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Breeding ecology of the Blackbird *Turdus merula* studied in the primaeval forest of Białowieża (Poland). Part I. Breeding numbers, distribution and nest sites [*]

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In the Białowieża National Park, NE Poland, the Blackbird populates the whole extensive forest as a forest-interior species. The following mean densities were recorded in primaeval stands: 2.5 pairs/10 ha in riparian ash-alder, 2.2 in oak-lime-hornbeam and 0.7 p/10 ha in conifer-dominated stands. An approximate territory size was 1.1–4.3 ha, usually 2.2–2.7 ha, which is 11–43 times smaller of that found in Oxford Botanical Garden and some C-European urban parks. The density along the forest edge was slightly higher in some years only. In primaeval stands the species nests in trees, often in tree-holes, on average 5.3 (0.3–24) m above the ground. Nests placed above 7.5 m were twice more successful than the lower ones. The Blackbird's nesting in low bushes appears to be a feature reinforced under anthropogenic conditions, like its preference for the forest edge or its foraging in the open. It is argued that the Blackbird was primarily a species of old high-stemmed lowland and submontane forest.

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INTRODUCTION

This paper is the first in a series of studies on forest populations of two thrush species, Blackbird and Song Thrush *Turdus philomelos*, thriving under nearly primaeval conditions of the Białowieża National Park. The questions in this paper were what was the primaeval breeding habitat of the Blackbird? where did it nest? what were its original breeding densities?

The Blackbird is a widespread breeding species of Eurasia. During the last two centuries (Heyder 1955) it occurs in two distinct populations, in most regions sympatric: a natural population and a secondary population of human-transformed habitats, mainly urban ones (Luniak and Mulsow 1988). Fundamental European handbooks and summaries (Stephan 1985, Cramp 1988, Glutz and Bauer 1988) while describing Blackbird's biology rely largely on the knowledge of its W European populations resident in and well adapted to anthropogenic landscape (cf. Snow 1955, 1956, Lack 1966).

The Blackbirds of the western half of Europe were for centuries deprived of their pristine habitats (Hawksworth 1974, Peterken 1981, Rackham 1976, Simms 1971) and forced to invade secondary habitats characterized by their immature trees, shortage of dead timber, but having a bet-

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ter developed bush-layer instead (Tomia-łojć 1991). Also in the western part of C Europe secondary young stands have prevailed for centuries; only since the late 18th century foresters have turned to growing high-stemmed forests (Thomasius 1978).

The Białowieża Forest, as a hunting ground of rulers, has largely escaped those changes, with several of its stands surviving till the present in their nearly primaeval state (Faliński 1986, Tomiałojć 1991, Tomiałojć et al. 1984).

It can be suspected that the knowledge of the Blackbird's reproductive ecology is strongly biased. Attempts to study its forest populations (Snow 1956, 1958, Graczyk and Klejnotowski 1966, Dyrcz 1963, 1969, Mulsow 1980) concentrated in study areas either in forests under long-term human impact, or small woods subject to urban influence from the neighbouring large cities. It was uncertain that those Blackbirds still retained the primary features in their ecology.

One of the major aims of our teamwork in the Białowieża National Park (Tomiałojć et al. 1984, Tomiałojć and Wesołowski 1990, Wesołowski 1983) was to learn the original reproductive ecology of some bird species, earlier thoroughly studied in human-transformed habitats. A hypothesis was formulated (Tomiałojć 1980, Tomiałojć et al. 1984) that conspicuous differences were likely to occur between the primaeval and secondary bird populations and these would not be explained by a differentiating action of natural ecological factors alone. One of the most striking differences resulting from human impact are different levels of predation pressure under primaeval and secondary ecological conditions. For centuries humans have tended to eradicate predators from their neighbourhood (Tomiałojć 1980, Tomiałojć and Profus 1977, Wesołowski 1983).

The Białowieża Forest offers conditions allowing to test these expectations.

STUDY AREA AND CLIMATIC CONDITIONS

The Białowieża Forest (1250 km^2) is a forest complex situated in the center of Europe (c. 52°41′N and 23°52′E), in a transition zone between W European deciduous forests and NE boreal (taiga-like) ones. This finds its reflection in the occurrence of Norway spruce *Picea abies* as an admixture to all Białowieża treestands. Białowieża Forest is a relic remnant of vast forests once extending over most of Europe. Its present uniqueness is due to its lowland localization on relatively fertile soils, considerable size, its compactness and a nearly primaeval character of some of its fragments retaining a pristine flora and fauna.

The studies were carried out in the Białowieża National Park (BNP) which constitutes the largest patch (47.5 km^2) of practically unaffected primaeval lowland temperate European forest. Its more detailed characteristics is contained in monograph by Faliński (1986) and our earlier papers (Tomiałojć et al. 1984; Tomiałojć and Wesołowski 1990, Tomiałojć 1991). It should be stressed that the BNP area constitutes a central part of the Forest, isolated from extensive farmland by a buffer zone of managed stands, 7–15 km wide. Only in the south it adjoins the Białowieża Glade (13 km^2), a rural "island" formed late in 17th century. The area of BNP has a typical lowland character (about 160 m above sea level); its geographical latitude is equivalent to that of Berlin and London.

Primaeval tree stands of BNP differ from the surrounding managed forest in being much older, species-rich, multilayered, uneven-aged, very high, patchy (due to dominant-tree saltation and some larger

windbreaks), rich in dead timber and clearly more humid. They are known to harbour an extremely diverse, species-rich, and especially predator-rich, fauna (Tomiałojć and Wesołowski 1990).

A monitoring of bird numbers, Blackbird included, was done in 1975-90 on permanent census plots selected in three main types of BNP old-forest habitats:

— riparian ash-alder (further AA) or alder-dominated stands of *Circaeo-Alnetum* or *Carici elongate-Alnetum* types, constituting an optimal breeding habitat for the Blackbird;

— oak-lime-hornbeam stands (further OH) on dry-land brown soils, of *Querco/Tilio-Carpinetum* association, with a poor bush layer;

— conifer-dominated mixed stands (further MC) of *Peucedano-Pinetum* or *Pino-Quercetum* associations, located on poor sandy elevation, a marginal habitat for the Blackbird.

For detailed studies of Blackbird and Song Thrush breeding ecology the following census plots were chosen:

— Plot K (33 ha), comprising a patch of 130-year old riparian AA stands adjoining the Białowieża Glade and remaining in nearly primaeval state, except two patches with traces of local logging some 70 years ago. This is a mosaic of wet and drier places, with some intrusions of OH forest. An admixture of medium sized spruces should be mentioned. Of all the plots studied this has the best developed young-tree-, bush- and herb-layers. Once a sharp edge between this habitat and the neighbouring marshy meadows, after 1972 it gradually became screened by a secondary growth of alders in front of the forest wall.

— Plot W (50,5 ha), comprises c. 180-year-old OH stand adjoining the Białowieża Glade. Its canopy is very diversified structurally, three-layer, the height of trees being usually over 30 m, some well over 40 m, and a much less developed bush- and herb-layers. Like in other habitats there is an admixture of spruces, represented by large trees less suitable for the Blackbird. A specific feature of this forest tract is its heavier than elsewhere in BNP grazing and browsing pressure of game (deer and wild boars) due to a "fence-effect" - the fence prevents game penetration into the Białowieża Glade farmland.

— Plot C (36 ha), is a forest-interior OH tract resembling that of plot W, but differing in a stronger dominance of hornbeams and lower patchiness. Among herb vegetation monotonous patches of garlic *Allium ursinum* prevail.

— Plot NW (25 ha) was only superficially studied, being a marginal habitat of the Blackbird. It is covered by uniform, almost even-aged, stand of spruce and pine, with a slight admixture of deciduous trees *Populus tremula*, *Betula verrucosa*, *Quercus robur*, and in some patches an under-layer of young hornbeams. There is barely any bush- and herb-layer there. Some recent windbreaks add to the complexity of this habitat.

The climate of Białowieża Forest is of subcontinental type; winters are usually snowy (50 cm on average) and last for one to three month (mean January temperature – minus 4.3 C); summers are relatively warm (mean July temperature – 17.6 C). Mean annual precipitation is 624 mm (426-857). The period between 1986 and 1990 deviated, however, from long-term averages and from the previous decade, by being drier and warmer during the spring. The meteorological data for the last years show that:

— Year 1986 – was characterized by a severe snowy winter, followed by a very warm, dry spring (chiefly in April and May).

— Year 1987 – a very cold and prolonged winter followed by one of the coldest and latest springs with a high rainfall in May.

— Year 1988 – after a mild winter the spring was very cold and dry in April, but with high temperatures and rainfall in May and June.

— Year 1989 – after exceptionally mild and snowless winter the leafing of trees was a fortnight earlier, but later in May and June a severe drought developed.

— Year 1990 – after the second snowless winter the spring was unusually early, but in April and May the drought occurred again.

METHODS

A complex approach to studying Blackbird's breeding ecology was adopted, with the aim to estimate its numbers, distribution of territories and nest-sites most accurately. The focus was on obtaining true breeding densities, not relative indices. During 1986-89 on the plots chosen for detailed studies on thrush ecology 20–30 visits were made yearly to each site, which is 10–12 visits per one brood. The area was checked from early April till early or mid July. Besides all kinds of bird activity recorded in standard mapping method (IBCC 1969) the following were additionally considered:

— intentionally increasing the detection of the neighbours active contemporarily and producing cues of high territorial importance (cf. Tomiałojć 1980a),

— paying half of the visits during twilight (dawn or dusk) when thrushes are most active vocally (Tomiałojć and Lontkowski 1989),

— intensive searching for nests, which, when there is no leaf cover, were found in c. 75, sometimes in 95 per cent,

— colour-ringing some individuals (33 adults in 4 years) which added to the accuracy of many observations.

All the signs of the Blackbird's activity were plotted on 1:1000 maps, using for orientation a grid system 50 x 50 m established on census plots. The maps were kept up-dated after each visit, which helped to reveal uncertain cases and then, during the following visit to the spot, to solve them by prolonged observations in the place of the supposed boundary between territories.

During earlier years (1975-85) and contemporarily with this detailed study, on other and on the same census plots, the standard bird counts for monitoring purpose were carried out by other persons from our team. The field tests have shown that our improved version of the mapping technique (Tomiałojć 1980a), applied for monitoring purposes, produces the Blackbird density figures reflecting 98% true numbers (Tomiałojć and Lontkowski 1989). This allows our 17-year census data to compare directly with the results of more intensive study. High number of nests found, several of them being occupied simultaneously on neighbouring territories, allowed to double-check the number of territories drawn relying on other, mostly song, cues. The accuracy of breeding number estimates is, thus, comparable to that from urban studies. On the contrary, the estimates of the size and shape of particular territories are less precise than in the studies on other bird species in BNP (Wesołowski 1981, 1983, 1985), or in some Blackbird urban studies. The size of most territories larger than elsewhere, diminishes, however, the possibility of serious errors in detecting their boundaries. Territories shown on the maps are, thus, approximate estimates obtained by drawing lines surrounding all the records of male song, location of the nests found and

directions and distances of feeding flights (cf. Kendeigh 1944). In the cases when the data had to be allocated to a particular brood period, it was arbitrarily assumed that nesting started before 15 May belonged to the first brood, that started between 16 May and 15 June to the second, and that started after 15 June to the third one.

Alongside bird numbers also caterpillar (*Geometridae* and *Tortricidae*) abundance was monitored since 1975 in the plot W, and additionally in other OH census plots (Tomiałojć and Wesołowski 1990). The leaf-eating caterpillars were counted on standardized in size (50 x 50 cm of surface) lower twigs of hornbeams during second half of May. Each year (60) 100-120 samples were collected. For Blackbird the falling to the ground caterpillars constitute in OH stands second most important food category, after earthworms.

RESULTS

Population size, density and stability

The long-term census work conducted on c. 187 ha of the BNP stands indicates that the Blackbird numbers fluctuate around a fairly steady level (Fig. 1). Assuming the 1977 values as 100%, the fluctuations remain within 97–137%. No clear trends were noticed, but, instead, a suggestion can be made about the traces of a 4–5-year cycle in the data: comparing average densities for the three consecutive 5-year periods reveals that in 1980-84 they were markedly higher (2.4 and 2.9 p/10 ha in plots W and K) than during the earlier and later periods (Tab. 1). More accurate data from the intense study period 1986-90, collected from 108 ha of primaeval stands, confirm this pattern (Tab. 2).
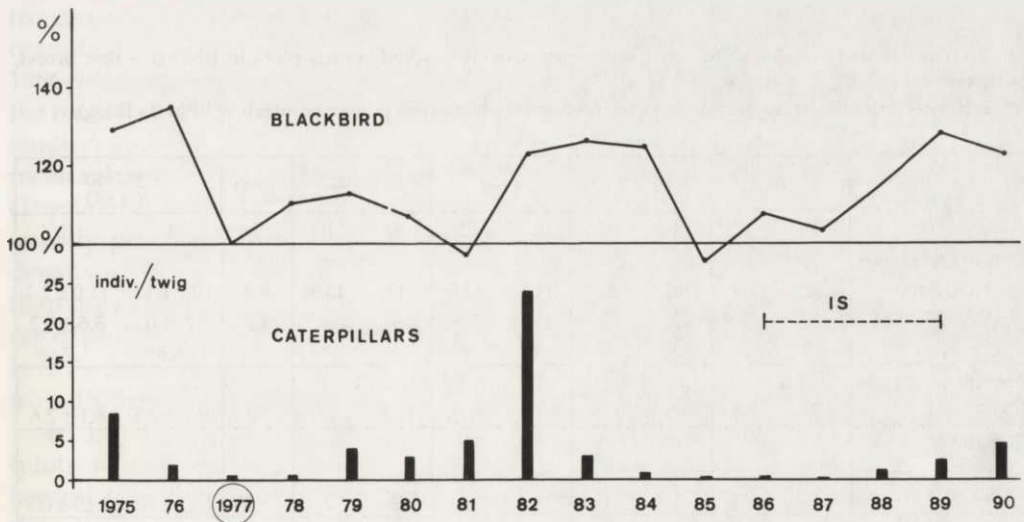

Fig. 1. Long-term changes in BNP Blackbird numbers (expressed as an index assuming the 1977 numbers being equal to 100%) and in caterpillar abundance (expressed as caterpillar number per standard hornbeam twig - see text). IS – period of intensive study.
Ryc. 1. Wieloletnie zmiany liczebności kosa i gąsienic w BPN. IS – okres intensywnych badań.

Tab. 1. Densities (p/10 ha) of Blackbirds according to standard censuses for monitoring purpose. Symbols – see "Study area ..."
Tab. 1. Zagęszczenia (p/10 ha) kosów - wyniki standardowych liczeń na powierzchniach badań monitoringowych.

	1975	76	77	78	79	80	81	82	83	84	85	86	87	88	89	X̄ ± SD	
Plots in AA stands																	
K (33 ha)	1.9	1.9	1.9	3.0	2.1	2.1	2.9	3.0	3.0	3.3	2.7	2.1	1.7	2.4	3.5	2.5	0.8
L (25 ha)	2.4	2.6	–	–	–	2.0	1.8	3.0	2.6	2.4	2.2	2.4	2.8	2.8	2.6	2.5	0.3
H (25 ha)	2.6	3.6	2.2	2.6	2.3	–	–	–	–	–	–	–	–	–	–	2.7	0.8
Plots in OI I stands																	
W (25.5 ha)	1.9	1.9	1.8	1.4	1.9	2.7	1.8	2.1	2.9	2.3	1.8	2.3	2.2	2.2	2.7	2.1	0.4
CW (24 ha)	2.1	2.1	0.8	1.7	1.9	2.1	1.7	1.5	1.7	1.9	1.5	2.3	2.0	2.1	1.5	1.8	0.4
CE (24 ha)	1.9	2.5	1.7	1.7	1.5	–	–	–	–	–	–	–	–	–	–	1.9	0.4
MS (30 ha)	2.2	2.7	2.0	1.3	1.6	1.5	1.2	1.8	2.0	1.7	1.3	1.8	2.0	2.0	1.8	1.8	0.4
MN (24 ha)	3.1	2.3	1.7	1.9	2.5	–	–	–	–	–	–	–	–	–	–	2.3	0.5
Plots in MC stands																	
GB (32 ha)	0.6	0.5	0.6	–	–	–	–	–	–	–	–	–	–	–	–	0.6	0.1
N (50 ha)	0.8	1.0	0.5	0.6	0.6	0.7	0.6	0.9	0.7	0.9	0.4	0.4	0.4	0.6	0.7	0.6	0.2

Tab. 2. True numbers of Blackbird territories in intensively studied census plots in BNP (I – first brood, II – second brood)
Tab. 2. Rzeczywista liczba terytoriów kosa na intensywnie badanych powierzchniach w BPN (I i II lęg).

Year	1986		1987		1988		1989		1990	Average X̄ ± SD	
	I	II	I	II	I	II	I	II	I	I	II
Plots in OI I stands											
1. W (50.5 ha)	10	9.5	9.5	8.5	11.5	12.5	13	13.5	9.3	10.7 ± 1.6	11.0 ± 2.3
1a. WW (25.5 ha)	5	5	5	5	6.5	7.5	5	5	4.7	5.2 ± 0.7	5.6 ± 1.2
2. C (36 ha)	6.5	?	?	?	?	?	?	?	?	6.5	?
Plots in AA stands											
3. K (33 ha)	7	7.5	7	6.5	8	6.5	11.5	12	12	9.1 ± 2.5	8.1 ± 2.6
Plots in MC stands											
4. NW (25 ha)	0.75	0.75	1	1	1	1	2	2	1.5	1.25 ± 0.5	1.25 ± 0.5
Total (plots W,K,NW = 108.5 ha)	17.7	17.7	17.5	16	20.5	20.0	26.5	27	27.5	21.9 ± 4.8	20.2 ± 4.8

Some decrease in numbers coincided with the preceding severe winters (1977, 1981, 1985-87) in C Europe, except that there was no decrease after the cold winter 1978/79. Thus, the Blackbird numbers seem to depend on the severity of winters ($r = 0.4501$, or even $r = 0.5326$ when calculated with a time-lag of one year) as long as conditions in C Europe show parallelisms to conditions on the species' wintering grounds. This influence may be exerted in two ways: a) directly by a reduction in the number of individuals surviving till next spring, or b) by acting through the caterpillar abundance of the previous year (correlation with next year Blackbird numbers is: $r = 0.4523$), the latter factor may itself be regulated by the severity of winters ($r = 0.2123$).

Breeding densities of the Blackbirds in BNP were calculated from two sets of results: from monitoring data (Tomiałojć et al. 1984, Tomiałojć and Wesołowski 1990, Tab. 1), and from intensive studies on some census plots in 1986-90 (Tab. 2). In the case of OH stands the average densities for 1986-90, c. 2.2 pairs/10 ha, agree well with the results from a larger set of census plots studied during 1975-79, when the yearly mean value was between 1.6 and 2.3 p/10 ha (Tomiałojć et al. 1984). In ash-alder stands (mostly plot K), however, recent average density of 2.5 p/10 ha appears to be lower than the results obtained from a wider array of plots (Tab. 1) studied simultaneously (2.7 – 3.5 p/10 ha), but is similar to those from 1975-79 (2.2 p/10 ha).

In both largely deciduous habitats (plots K and W) the averaged densities became identical in the last period. Hence the relative suitability of these habitats for the Blackbird was equal, in spite of some differences in structure. When a wider array of plots is analysed (Tab. 1), however, AA habitat in most years turns out to be slightly denser populated – 2.5 p/10 ha – than OH stands. On the contrary, the conifer-dominated stands (MC) are a suboptimal habitat for the species, as its densities were over 3 times lower there than in the deciduous fragments. The average density in coniferous plot NW was (0.3) 0.6–0.9 p/10 ha, though the so-called ecological density, in actually occupied patches alone, was about twice as high.

Distribution within the forest habitats

The Blackbirds breed in primaeval and managed stands throughout the whole Białowieża Forest area, even in its innermost fragments 7–15 km distant from extensive open habitats. They are there true forest-interior dwellers.

The distribution of territories shown on species maps allow to claim that Blackbird saturates both deciduous habitats completely. In coniferous stands, contrarily, large patches remain outside the territories.

The approximate size, shape and distribution of the Blackbird song/breeding territories were studied in detail in a fairly uniform OH habitat (plot W) and in a mosaic AA forest (plot K). All the territories from the 4-year period were plotted on the working maps. In the process, some sections of the territory boundaries had to be drawn as intermediate ones between the first brood and the second brood of the pair. Such between-brood shifts were however, infrequent and insignificant in relation to the territory size. The maps reveal a slight preference for some forest patches (occupied each year), even if apparently similar in structure to the other ones. The preference was rather weak, especially in uniform OH stands. This can be judged from numerous year-to-year shifts of a particular territory, visible not only in OH, but even in more patchy AA stands. In both habitats the distribution pattern was

more flexible in the forest interior zone than along the forest edge. The forest-edge line creates a rigid barrier to the shifts taking place apparently under pressure of neighbours, with disregard of minor within-habitat subdivisions.

Another measure of habitat preference can be based on the distribution of nests found. It was possible to calculate that the patches falling each year within a Blackbird territory constitute jointly about 25% whole plot W, and about 27% plot K. Such patches contained almost a half (48%, n = 71) of all the Blackbird nests found in plot W and as much as 58% (n = 57) nests in plot K. Moreover, if accepting a less rigourous delineation of the preferred patches, assuming as such the sites included into Blackbird territories during at least three years, then as many as 80% and 88% nests found respectively fall within preferred forest patches.

Some patches in our plots are structurally different from the other ones, e.g., in the largely uniform OH stand of plot W the belt between grid lines 13 and 16 (7.5 ha in size) comprises a stand heavily disturbed by wind, with few big trees left standing and a considerable amount of uprooted ones. In spite of this, there was no difference in the local density of the Blackbirds between this patch and the undisturbed fragments of the plot. The average densities were identical (2.2 p/10 ha) in both areas, though in 1986-87 they were somewhat higher in the windbreak patch, while in 1988-89 the situation was reversed. Likewise some differences in the soil humidity recognizable in the plot W did not find reflection in the Blackbird distribution. More pronounced were the intra-habitat differences in its distribution in the mosaic swampy stand in plot K. But even there only two patches of a forest regrowth, after a logging of about 70 years ago, are still unoccupied. The boundaries of territories do not follow division lines between the patches of AA and the "islands" of OH stands. It should be added, however, that for unknown reasons in 1975-85 the Blackbirds tended to occur in clearly higher densities in AA (up to 3.7 p/10 ha) than in OH stands. Such a preference disappeared during recent years, which may be a consequence of the drought periods which more dramatically change conditions of muddy soil than of drier brown forest soils.

The BNP stands offer a rare opportunity to study the edge effect in its original form in undisturbed extensive forests. The response to the forest edge was analysed in detail elsewhere (Tomiałojć, in prep.). It has been found that the Blackbirds occur in the 200 m wide edge zone on average in slightly higher, though not very consistently, densities. In some years clearly higher densities were recorded deep in forest interior, even in census plots 1–3 km away from the nearest edge.

Territory size

Though in BNP the accuracy of territory boundary delineations was lower than that in urban studies, in deciduous stands, with their higher density of the species and its sharper area defence, the error seems to be acceptable in the analysis. The territory sizes calculated from detailed working maps have appeared to be larger in OH than in AA stands in accordance with earlier observations (Tomiałojć et al. 1984). In plot W they were 2.7± 0.6 ha on average (n = 40, span 1.4-4.3 ha) while in riparian plot K 2.2 ± 0.7 ha (n = 30, span 1.1–3.0 ha). During recent years this difference became smaller than previously.

It should also be added that the largest (4.3 ha) territory found in 1988 within the plot W belonged to an adult male (ringed

in 1987 as adult), most probably a bigamist, judging from the timing and distribution of four nests found in his territory during that particular season.

Nest-site distribution

Most Blackbird nests in the BNP are located in living trees, only 0.7–1.5% being in bushes or in similarly structured freshly fallen tree crowns. Usually the most numerous tree species is used: hornbeam in OH stands, alder in AA, and spruce in MC ones (Tab. 3). A closer analysis reveals that some preference may be involved. In OH stands, for which tree counts on 40 circular plots of radius 10 m were made in autumn 1989 (T. Wesołowski, unpubl.), the comparison of the hornbeam share in stands and among nesting trees shows that this species is twice more frequently selected for nesting than could be expected from random sample. The hornbeam is selected for its plentitude of cracks, holes and offshoots in old trunks, offering a good support and shelter for rather heavy and conspicuous Blackbird nests. The other trees, contrarily, were clearly underrepresented in this sample, especially the smooth-bark lime.

In conifer-dominated stands mostly spruce and pine are selected for nesting. Own data are too scanty (Tab. 3), and for methodical similarity they can be compared only with a sample of 130 nests studied in the managed, mostly young, mixed-coniferous forests near Poznań, W Poland (Graczyk and Klejnotowski 1966). Also there the Blackbird nests were mostly in spruces (62%) and pines (27.7%). How-

Tab. 3. Location frequency of Blackbird nests according to the species of nesting tree (1975-89). * after T. Wesołowski, unpubl.

Tab. 3. Częstość (%) umieszczenia gniazd kosa na różnych gatunkach drzew.

Forest type Nesting tree	OH		AA	MC
	Frequency of trees*	nests	nests	nests
Carpinus betulus,	36.4	63.1	9.5	–
Vykhrots (upturned root systems)	?	11.6	29.9	7.6
Picea abies	18.8	11.6	17.7	38.5
Alnus glutinosa	2.2	1.5	22.7	7.6
Dead stumps	?	2.0	6.8	7.6
Tilia cordata	24.5	2.0	2.7	–
Quercus robur	3.3	2.0	2.0	–
Fraxinus excelsior	0.3	–	4.0	–
Acer platanoides	6.7	2.0	0.7	–
Corylus avellana	+	0.5	2.0	–
low bushes	+	1.5	0.7	–
Betula verrucosa	0.9	–	1.4	–
Populus tremula	1.8	1.5	–	–
Ulmus laevis	5.1	0.5	–	–
Pinus silvestris	–	–	–	23.0
Other	–	–	–	7.6
Total (n)	100% (330)	100% (200)	100% (147)	100% (13)

ever, "christmas-tree-shaped" spruces were preferred there in the absence of structures typical of primaeval stands.

More important is how the Blackbirds locate or hide their nests. Seven types of nest locations were recognized in the BNP (Fig. 2). The relative frequency of some locations differs between AA and OH stands (Tab. 4), presumably due to some general differences in the habitat structure. In OH stands 73% nests were in living trees, while in AA only 44%, the remaining 30% being located in vykhrots and 21% in snags. Almost 20% nests in AA stands and 48% in OH were in tree-holes, semi-holes or other cracks of old trunks. Thus, in BNP as many as 70% nests in OH and 62% in AA

were found in structures virtually nonexistent in intensively managed forests.

The way the nests were placed in tree crowns or vykhrots was analysed to check if there is any preference for particular sides (Tab. 5). During the first brood they were placed fairly randomly with respect to the direction from a tree trunk or a centre of vykhrot, with an insignificantly higher share of northern orientations. During later broods a slight prevalence of southern orientations may be noticed. This agrees with the postulated Blackbird's preference for nesting in the shadow (Stephan 1985).

The average height above the ground at which nests were located in BNP was considerable (Tab. 6). In AA stands it was
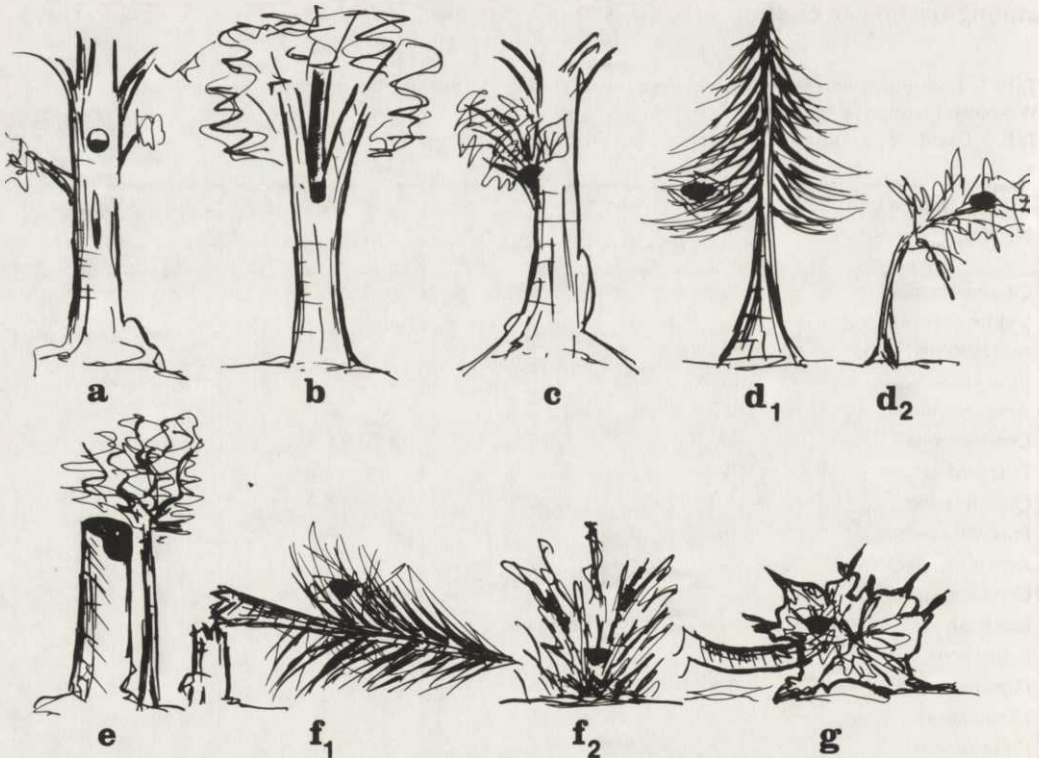

Fig. 2. Main types of Blackbird nest location in BNP. For frequency data see Tab. 4.
Ryc. 2. Główne sposoby umieszczania gniazd kosa w BPN (patrz tab. 4).

Tab. 4. Ways of locating Blackbird nests in BNP. (Data from 1975-89)
Tab. 4. Sposób umieszczenia gniazd kosa w BPN. a – dziuple i zagłębiania pni, b – w rozwidleniu pnia, c – w odroślach przy pniu, d – na gałęzi lub zgiętym młodym drzewie, a-d – żywe drzewa, e – na powalonym pniu, f – w krzewach lub na gałęziach powalonego drzewa, g – w wykrotach.

	OH	AA	OH + AA
a. Tree holes and shallow holes	48.6	19.1	35.5
b. Bifurcation of big stem	11.3	9.9	10.7
c. At the stem in offshoots	9.6	9.9	9.8
d. On the branch or bent young tree	3.9	4.9	4.4
a-d. Live trees	73.4	43.9	60.4
e. On dead stump (snag)	9.1	21.3	14.5
f. In bush or branches of fallen tree	5.7	4.2	5.0
g. on vykhrots	11.9	30.5	20.2
Total (n)	(177) = 100%	(141) = 100%	(318) = 100%

Tab. 5. Orientation of Blackbird nest location in relation to tree stem as axis, or to the centre of vykhrots (1975-1989).
Tab. 5. Kierunek umieszczenia gniazda kosa w stosunku do pnia lub środka wykrotu.

Directions	I st brood			II and III broods			Total	
	(%)	n		(%)	n		(%)	N
S		19			9			
SW	(32.6)	5	32	(42.1)	2	16	(35.3)	48
SE		8			5			
N		23			9			
NW	(43.9)	11	43	(34.2)	0	13	(41.2)	56
NE		9			4			
W		11			3			
	(23.5)		23	(23.7)		9	(23.5)	32
E		12			6			
Total	(100%)	98		(100%)	38		(100%)	136

Tab. 6. Average height (m) and span of nest location in BNP.
Tab. 6. Wysokość umieszczenia gniazda w BPN.

Habitat		ears		Total
		1975-1985	1986-1989	1975-1989
AA	n	102	50	153
	span	0.3–24	1–21	0.3–24
	X̄ ± SD	3.82 ± 4.5	4.53 ± 4.5	4.07 ± 4.5
OH	n	124	74	198
	span	1–21	1–17	1–21
	X̄ ± SD	6.66 ± 4.9	5.34 ± 4.0	6.23 ± 4.6
Totals	n	226	124	350
	span	0.3–24	1–21	0.3–24
	X̄ ± SD	5.41± 4.7	5.04± 4.2	5.33 ± 4.7

Tab. 7. Changes in nest height location with the progress of breeding season.
Differences during 1985-89 statistically significant (test $X = 12.7$, df. 5, $p < 0.02$), while for the whole period not significant.
Tab. 7. Zmiany wysokości umieszczenia gniazda w ciągu sezonu lęgowego.

Height above the ground (in m)	1st brood (before 15 V)	2nd brood (15 V-15 VI)	3rd brood (after 15VI)	Total
Years 1985-89:				
0–5 m	69.5	56.3	41.2	62.8
> 5 m	30.5	43.7	58.8	37.2
Totals	100% (n=118)	100% (n=64)	100% (n=17)	100% (n=119)
All years 1975-89:				
0–5 m	70.5	50.5	59.2	63.5
> 5 m	29.5	49.5	40.8	36.5
Totals	100% (n=193)	100% (n=95)	100% (n=17)	100% (n=315)

4.1 m (n = 152) and in OH stands even 6.2 m (n = 198). Remarkably enough, no ground nests were found. Moreover, the data show that nests built during the first brood tend to be located lower than during later broods (Tab. 7). The difference was consistent through years. E.g. in 1985-89, when nests were searched uniformly in all forest-layers, the share of first-brood nests located higher than 5 m above the ground was 30.5% (n = 118), among second-brood ones 43.7% (n = 64), while in the third brood 58.8% (n = 13); the difference is highly significant (X = 10.45; p < 0.001).

There can be two possible explanations to such a change in time. The first one

assumes a bias introduced into data by the presence of observers. To check this the nests found during 1975-85 (when the frequency of our visits was three times lower) were analysed separately from those ones from the period of intensive study (1986-89). The average height of nesting during earlier years appeared to be not lower, and in OH stands even slightly higher, than during the second period (Tab. 5).

The proper explanation is that early in spring the lack of good leaf cover makes higher nests too conspicuous to avian predators. Later in the season, developing leaves may allow to hide nests at higher layers, where nesting adults seem to be less exposed to a danger of unexpected attack by mammalian, mostly ground-bond, predators.

Nesting losses in relation to nest-sites and their distribution

In BNP the lowest nesting losses were found (Tab. 8) among the Blackbird nests located in:
— bushes and crowns of fallen leafy trees (a small sample),
— bifurcations of thick trunks;
— tree-holes and semiholes.

On the contrary, the highest losses were suffered by the Blackbirds nesting on single-standing dead snags and on vykhrots, chiefly on those with sandy soil, found in OH stands. Even identical nest location may cause different consequences in different habitats (Tab. 8), depending on camouflaging properties of the vegetation and/or kinds of predators involved. E.g., vykhrots in AA stands contain black muddy soil among roots, which remains solid after drying up and usually does not cover eggs in nests, while the sandy soil of OH vykhrots usually does. Additionally, AA vykhrots are better hidden among high herb and bush vegetation, whereas in OH forest they attract attention of predators being not only more exposed but also more easily accessible. AA vykhrots are not seldom surrounded by water holes or muddy patches preventing the predator access (Wesołowski 1983).

Relatively high nesting losses among broods started on vykhrots or in snags, i.e. structures low and exposed to predators' eyes, suggest that these places serve as the low-quality substitutes when the better sites are in shortage. This agrees with the fact that the percentage of low nests, and the

Tab. 8. Nesting losses (in %) of Blackbirds during 1975-89 in relation to the habitat and nest location type.
Tab. 8. Straty lęgów (%) kosa (1975-89) w zależności od środowiska i sposobu umieszczenia gniazda.

Habitat	OH		AA		Totals	
Nest location	%	(n=100%)	%	(n=100%)	%	(n=100%)
a. Tree holes	65.6	(61)	59.1	(22)	63.8	(83)
b. Main stem bifurcation	40.0	(15)	81.8	(11)	57.7	(26)
c. At the stem in offshoots	66.6	(9)	66.6	(9)	66.6	(18)
d. On the branch	?	(2)	?	(5)	71.4	(7)
e. Dead stump	87.5	(16)	70.8	(24)	77.5	(40)
f. Bush or fallen tree	40.0	(10)	50.0	(4)	42.8	(14)
g. Vykhrots	85.0	(20)	69.3	(39)	74.6	(59)
Average	66.2	(133)	68.4	(114)	67.2	(247)

Tab. 9. Nesting losses in relation to the height of nest location in BNP (Years 1975 - 1989).
Tab. 9. Straty lęgów w zależności od wysokości umieszczenia gniazda (dane z BPN 1975-1989).

Habitat	AA		OH		Average	
Height (m)	%	(n)	%	(n)	%	(n)
0 – 2.5	70.8	(65)	71.2	(45)	70.9	(110)
2.6 – 5.0	64.0	(25)	75.0	(36)	70.5	(61)
5.1 – 7.5	66.7	(6)	71.4	(21)	70.4	(27)
7.6 – 10.0	50.0	(6)	33.3	(12)	38.9	(18)
> 10.0	71.5	(7)	28.6	(14)	42.9	(21)
Totals	67.9	(109)	64.1	(128)	65.8	(237)
Differences (X test):	not signif.		signif. at p<0.02		signif. at p<0.02	

number of locations in such structures, decrease with the leaf development (Tab. 7).

Rarely occurring in old forests bushes or fallen leafy trees may offer a slightly better cover to the Blackbird nests, as 27.5% (n = 29) were successful, in contrast to 24.5% (n = 113) among those in snags and vykhrots; the difference is not statistically significant, however, probably due to a small sample size.

Surprizingly (Tab. 9) in BNP the nesting success was two times better among the broods commenced in nests placed higher than 7.5 m above the ground, than in the nests located lower. The difference is statistically significant (at p < 0.002), especially in OH stands.

It is intriguing why, especially in AA stands, the reversal of proportions between the destroyed and successful nests took place with time. In 1975-85 nesting losses in AA stands, as well as along the forest edge, were lower than in the forest-interior, while in 1986-89 no such difference was noticed, and even a slight opposite tendency occurred. When the data are split according to the particular year it appears that in 1987-89 there was a clear tendency for lower losses to occur at the forest edge, while in 1986 the reverse was true.

The forest Blackbirds are very versatile with respect to the nest site choice. To analyse this aspect the attempts were made to observe if particular females tended to choose the same type or the same height of the nest site during their successive breeding attempts. The result was negative, with the same females switching consistently (n = 11) from one type of nest site to another and changing their nesting heights as well. As a consequence the Blackbird probably retained a conservative egg colouration of the thrush ancestor, while the Song Thrush evolved a very advanced nest construction and specific egg colouration (Bocheński 1968, Tomiałojć, in prep).

DISCUSSION: WHAT WAS THE PRISTINE DENSITY AND HABITAT CHOICE OF FOREST BLACKBIRDS?

Population density and its stability.

A fundamental feature of the forest Blackbird in BNP, and of its other undisturbed forest populations in CE Europe, is a relatively low breeding density. Usually it ranges from 1 to 3 pairs/10 ha, which makes a substantial difference with the 5.0–24.0 p/10 ha values reported from several W European small woods or fragmented forests (Snow 1958, Mulsow 1976,

Karlsson and Källander 1977, Glutz and Bauer 1988). It differs still more from densities found in some down-town parks of Copenhagen, Oxford, Edinburgh, Berlin, Poznań, Prague or Budapest – up to 40-70 p/10 ha (Lind 1955, Snow 1958, da Prato 1980, Stephan 1985, Stastny et al. 1987, Mizera 1988, author's obs. from Budapest).

As long as forest Blackbirds were studied only in managed or suburban woods, there was no certainty if their density, lower than in urban parks, resulted from a simplification of the managed stands kept at younger age, or from another reason. In view of the BNP data, fairly low Blackbird density in forests appears to be a pristine feature. It is also possible to reject another suggestion (Dyrcz 1969), namely, that low densities in eastern forests, including the BNP, result from a relatively recent their colonization by the species. This hypothesis is in conflict with paleozoological data (see below) and with our 17-year bird monitoring results which show the absence of an increasing trend in the forest Blackbird numbers.

Contrarily, the densities found in the BNP are clearly higher than those in more eastern and north-eastern forests, where they usually remain below 1 p/10 ha (Dyrcz 1969, Malchevskiy and Pukinskiy 1983). Densities similar to BNP data, were found in other larger forests of C and E Europe: 1–4 p/10 ha (Stephan 1985, Glutz and Bauer 1988). For a deciduous forest on fertile alluvial soils in the Odra River valley near Wrocław the density was estimated as 1.3–1.4 p/10 ha (Dyrcz 1963, 1969). I suspect that they were underestimates, being based on the number of nests found, as these are usually incompletely counted. The suggestion is confirmed by the mapping-technique results collected in another Odra-valley forest near Wrocław, where the densities of song-territories (with some nests

found) were estimated to be 3.3–3.8 p/10 ha in forest-interior old stands and 4.7–5.8 p/10 ha in an immature oak-stand with a long forest-edge belt of thorny thickets (Tomiałojć and Profus 1977).

The question is: why are the Blackbird densities in primaeval vast forests low? At least three not necessarily exclusive explanations can be proposed.

1. The low densities may be a coevolutionary consequence of the long-term coexistence with a diverse group of predators (Tomiałojć 1980, Tomiałojć and Profus 1977, Tomiałojć at al. 1984, Martin 1988);

2. The low breeding densities of a migratory population of a species may result from a population limiting factors acting on wintering grounds.

3. The food resources of primaeval forest might be in shortage during the breeding season.

The second explanation seems to be falsified by equally low densities reported from the last extensive W European forests (the New Forest of England – after Glue 1973, and Fort de Citeaux in Burgundy – after Ferry and Frochot 1968, 1985) in spite of a non-migratory status of those Blackbird populations. The food shortage hypothesis is questionable in view of the forest territory size being 11–14 and in extreme cases even 43 times larger than that in the Oxford Botanical Gardens or in other down-town parks, where territories may be reduced to 0.16–0.24 ha, sometimes even to 0.1 ha (Snow 1956, Lind 1955). The estimates of the invertebrate (chiefly earthworm) biomass and availability in deciduous forests versus urban parks are not dissimilar to a comparable extent, as well as several other facts discussed elsewhere (Snow 1958, Tomiałojć in prep.) also speak against the third explanation.

Original habitat preferences

Several suggestions concerning the original nesting habitat of the Blackbird can be found in the literature. These are:

— humid mountain forest (Stephan 1985);

— bushy formations (Havlin 1962, 1964);

— forest edges (Furrer 1980, Stephan 1985);

— old lowland and submontane forests (this study).

The arguments for the Blackbird origin from humid mountain stream-side forests have been seen in its present geographical and vertical distribution. Stephan (1985) indicated, supporting his line of reasoning by an extensive literature overview, that in Asia Blackbird occurs largely in mountains, reaching the timberline. This is thought to indicate that it has evolved originally as a mountain species and only recently spread to the lowlands. The following arguments can be presented against such a conclusion:

a) Fossil remains allocated to Blackbird have been found in most of southern half of Europe north to Ireland, England, France, S Germany, S Poland, Ukraine and S Russia (Lambrecht 1933, Brodkorb 1978, Bocheński 1974, 1988, Bocheński jun. 1990 etc.). Even assuming that in single cases a misidentification of *T. viscivorus* might have happened (Z. Bocheński in litt.) the number of well preserved remains alone is so high that the occurrence of Blackbirds in European lower elevations already in the late Pleistocene, early Holocene and during medieval times (Waluszewska-Bubień 1973) cannot be denied. The oldest finding, probably concerning *T. merula*, is that known from Brno vicinities, Moravia, from mid Pleistocene, some 500 000 years BP (Janossy 1972);

b) The Blackbird densities are the highest in lowland forests and decrease with increasing altitude (Kovshar and Shuyko 1984, Glutz and Bauer 1988);

c) The present distribution of forests in SW and C Asia may be recently restricted by an aridisation of the region due to climatic changes and/or destruction of lowland forests by ancient civilizations. An easiness with which Blackbird colonizes the oases of cultural landscape in the lowlands (Kovshar and Shujko 1984) suggests that the present-day absence of this species at C Asian lower altitudes may be a recent phenomenon.

Also for other reason it seems improbable that Blackbird was originally an exclusively mountain bird. The Palearctic region was a centre of dispersal for the whole group of thrushes (Ripley 1986). Out of 14 species of the genera *Turdus* and *Zoothera* 13 are known to occur in lowlands, while only 4 species, including the Blackbird, extend their breeding ranges above the elevation of 2000 m a.s.l. (Dementiev et al. 1954, Glutz and Bauer 1988). Yet in all these cases, except *Turdus torquatus*, the majority of individuals form lowland or submontane populations. Thus, the fact that at present C-Asian Blackbirds are limited to mountain forests may be either a regional feature or recent phenomenon. After all, the main part of the species breeding range is still in the lowlands of Europe and SE China (see map in Glutz and Bauer 1988).

The increase in the Blackbird numbers predicted theoretically and confirmed for some regions, or its spread into new areas, e.g. in N Scandinavia and Russia (Malchevskiy and Pukinskiy 1983, Glutz and Bauer 1988) can be explained as a consequence of recent anthropogenic changes or climate amelioration (Cramp 1988) rather than as an evidence of the continuation of

its original expansion from mountains to lowlands. Not only our 17-year monitoring results exclude an occurrence of a steady increase in the forest Blackbird numbers, but the same is valid for the whole last 25-year period. Already during late 60ies our faunistic investigations of NE and E forests of Poland revealed that the Blackbird numbers in several swampy nature reserves were comparable to those in the BNP. It seems that some conclusions on the increase of the Blackbirds in forests were based on data from human-transformed woods situated amidst anthropogenic habitats. Such cases, however, may be better explained as a result of an overspill of the Blackbirds from highly productive anthropogenic habitats, chiefly human settlements, to the neighbouring woods (e.g. Tischler 1941, Lind 1955, Batten 1973, Mulsow 1976, Karlsson and Kallander 1977, Bruch et al. 1978, Stephan 1985 etc.).

It seems also unlikely that the Blackbird originally was a bird of bushy formations, as suggested by Havlin (1962, 1964) and Lack (1966). Most bushy formations of the present Europe are of anthropogenic character, even those in the Mediterranean region (Blondel 1988). The other ones remain geographically or altitudinally outside the Blackbird's breeding range. The only partly bushy habitat suitable for the Blackbird could be found in pristine times in riparian forests, where primary and secondary succession occurs. However, the high adaptability of present-day Białowieża Blackbirds makes it doubtful if they ever avoided nearby located high-stemmed primaeval stands. Nesting high, even in treeholes, found recently in primaeval populations studied in two distant regions, in BNP and in the Alatau Mts near Alma-Ata, suggests that this is a pristine feature of the species breeding ecology (Tab. 10).

It was also suggested that the Blackbird is a thrush adapted to forest-edges or forest ecotone habitats. Again, a question arises: is this a pristine or a secondary feature? In view of the results from BNP, as well as

Tab. 10. Percentage of Blackbird nests located in bushes. NR – nest-record scheme data, LS – intensive local study data.
Tab. 10. Udział procentowy gniazd kosa umieszczonych w krzewach dane z ogólnych kartotek lęgowych (MR) oraz wyniki lokalnych badań (LS).

	Kind of data, region	%	Author
NR	Czechoslovakia – all habitats	28.3	Pikula & Beklova (1983)
	Czechoslovakia – forests	60–91	Havlin (1962)
	Poland – forests	15–33	Wesołowski & Czapulak (1986)
	Switzerland – farmland	35.5	Glutz & Bauer (1988)
	Switzerland – forests	12.3	Glutz & Bauer (1988)
	South-Poland – forests	6.7	Bocheński (1968)
LS	SW-Poland – deciduous and mixed forests	25	Dyrcz (1963, 1969)
	Kazakhstan – coniferous forests	2.7	Kovshar & Shuyko (1984)
	W-Poland – mixed conif. plantations	c. 1	Graczyk & Klejnotowski (1966)
	BNP – primaeval forest	0.7–1.5	This study

from faunistic observations from other forests of NE Poland (own data) and of Graczyk and Klejnotowski's (1966) data from W Poland, it is certain that the Blackbirds which live in extensive forests show no strong preferences for the forest edge (Tomiałojć, in prep.).

There is an additional argument in favor of such an explanation. The Blackbird is known for its low-frequency song (mainly in the range of 1.5–4 kHz) which is a typical feature of true forest-interior birds. Some tropical thrushes and wrens inhabiting primary forests have equally low-frequency songs (D. Snow, in litt.). Such notes are known to carry more efficiently through forest vegetation. Actually the Białowieża Blackbirds tend to sing low in the canopy, in contrast to the Song Thrushes singing from tree tops (Tomiałojć and Lontkowski in prep.).

The BNP Blackbirds do not display consistently any strong preference for forest edge, nor do they exploit food resources from the adjoining open areas. Theoretically, one could expect a stronger tendency to appear in the open to be developed in the E European migratory population of the species, than among the resident W European one. After all, the former but not the latter birds have to cross open areas during their migrations and while wintering in the Mediterranean region. An opposite is observed in nature, which means that some other factors are responsible for the differences in the behaviour of various populations. It can be suggested that an overpopulation once triggered in western habitats by anthropogenic factors, chiefly by reduced predator pressure and/or improved wintering conditions, was a major ecological force pushing the individuals to accept foraging in the open, even far from cover. In consequence, western populations developed an ability to thrive in half-

open habitats (Furrer 1980), while on treeless islands off Great Britain they even adjusted to living in truly open habitats (Cramp 1988). As most such places once were covered with high forests (Dimbleby 1976, Birks 1977, Rackham 1976), such a habitat choice must be a recent feature. Secondarily transformed Blackbird populations apparently ceased to be afraid of penetrating open habitats. It remains to be tested by experimental studies to what extent this kind of change was based on a selection of genetically less nervous individuals, or to what it was a phenotypic adjustment of their behaviour (Tomiałojć 1985).

Concluding, the Blackbird is a thrush originally populating dense high and mature forests, preferably humid, both in lowlands as at lower mountain elevations. It is noteworthy that an equally dark-coloured thrush, *Zoothera sibirica*, from the taiga along Yenisey river, Siberia, shows a preference for riparian forests, especially willow formations, and does not occur high in the mountains (Rogacheva 1988).

Pristine nest-site preferences

The BNP findings contrast with most other European results with respect to the prevailing type of nest-sites accepted by the Blackbirds. This justifies the question on what was the pristine localization of their nests. The crudest division of nesting sites into those in bushes (or crowns of fallen leafy trees) and others (Tab. 10) should be analysed with caution, as, obviously, such data contain a more or less serious bias. Especially the data collected randomly within the frames of national nest schemes tend to overestimate the percentage of low nests (Wesołowski and Czapulak 1986).

In spite of this a considerable difference found between the Polish and Czechoslo-

vakian nest-record scheme data, as well as between those and the S Polish scheme (Bocheński 1968), suggests strongly a true variability in nest-site choice (Tab. 10). More trustful are data from the set of intensive local studies, among which the results from the region of Wrocław, SW Poland (Dyrcz 1963, 1969) deviate considerably. Knowing those study areas personally I would explain this deviation by a presence of exceptionally rich bush-layer not destroyed by (largely absent) big herbivores, combined with a relatively young (as for oaks), thinned and structurally still immature tree stand. A general message from the Table 10 is clear: only primaeval mountain forests of Kazakhstan and largely coniferous plantations in W Poland have percentage of Blackbird nests placed in bushes as low as in the BNP. Thus, a high percentage of bush nests usually reported in literature (Stephan 1985, Glutz and Bauer 1988) may be a secondary feature. E.g. Bocheński (1968) found 33.9% bush nests among his garden sample, and only 6.7% among those from natural forests.

Also the nesting tree selection is different in primaeval forests as compared with that in the other habitats. A clear preference for the hornbeam in the BNP (Tab. 3) can be confronted with only 3.2 (max. 5.7) and 2.9% nests found in this tree in the country-wide Polish and Czechoslovakian samples (Wesołowski and Czapulak 1986, Pikula and Beklowa 1983). Instead, the latter contain 21.3 and 25.8% Blackbird nests located in the spruce, a tree which has been secondarily replenished and transformed structurally. Therefore, it better meets the Blackbird's requirements there than the same tree species in the BNP. In Polish and Czechoslovakian anthropogenic habitats also other nesting plants occur, such as thorny bushes or half-trees, which are virtually absent in the BNP.

Considerable changes in the height of nesting took place in the process of anthropogenic transformations,. Starting from the apparently primaeval nesting height of 4.3–5.3 m above the ground (Kovshar and Shujko 1984 and this study) the Blackbirds inhabiting human-made habitats switched to nesting as low as 1.3–2.4 m (Bocheński 1968, Dyrcz 1969, Pikula and Beklova 1983, Glutz and Bauer 1988). Strong prevalence of low and bush nests in secondary populations stems from a combined action of three factors: lower share of high old-growth forests in anthropogenic landscape; increased share of bushy vegetation owing to secondary succession and lowered pressure of big herbivores; different composition of the predator guild, with several mammal predators absent, while acting from above avian predators (corvids) are apparently more abundant than under primaeval conditions (cf. Tomiałojć 1980). It should be stressed that the present-day bushy secondary-forest plantations restored on clear-cut areas had almost no counterpart in pristine forests, except perhaps after fire. Examples of the forest regeneration on some windbreaks, which appeared in the BNP some 25 years ago and quite recently, indicate that wind-disturbed primaeval stands do not necessarily pass through a bush-thickets stage (Tomiałojć 1991). The young-tree under growth usually survives the disturbance and quickly (after 2–4 years) restores a new canopy. In the process mostly thin and unbranched stems begin to dominate, offering neither support nor shelter to bulky Blackbird nests. At this stage of forest regeneration the species nests mostly on snags or vykhrots remaining after broken old trees for a period of 10–20 years.

In the BNP no Blackbird nests were found on the ground. Such a way of nesting seems to be hindered there by a con-
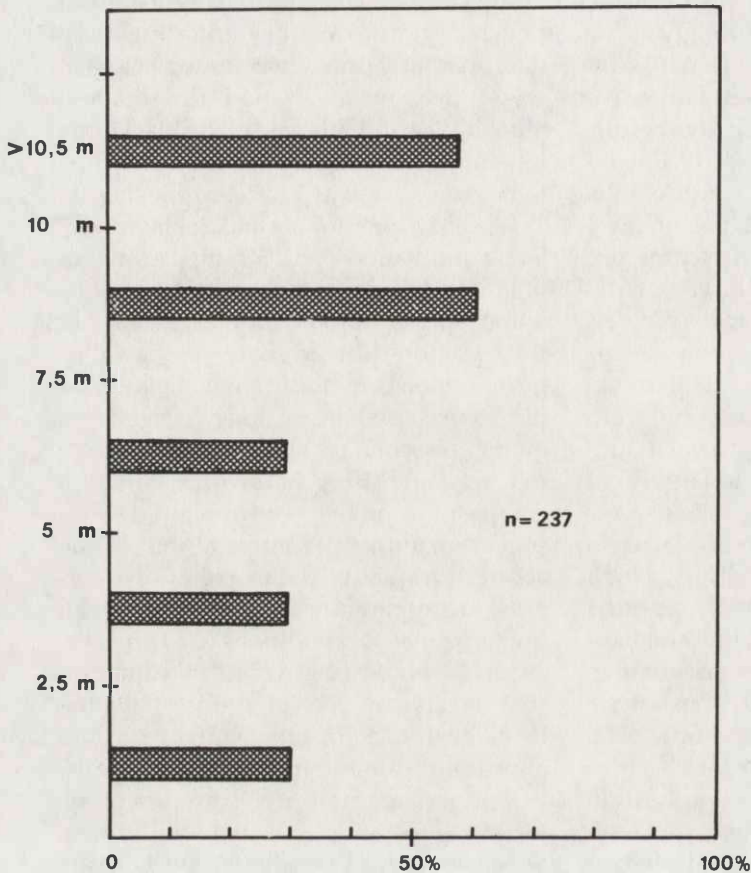
Fig. 3. Blackbird's nesting success in BNP in relation to the height of nest site.

Ryc. 3. Sukces lęgowy kosa w BPN przy różnych wysokościach umieszczenia gniazda.

siderable number of big animals, carnivores and hoofed mammals, which can easily destroy ground or very low nests. Blackbird ground nests in Czechoslovakian and Polish national samples form only 0.7-1.1% all nests (Pikula and Beklova 1983, Wesołowski and Czapulak 1986), in Switzerland they constitute 3.9% (Glutz and Bauer 1988), presumably occurring more frequently at higher altitudes, while in a Finnish sample they form as much as 14% (von Haartman 1969), or even 32% if easily accessible very low nests are included. They are also said to prevail in some areas of the former Soviet Union (Dementiev et al. 1954). Such nests are still more frequent on some islands off Great Britain (Cramp 1988). All this suggests that Blackbird ground or very low nests tend to occur in habitats or regions where big animals are not numerous or absent, e.g. in the Far North, in higher mountains, on islands. Especially the absence of gregarious and usually numerous wild boars *Sus scrofa* and big hoofed browsers (like *Cervus elaphus*, *Alces alces* and *Bison bonasus*) may be of importance, as they are known to exert a strong impact on lower layers of the forest (Faliński 1986), destroying bird ground nests (Wesołowski 1985). It seems that
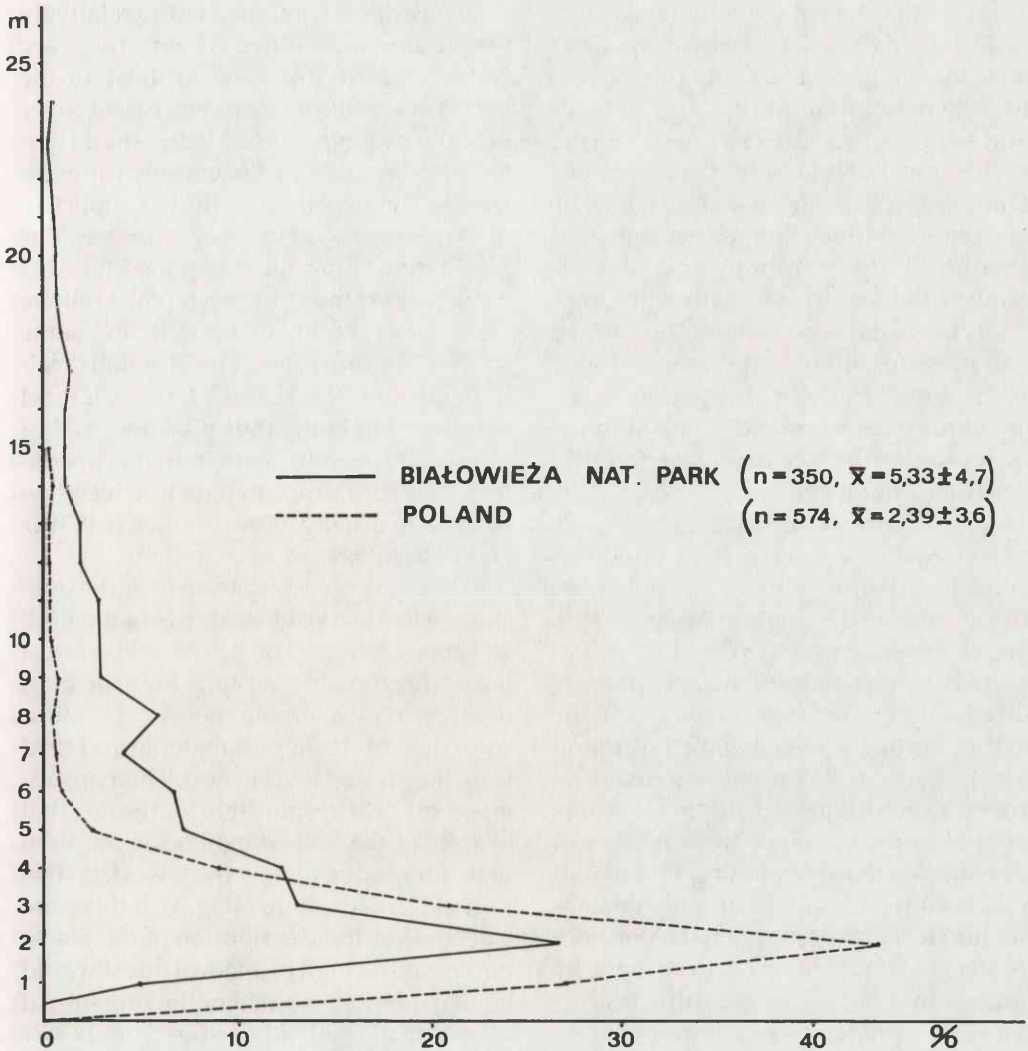
Fig. 4. Vertical distribution of Blackbird nests in BNP and in some forests of southern Poland (combined data of Bocheński 1968 and Dyrcz 1963, 1969).
Ryc. 4. Rozmieszczenie pionowe gniazd kosa w BPN i w wybranych lasach południowej Polski.

just because of the limited presence of these creatures the Redwing *Turdus iliacus* near Sankt Petersburg locates 20% nests on the ground (Malchewskiy and Pukinskiy 1983), in S Finland even 31%, and the proportion tends to increase northwards (Tyrvainen 1969), while in the Białowieża Forest almost all nests of this species are known from elevated sites.

The problem with this interpretation is that the true abundance of big animals in pristine times is unknown (Tomiałojć 1991), i.e. if it was higher or lower than in the present wildlife refuges like BNP. Jud-

ging from the present-day situation in BNP it can be suggested that also in pristine times the big game tended to be distributed unevenly in the forest. Such animals exert stronger pressure on some preferred patches, chiefly "island-like" situated OH stands (Faliński 1986; own observ.), while more lightly influencing the vegetation in other forest types (swampy or coniferous stands, windbreaks) as less attractive trophically and/or less accessible. Thus, heavy local pressure of big herbivores on lower layers of the forest not always denotes an unnatural phenomenon developed in the preserves with excessive (secondarily high) game numbers.

An exceptional case of the Blackbird's rather frequent nesting on the ground was found in urban conditions of Tiergarten park in downtown Berlin (Anders 1979). This shows that an underdevelopment of bush-layer may yield two contrasting results: either nesting high in trees as in the BNP, or nesting in trees and on the ground as in Tiergarten. The second case requires, however, an additional condition to be met – a kind of protection of some patches of the habitat against trampling by animals and/or humans. This example confirms that the structure of the habitat alone does not decide about the ways of using it by nesting birds, but the pressure of a destructive action (predation or trampling) of other beings is a dominant factor (cf. Tomiałojé 1980).

Some studies in managed forests concluded that the height of Blackbird nest sites declines with the progress of the season (Dyrcz 1963, 1969, Glutz and Bauer 1988). The BNP results contradict this (Tab. 4). This discrepancy can be explained by structural differences between the average managed and primaeval forests. Most managed stands, including those studied near Wrocław (Dyrcz 1963, 1969), have a luxu-

riant bush layer combined with a relatively simple structure of tree crowns; these are features exactly opposite to those in the BNP. Hence, the development of leaf cover in both forest types offers increasingly better nesting conditions in entirely different layers. The explanation finds support in the differences in nesting success. The Blackbird nesting success in the BNP was twice higher among the nests placed above 7.5 m than the lower nests in the same habitat. The difference (Fig. 3) is statistically significant ($X = 12.8$, df. 4, $p < 0.02$) and was found in both kinds (OH and AA) of stands. This result, again, remains in contrast to other European data in which low nests were usually more productive (Glutz and Bauer 1988).

Thus, it is necessary to answer the question: why do most Blackbirds in the BNP still breed below (Fig. 4) the safest forest layer? Presumably nesting high in trees involves a considerable energy expenditure for delivering the nest material and food from the ground level to nest. This constraint seems to be responsible for the fact that in spite of the BNP stands being 35–40 m high, for nesting mostly the lowest, c. 10 m thick, layer is exploited (Fig. 4). If this were true, the vertical distribution of the Blackbird nests in a high primaeval forest would be shaped by a resultant of the pressure of mammalian predators acting from below and the energy restrictions preventing nesting too high, where additionally the nests may be too conspicuous to avian predators, especially during the early spring period. Once it was believed that Blackbird's rare nesting in tree-holes of some urban parks denotes a new adaptation being developed to meet urban conditions (Graczyk 1960). The data from BNP show, however, that such a nesting in cities is a return to the ancient trait which has largely been lost in man-shaped habitats.

CONCLUSIONS

The pristine Blackbird populations were most probably characterized by the following features:

a) Fairly uniform breeding distribution in almost all forest habitats, with lower numbers in poor coniferous stands and only slightly and inconsistently higher than average along the forest edge.

b) Moderate nesting densities, 1–4 p/10 ha in mainly deciduous and below 1 p/10 ha in coniferous stands. Still lower densities reported from several managed forests of C-Europe seem to result from a secondary simplification of the habitat structure by management, which lowers their suitability for the Blackbird nesting. Contrastingly high densities – 5–24 p/10 ha - of several W European woods seem to arise from a secondarily enhanced Blackbird productivity and/or survival in surrounding them anthropogenic habitats.

c) During the breeding season the Blackbirds originally tended to avoid open areas; they collected their food almost exclusively within the forested area itself.

d) For nesting they used to select mostly old trees, preferring hornbeam rich in holes, crevices and offshoots in deciduous stands, and spruce in coniferous ones. The bushes, though also preferred, were less frequent in comparison to the present-day situation in managed forests. In BNP 62–70% Blackbird nests were found in structures nonexistent in managed stands.

e) The average nesting height was about 4 to 5 m above the ground; nesting on the ground was impossible in most regions, being prevented by wild boars and other big game.

f) High located nests (above 7.5 m) produced more offspring than the lower ones, contrarily to the situation in managed stands. The height of nesting seemed to be controlled by the following factors: vegetation structure in a given period of the breeding season, action of predators, and energy costs arising from ground foraging and delivering food high up to the nests.

In the present-day, still largely undisturbed, forests of the Białowieża National Park the Blackbird breeds in fairly high and stable numbers, without an increase tendency. The range of its year-to-year density fluctuations is up to 1.5 fold, their pattern roughly agreeing with the incidence of severe winters in C-Europe and with the changes in caterpillar abundance (Tomialojć, in prep.). The population remains a typical forest-interior one and migratory.

To sum up, the Blackbird is a thrush which has evolved inside the relatively fertile, humid and high-stemmed forests of the lowland and submontane elevations. Its present-day preference for the forest-edge zone and bushy vegetation, as well as its occurrence in the open landscape or in conifer-dominated forests, seem to have been strengthened recently. This has occurred under pressure of anthropogenic changes such as: management and reduction of forests, improvement of wintering conditions, decreased predation pressure, adjustment or adaptation to penetrating newly-created open habitats.

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STRESZCZENIE

[Ekologia rozrodu kosa *Turdus merula* w pierwotnym lesie Puszczy Białowieskiej. Część 1. Liczebność, rozmieszczenie i miejsca gniazdowania.]

Ekstensywne obserwacje nad występowaniem i ekologią kosów leśnych zamieszkujących niezaburzone drzewostany Białowieskiego Parku Narodowego (dalej BPN) prowadzono przez 17 lat na stałych powierzchniach próbnych przy okazji liczenia ptaków dla celów monitoringu. Równolegle, w latach 1986-89, częściowo w 1990, przeprowadzono znacznie bardziej szczegółowe badania ekologii tego gatunku na dwóch powierzchniach próbnych – lęgowej (K) i grądowej W (i tylko w 1986 także na pow. C), szczegółowiej scharakteryzowanych wcześniej (Tomiałojć, Wesołowski i Walankiewicz 1984).

Niniejsza praca omawia sposób występowania gatunku w BPN tak w przestrzeni, jak i w czasie. Standardowa ocena liczebności kosów została przy tem sprawdzona (Tomiałojć i Lontkowski 1989) poprzez skonfrontowanie standardowych wyników liczenia metodą kartograficzną ze znacznie bardziej szczegółowymi danymi wywiedzionymi z większej liczby kontroli (20–30 w sezonie), wykrycia większości gniazd oraz kolorowego obrączkowania części osobników.

Stwierdzono, iż kosy zamieszkują cały obszar Puszczy włącznie z wnętrzem zwartych wysokich drzewostanów, w strefie brzegu lasu wykazując (nie corocznie) tylko nieco podwyższoną liczebność. Gęstość populacji lęgowej wynosiła w lesie lęgowym średnio 2,5 p/10 ha, w grądowym 2,2, a w borach 0,7 p/10 ha (tab. 1). Rzeczywistą liczbę terytoriów, a nie uzyskaną standardową metodą kartograficzną, zawiera tab. 2. Wyliczona z tych dokładnych obserwacji przybliżona wielkość terytoriów w drzewostanach o przewadze drzew liściastych zwykle wynosiła 2,2–2,7 ha, skrajnie 1,1–4.3 ha. Były więc one 11–43 razy większe niż w niektórych parkach miast europejskich. Liczebność kosów w ciągu 17 lat wahała się w granicach 97–137% w stosunku do stanu w r. 1977 uznanego za 100% (ryc. 1). Przy tym ujawniła się dodatnia korelacja liczebności kosów z obfitością gąsienic *Geometridae* i *Tortricidae* w roku poprzedzającym, a także, choć z wyjątkami, z ostrością poprzedzających zim. Nie zauważono trendu wzrastającego w liczebności tej populacji.

Rozmieszczenie terytoriów kosa wewnątrz pierwotnych drzewostanów BPN nie wykazywało wyraźnej zależności od dostrzegalnych w terenie różnic w strukturze środowiska (np. rozległe wyłomy) lub wilgotności podłoża, choć rozmieszczenie gniazd to sugerowało: większość gniazd została znaleziona w miejscach, które przez cztery lub przynajmniej trzy lata wchodziły w obręb terytoriów tego gatunku, a więc, preferowanych. Sugeruje to, że preferencja dotyczy miejsc ukrywania gniazd, a nie miejsc żerowania.

W starych drzewostanach BPN kos gnieździ się wysoko nad ziemią (tab. 6) – średnio 5,3 m (0,3–24 m), głównie na drzewach liściastych (tab. 3). Wraz z upływem

sezonu gniazda są umieszczane coraz wyżej (tab. 7), co sugeruje że wcześnie wiosną wyższe piętra lasu zapewniają słabą osłonę. Stosunkowo wysokie gnieżdżenie się wynika w BPN z niedorozwoju warstwy krzewów i podrostu spowodowanego niedostatkiem światła oraz silną presją dużych ssaków kopytnych. Prawie 20% gniazd kosa w łęgach i 50% w grądach bywa zakładanych w dziuplach i półdziuplach (tab. 4), a znaczna część także na kikutach martwych drzew i wykrotach (ryc. 2). Tylko 0,7–1,5% gniazd bywa w krzewach lub koronach powalonych drzew (tab. 4). Zatem aż 62–70% gniazd kosa w pierwotnych drzewostanach bywa zakładanych na strukturach niemal zupełnie nie występujących w odmłodzonych przez gospodarkę lasów użytkowych. Nie stwierdzono wyraźnej preferencji stron świata w umieszczeniu gniazd, choć w okresie pierwszego lęgu jakby zaznaczała się słaba przewaga lokalizacji od północnej strony drzewa (tab. 5). Gniazda otwarte niemal zawsze są w głębokim cieniu, tym bardziej że w wysokopiennym lesie promienie słoneczne tylko bardzo krótko w godzinach południowych mogą penetrować niskie piętra.

Gniazda zakładane w krzewach i leżących drzewach oraz te w dziuplach ponoszą nieco niższe straty z powodu drapieżnictwa niż pozostałe (tab.8). Stwierdzono statystycznie istotną różnicę pomiędzy nasileniem strat lęgowych wśród gniazd zakładanych na różnych wysokościach: lęgi powyżej 7,7 m nad zie-

mią ponosiły dwukrotnie niższe straty niż gniazda niskie (tab. 9, ryc. 3). Jest to rezultat odwrotny od uzyskiwanego w lasach zagospodarowanych, a wynika z przeciwstawności strukturalnej tych dwóch typów lasu: lasy zagospodarowane mają silniej rozwinięte dolne warstwy lasu a niedorozwinięte (z powodu młodego wieku) warstwy wyższe, gdy w lesie pierwotnym jest odwrotnie.

Mimo wyższych strat większość gniazd była jednak lokowana dość nisko (ryc. 4), co świadczy że jakiś inny czynnik musi przeciwdziałać wysokiemu gniazdowaniu. Przypuszcza się, że są nim koszty energetyczne wzlatywania z powierzchni ziemi do wysokich gniazd, a wczesną wiosną dodatkowo także nadmierna ich widoczność.

Wychodząc z faktów stwierdzonych w BPN wyprowadza się wnioski co do sposobu rozmieszczenia i gniazdowania tego gatunku w czasach dawnych. Argumentuje się, że kos pierwotnie był mieszkańcem wnętrza niżowych i podgórskich dojrzałych lasów, zwłaszcza wilgotnych, bez wyraźnej preferencji obrzeży leśnych kompleksów. Nie mógł on być związany z formacjami krzewiastymi, gdyż te zwykle były ograniczone w swym występowaniu przez presję dużych ssaków kopytnych. Przedstawiono argumenty paleontologiczne, historyczne i ekologiczne przemawiające przeciw hipotezie (Stephan 1985), iż kos wyewoluował jako gatunek drozda zasiedlającego lasy górskie i dopiero wtórnie rozprzestrzeniającego się na niziny.