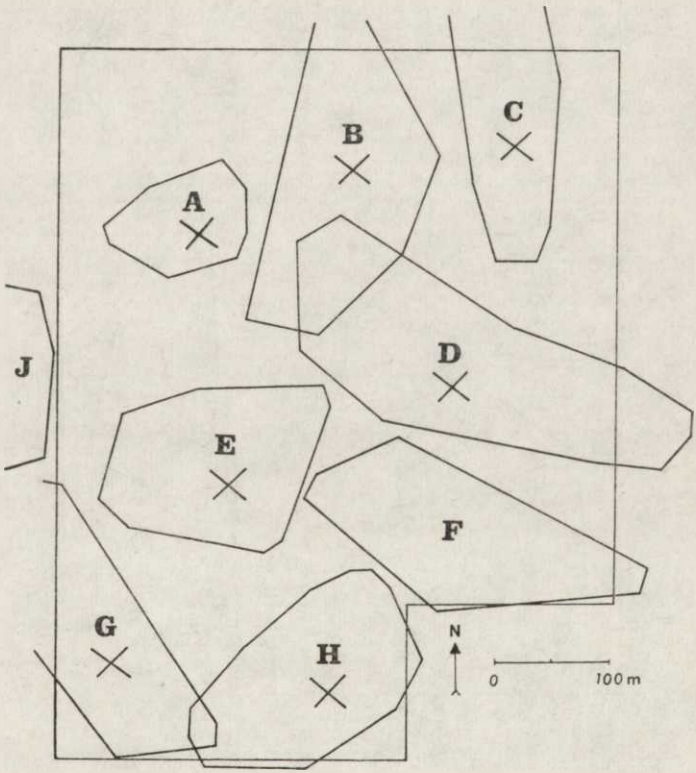

Fig. 5. Distribution of *P. major* territories in the managed oak-hornbeam plot before the removal experiment

Males were removed from territories marked with ×-signs

Ryc. 5. Rozmieszczenie terytoriów bogatek na powierzchni w grądzie zagospodarowanym w okresie poprzedzającym eksperyment

Samce usunięto z terytoriów zaznaczonych krzyżykami

trees, which resulted in rather elongated shapes of the territories seen in Figure 5. All the males, except male B, were paired.

On 26 and 27 April, when the females were building nests or commencing egg-laying, the birds of both sexes were removed. Altogether seven males (A, B, C, D, E, G, and H) and eight females (from territories A, C, D, E, F, G, H, and J) were removed.

On 1 May the first new male (K) was observed, on 5 May two additional ones (L and M) were recorded, no further males appeared after that date (controls on May 10, 14, 22, June 12, 19). Distributions of territories of these males, as well as those which were presumed to be the same birds as before the experiment is shown in Figure 6.

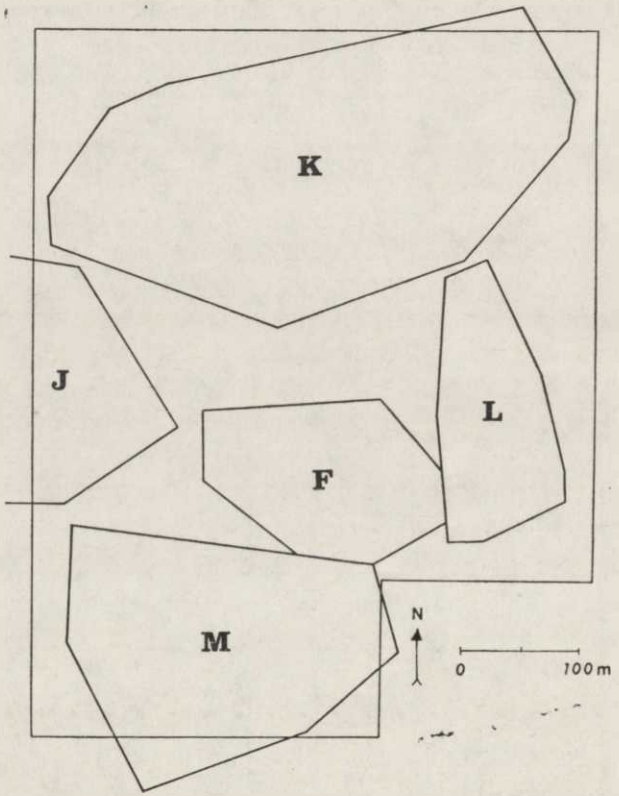

Fig. 6. Distribution of *P. major* territories in the managed oak-hornbeam plot c. 10 days after the removal experiment

Other explanations as in Fig. 3

Ryc. 6. Rozmieszczenie terytoriów bogatek na powierzchni w grądzie zagospodarowanym około 10 dni po usunięciu ptaków

Pozostałe objaśnienia jak na ryc. 3

The first new female was detected in territory M on 3 May, the second, and the last one, in territory F on 10 May. In none of these territories was breeding definitely proved, though a pair inspecting a hole was observed in territory F on 10 May, and courtship feeding was seen in territory M on 19 June.

Summing up, the repopulation of the plot was incomplete, only three new males and two females appeared. This was accomplished in less than two weeks following the removal. No birds settled later on. Thus, even in this low numbers year, there were some non-breeding males in the population, deprived of a chance to breed due to social intolerance. In the case of females similar conclusion must be treated as a very tentative one, as one cannot rule out the possibility that their late settlement could be due to other factors, like for example retarded gonadal developement.

GENERAL DISCUSSION

Even if all *P. major* repopulating our plot in 1985 had settled and attempted to breed along with the birds present in the pre-removal period, this would not have substantially changed the breeding numbers that year. Coming back to our main question posed earlier "why low densities in the Białowieża population" we can now answer that, though the area was saturated with birds, and some birds were even prevented from breeding in 1985, the social interactions had only a subsidiary, to the number of birds present at the beginning of spring, effect on breeding densities then. They could have stronger impact in 1984 and other high-numbers years (1981–1983, Fig. 4), but in the years 1978–1979, when numbers of the tits reached the lowest level, there were probably even not enough birds to saturate the plots. As the *P. major* numbers in seven out of eleven study years was of the same order as their numbers in 1985 (*cf* Fig. 4) or less, hence in the majority of years, low numbers in the Białowieża population probably result mainly from the limited number of birds present early in the spring. Social interactions would be then more important only in the years in which higher numbers are observed.

The low numbers of tits present at the onset of spring can result from lower than in other areas production of young and/or lower survival and/or immigration not balanced by emigration. We have no data pertaining to the latter possibility, but there is some circumstantial evidence speaking in favour of both the former possibilities.

The Białowieża birds breed in natural holes in which the breeding success is usually lower (*e.g.* Löhrl 1957, Nilsson 1975, 1984) than in nest-boxes in which many tits studied in Western Europe breed.

Moreover, the nest predation rates in the Białowieża Forest are usually very high (*e.g.* Wesołowski 1983, 1985), whereas in West European woods the predator fauna is very impoverished and nesting losses lower (Dhondt

1970, Tomiałojć 1980a, Tomiałojć *et al.* 1984, Wesołowski 1983). This difference could also result in a lower than elsewhere production of young in the Białowieża population.

It is well known that severe winters combined with inaccessibility of food can reduce numbers of *P. major* (*e.g.* von Haartman 1973, van Balen 1980, Källander 1981, Bejer and Rudemo 1985). There are also some signs that the mortality of tits in northern populations can be higher than in the populations from areas with milder winters (Orell and Ojanen 1979).

The Białowieża *P. major* do not stay for winter at the Forest but, since their numbers in neighbouring villages increase substantially at winter time (Wesołowski unpubl.), it seems reasonable to assume that a substantial fraction of them spend winter somewhere in the neighbourhood of the Forest. If this is so, then they have to cope with much more severe winters than their West European counterparts; the mean January temperature in the region is −4.3°C, and snow cover (*c.* 0.5 m deep) lasts on average for 92 days (Tomiałojć *et al.* 1984).

Wintering conditions of the Białowieża *P. major* could be still worsened by the rather limited capacity of their presumed wintering grounds. The tits from Western Europe, which breed in small isolated "islands" of woods can disperse in winter time over a "sea" of densely human populated anthropogenic habitats, where there are additionally supplied with food. On the other hand, the birds from the Forest and other large forest complexes of the region (forests still cover over 30% of NE Poland) would have to emigrate to farmland sparsely populated by people (50–60 persons/km^2), almost devoid of larger settlements.

Summing up, low spring numbers of the Białowieża *P. major* could result from lower than in other populations production of young and/or higher breeding season and winter mortality rates. Checking these possibilities is impossible with the data available. It will need further studies.

When Brown's (1969, 1975) reviews of population limitation by territorial behaviour appeared, almost all the available data confirming this possibility originated from habitats highly man-modified, and densely populated by birds. Hence Brown posed a question if the population control by territorial behaviour was a by-product of unusually high densities in secondary habitats, or if it also could occur in more natural conditions. All earlier removal experiments with *P. major* (Krebs 1971, 1977, 1982) could not be helpful in resolving this problem. The removed birds (both males and females) in Krebs's experiments were rapidly replaced by newcomers, some of which had been previously non-stationary, thus confirming the limiting role of territorial behaviour. Yet these experiments were carried out in an isolated wood (Wytham Wood near Oxford, England) which was very densely populated by the tits (densities about ten times higher than in Białowieża Forest, *cf* Fig. 1) breeding almost exclusively in nest-boxes.

This study, as well as an earlier one on *Troglodytes troglodytes* (WESOŁOWSKI 1981), were carried out under close-to-primaeval conditions. They showed that even in such a situation, at very low bird densities of 2–3 p/10 ha, territory holders were able to prevent some males from establishing territories. Thus the population control by territorial behaviour is not limited to the secondary situations, it can be important also under primaeval conditions.

Apart from the main subject of our discussion, another phenomenon, *i.e.* large territories in the Białowieża *P. major* seems worth discussing here. Though the exact size of territories has not been measured by us, yet, as it can easily be seen from Figures 2, 3, 5, and 6, they were at least several hectares large. This remains in sharp contrast with results from denser populated areas, where the average territory size is often under a hectare (*e.g.* DHONDT 1971, KREBS 1971, 1977).

Why do the tits in the Forest keep such large territories instead of holding much smaller ones? Defending the larger territories is connected with additional time and energy expenditures, which one would not expect to be spent without some extra benefits (BROWN 1964). In fact the defence costs at the Forest could be lower, as the number of would-be settlers per unit area was probably much lower than in the denser populated areas. Nevertheless these costs could be still lowered if the birds possesed smaller territories. Then what could be the benefits?

One possibility is that food in the Białowieża Forest is much less abundant than in the areas densely populated by the tits, and the Białowieża birds have to posses larger territories in order to secure the same amount of food. As densities in the Forest were over ten times lower than in the areas densest occupied by *P. major* (*cf* Fig. 1) it would mean that in the Forest there was over ten times less food per unit area than *e.g.* in English woods. This suggestion does not seem tenable as invertebrates in the Białowieża stands are usually abundant and, if anything, there is probably not less, but more invertebrate food (TOMIAŁOJĆ *et al.* 1984) than in, for example, English woods in which the tits are so abundant.

Another possibility could be that the tits hold large territories in order to avoid predation. KREBS (1971) demonstrated that the dispersion of nests was advantageous – nest predation rates in his study area near Oxford were negatively correlated with the distance to nearest occupied box. As predator pressure in the Białowieża Forest seem to be higher (*cf* above) than in KREBS's study area, the Białowieża *P. major* could benefit even more from the dispersion of nests than the English tits, and the costs of possessing larger territories could be offset by lowered chances of nest loss due to predation.

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STRESZCZENIE

[Dlaczego niskie zagęszczenia *Parus major* w Puszczy Białowieskiej? — eksperymenty z usuwaniem ptaków]

Bogatka *Parus major* gnieździ się w Puszczy Białowieskiej w zagęszczeniach znacznie niższych niż na innych obszarach Europy (ryc. 1). Nie wynika to z braku dostatecznej liczby miejsc gniazdowych.

Dla rozróżnienia, czy powodem jest tu mała liczba ptaków obecnych na przedwiośniu, czy też liczebność ograniczana jest przez zachowanie socjalne w okresie wiosennym, usuwaliśmy ptaki z frakcji lęgowej. Oczekiwaliśmy, że jeśli liczebność jest ograniczona czynnikami socjalnymi, to po opróżnieniu obszaru z terytorialnych ptaków powinny się na nim osiedlać nowe osobniki. Eksperymenty przeprowadzono w lasach grądowych, w okresie budowy gniazd i składania jaj. Powierzchnie zostały wybrane tak, aby były możliwie najbardziej oddalone od siedzib ludzkich.

W 1984 r. eksperyment przeprowadzono na powierzchni MS położonej w Białowieskim Parku Narodowym. Z powierzchni (ryc. 2) usunięto pięć samców. W ciągu kilku dni zostały one zastąpione przez identyczną liczbę nowych ptaków (ryc. 3). W 1985 r. eksperyment przeprowadzono w zagospodarowanej części Puszczy. Warunki jego przeprowadzenia były bardziej krytyczne, gdyż liczebność bogatki była znacznie niższa niż w 1984 r. (ryc. 4). Z powierzchni (ryc. 5) usunięto siedem samców i osiem samic. Na ich miejsce osiedliły się tylko trzy nowe samce i dwie samice (ryc. 6). Tak więc, chociaż również w 1985 r. część ptaków została wykluczona z rozrodu przez zachowanie socjalne, ich liczba była tak mała, że nawet gdyby wszystkie one mogły się osiedlić, nie zwiększyłoby to w znacznym stopniu zagęszczenia. Podstawowym czynnikiem wyznaczającym poziom liczebności była więc w tym przypadku liczba ptaków obecnych na przedwiośniu. Ponieważ liczebności takie jak w 1985 r. lub niższe

obserwowano w siedmiu z jedenastu sezonów obserwacji, można przypuszczać, że niskie zagęszczenia bogatek w Puszczy Białowieskiej są warunkowane głównie przez liczebność ptaków na przedwiośniu. Ich liczebność w tym okresie może być przeciętnie niższa niż na innych obszarach z różnych powodów. Jednym z nich może być gorsza produktywność lokalnej populacji. Bogatki białowieskie gnieżdżące się w dziuplach naturalnych, na obszarze o bardzo silnej presji drapieżnictwa, mogą ponosić znacznie wyższe straty w lęgach niż bogatki zachodnioeuropejskie, gniazdujące głównie w skrzynkach lęgowych, na obszarach o silnie zubożonej faunie drapieżników. Innym czynnikiem może być wyższa śmiertelność w sezonie nielęgowym. Nie wiadomo, gdzie spędzają zimę bogatki białowieskie. Jeśli jednak — jak można przypuszczać — znaczna część z nich pozostaje w okolicach Puszczy, to warunki ich zimowania (silne mrozy, długo zalegająca pokrywa śniegowa, mniejsze zagęszczenie ludności) są znacznie trudniejsze niż na zachodzie Europy. Może to prowadzić do silniejszej, niż na innych obszarach, zimowej redukcji liczebności.

Białowieskie bogatki posiadają bardzo duże terytoria. Wydaje się to być bardziej przystosowaniem do rozproszenia gniazd w przestrzeni, sprzyjającym uniknięciu drapieżnictwa, niż wynikiem ich dopasowania do lokalnych zasobów pokarmu w porze lęgowej.