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# Breeding ecology of the Blackbird *Turdus merula* studied in the primaeval forest of Białowieża (Poland). Part 2. Reproduction and mortality*

**Abstract.** The forest Blackbirds in the Białowieża National Park constitute a migratory, monogamous, double-brooded population with a low frequency of inter-male and inter-female aggression. During most years they meet good feeding conditions reflected in: a large clutch size (4.5, in May even 4.8), high amount of food brought to nestlings, intensive mid-day feeding them, rarity of nestling starvation. Nesting losses (50–92%, mean 68%) were in 98% caused by predation or a threat of it. An average nest produced 1.3 nestlings, at a variable nesting success (8–50%). On average 2.5 young per pair fledged yearly; the most successful pairs reared 8–9 young. Nesting losses varied (50–81%) between habitats, seasons and years. The predators switch to other prey: in a low-rodent year they killed four times more Blackbird nestlings than in a rodent year, and in high-caterpillar years smaller predators left more bird eggs undestroyed. Breeding ecology of Blackbirds in the primaeval forest is shaped mostly by a strong predation pressure varying in space and time.

## INTRODUCTION

The rates of Blackbird reproduction and mortality were investigated repeatedly, though almost exclusively in transformed populations from anthropogenic habitats (Snow 1955–1969, Lack 1966, Steinbacher 1953, Erz 1964, Havlin 1962–1964, Mulsow 1976, 1980, Stephan 1985, Glutz & Bauer 1988, etc.), among others in Poland (Graczyk 1959, Dyrcz 1963, 1969, Mizera 1988). Even attempts at collecting data for forest populations (Snow 1955, 1958, Graczyk 1961, Graczyk & Klejnotowski 1966, Dyrcz 1963, 1969) were made either in suburban forests influenced by cities to an unknown degree or in woods affected for ages by extensive farmland surroundings, or – finally – in immature forests for a long time under simplifying their structure management (Tomiałojć 1993).

The study in the Białowieża National Park (BNP below) intended to reveal original ecological parameters of a Blackbird population thriving under nearly primaeval conditions. These data may serve as a reference point to verify some earlier interpretations of

the co-occurrence in this species of two distinct (forest and urban) forms. The main hypothesis underlying this study is that under conditions of a nearly primaeval forest, known to have retained most of its pristine predators (Tomiałojć *et al.*. 1984, Tomiałojć 1991), the predation pressure should be a major factor shaping breeding ecology of forest birds. Earlier we attempted to demonstrate this with the use of the patterns in the bird community organization (Tomiałojć *et al.*. 1984, Tomiałojć and Wesołowski 1990), switching also to particular species investigations (Wesołowski 1983, 1985). This paper is the second one in a series devoted to forest Blackbird breeding ecology (cf. Tomiałojć 1993).

## STUDY AREA AND CLIMATIC CONDITIONS

The observations were carried out within the Białowieża National Park (BNP) comprising 47.5km² of primaeval forest habitats never subjected to extensive logging and bearing only slight and local traces of

some human impact. This core area is surrounded by a 7–15 km belt of managed stands of the Białowieża Forest (1250 km$^2$). The primaeval stands in BNP differ from the managed part of the Forest in being much older, species-rich, multilayered, unevenaged, very high, patchy, rich in dead timber and clearly more humid. They are known to harbour an extremely diverse, species rich, chiefly predator-rich, fauna. For more information see Faliński (1986), Tomiałojć *et al.* (1984), Tomiałojć and Wesołowski (1990), Tomiałojć (1991, 1993).

Extensive preliminary Blackbird observations during 1975–1985 were carried out alongside with the bird censuses on several plots selected in three main types of the BNP old-forest habitats:

– Riparian ash-alder (called AA below) and alder stands of *Circaeo-Alnetum* and *Carici elongate-Alnetum* associations, constituting an optimal habitat for Blackbirds;

– Oak-lime-hornbeam (called OH below) stands (*Querco/Tilio-Carpinetum*) on dry-land fertile brown soils, but with an underdeveloped or absent bush layer;

– Mixed-coniferous (called MC below), with admixture of deciduous trees, stands of *Peucedano-Pinetum* and *Pino-Quercetum* on sandy elevations, a marginal habitat for the Blackbird.

For detailed study (1986–1989) of thrushes, the Blackbird and the Song Thrush, the following permanent census plots were selected:

– Plot K (33 ha), comprising an old riverine AA stand adjoining the Białowieża Glade. This is a mosaic of wetter and drier places with some intrusions of OH forest;

– Plot W (50.5 ha in its extended version) comprises an old OH stand at the forest edge, very poor in bushes due to a heavy pressure from big herbivores;

– Plot C (36 ha) represents an equivalent to plot W situated in the forest-interior part of BNP, and less influenced by big herbivores;

– Plot NW (25 ha), a spruce-pine stand with an admixture of some deciduous trees, situated in the middle of BNP. This is a marginal breeding habitat for the Blackbird (see also Tomiałojć *et al.* 1984 and Tomiałojć 1993).

The climate of the Białowieża Forest is of the subcontinental type, with severe snowy winters and relatively warm summers. The mean annual rainfall is 624 (426–857) mm. The period of 1986–1990 deviated from the long-term averages, especially from the previous decade, in being warmer and much drier (Tomiałojć 1993).

## METHODS

An intensive study of the functioning of fragments of the Blackbird population inhabiting optimal BNP habitats was preferred to extensive collecting scattered data from a larger or the whole Forest area. This was done to keep the results comparable to other intensive local studies (Snow 1955, 1958, Dyrcz 1963, 1969) and to avoid the bias of extensive studies, which are based mostly on easily found, lower-located nests (Wesołowski & Czapulak 1986). It is supposed that the nests that are easier to find to a human observer are also more exposed to destruction by predators.

### Nest searching

Searching for Blackbird nests in the high multilayered (OH) or bush-rich (AA) old tree stands was a difficult task because many of them were located high in tree crowns and/or tree holes, and the birds were extremely secretive. Usually 70–80% nests were found, during the first brood even 90–95%. The nests found were recorded on detailed maps (1:1000), their location and contents noted and subsequent occupation checked every 3–5 days. The search for nests largely based on surveying with the help of binoculars every place in the tree crowns likely to contain a nest. In c.20% cases the behaviour of adults was a helpful clue; noticing a female flying high through tree crowns was a strong clue indicating an equally high nest location. Such a binary technique should have reduced an unavoidable bias of underestimation of high-nest numbers.

To the nesting tree a small colour mark was attached to help rediscover it. The marks were usually placed several metres away from the nests not to indicate them to predators. The contents of most nests was checked with the help of a mirror attached to a pole. This method worked with the nests up to 7 m above the ground, preferably containing eggs (counting nestlings was hardly possible this way). High nests located away of the trunk were also checked with the mirror. Such a method, alongside with the prevailing

high location of nests (Tomiałojć 1993), has apparently reduced a percentage of nest desertions, very low indeed in this study.

For analysing the nesting success (or losses) all the nests for which the fate of the brood could be inferred at least from traces (egg shells, nestling remnants, scales after nestlings fledged, etc.) were taken into account. Thus, not only the nests that had been found active, but also those depredated before found. This was so because the chances to find them by a visually oriented observer were identical. In view of this, it was not necessary to calculate a nest exposure using May-field's (1961) method, the more so that it is said to have some disadvantages (Hensler 1985). In this paper the overall breeding success or failure per breeding attempt is analysed, except for a separate analysis of the losses suffered during the egg- and the nestling-stages.

In four years of intensive work the data on 118 Blackbird nests were collected. As the plots K and W were populated by 18–19 pairs, this denotes 1.5 nests found per each territory yearly. This material was supported by 242 nests found in BNP during 1975–1985, the information for many of those being less complete.

### Ringing and colour-ringing

Attempts to ring Blackbirds were reduced in success because of an extreme shyness of forest individuals. They brought the following outcome :

– The Blackbirds refused to be lured to mist-nests by the play-back of their songs or calls;

– Unsuccessful were the attempts to attract them by exposing food (apples), stuffed predators (*Garrulus glandarius*, *Mustela nivalis*, even *Tyto alba* rotating automatically its head) or stuffed conspecifics;

– Capturing adults at the nests with eggs caused desertions and had to be neglected.

Consequently, capturing adults was restricted to low nests and only those which remained till the stage of larger nestlings. Totally during 1986–1989 only 33 adults were colour-ringed and 130 nestlings or fledglings ringed. Earlier (1976–1985) in BNP additional 83 nestlings or fledglings and 19 adults had been ringed with metal rings.

### Observation sessions at the nests

An exceptional shyness of forest Blackbirds forced the use of collapsible blinds put 7–15 m from the nest to learn about the behaviour of particular pairs. Totally 140 hours were spent in blinds arranged at 18 nests. While interpreting the results it was necessary to clear the data off the evident cases when the bird behaviour was disturbed by the presence of the blind. The following additional precautions had to be made: the observer had to approach the blind (arranged on the previous day) with another person who later left the spot overtly. In single cases observations had to be ceased even in spite of all the precautions made, as the adults refused to feed their nestlings or did this approaching the nest stealthily, even on foot (in the case of low nest location), and leaving it with nervous calls.

### Monitoring of the caterpillar numbers

To estimate the food resources, since 1975 the numbers of leaf-eating caterpillars (*Geometridae* and *Tortricidae*) were counted on standardized in size (50 x 50 cm surface) lower twigs of hornbeams in plot W (and additionally on other plots). Each year during the second half of May 60–120 samples were collected (Tomiałojć and Wesołowski 1990). It should be stressed that the period of intensive study covers the years of a very low abundance of leaf-eating caterpillars. As our monitoring has revealed (Tomiałojć 1993, Tomiałojć et al. 1984, Tomiałojć and Wesołowski 1990), the years 1985–1986 were characterized by the lowest numbers of those invertebrates (about 960–2200 times less than the peak numbers in 1982 and 1992–1993).

## RESULTS

### a. Migratory status, mating system, site-tenacity

**Migratory status.** The Białowieża Blackbirds form a migratory population with only single males of unknown origin sporadically attempting to overwinter in human settlements or along the unfrozen streams in the Forest (Dolbik 1974, Borowski & Okołów 1988). Similar was reported from the nearby situated Lublin province already for the years 1850–80 (Taczanowski 1882). The earliest migrants return during the first half of March, with the earliest song recorded on 16 March 1975. The forest Blackbirds do not stay year-round on their territories even if wintering in the Forest, which contrasts with the findings from W Europe and S Sweden (Karlsson & Källander 1977).

– **Mating system and territorial behaviour.** In BNP the Blackbird is a classical monogamous and territorial species, though this does not mean that the whole food is collected within the boundaries of the species' territory (cf. Snow 1958). Cases of foraging flights to exterritorial young stands in front of the old-forest wall or, rarely, to open areas were recorded. Attempts to disclose the polygamy gave only two indications, both in OH stand (plot W). An almost certain case was that of a bigamy of a colour-ringed male which in 1988 was holding an exceptionally large territory (4.3 ha) at the forest edge. Four nests were found within this territory and their distribution in time and space suggested the presence of two females. Moreover, a nest found there on 25 May 1988 contained 7 eggs, an unusually high number, presumably laid by two females.

In BNP the Blackbird males demonstrate a full and intelligible system of grades in territory defence, from proclaiming it by song, through "parades" and threat postures, chasing the intruding 1st-year males, to rare brief fights. Prolonged fights have not been recorded. Persistent chases of 1st-year intruder males, lasting up to 0.5 hour, were performed within a radius of 50–70 m, thus, over most part of the owner's territory. These were recorded once or twice per season. Thus, in contrast to observations from urban dense populations (Snow 1958, Mulsow 1980, Luniak and Mulsow 1988), the BNP forest males demonstrate a low frequency and intensity of territorial encounters and, apparently, it is not necessary for them to develop a system of hierarchy (pecking order).

A more interesting is a differentiated level of female aggressiveness among various habitats. In spite of a noisy and prolonged character of inter-female fights, during 20-year period in BNP no such cases were recorded. Contrarily, in the Budapest parks, with the breeding density c. 20 times higher than in BNP (own rough estimate), during two mornings in the late March 1986 not less than 9 fights were observed, some of them extremely fierce. This may be supported by own incidental observations of fights in densely populated Oxford parks, as well as by a number of reports suggesting that such behaviour is something usual among urban Blackbirds (Heyder 1953, Snow 1956, Löhrl 1984, Stephan 1985). Heinroth and Heinroth (1924–1931), associating such fights with high density, even assumed them to be a species-specific feature (Steinbacher 1953). The BNP data contradict such conclusion and suggest that female-female fights are a degeneration symptom of very dense populations. Moreover, under urban conditions high amount of stress resulting from a close proximity of other females (3–5 m in the Budapest parks – author's observation) may also cause a reduction in the clutch size, known to depend negatively on the population density (Gnielka 1991). This may be another, though not exclusive, explanation for the reduced clutch size in urban habitats, so far related to inferred food shortage.

– **Site tenacity.** Out of 33 colour-ringed adults only five returned to the area of the previous-year breeding. These were: a male ringed as adult in 1987 returned to the neighbouring territory in 1988; another earlier colour-ringed male occurred in 1989 in plot W (the colour combination of its rings could not be identified); in 1989 a return of a colour-ringed female, marked some 250 m away in 1988, was stated. During 1990 two cases were added; a male ringed as adult in 1989 returned to the same territory, and a female was seen in plot K, but the colour-ring combination could not be identified.

Concerning the natal tenacity, no single individual of 130 (plus 83 from earlier years) fledglings or nestlings was rediscovered in the area of birth.

These results, quite different from what has been found for the Song Thrush (author's data), may partly be an artefact, as almost half of the Blackbirds present on their territories could not be identified so as to exclude the presence of metal rings. Moreover, a larger size of the Blackbird's territories might have caused that even shifts by one-two territories away resulted in falling beyond the boundaries of the study plot. Theoretically, a shock after being ringed might have forced some birds to move elsewhere after the brood had been completed. However, out of 21 precisely analysed cases of ringing adults at the nests their territories were still occupied during the second brood by some (the same?) pairs. In one case a male ringed on 15 May disappeared from his territory and an unringed one was seen instead. Remarkably enough, out of 20 males of known age found on our regularly visited plots K and W only in four cases they were old individuals. On the contrary, sporadic visits to the forest-interior plots, chiefly to those with AA stands (plots L and H) made in the same years, suggested the share of old males being roughly 50%. Thus, adult males may avoid the plots frequently visited by ob-

servers, or the forest-edge zone at all for other reasons than the presence of humans. A high percentage of adult males was found in the Wytham Wood near Oxford (Snow 1958) though this habitat is comparable to the forest-edge sections of BNP.

It cannot be stated whether the migratory BNP population of the Blackbird shows a lower nesting and natal tenacity than the resident British one (Snow 1958, Greenwood and Harvey 1976), though scarce data at hand suggest this.

**Reproductive parameters of the forest Blackbirds**

**Sex ratio, status of males.** Unmated Blackbird males proclaimed their lonely status by intensive singing only for a few days. Later in such places mated pairs and nests were found. Only in 1988 a lonely male singing in the "bachelor" way stayed on the plot K at least from 1st to 28th June. Such males did not evoke aggression in the neighbouring mated males, e.g. on 5 May 1989 on plot K during six hour observations from a blind a lonely first-year male sang persistently only 50 m away from a nest with nestlings. The owner of the nest, also a first-year male, collected food exactly under the tree from which the bachelor was singing, and did not try to expel him. During the second brood this bachelor male found a mate and, extending his small territory, captured a large part of the territory of the neighbour, thus pushing him aside. In a few cases, when feathers of females were found close to the nest suggesting their death, the males remained on their territories during the second brood. Their behaviour suggested that : – some remained solitary (1 male); – some probably found a new mate (3 cases); – the identity of a new female was confirmed (1 case). The second category is uncertain with respect to the female identity as some of them might have survived the attack of the predator even losing large feathers. Thus, the BNP males and females have a chance to find a new mate even late in the season. It is unclear whether these are bachelor individuals or birds that lost their previous mate and/or deserted previous territory. It is certain, however, that if a surplus occurs, it is by no means as considerable as in the Song Thrush studied at the same time and place (author's data).

**Timing of breeding, number of broods.** The breeding season of Blackbirds in BNP, understood as the period when eggs or nestlings occur, lasts from c.8–10 April to late July. The last eggs are laid at the
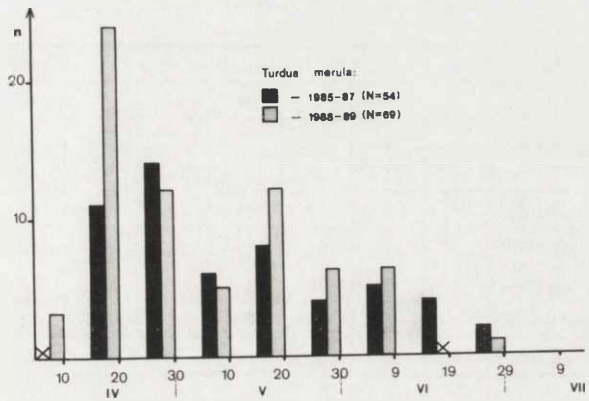


Fig. 1. Timing of breeding season in the BNP, expressed by the number of Blackbird clutches commenced during each of ten-day periods.

[Ryc. 1. Przebieg sezonu lęgowego w BNP, wyrażony liczbą lęgów kosa rozpoczętych w poszczególnych dekadach.]

end of June (Fig. 1). Most pairs rear two successful broods a year, or undertake 3–4 breeding attempts. The occurrence of unquestionable third broods has not been ascertained though some facts suggest their possibility: in 1989 a colour-ringed female reared the first brood between c. 12 April and 13 May while the second one between 15 May and 15 June (the nestlings left the nest prematurely on 12 June). Thus, there was a chance to rear the third brood late in June and in July. Fresh clutches found in BNP late in June may denote a third brood, though most of them seem to be rather clutches repeated after failures. Consequently, the forest Blackbirds show a somewhat lower natality than that of the Song Thrush in the same area (author's data). The Blackbird's egg-laying season in BNP, though begins a fortnight later than near Oxford or in Switzerland (Snow 1958, Glutz and Bauer 1988), ends exactly at the same time, i.e. late in June. This may reflect a common constraint, although only a few environmental factors seem to influence in a similar way both the migratory Białowieża population and the resident English one.

**Clutch size.** Variation in clutch sizes of forest Blackbirds is shown in Table 1. Average clutch size in BNP was very high (Tab. 2), particularly in AA stands. For unknown reasons the parameter is unstable in time, however. The statistically significant decrease in the years 1986–1989 (Tab. 2) resulted largely from a

Table 1. Number of clutches of a particular size (BNP data).

[Tabela 1. Wielkość zniesień kosa (dane z BPN).]

| Habitat and year | | Number of eggs in clutch | | | | | Total |
|---|---|---|---|---|---|---|---|
| | | 3 | 4 | 5 | 6 | (7) | n |
| AA | 1975–85 | 1 | 12 | 25 | 2 | – | 40 |
| | 1986–89 | 2 | 25 | 21 | – | (1?) | 48 |
| Total for AA: | | 3 | 37 | 46 | 2 | (1?) | 88 |
| OH | 1975–85 | 1 | 11 | 19 | 6 | – | 37 |
| | 1986–89 | 2 | 21 | 17 | – | – | 40 |
| Total for OH: | | 3 | 32 | 36 | 6 | – | 77 |
| Grand total AA+OH | | 6 | 69 | 82 | 8 | (1?) | 165 |

stitute even larger part, probably c. 90%, of the whole food, because of a considerable size of this prey. The second position on the list in OH stands occupied the leaf-eating caterpillars *Geometridae* and *Tortricidae*, while in the AA swampy stands – the insects of the *Tipula* sp. type and some larvae as well as leaches *Hirudinea*.

To measure the feeding intensity the observations were carried out incessantly throughout the whole day at a nest with four 8-day-old nestlings. Uniform scattering of the feeding sessions throughout the day-time (Fig. 2), whether at sunny midday hours or at twilight, shows that in the high-forest Blackbirds can

Table 2. Mean clutch size in different periods (BNP data).
Note: Thie difference between the totals for 1975–1985 and 1986–1989 is highly statistically significant (t-test, p<0.001).

[Tabela 2. Średnia wielkość zniesień w różnych okresach.]

| | April | | May | | June | | All | |
|---|---|---|---|---|---|---|---|---|
| | $\bar{x} \pm$ SD | (n) | $\bar{x} \pm$ SD | (n) | $\bar{x} \pm$ SD | (n) | $\bar{x} \pm$ SD | (n) |
| Years 1975–85 | 4,65± 0.56 | (26) | 4.91± 0.60 | (34) | 4.58± 0.87 | (17) | 4.75± 0.67 | (77) |
| Years 1986–89 | 4.92± 0.53 | (55) | 4.56± 0.58 | (23) | 4.50± 0.70 | (10) | 4.38± 0.57 | (88) |
| Total | 4.40± 0.56 | (81) | 4.77± 0.62 | (57) | 4.55± 0.80 | (27) | 4.54± 0.76 | (165) |

sharp drop in the 1986–1987 clutch size in swampy AA stands. It could not be caused by low caterpillar resources (Tomiałojć 1993) as this kind of food is less important and less variable in riparian forests. Within-in-seasonal changes of the average clutch size were similar to those found in other populations (Snow 1958, Dyrcz 1963, Havlin 1963a, Glutz & Bauer 1988, Wesołowski & Czapulak 1988), e.g. 4.4 in clutches started in April, 4.77 among those from May and 4.55 among June ones. Being similar in pattern, the values from BNP remain consistently the highest.

**Nestling diet, feeding frequency.** Difficulties with the use of traditional methods (neck-rings, examining stomach content) of studying the diet of this high-nesting and very shy species forced the adoption of another approach. The composition of food portions (beakfuls) brought to nestlings was identified by means of binoculars (11 x 40 and 20 x 60) from a blind arranged 7–15 m at low nests. The main food of the nestlings appeared to be the earthworms *Lumbricidae*, found in 66–86% of identified portions (Tab. 3). When considered by biomass the earthworms would con-

Table 3. Various prey types in the food brought to Blackbird nestlings. (Based on 132 hours of observation at 17 nests).
Note: The total number (N) of beakfuls with identifiable prey is lower than the sum of "n" because in some portions more than one prey type has been identified.

[Tabela 3. Skład pokarmu przynoszonego pisklętom kosów. (Wynik 132 godzin obserwacji przy 17 gniazdach).]

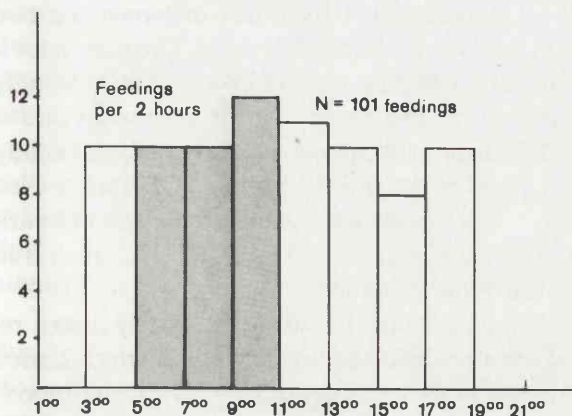| Kind of prey | AA | | OH | |
|---|---|---|---|---|
| | n | (%) | n | (%) |
| Earthworms | 118 | (67) | 188 | (87) |
| Caterpillars *Geometridae* and *Tortricidae* | 14 | (8) | 32 | (15) |
| *Larvae* of *Tipula* ? | 38 | (21) | 20 | (9) |
| Winged insects | 23 | (13) | 8 | (4) |
| Leaches *Hirudinea* | 17 | (10) | 0 | (0) |
| Big white *larvae* | 19 | (11) | 3 | (1) |
| Molluscs and *larvae* of *Cossus cossus* | 4 | (2) | 7 | (3) |
| *Hydrophilus* beetle | 2 | (1) | 0 | (0) |
| Butterflies | 1 | (0.6) | 0 | (0) |
| Dragonflies | 1 | (0.6) | 0 | (0) |
| Sample size | 177 | (100%) | 217 | (100%) |

Fig. 2. Pattern of daily nestling feeding intensity in the BNP. Results of continuous observation at a nest in OH habitat on 19 May 1988; shaded part is equivalent to a standard 6-hour session constituting 40% of daily feedings (Tab. 4) applied at the remaining 16 nests of the species.

[Ryc. 2. Rozkład karmień piskląt w BPN.
Dane zebrane przy gnieździe badanym w ciągu 19 maja 1988 w grądzie; zaciemniona część, stanowiąca 40% karmień, odpowiada 6-godzinnym obserwacjom prowadzonym dodatkowo przy każdym z 16 innych gniazdach (Tab. 4).]

forage daily for a longer time than when under urban conditions. This conclusion found support in results of 6-hour observation sessions at the remaining 16 nests (Tab. 4) where no decrease in feeding frequency at mid-day hours was noticed either.

The males fed nestlings more intensively than the females, contrarily to results of Graczyk (1961), particularly when young required brooding. Feeding by the females was even less important than the Table 4 suggests because, as a rule, they brought portions constituting only c. 1/3 of beakful load of males. The females tended to bring mostly caterpillars and unidentifiable small items, while the males usually brought 4–7 large earthworms. While the females tended to forage a few to 50 m from the nest, the males, judging from their flights and voices heard, flew much farther and usually in different directions from those exploited by the females.

A considerable individual variability in feeding frequency was noticeable. In the OH stand two females, both tending four about 13-day-old nestlings, fed 2.5 and 5.6 times per hour. Their males fed compensatingly: 5.8 and 3.3 times per hour respectively. In another nest 8-day-old nestlings were fed by the fe-

male with a high frequency of 8.1 times per hour while her partner, singing in the meantime, fed 3.8 times only. Such a variability made it impossible to disclose any consistent between-habitat differences. A conflict of interests between the members of a pair, which produced a wide array of results, seems to be the better explanation here.

To small nestlings parents bring small prey. They do not fragment, however, long earthworms and sometimes deliver large live leaches. Dramatic moments were noticed, e.g. when two nestlings attempted to swallow a large earthworm simultaneously, starting from its opposite ends. A six-minute struggle exhausted them, without prompting any help from the female present at the nest. In another case a large leach attached to the beak of a Blackbird male who for 3 minutes fruitlessly persisted in putting it into the gape of a nestling and subsequently pulled it out while raising his head. In such cases the adult eventually swallowed too large prey itself. According to Dyrcz (1969), Blackbirds bring some earthworms in fragments. Probably fragmentation of prey is not made on purpose but happens while pulling earthworms out of the earth holes. In dry urban soil they may be fragmented while not in the humid forest one.

Table 4. Intensity of Blackbird nestling feeding in relation to their age and to the parent's sex. (Data from 132 hours of observation.)

[Tabela 4. Intensywność karmienia piskląt kosa w zależności od ich wieku oraz od płci rodziców. (Wynik 132 godzin obserwacyjnych.)]

|  | Nestlings age | | | | | |
|---|---|---|---|---|---|---|
|  | 1–3 | | 4–8 | | 9–14 | |
|  | M | F | M | F | M | F |
| Hours of observation | 36 | 36 | 72 | 72 | 24 | 24 |
| Feedings per hour | 2.2 | 1.6 | 3.2 | 2.7 | 4.3 | 4.0 |
| M+F | 3.8 | | 5.9 | | 8.3 | |

## Offspring mortality

**Nesting losses and their timing.** Nesting losses vary with the progress of season (Tab. 5) which reflects first of all a change in the protective impact of the leaf-cover (Snow 1958, Havlin 1963a, Stephan 1985). In BNP the nesting losses among the first-brood nests were by a dozen or so per cent higher, during 1986–1989 even by 20%, than those among the broods started after mid May (Tab. 5). A statistically signifi-

Table 5. Nesting losses with the progress of the breeding season. Note: The differences between the 1st and the 2-3rd brood statistically significant ($\chi^2$ test, p<0.05).

[Tabela 5. Straty lęgowe w przebiegu sesonu lęgowego.]

| | | 1st brood (before 15 May) | | 2–3rd brood (after 15 May) | |
|---|---|---|---|---|---|
| | | % | (n) | % | (n) |
| AA | 1975–84 | 70.0 | (40) | 59.1 | (22) |
| | 1985–89 | 82.6 | (23) | 60.7 | (28) |
| | Total | 74.6 | (63) | 60.0 | (50) |
| OH | 1975–84 | 69.7 | (33) | 63.6 | (22) |
| | 1985–89 | 70.6 | (51) | 50.0 | (26) |
| | Total | 70.2 | (84) | 56.2 | (48) |
| Total AA+OH | | 72.1 | (147) | 59.2 | (98) |

cant increase in nesting losses in AA stands – from 70 to 82.3% – manifested itself also between the two periods of 1975–1985 and 1986–1989. The reason for it remains obscure. The nesting losses varied strongly between years (Tab. 6): during the very bad years of 1984–1985 in both deciduous habitats analyzed jointly they reached 80.8% (n = 47 nests), in OH stands even 92% (n = 25). Consequently, the whole span of variation in nesting losses was from 50 to 92% which is an almost two-fold difference.

**Kinds of nesting losses.** Most nesting losses resulted from predation or the threat of it, which caused desertion of broods after disturbance. Out of 166 broods lost only two were due to some accidental events such as covering the eggs in a tree-hole by rotten wood powder or knocking down the nest by wind. Even if we

Table 6. Variation in nesting losses and success among years as related to egg or nestling stage.

[Tabela 6. Zmienność strat lub sukcesu lęgowego pomiędzy latami w rozbiciu na stadium jaj i stadium piskląt w gnieździe.]

| Year | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | Total | Average |
|---|---|---|---|---|---|---|---|---|
| Eggs laid (nests) | 93 (22) | 51 (12) | 63 (15) | 53 (13) | 102 (24) | 120 (28) | 482 (114) | 4.22 per brood |
| % of eggs lost | 33 | 43 | 54 | 34 | 44 | 24 | 39 | – |
| Hatched Eggs | 31 | 29 | 29 | 35 | 57 | 91 | 272 | 2.38 per brood started |
| % of nestlings lost | 13.0 | 34.5 | 11.1 | 35.8 | 27.4 | 44.2 | 27.6 | – |
| Nestlings fledged | 27 | 19 | 22 | 16 | 29 | 38 | 151 | 1.32 per brood started |
| % of eggs producing fledglings | 29.0 | 37.2 | 35.7 | 30.2 | 28.4 | 31.6 | 31.3 | – |

Table 7. Types of nesting losses among the BNP Blackbirds.

[Tabela 7. Rodzaje strat lęgowych u kosów z BPN.]

| Detailed specification | 1984–86 | | 1987 | | 1988 | | 1989 | | Totals | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | AA | | OH | |
| | AA | OH | AA | OH | AA | OH | AA | OH | n | % | n | % |
| Larger shell fragments (corvids) | 4 | 9 | 0 | 1 | 5 | 2 | 2 | 1 | 11 | 25 | 13 | 20 |
| Nest with tiny eggshell fragments (destructed by small mammals) | 2 | 8 | 0 | 2 | 1 | 1 | 1 | 1 | 4 | 9 | 12 | 19 |
| Eggs missing nest not damaged | 2 | 9 | 4 | 0 | 2 | 5 | 0 | 11 | 8 | 18 | 15 | 23 |
| Nestlings missing prematurely | 1 | 1 | 3 | 1 | 4 | 1 | 5 | 3 | 13 | 31 | 6 | 9 |
| Clutch/brood missing, nest intact | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | – | 1 | 2 |
| Clutch deserted (Man?) | 0 | 3 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 2 | 4 | 6 |
| Eggs/nestlings lost, feathers of female suggesting death | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | – | 5 | 8 |
| Nestlings dead, not emaciated (female killed?) | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 2 | 1 | 2 |
| Remnants of nestlings eaten (mustelid) | 1 | 4 | 0 | 0 | 2 | 0 | 3 | 3 | 6 | 14 | 7 | 11 |
| Total | 10 | 38 | 7 | 4 | 15 | 9 | 12 | 13 | 44 | 100% | 64 | 100% |

include two other nests located on sandy vykhrots (root plates of fallen trees) and filled with sand before the eggs were laid in, and seven cases of full clutch desertion by females (two after ringing them), the total losses due to such factors remain negligible. The more so that some desertions could be apparent and resulted from the female's death far from its nest. Thus, at least 95% nesting losses in BNP were due to predation, or as much as 98% due to predation and the attempts to avoid it by deserting the nest.

Two main kinds of nesting losses are recognized: during the egg stage and during the nestling stage. Not always data precise enough can be collected, hence several calculations treat them jointly. For a more complete sample from 1986–1989 the following way of differentiating has been chosen (Tab. 7). When data combined for all years are analysed the proportion of overall losses is similar during the two periods of study (1975–1985 and 1986–1989): about 68–69% of eggs/clutches were lost in both periods. The data for 1986–1989 suggest that the egg losses were somewhat higher (37%) than the nestling losses (31.6%). These proportions change, however, when analysed year by year: during 1986 the rate of nestlings killed was four times lower than during 1989, and in the former year the egg losses were five times higher than those of nestlings. Separate calculations for egg stage and nestling stage help to identify the causes of failure.

The data can also be split into lower categories, apparently dependent on kind of predator, time and habitat. A traceless disappearance of eggs or nestlings is the most frequent category (Tab. 7). The fact that in several nests known to contain nestlings after their premature disappearance the inner layer of nest showed some damage or disorder suggests that the

nestlings had attempted to prevent being pulled out of the nest by a predator. The second category comprises clutches destroyed by rodents, the Red Squirrel *Sciurus vulgaris*, dormice *Glyridae* or mice *Muridae*. After their attack, usually on eggs, tiny fragments of chewed eggshells were left. In OH stands, known to abound with rodents (Aulak 1982), such signs were found in 22% of all identifiable failures. Another group of nest predators are corvids, mostly the Jay *Garrulus glandarius*, sporadically the Raven *Corvus corax*, and locally probably the Nutcracker *Nucifraga caryocatactes*. The nests depredated by them can be recognized by large eggshells inside or under the nesting tree.

The nests with nestlings were a target of attacks by mustelids, chiefly martens *Martes* sp. Such nests contained remains of eaten nestlings, sometimes the female's feathers. Losses of that kind were frequent during 1989. Among BNP birds of prey, attacks on Blackbird nests have been documented for the Buzzard *Buteo buteo* and Tawny Owl *Strix aluco* (Jędrzejewski *et al.*., in press). Per analogy to Uttendörfer's (1952) data from Germany and to author's own data from BNP for the Song Thrush, it can be presumed that also the following animals may cause losses among Blackbirds: *Mustela putorius, M. erminea, M. nivalis, Vulpes vulpes, Nyctereutes procyonoides, Lynx lynx, Sus scrofa, Accipiter gentilis, A. nisus, Pernis apivorus, Hieraaetus pennatus, Aquila pomarina, Bubo bubo, Asio otus, Aegolius funerous, Glaucidium passerinum*, etc. The full list of predators on Blackbirds is presumably as long as in the case of the Song Thrush in BNP (author's data), only lower density of Blackbirds prevented collecting more complete data.

A small percentage of the eggs failed to produce fledglings for reasons other than predation. Here the so-called partial losses in otherwise successful nests were taken for analysis (Tab. 8). The percentage of the eggs lost was the highest in 1986 (17% failed to give nestlings) while the lowest in 1989 (only 2%). The mean clutch size was also the lowest in 1986 which co-occurred with the low caterpillar numbers of that year (Tomiałojć 1993). Partial reduction in the nestling number, suggestive of nestling starvation, was recorded only in a single case in 1986 (Tab. 9). However, during 1986 the predation pressure on Blackbird nestlings was the lowest, compensating successfully for other disadvantages so that the overall nesting success was quite high (Tab. 10).

Table 8. Reduction (partial losses) in egg number. (Clutches completely destroyed have been omitted).

[Tabela 8. Straty częściowe wśród jaj w gniazdach trwających pomyślnie do wylęgu.]

| Year | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | Total or average |
|---|---|---|---|---|---|---|---|
| Eggs laid (number of clutches) | 33 (7) | 30 (6) | 41 (10) | 38 (8) | 58 (13) | 94 (21) | 294 (65) |
| Hatchlings | 27 | 29 | 34 | 35 | 53 | 92 | 270 |
| Reduction in % | 18 | 3 | 17 | 8 | 9 | 2 | 8.2 |

Table 9. Partial losses among nestlings in successful broods.
(Broods totally destroyed have been omitted).

[Tabela 9. Straty częściowe wśród piskląt w pomyślnie zakończonych lęgach.]

| Year | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1984–89 |
|---|---|---|---|---|---|---|---|
| Eggs laid (successful nests) | 29 (6) | 20 (4) | 34 (8) | 18 (4) | 32 (7) | 40 9) | 173 (27) |
| Hatchlings | 24 | 19 | 27 | 16 | 29 | 40 | 155 |
| Fledglings | 23 | 19 | 26 | 16 | 29 | 40 | 153 |
| Reduction–% related to eggs laid | 21 | 5 | 24 | 11 | 9 | 0 | 11.5 |

Table 10. Nesting success in particular years and habitats.
Note: Statistically significant differences occur only in AA data between 1975–1986 and 1987–1989, as well as between habitats within three periods treated separately ($\chi^2$ test, p<0.05).

[Tabela 10. Udatność lęgów w poszczególnych latach i biotopach.]

| | AA | | OH | | AA+OH | |
|---|---|---|---|---|---|---|
| | % | n | % | n | % | n |
| Period I: | | | | | | |
| –1975–85 | 35 | 52 | 42 | 43 | 38 | 95 |
| Period II: | | | | | | |
| –1984–85 | 35 | 20 | 12 | 26 | 22 | 46 |
| –1986 | 50 | 6 | 28 | 18 | 33 | 24 |
| Period III: | | | | | | |
| –1987–88 | 15 | 23 | 48 | 29 | 34 | 52 |
| –1989 | 25 | 16 | 43 | 21 | 35 | 37 |
| Totals | 30.3 | 117 | 35.7 | 137 | 33.1 | 254 |

## Nesting success and production of fledglings

The nesting success is defined here as the percentage of broods from which at least one young fledged. It varied in BNP between years from 30 to 35%, on average being 33% (Tab. 6 and 10). A more precise way of measuring it, however, is when only the nests with a known number of eggs laid are taken into consideration. Moreover, lumping data from several years may blur even considerable differences. For example, the fledgling success in trophically poor year 1986 was even higher (35.7% of total number of eggs) than in 1989 (31.6%; Tab. 6) owing to a stronger predation pressure in the latter year. The 1984–1985 period was in BNP exceptionally bad for Blackbird reproduction, as for some other passerines (author's data). The nesting success of Blackbirds was only 19.2% (n = 47 nests),

being especially low in OH stands: 8.0% (n = 25). In those two years the caterpillar index dropped to its lowest values (0.2 and 0.025 caterpillar per standard twig respectively), i.e. over 1000 times lower than in the gradation years 1982 and 1992, creating a shortage of alternative food for predators. However, already in 1986 the nesting success in OH stands was already 1.7 times higher (Tab. 10), during 1987–1989 even 4.2 times higher. Therefore, bad reproductive years are those when several inhibiting factors coincide, like low caterpillar numbers, dry weather and high predation pressure.

Long-term data, when lumped together, may conceal even contradictory results. For example, a sharp change occurred between the breeding season of 1986 and 1987 in both intensively studied habitats of BNP. While earlier (1975–1986) the nesting success had been lower in OH than in AA stands, later it started to improve in the former habitat, increasing from 28.8 to 43.7%. In AA stands, on the contrary, it was fairly high (35.9% on average) till 1986 and then decreased to 19.2%. The last difference is statistically significant ($\chi^2$ = 3.99, p<0.05); the reasons for its manifesting are obscure. The change might reflect an accidental or local event, though simultaneous drop in the average clutch size (Tab. 2) suggests a true deterioration of living conditions in AA habitat. Field observations indicate that a drop in the ground-water level has occurred in BNP recently, which may have a stronger impact on availability of invertebrates in swampy AA stands whereas OH stands, with their mineral soil covered by a more continuously distributed leaf litter, retained some humidity even during drought periods. To check this, on 2–4 July 1989 samples (50 x 50 cm and 5 cm deep) of soil and leaf litter from both habitats were analysed. In OH stands earthworms and *Myriapoda* were actually more numerous than in AA stands (Tab. 11), especially when compared with their dry-mud patches which during drought preserve hardly any larger invertebrates.

As not all Blackbird nests were found, theoretically the reproductive output calculated from known nests may deviate from the true pattern. To check this, a different way of measuring the reproduction level has been applied. It was based on the territory (pair) as a unit. Out of 17–19 pairs occurring in a particular year on the plots W and K only exceptionally a pair or two managed to rear successfully two broods a year. The

record of such cases is as follows: 1986 – one case, 1987 – one, 1988 – one, 1989 – two cases (on two territories). These results do not differ from those traditionally calculated, and exclude possibility of a bias due to overlooking nests with a different depredation rate. Also these data confirm that a change in predation pressure actually occurred between 1986 and 1987, reversing the proportions between OH and AA stands: during 1987–1989 more successful families were found in OH stands (0.77 per average territory) than in AA ones (only 0.36).

Table 11. Number of larger invertebrates in forest litter/soil samples during early July 1989 drought period.

[Tabela 11. Liczebność większych bezkręgowców w próbkach ściółki i gleby leśnej podczas suszy w lipcu 1989.]

|  | OH | AA | | Total |
|---|---|---|---|---|
|  |  | island | dry mud |  |
| Sample size | 20 | 10 | 10 | 40 |
| *Lumbricidae* | 7 | 2 | 1 | 10 |
| *Millipedia* | 1 | 2 | 0 | 3 |
| *Carabidae* | 1 | 1 | 1 | 3 |
| *Myriapoda* | 4 | 1 | 0 | 5 |

Table 12. Number of Blackbird fledglings reared in BNP per territory per season. NF – number of families noticed per average territory, NY – number of fledglings per average territory.
Note: The values have been calculated according to the formula NF = $F_1 + F_2$ / T, where $F_1$ and $F_2$ denote numbers of families with fledglings (from the first and second brood) and T – the average number of territories occupied during both broods in a plot. The formula NY = NF x Y means the number of young reared in a territory, where Y denotes the average number of fledglings in a successful brood (extracted from Tab. 9).

[Tabela 12. Liczba podlotów kosa w BPN w przeciętnym terytorium i roku. NF – liczba rodzin w przeciętnym terytorium rocznie, NY – liczba podlotów w przeciętnym terytorium rocznie.]

|  | AA | | OH | | Totals | |
|---|---|---|---|---|---|---|
|  | NF | NY | NF | NY | NF | NY |
| 1986 | 1.0 | 3.25 | 0.61 | 1.98 | 0.8 | 2.6 |
| 1987 | 0.3 | 1.2 | 0.83 | 3.3 | 0.6 | 2.4 |
| 1988 | 0.2 | 0.87 | 0.75 | 3.1 | 0.5 | 2.2 |
| 1989 | 0.6 | 2.57 | 0.76 | 3.4 | 0.6 | 2.8 |
| Average 1987–89 | 0.39 | 1.63 | 0.77 | 3.26 | 0.6 | 2.5 |

Production of fledglings per pair per season has been obtained by multiplying the number of families with young (Tab. 10) by the average size of successful brood (Tab. 12). The mean value is 2.5 young/territory/season, with fluctuations between 0.87 and 3.37, depending on the year and habitat. The exceptional pairs, however, produced up to 9 young (one female was colour-ringed which proves that the same individual reared 9 young in a season).

**Mortality of adults**

The oldest Blackbird ringed in Poland survived for at least 20 years and four months (Rydzewski 1978). This allows to estimate the amount of experience which some individuals may accumulate during their lifetime. Unfortunately, it is unknown in what kind of habitat such a long survival took place; some cases allow to suggest that longevity of individuals from human-made habitats may exceed that from a primaeval forest (Tomiałojć 1980b).

During this study some data on adult female mortality have been collected. Out of 17–19 pairs breeding each year on two plots seven cases of highly possible female death were recorded: 1986 – 3 cases, 1987 – 0, 1988 – 1, 1989 – 3. This would mean c. 9% of females present, which is uncertain, however, as only two corpses were actually found. In the remaining cases the judgement was based on finding contour feathers of females and their constant absence at the nest. During 1977–1992 there were six additional cases suggestive of the female death. All these 13 cases can be classified as follows:

– female's (killed or injured) feathers found in or at the nest and her constant absence (7 cases);

– died of cold, not injured nor emaciated, nestlings found in the nest (4 cases), which suggests that the female died far from it as no cases of deserting the nestlings after even serious disturbance are known (Havlin 1963a);

– deserted complete clutches with well-developed embryos (2 cases), without a stronger disturbance by the observer.

In one of the first-group cases feathers were found a few metres from the low nest with the young survived, which suggests that the female had been killed by a predator during her injury-feigning, the behaviour actually observed among the BNP individuals.

The three young were reared successfully by the wi-
dowed male, which at the end of the feeding period
weighed only 84 g. Another unusual case presents a
female found dead in her empty nest in a half-hole. She
had a wound of her breast. This suggests that a mam-
malian predator injured the female, then extracted the
nestlings (too young to escape) and the female re-
turned to nest to die on it later on.

Symptomatically, out of 13 cases of suspected or
confirmed female death in all but two cases their nests
were located low above the ground (0.8–3 m), all
below the average for BNP (5.3 m). Moreover, all five
cases of full clutch desertion concerned nests 1.3–2.5
m above the ground. Thus, low location of Blackbird
nests in BNP seems to bring a personal risk to females.

Full-grown Blackbirds fall prey to predators, in
particular the avian ones, also far from the nest. Dur-
ing 1976–90 we recorded 9 cases of Blackbird remains
in BNP and 45 of the Song Thrush, in spite of the
former species' plumage being more contrasting with
the leaf litter. The five times lower frequency of falling
prey agrees well with 4–5 times lower abundance of
Blackbirds in the Forest as compared to Song
Thrushes. The BNP data on adult Blackbirds falling
prey to avian predators broadly agree with earlier
results from England, Holland and France (Newton
1986, Tinbergen 1946). In those countries, where the
Blackbird is more numerous than the Song Thrush, the
remains of predated individuals of the former species
are during the breeding period less frequent than
those of the latter one, while during non-breeding
period just opposite is true. Uttendörfers' (1952) data
from Germany demonstrate a slight predominance of
Song Thrush remains. The BNP data show that adult
Blackbirds during the breeding season, when they
rather do not leave forest habitats, avoid being killed
equally efficiently as Song Thrushes (author's data).
Both species experience here fairly low predation
pressure on adults from avian predators. A relatively
high share of these two species in some W European
data comes from the fact that those were frequently
the remains of inexperienced or poorly flying young.
Moreover, a considerable part of them were from the
non-breeding season when thrushes extensively pene-
trate open habitats, in which Blackbird appears to be
more vulnerable to predation than the Song Thrush
(Newton 1986).

DISCUSSION

### Pristine features in breeding ecology of the forest Blackbirds

The knowledge of Blackbird ecology comes mostly
from the part of Europe deeply transformed by hu-
mans (Snow 1958, Cramp 1988, Glutz and Bauer 1988,
Stephan 1985). Even the best known regional popula-
tion, however, cannot offer a complete model of func-
tioning of a whole widely distributed species. To
develop a balanced view of the Blackbird's ecology, it
would be necessary to conduct studies of its distinct
populations, such as migratory versus resident ones,
primaeval versus those from secondary anthro-
pogenic habitats, or geographically – those from the
margins and those from the centre of the breeding
range or the Mediterranean versus Central-European,
etc. This study describes breeding ecology of a migra-
tory Blackbird population from the centre of its breed-
ing range, inhabiting the least disturbed lowland
forest habitats. Unusual shyness of the forest Black-
birds made it impossible to collect adequate data on
many aspects of their breeding ecology, yet what has
been achieved allows to construct a fairly balanced
summary. In accordance with earlier suggestions by
Snow (1955, 1956, 1958), Dyrcz (1963, 1969), Glutz and
Bauer (1988) or Luniak and Mulsow (1988), it has been
revealed that the Blackbirds of primaeval forests live
under conditions dramatically different from those
faced in suburban or farmland habitats.

**Migratoriness of forest Blackbirds.** In the past
when most parts of our continent were covered with
extensive forests, most of the European Blackbirds had
to migrate for winter to the areas with a milder climate,
as well as to descend from mountains to the lowlands,
as this happens till now near Alma-Ata or in Switzer-
land (Kovshar and Shujko 1984, Glutz and Bauer
1988). Small patches of forest-devoid land in the
ancient southern Europe must have denoted a smaller
carrying capacity of the European wintering grounds
in past millennia. Though I do not suggest that all
pristine Blackbird populations were migratory, yet
during the last two-three thousand years the zone
populated by resident or partially migratory popula-
tion of the species must have expanded to the north-
east considerably (cf. Lack 1943–44).

The change from migratory to resident way of life
must have triggered several transformations in breed-

ing ecology of the populations involved. Such features of the west-European Blackbirds as: the year-round territoriality, an early and prolonged breeding season, a relatively high production of young, presumably enhanced survival until the next breeding season and, consequently, a higher breeding density all result, at least partly, from the change from the migratory to the resident way of life. Moreover, such a change may have allowed a finer adaptation to local conditions (Mayr 1963) which in migratory populations was inhibited by environmental requirements of the winter grounds and stopover sites. From this hypothetical perspective the prediction can be drawn that the Blackbirds which breed in the last extensive forest tracts of Western Europe should largely leave those forests for winter. For checking this, two areas seem to be most suitable: the New Forest in southern England and some extensive forest complexes in Burgundy.

**Breeding density in different habitats.** A detailed analysis of the breeding density of several Blackbird populations was presented earlier (Tomiałojć 1993). Here, however, having data on reproduction and mortality of primaeval populations, it is possible to evaluate the reasons for sharp differences in density, and the ecological consequences of overcrowding which occurs in some anthropogenic habitats.

Regarding the first problem, it is necessary to remind that the colonization of urban habitats by Blackbirds started as early as in the 18th century and after 1840–1850 it has become a widespread phenomenon in the western part of the continent (Stephan 1985, Tomiałojć 1985, Glutz and Bauer 1988, Luniak and Mulsow 1988). For a century or so (which means for a hundred or so generations!) urban populations of the species were reproducing at the absence of main predators, both the nest predators and the predators on adults. At that time urban Blackbirds suffered low nesting losses, reaching as high nesting success as 50–60%, which roughly equals the production of 4–5 fledglings per pair yearly (e.g. Snow 1955, 1958; Havlin 1963a). For a hundred or so years some urban Blackbird populations produced twice as many fledglings as it is necessary to maintain a primaeval forest population (producing 2.5 young per pair) at a stable numerical level. The period of so high production of young terminated in most cities with colonization of them by corvids, chiefly the Magpie *Pica pica* and Crow *Corvus corone*, and locally also martens *Martes*

*foina, M. martes* (cf. Tomiałojć 1980). Since then, even from the same urban habitats, very high nesting losses started to be reported, reaching 70–88% or even more (Stephan 1985, Glutz and Bauer 1988, Mizera 1988), because in relatively transparent urban habitats corvids not only can find bulky Blackbird nests more efficiently, but also additionally may kill fledglings devoid of sufficient bush-cover. For this reason several recent urban studies have again registered very high breeding losses, exceeding even those in the rural habitats that usually contain dense hedgerow- or spruce-plantation-thickets hardly penetrable to corvids, and those in natural extensive forests which do not abound in stronger corvid species. This scenario of historical events explains why any automatically lumped urban data, as representing often different periods of the described process, fail to give a clear picture of the dependences described (Tomiałojć 1985).

The best case to illustrate the reversed course of events is that from Poznań, W Poland. In the Sołacki Park of Poznań during 1950s, the period when most predators were absent, the Blackbird densities continued to increase and the nesting success was at least 34% (Graczyk 1959, 1960, 1961). In 1970s the density reached 27.6 p/10ha, locally even 45.2 p/10 ha (Mizera 1980). However, after the arrival and increase in numbers of Hooded Crows and Magpies, when the Blackbird's nesting success dropped to mere 11.5%, its density decreased to c. 18 p/10 ha (Mizera 1988). An analogous sequence of events, terminating with the restoration of predation pressure on the urban Woodpigeons, had been earlier described for the Wrocław urban parks (Tomiałojć 1980). Both examples suggest that the local population size may depend on a long-term level of offspring production, contrarily to a conclusion reached by Lack (1966).

In contrast to what is known for mammals (Christian 1950), the level of offspring production in birds may be positively correlated with the breeding density (e.g. Tomiałojć 1980, Shields *et al.*. 1988). Only under extreme conditions of overcrowding, such as those found in some urban populations, may the correlation be negative.

A very high density may disrupt, however, several behavioural adaptations. Literature on the Blackbird reproductive behaviour abounds in unusual cases, such as heavy territorial fights, chiefly between fe-

males, a complicated pecking order among males, polygamy, the breeding season prolonged up to four broods a year, repeated use of the same nests, double clutches, unusual nesting sites, two females incubating or brooding in one nest, etc. (Stephan 1985, Glutz and Bauer 1988, Luniak and Mulsow 1989 and others). Most, if not all, cases of such exceptional behaviour, virtually unknown in the forest populations, were found in anthropogenic habitats densely populated by Blackbirds. Therefore, it should be classified as secondary, usually forced, deviation from the original very different behaviour of the species.

## Conditions of the Blackbird reproduction in BNP.

**Feeding conditions during the breeding season.** During the breeding season in the mainly deciduous habitats of BNP the Blackbird usually meets very good or fairly good feeding conditions. This conclusion can be supported by various evidence: large clutch size, fairly stable breeding density, diverse diet and usually high availability of the two most frequent kinds of prey (earthworms and caterpillars), high frequency of feeding young, feeding them evenly the whole day round, no starved nestlings even during bad years, etc.

The amount and predictability of food resources are thought to find a reflection in the clutch size (Ricklefs 1980). The Blackbird's average clutch in BNP is larger (4.5 on average, in May even 4.8) than in W Poland (Graczyk 1961, Dyrcz 1969, Wesołowski and Czapulak 1986) and other parts of Europe (Cramp 1988, Glutz and Bauer 1988). In fact it is among the highest values ever reported (von Haartman 1969, Payevskiy 1985, Glutz and Bauer 1988), which suggests that food resources available to females during egg-formation are in BNP richer than elsewhere. This is not surprising, considering that the Blackbird territories in BNP are 11–43 times larger (Tomiałojć 1993) than in urban and suburban populations.

The question arises why the Białowieża Blackbirds defend so big territories? Generally, the nestling diet in BNP resembles that in other European habitats (Snow 1958, Dyrcz 1969, Glutz and Bauer 1988). Only the results of a study conducted in a dry climate near Budapest (Török 1981) are exceptional: the nestlings were fed mostly with caterpillars, adult *Coleoptera* and *Diptera*. The earthworms, animals known to occur in their highest numbers and biomass in the lowland deciduous forests (Siivonen 1941, Graczyk 1959, Za-

jonc 1971 etc.), constitute the main nestling food in BNP. Their exceptionally high biomass – c. 36.5 $g/m^2$ – was revealed in the Niepołomice Forest, S Poland (Rożen 1987), in a habitat very similar to that which occurs in plot W and some parts of plot K in BNP. The earthworm biomass in OH stands is comparable also to that in the lawns of the Polish urban parks (Graczyk 1959), though one should take into account considerable differences in earthworm availability in those two habitats. A high deciduous forest shades the ground, preserving humidity, and creates an opportunity to forage even during the mid-day hours (Fig. 2). In urban parks, contrarily, collecting earthworms is temporarily and spacially restricted by sunny weather and by presence of humans.

Food availability may be revealed by measuring the frequency of feeding nestlings. In a deciduous (Sołacki) park of Poznań, Graczyk (1961) found that 53 and 86 beakful loads of food were delivered daily to two nests under incessant observation. Assuming the average weight of load to be 1.2 g he estimated daily amount of food at 64 and 103 g. Using Graczyk's way of calculation, in 101 feedings recorded at a nest in BNP at least 120 g of food had to be delivered per day. The feeding intensity at remaining 17 nests was equally high (Tab. 3).

The leaf-eating caterpillars constitute the second most important food category for Blackbirds. During 1985–1989 their abundance in BNP was increasing from a minimum value in 1985 (0.025 caterpillar/standard twig) to a value 76 times higher in 1989. In good caterpillar years the Blackbird nestlings' food is composed of earthworms and caterpillars in fairly equal proportions. Moreover, the Blackbird numbers fluctuate at a positive correlation with the caterpillar index (r = 0.4523) and show relation to amount of precipitation in April–June (assumed to reflect earthworm availability) when a time-lag of one year is introduced, which suggests that the species numbers depend on the previous year food resources and its success in reproduction (Fig. 1 in Tomiałojć 1993).

In spite of such a delayed positive correlation between the food conditions and Blackbird numbers, this dependence need not necessarily be strong. There is another essential factor involved, the nest predation and predation on adults, which appears to influence stronger than the food resources. For example, in 1986, when the trophic conditions were still very poor,

which was reflected in a low clutch size and considerable partial losses of eggs, the food shortage was compensated by a weaker predation pressure on Blackbird nestlings (only 11% were destroyed), apparently owing to the abundance of alternative prey – the rodents (Jędrzejewski *et al.*, in press). Consequently, the overall nesting success in 1986 approximated that in later years (1988) when caterpillars and earthworms occurred in much larger numbers. Thus, even as trophically bad years as 1984–1986, in an old deciduous forest are not necessarily tantamount to periods of "ecological crunches", as this was in grassland habitats (Wiens 1977). A multilayer and very diverse community of a deciduous forest seems to be too complex to show up the impact of bad seasons. This conclusion remains in line with general climatic and trophic features of deciduous temperate forests, characterized by high biomass and diversity of plants and animals (Ricklefs 1990, Faliński 1986, Tomiałojć 1991). Especially high diversity and biomass of the herb-layer entomofauna, four times higher than in MC stands, has been found in an AA forest tract (Borowski and Dehnel 1952, Olechowicz 1984). Moreover, if the pres-

ent study had been conducted not in the period of 1984–1989 (the lowest caterpillar numbers, a low precipitation index), the results would have even stronger documented that food resources exert only a slight limiting influence on the forest Blackbird numbers and the species' nesting success.

All the clues analysed support the conclusion that during the breeding season the Blackbirds inhabiting deciduous stands of BNP usually meet with very good feeding conditions, which agrees with the suggestion (Snow 1958a, Lack 1966) that neither in the Wytham Wood near Oxford did the food resources play any important role as a factor limiting the Blackbird population size.

### Nesting success in BNP and elsewhere

The scarce data so far available have indicated that the nesting success of forest Blackbirds was usually low or very low, in British woods being only 12–14% (Snow 1955, 1958a, Lack 1966). Its very low value from the Wytham Wood was thought to result from a secondarily easier access of corvids to Blackbird nests frequently exposed by management forming an open-
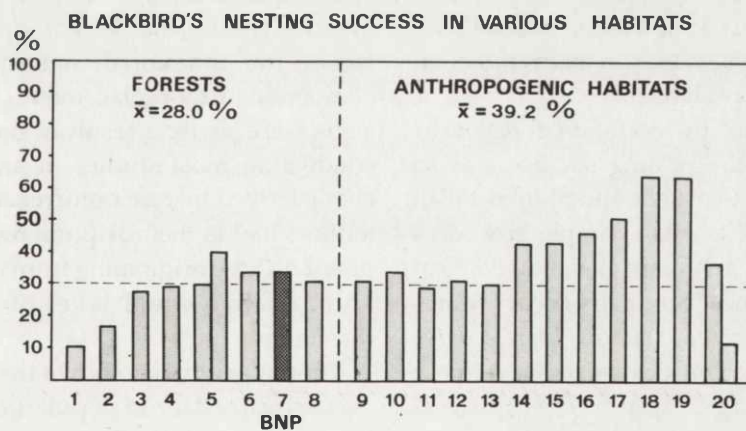


Fig. 3. Blackbird's nesting success in the European forests and woodland-like habitats.
Forests: 1 – Wytham Wood near Oxford (Snow 1958, Snow and Mayer-Gross 1967), 2 – mixed coniferous plantations n. Poznań (Graczyk and Klejnotowski 1966), 3 – riverain forest n. Halle (R. Gnielka after Stephan (1985), 4 – various forests n. Poznań (Graczyk 1961), 5 – deciduous wood n. Wrocław, various years (Dyrcz 1963, 1969), 6 – mixed forest n. Wrocław (Dyrcz 1969), 7 – mainly deciduous forest in BNP (this study), 8 – oak forest, Romania (Gal 1967).
Other habitats: 9 – parkland, Exeter University (Osborne and Osborne 1981), 10 – various habitats, Lincolnshire (Baron, after Osbornes), 11 – English gardens and farmland (Snow and Mayer-Gross 1967), 12 – Polish non-urban habitats (Wesołowski and Czapulak 1986), 13 – rural areas in London (Batten 1973), 14 – various suburban habitats, Hamburg (Mulsow 1976), 15 – suburban park, Wrocław (Dyrcz 1963), 16 – various urban habitats, Germany (Erz 1964), 17 – some exceptional gardens in England (Snow and Mayer-Gross 1967), 18 – various non-urban habitats, Czechoslovakia (Havlin 1963), 19 – urban habitats, Czechoslovakia (Havlin 1963), 20a – urban park in Poznań during 1951–55 (Graczyk 1961), 20b – same park in Poznań during 1975–1983 (Mizera 1988).

[Ryc. 3. Udatność lęgów kosa w europejskich lasach i środowiskach lasopodobnych.]

canopy forest. An equally low value was revealed for coniferous monocultures near Poznań (Graczyk and Klejnotowski 1966), a habitat marginal to Blackbirds. When such extreme results are ignored as originating from human-transformed habitats, the nesting success from more natural forests, including BNP, approximates 31% (Fig.3). This is still a low figure when compared with data from other, chiefly urban or rural, habitats (Cramp 1988, Glutz and Bauer 1988, Stephan 1985). A very high nesting success of the forest Blackbirds in Czechoslovakia (62.4% according to Havlin 1963) strongly deviates from the background of other forest data (Fig. 3), including similarly collected Polish nest-record scheme data where the success was 30% (Wesołowski and Czapulak 1986). This disagreement between the data from two neighbouring countries may have resulted from two additive causes. The first one is a methodological inconsistency in the habitat classification, as Havlin's "forest habitats" actually meant "non-urban ones" with the majority of data apparently originating from rural woods or mid-field copses, not from extensive forests. The other reason may be sought in a different level of predation pressure in both countries, as in Czechoslovakia corvids seem to be less numerous (own obs.). Thus, the absence of a sharp contrast between the nesting success in urban habitats reported by Havlin (1963, 1963a, 1964) remains rather an exception among the European data.

It is also unclear why in mountain forest near Alma-Ata, Kazakhstan, the nesting success was so high: 56.4%, n = 39 nests (Kovshar and Shujko 1984). Was it a consequence of a small sample size, or a regularity typical of high mountain elevation (2800 m a.s.l.) where only a few nest predators occur? Moreover, the predators indicated, namely *Martes foina*, *Sciurus vulgaris*, *Pica pica* and *Corvus corone*, appear inefficient in penetrating dense spruce crowns, at least the latter two and under European conditions.

At the nesting success of 31%, and two broods per year, the reproduction output in the BNP deciduous stands is c. 2.5 fledgling/pair/year. It is identical with that in London rural habitats, although much lower than in London urban and suburban populations (3.46) or those in Hamburg (3.9) and the Oxford Botanical Gardens (4.1) (Snow 1958, Batten 1963, Mulsow 1980).

The fact that a relatively low production in BNP still allows to maintain the population on a steady

level (Tomiałojć 1993) suggests that a higher reproductive rate in urban habitats actually denotes an overproduction of fledglings, which leads to an overspill of excessive individuals to the surrounding habitats or other cities (cf. Mulsow 1980). It agrees with the earlier presented scenario of historical events in the course of the species' adaptation to the anthropogenic landscape. This way of reasoning is based, however, on the unproven assumption of equal adult or postbreeding mortality of juveniles in the compared habitats.

## Predation pressure in the Blackbird population dynamics under primaeval and secondary conditions

Since long ago predators have been known to be the main cause of nesting failures in small birds. Yet, Lack (1966), when evaluating the results of a dozen or so population dynamics studies of birds, or Havlin (1964), while discussing his Moravian study of two Blackbird populations, both concluded that the nest predation had only a slight influence on population dynamics and population size. At that time there was no clear relation found between the number of fledglings and the recruits into the breeding population. It was also argued (e.g. Murton 1958, 1972) that in multi-brooded species, like the Woodpigeon *Columba palumbus* or the Blackbird, nesting losses are easily compensated by replacement clutches. Such conclusions were partly a result of the bias on the score of conducting most studies in anthropogenic habitats characterized by rare occurrence of predators. Earlier authors had to their disposal mostly only one type of data, i.e. those originating from man-changed habitats with a fairly equal level of predation pressure throughout.

Present study has shown that the nesting losses in an undisturbed forest population may vary within the frames much wider than once expected, and that in 95–98% they are caused by nest predation. Partial losses, in nestlings in particular, could be attributed to food shortage, even if it acts through predators taking the opportunity when there are no adults at the nest as they have to search for food longer. It does not, however, change the fact that only two of 155 hatched nestlings (1.3%) failed to fledge from otherwise successful nests (Tab. 9). Such a low level of nestling mortality for other than predation reasons was found even during trophically the worst years.

The nest predation in BNP, when analysed jointly for all years, was slightly higher during the egg stage (39% losses) than the nestling stage (27.6% losses). However, when looking at yearly data, these two types of nest mortality appear to fluctuate considerably and independently (Tab. 6): in 1989 the nestling losses were four times higher than those in 1986, while the losses in eggs in 1986 were five times those on nestlings. The reasons for this appeared to be in the differences observed in predator activity. In the caterpillar outbreak years (1975, 1982, 1992–1993) smaller nest predators, such as jays, squirrels, dormice, mice, woodpeckers, were recorded to feed on caterpillars (Tomiałojć *et al.* 1984; mammalogical data), thus leaving more bird nests unattacked. During the 1986 breeding season the Blackbirds faced not only the lowest amount of caterpillars, but also scarcity of earthworms owing to drought conditions. Moreover, the shortage of caterpillars made small predators concentrate on bird nests, which found reflection in the highest partial losses among nests with eggs. On the contrary, in 1989 (with 12 times more caterpillars) most Blackbird eggs survived, but instead, the nestlings became the target of attacks by larger predators (mustelids, raptors and owls) facing a shortage of the alternative food, rodents, being then at their lowest level (Jędrzejewski, Szymura and Jędrzejewska, in press; own observ.). A similar pattern of changes in nest predation has been noticed in the simultaneously studied Song Thrush (Tomiałojć, in prep.), which offers an independent supporting evidence. These observations show that changes in food resources availability may be tightly interwoven with the phenomenon of predators switching to other prey. Dramatic differences found between different (primaeval and secondary) populations of the Blackbird appear to result to a much larger extent from differences in predation pressure than from differences in food resources.

The examples of reproductive ecology of the Blackbird, Woodpigeon (Tomiałojć 1980) or of Wren *Troglodytes troglodytes* (Wesołowski 1983), studied under two contrastingly different field conditions, indicate that a consistently acting strong predation, or contrarily, a prolonged decrease in the predation pressure, may change not only the population density of the prey species, but, as a consequence, many traits in its ecology as well. A very dense and a very scattered

population represent the two dramatically different ecological situations in which the species can be thriving. The four-fold fluctuations (0.87–3.37 juv./pair/season) in fledgling production of the BNP Blackbirds, or even five-fold when confronted with that in the Oxford Botanical Gardens, are comparable to the differences revealed earlier (4–6fold) between various Woodpigeon populations (Tomiałojć 1980). The span of that size is, thus, not an exception, but appears to be a rule in the case of so adaptable bird species. In earlier studies, when known production of young varied only by half or less, the conclusions by Lack (1966), Havlin (1964) or Murton (1958, 1972) were justified. However, since it is known that the production of young may vary several-fold, the claim that there is no direct relation between the number of fledglings produced and the next-year number of recruits needs verification. The history of bird adaptations to anthropogenic, mostly urban, conditions strongly suggests that almost a two times higher production of young (4.1 versus 2.5 juv./pair/season in the Blackbird), if long-lasting, always led to an ecological and geographical expansion of the species.

## CONCLUSIONS

1. Under primaeval forest conditions the Blackbird reproduction and nest mortality fluctuate strongly: nesting losses vary between 50 and 90%, while production of young per season almost four times (0.87–3.37).

2. The forest Blackbirds produce on average 2.5 young per pair per season, which is a half of the value revealed for some urban populations. As such a low rate is apparently sufficient to maintain the forest population at a stable numerical level, those urban populations are excessively productive.

3. Limitation of the forest population productivity is exerted by heavy predation, and it co-occurs with high natality.

4. In old deciduous stands serious food shortage conditions hardly occur.

5. The action of the trophic factor appears to be tightly interwoven with that of predators. In some years raptors and mustelids focus on thrush nests as the alternative prey. In caterpillar-outbreak years smaller predators (rodents, corvids, woodpeckers) switch to feeding on caterpillars, leaving more bird

nests unraided. Hence, a high fledgling production in a caterpillar year results not from better nourishment, but mainly from less destruction of broods.

6. The conclusion concerning a relative importance of food resources availability and predation pressure might have been even stronger in favour of limitation by predation if this study had been performed in the years with average (better) food resources. This example shows that short-time studies, without a knowledge of the population's earlier and subsequent size and food conditions of its habitat across many years may be misinterpreted.

## ACKNOWLEDGMENTS

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## STRESZCZENIE

**[Ekologia rozrodu kosa *Turdus merula* w pierwotnym lesie Puszczy Białowieskiej. Część 2. Rozrodczość i śmiertelność.]**

Wyniki niniejsze są oparte na poznaniu losów 360 lęgów kosów leśnych, obserwacjach 33 kolorowo obrączkowanych osobników dorosłych, zaobrączkowaniu 213 piskląt lub podlotów oraz na rezultatach 140 godzin obserwacji prowadzonych z ukrycia przy 18 gniazdach z pisklętami. Gniazdowanie wysoko na drzewach oraz nadzwyczajna płochliwość kosów w

Białowieskim Parku Narodowym (BPN) ograniczyła możliwość uzyskania niektórych danych charakteryzujących biologię rozrodu populacji zasiedlającej ten niezaburzony las strefy umiarkowanej.

Białowieskie kosy tworzą wędrowną i monogamiczną populację o niskiej częstotliwości walk pomiędzy samcami, a zwłaszcza pomiędzy samicami. Zauważono istnienie niewielkiego tylko odsetka osobników samotnych, przy czym niemal wszystkie one po pewnym czasie znajdowały partnerów do rozrodu. Okres rozrodczy trwa od 8–10 kwietnia do końca lipca (Ryc. 1); udowodniono odbywanie dwóch lęgów przez większość populacji, a oznaki wskazują na rozpoczynanie przez niektóre osobniki także trzeciego lęgu. Jedna z najwyższych w Europie średnia wielkość zniesień (Tab. 1–2) ulegała zmianom w czasie: w latach 1986–1989 obniżyła się do 4.38 zamiast uprzednich 4.75 jaj, zwłaszcza w lęgach.

Zabrano dowody świadczące o dobrych lub bardzo dobrych warunkach pokarmowych panujących w BPN. Nawet w najmniej korzystnych latach 1984–1986 kosy jeszcze zdołały wychować niemałą liczbę potomstwa, dzięki temu że równocześnie z pogorszeniem warunków pokarmowych (najniższa liczba gąsienic *Geometridae* i *Tortricidae* oraz susza zmniejszająca dostępność dżdżownic) wystąpiło osłabienie presji drapieżników atakujących pisklęta, wobec obfitości pokarmu zastępczego – gryzoni. O dobrych warunkach pokarmowych świadczy też wysoka wielkość zniesień, intensywne karmienie piskląt nawet w godzinach południowych (Ryc. 2), znaczna ilość przynoszonego im pokarmu, wyjątkowość (prawdopodobnie 1 przypadek) śmierci piskląt, którą można przypisać trudnościom aprowizacyjnym a nie wynikającej ze śmierci samicy. Odnotowano silne indywidualne zróżnicowanie intensywności karmienia piskląt (na ogół intensywniej karmiły samce – Tab. 4), a nie stwierdzono istotnej statystycznie różnicy w intensywności karmienia pomiędzy lęgiem a grądem.

Straty lęgowe (średnio 67%) wahały się z roku na rok (50–92%) oraz malały w trakcie sezonu. Aż 95–98% z nich było spowodowanych działaniem różnorodnych drapieżników (Tab. 7), które niszczyły średnio 37% jaj i 31.6% piskląt. Udatność lęgów (sukces lęgowy) w BPN wynosiła średnio 33% (Tab. 6 i 10), w szczególnie niekorzystnych latach obniżając się do 19.2%, a w grądach nawet do 8.0%. W trakcie badań wartość ta silnie zmalała dla gniazd w lęgach, a wy-

raźnie wzrosła w grądach, co zdaje się być skutkiem suszy ale i być może spadku liczebności gryzoni jako alternatywnego pokarmu dla drapieżników. Produkcja podlotów wynosiła średnio 2.5 (0.87–3.37) na terytorium i rok, wykazując silne wahania zależne od biotopu i roku.

Śmiertelność wśród ptaków dorosłych była dość znaczna w przypadku wysiadujących samic (zwłaszcza przy nisko umieszczonych gniazdach), a zdaje się być niewysoka wśród ptaków dorosłych i samodzielnych młodych jeśli przebywających w obrębie lasu, co w porze lęgowej jest dla kosów leśnych regułą.

Poprzez porównanie z zachodnimi populacjami osiadłymi argumentuje się, że wędrowność leśnych kosów jest cechą pierwotną gatunku, utraconą na zachodzie wtórnie. Zmiana ta pociągnęła za sobą głębokie przeobrażenia w ekologii i biologii zachodnich populacji umożliwiając im całoroczny terytorializm, nasiloną rozrodczość, a zarazem obniżoną śmiertelność, co dało przynajmniej podwojenie wskaźnika produkcji podlotów. Oznacza to, że przez 100–150 lat (i pokoleń ptasich) kosy miejskie produkowały dwukrotnie więcej młodych niż to jest potrzebne populacji białowieskiej dla utrzymania stałego poziomu liczebności. Przytoczono przykład badań w Poznaniu (Z. Graczyka i T. Mizery), wykazujący że ta sama populacja kosów przy braku istotnych zmian w strukturze i troficzności środowiska może produkować diametralnie różną liczbę młodych, zależnie od okresu historycznego (a więc braku lub obecności drapieżników gniazdowych w parkach miejskich).

Spośród dwóch głównych czynników – obfitości pokarmu i oddziaływania drapieżnictwa – ten drugi czynnik w warunkach BPN okazał się mającym wielokrotnie większe znaczenie dla dynamiki populacji kosa. Nikły odsetek ubytków w populacji powodowanych ewidentnie niedożywieniem (przy wielkich stratach z powodu drapieżnictwa) jest tym bardziej wymowny, że wynik ten uzyskano w okresie najtrudniejszym pokarmowo w całym 20–letnim czasie badań w BPN (por. liczebność gąsienic wg Ryc. 1 w: Tomiałojć 1993). W żyznym głównie liściastym lesie strefy umiarkowanej zdają się zatem nie występować lub występować nadzwyczaj rzadko okresy krytyczne ("ecological crunches") znamienne dla ekosystemów trawiastych.

Dominujący czynnik ograniczający – drapieżnictwo gniazdowe – działa w powiązaniu z obfitością

zasobów pokarmowych, co stwarza możliwość błędnych interpretacji. I tak, stwierdzenie silnej pozytywnej korelacji pomiędzy zasobami pokarmu a liczbą wychowanych podlotów nie jest jeszcze dowodem działania tej zależności biologicznej. Obserwacje nasze i teriologów w BPN wykazały bowiem, że w latach eksplozji gąsienic drobni niszczyciele lęgów ptasich (wiewiórki, inne gryzonie, sójki, większe dzięcioły) same przestawiają się na żer na gąsienicach pozostawiając więcej gniazd ptasich niezniszczonych. Wyższa udatność lęgów jest więc nie tyle wynikiem lepszego odżywienia kosów, lecz wynikiem osłabienia presji drapieżników na ich lęgi. Podobnie w roku 1986, przy wysokiej liczebności gryzoni, większe drapieżniki (głównie mustelidae, a także puszczyk i myszołów zwyczajny) zabiły tylko 11% piskląt kosów, gdy w roku 1989 (przy braku gryzoni) aż 44% (i to pomimo kilkakrotnie większej obfitości gąsienic – drugiego co do ważności pokarmu kosów – Tab. 3). Oznacza to, że przestawianie się drapieżników na pokarm alternatywny jest jednym z głównych mechanizmów uwalniających populację kosa od ich silnego oddziaływania ograniczającego.

Tak różna śmiertelność gniazdowa kosów leśnych i miejskich wywołuje dwukrotną, a w skrajnych przypadkach 5-krotną, różnicę w liczbie wychowanych podlotów na parę lęgową rocznie. Jest to zróżnicowanie równe temu stwierdzonemu wcześniej dla grzywacza, co wskazuje na istnienie pewnej prawidłowości a nie wyjątkowości w tak wielkich różnicach odnotowanych pomiędzy niezaburzonym lasem a środowiskami antropogenicznymi.

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