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A city as an object for synecological studies: a search for density compensation among birds breeding in urban woodlands

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SUMMARY

Unexpectedly high breeding densities developed by some bird species in urban and other man-modified green areas seem to be widespread. This paper is an attempt at an analysis of the woodland birds of Moscow City in the context of species impoverishment, ecological release, and density compensation. There seem to be no reasons to talk about species impoverishment or decrease in the number of forest species in large urban woodlands (> 2.5-3 km^2) except for components related to habitat loss or heavy disturbance, at least at the temporal scale of 5-10 decades. The exclusion concerns shy and/or large-sized species which have disappeared mostly at early suburban stages. Species enrichment rather than impoverishment has occurred in the only long-studied large woodland island in the transitional period between suburban and urban stages. There are no grounds to suspect density compensation caused by competitive release or competitive exclusion between or during these stages. On the contrary, two pairs of ecologically similar congeners (Blue Tit *Parus caeruleus* and Great Tit *Parus major*, Song Thrush *Turdus philomelos* and European Blackbird *Turdus merula*) have developed high local densities during the same or overlapping periods. In the interior part of the model forest, the nesting success in a number of years is fairly high in three of these species. The fact that the percentage of successful nests in Song Thrush has been moderate or moderately high in some years comes as a surprise because Moscow City has supported a huge and dense population of Hooded Crow *Corvus cornix*, a major predator on open nests. As in many other large woodlands of the city, the assemblage of potential nest predators in the forest studied has not been species-poor but several important natural predators (e.g., Pine Marten *Martes martes*) have been absent as residents. Thus, partial release from nest predation could be among the mechanisms responsible for the high local densities which have currently been observed in some passerine birds in these and some other Moscow woodlands. On the other hand, the nesting success in the study species is not too high to suspect that it could be the only determinant of the above pattern. A wider set of urban sites and avian species must be studied in the region to test these findings for validity and generality.

Key words: urbanization, woodland bird, density compensation, species impoverishment, ecological release, interspecific competition, nest predation, nesting success

INTRODUCTION

Urbanization is an increasing component of land transformation in most parts of the globe. That is why a growing concern about impacts of urbanization on plant and animal populations, ecological communities and biotas has been seen in the past decades (e.g. Tomiałojć, 1982, 1988; Bezzel, 1985; Tsibulin, 1985; Klausnitzer, 1987; Konstantinov et al., 1996; Fernández-Juricic & Jokimäki, 2001; Marzluff et al., 2001a; Pickett et al., 2001; McKinney, 2002, 2006, 2008; Luniak, 2004; Marzluff & Donnelly, 2004; Adams et al., 2005; Chace & Walsh, 2006). However, the value of urban studies is not restricted to the spheres of applied ecology and protection of biological diversity. It is often overlooked that urban and suburban areas are promising model objects for conducting basic ecological research. Rapid changes in habitat mosaics, high patchiness, distinctiveness of boundaries between densely built-up areas (usually supporting poor species diversity), man-made green areas, and remnants of natural habitats modified to a different degree (and often having specific vegetation characteristics, e.g., well-preserved old-growth tree stands, unusual vertical and horizontal structures, exotic species among dominants) provide some unique possibilities for conducting studies in such fields as local- and metapopulation dynamics, intra- and interspecific interactions, ecological niche, community stability, island ecology, and biological invasions.

Relationships between evolutionary process (at the levels of species and supraspecific taxa) and historic transformation of ecological communities are one of the most complicated and controversial themes in evolutionary ecology (see Dunbar, 1960; Lewontin, 1969; Pianka, 1978; Zherikhin, 1978, 2003; Chernov, 1984, 1988, 1996; Meyen, 1987; Vakhrushev & Rautian, 1993; McIntosh, 1995; Rosenzweig, 1995). Modern cities and urban agglomerations are “young” landscapes on the evolutionary scale of time. In many regions, urbanization, at least at the early stages, increases the risk of local extinction in many native species and seems to decrease species richness in local biotas and assemblages (Bezzel, 1985; Jokimäki & Suhonen, 1993; Czech & Krausman, 1997; Clergeau et al., 1998; Marzluff, 2001; Jokimäki et al., 2002; McKinney, 2002; Adams et al., 2005; Chace & Walsh, 2006;

Venter et al., 2006 and references therein). This tests the adaptive potential in separate species and the interplay between heritability and phenotypic plasticity in population changes (Tomiałojć, 1985, 1988; Diamond, 1986; Luniak, 2004; Adams et al., 2005).

The following two broad-topical questions must be emphasized in the synecological context. First, it is important to estimate an extent to which general processes and mechanisms operating in populations and communities in urban landscapes can be paralleled with those shaping natural communities and biotas in extreme situations (e.g., during and after natural disturbances of different kind and duration) or extreme environmental conditions (e.g., in harsh or highly unstable climate). Second, the beliefs that urban landscape is a novel "adaptive zone" containing a considerable number of unoccupied ecological niches (Klausnitzer, 1987; Vakhrushev & Rautian, 1993; Luniak, 2004; Adams et al., 2005) and that urban assemblages of taxonomically related species are not entities but rather collections (Vakhrushev & Rautian, 1993) are plausible in reference to built-up areas. However, there is no *a priori* reasons to extrapolate these or any other generalizations concerning human-settlement areas on large man-made "green islands" or remnants of natural habitats embedded in an urban matrix (but see Sasvári et al., 1995; Jokimäki, 1999). For example, the tentative generalization that "the quality of the landscape surrounding the city does not seem to play a preponderant role in bird abundance and community structure" (Clergeau et al., 1998, p. 422) needs proofs in reference to urban green islands of different types and sizes (see, e.g., Tomiałojć, 1976, 1985, 1998 for some facts and arguments contradicting the suggestion cited).

Some authors (e.g., Fernández-Juricic & Jokimäki, 2001) emphasized that woodland fragments in urbanized areas often seem to be more structurally isolated from surrounding matrix than those in more natural types of fragmented landscapes. It is important to know in detail how and why do built-up surroundings affect local- and metapopulation structure, interspecific interactions, and community organization in green islands (Miller et al., 2001). For example, it was shown for some man-modified landscapes that species interactions in forest fragments, for example, the rates of nest predation and nest parasitism in birds (e.g., Andrén & Angelstam, 1988; Andrén, 1992; Paton, 1994; Robinson et al., 1995; Donovan et al., 1997; Flaspohler et al., 2001), can be substantially influenced by the matrix or adjacent habitats. Is the generalization valid for urban and suburban forest fragments of different sizes in different regions? How considerable are the differences in this respect between peripheral and interior parts of large woodland islands embedded in an urban matrix?

A large number of studies in community ecology have focused on birds. There are two broad "paradigms" concerning the mechanisms and processes shaping bird assemblages. Firstly, competitive interactions have been believed to create structured community patterns and govern their dynamics. Communities at any given moment have been considered to be either in or, as a result of disturbances or environmental variations, on the way to an equilibrium state rooted in from resource limitations and more or less "saturated" by species and individuals. Secondly, according to a different, "individualistic" viewpoint, mutually independent processes and events at separate species levels, including stochastic numerical variations, are of prime importance in shaping the assemblages which are often unsaturated by species and individuals (for a review, see Wiens, 1989a; McIntosh, 1995).

The first scientific data on the birds inhabiting European cities came from the XIX century. In some cities and suburban areas, regular ornithological observations were made during many decades (e.g., Batten, 1972; Cramp, 1980; Kelcey & Rheinwald, 2005). Changes of bird assemblages during long-term gradual or rapid urbanization were described in several studies (see Adams et al., 2005 for a review). The idea to use urban green areas as natural laboratories for ecological research was most insistently emphasized by ornithologists (e.g., Erz, 1966; Suhonen & Jokimäki, 1988; Il'ychev, 1990; Fernández-Juricic & Jokimäki, 2001). For example, in accordance with expectations, park area was shown to explain a high percentage of the variation in bird species richness (Luniak, 1983; Sasvári, 1984; Vizyová, 1986; Fernández-Juricic & Jokimäki, 2001; see also Gavareski, 1976; Tilghman, 1987; Friesen et al., 1995 for the parallel North American result) and to affect species turnover rate, with larger parks favoring species persistence (Fernández-Juricic & Jokimäki, 2001). However, a limited number of studies (e.g., Dyrcz, 1969; Tomiałojć & Profus, 1977; Tomiałojć, 1979, 1982, 1998, 1999; Jokimäki, 1999; Grégoire et al., 2002; Sorace, 2002) were conducted in urban green areas in which an attempt was made to connect population characteristics and adaptive potentials in separate species with interspecific interactions or bird assemblage organization. Among them, few works (e.g., Tomiałojć, 1998, 1999) were focused on the long-term processes and patterns (see Marzluff et al., 2001b).

In Russia, an interest in the processes of avifauna shaping in urban and urbanizing areas dawned in the late XIX and the first half of the XX centuries (e.g., Kaigorodov, 1898; Sheremet'ev, 1902; Bianki, 1907; Promptov, 1932; Belyaev, 1937, 1938; Formozov, 1947; Mal'chevskiy, 1950). Some natural areas located inside or in the outskirts of St-Petersburg (see Khrabryi, 1991 for a review) and Moscow (see below) were surveyed several times at sporadic intervals during many decades. However, most ornithologists avoided urban landscapes as sites for conducting regular and detailed field research. That is why short-term (1-3-year long) faunistic inventories and counts, sporadic observations, and nest-box supplementation projects sharply prevailed numerically over long-term ecological studies. The exceptions were few. Among them, long-term research of population dynamics of waterfowl in Moscow is especially meaningful (Avilova & Eremkin, 2001; Avilova et al., 2003). There is a need for detailed descriptive and experimental studies to test ecological hypotheses including some interesting but unproved theories of urban population establishment (Friedman et al., 2008) and shaping multi-species assemblages (Vakhrushev & Rautian, 1993) outlined mostly on the basis of faunistical observations.

In this chapter, I emphasize the importance of studies in urban "green areas" for elaborating some basic problems of community and population ecology. Attention is focused on the fundamental question of relationships between species richness and abundance. This paper is an attempt at an analysis of the woodland birds of Moscow City in the context of species impoverishment, ecological release and density compensation. Most examples come from my study conducted in large forest islands of the city, especially in the Main Botanical Garden of the Russian Academy of Sciences in Ostankino. The aim is to stress the issue and outline ways of reasoning rather than to give definitive answers. For this reason, field methods are described briefly. The details will be published elsewhere.

DENSITY COMPENSATION

The terms "density compensation" and "excess density compensation" were used by MacArthur et al. (1972) to indicate the patterns in which island populations have unexpectedly high densities (compared to similar mainland habitats) in the absence of some presumed competitors. It was recognized that the density increase in a species may occur without any change of the realized niche or arise from niche expansion. Although density compensation was believed to be mostly the result of competitive release, it was realized that the phenomenon may be caused also by other species interactions, e.g., decrease in predation or parasite pressures in insular conditions (see MacArthur & Wilson, 1967; MacArthur et al., 1972; Abbott, 1980; Faeth, 1984; Wiens, 1989b). Moreover, as noted by Abbott (1980), releases from interspecific competition and from predation were not distinctly distinguished in the literature for a long time.

Although initially this idea was applied to oceanic islands (Crowell, 1962; MacArthur et al., 1972; Abbott, 1980; Wright, 1980; Chernov, 1982), it is reasonable to expect that species impoverishment in non-insular conditions, e.g., caused by anthropogenic fragmentation of natural habitats, may also result in density compensation effects. For example, Tomiałojć (2000, p. 13) noted that the community-composition pattern of the type "fewer species but higher abundance of the remaining ones" was common among plant and animal assemblages which underwent synanthropization. More broadly, density compensation may be defined as an inverse relation between population density and species richness (McGrady-Steed & Morin, 2000). This theme overlaps with one of the basic biocenotic principles proposed by Thienemann (1939).

The interest to the niche shift and density compensation effects decreased to some extent in the 1980s, resulting from the disappointment in "competitive paradigm" and the belief that assemblages of taxonomically related species are integrated ecological entities (see James & Boecklen, 1984; Wiens, 1989a, b; McIntosh, 1995). Evidence of compensatory mechanisms was argued to be inconclusive (Abbott, 1980; Wright, 1980; Faeth, 1984; Wiens, 1989b). Actually, in many studies environmental conditions, habitat characteristics, and resource levels on the islands and the mainland were not closely similar. Usually, the degree of the similarity was not measured or estimated in acceptable ways. Moreover, considerable differences in resource availabilities have been found in some studies (Abbott, 1980). In most cases, higher population densities in insular conditions could be plausibly "explained" by mechanisms other than ecological release. Wiens (1989b) even used the phenomena of niche shifts and density compensation in oceanic islands as an example to illustrate difficulties of framing and testing process hypotheses in community ecology.

It may be said that lately an interest in the phenomenon has come back. Density compensation effects or their absence were mentioned in many studies. An increase in the number of vertebrate taxa for which a possible role of density compensation effects was discussed is symptomatic. The set initially composed mostly of lizards, birds, and small mammals (see Faeth, 1984) was enriched by fish (Fausch et al., 1994; Oberdorff et al., 1998), several groups of amphibians and reptiles (Hecnar & M'Closkey, 1997; Rodda & Dean-Bradley, 2002), birds of prey (Thiollay, 1998), bats (Stevens & Willig, 2000), and primates (Lawes & Eeley, 2000; Peres & Dolman, 2000; Gonzalez-Solis et al., 2001). Recently, this concept was emphasized in the context of a broader discussion about presumed compensatory mechanisms operating in ecological communities and biotas (Chernov, 2005). However, most arguments in favor of importance of density compensation in shaping bird assemblages remain unconvincing because of the lack of detailed field studies, especially manipulative experiments.

BIRD SPECIES RICHNESS AND POPULATION DENSITIES IN URBAN GREEN ISLANDS: THE LINE OF REASONING

It was noted by many authors that landscapes and habitats strongly modified or stressed by human activity, at least in the temperate zone, often have impoverished avifaunas compared to the natural ones in the same regions because of the local extinction of many native species (e.g., Gladkov & Rustamov, 1975; Bezzel, 1985; Friesen et al., 1995; Tomiałojć, 2000; Luniak, 2004; Adams et al., 2005). This generalization comes mostly from research conducted in initially forested landscapes for which anthropogenic pressures including urbanization often means habitat loss, fragmentation, and simplification of habitat structure (Miller et al., 2001). Tomiałojć and Wesołowski (Tomiałojć, 2000; Tomiałojć & Wesołowski, 2004) concluded that breeding bird assemblages in fragmented Western European woods are not only less species-rich because of the loss of large-size and shy species but are also composed of a higher proportion of species which have developed dense or very dense breeding populations than larger and less disturbed woodland tracts in Western and, especially, Eastern Europe (see also Tomiałojć et al., 1984; Tomiałojć & Wesołowski, 1990). The proposed east-west gradient in the breeding species richness of the woodland avifauna seems to result predominantly from differences in the intensity of human impact between the two parts of Europe.

Urbanization is one of the extreme forms of anthropogenic transformation and destruction of natural landscapes. Replacement of suburban habitats containing considerable proportions of green areas by densely built-up settlements usually results in a dramatic or substantial decline in breeding bird species richness, considerable changes in their composition, and high densities and strong numerical preponderance of few species well adapted to urban environment. For the present, in most urbanizing areas studied, breeding species enrichment due to synurbization (an adjustment of wild populations to specific conditions of the urban environment), reintroduction, and introduction was lower than breeding species impoverishment (Bezzel, 1985; Marzluff, 2001; Luniak, 2004; Adams et al., 2005; Chace & Walsh, 2006 and references therein). For green islands embedded in an urban matrix, it is also reasonable to expect some local species loss resulting in density compensation effects due to ecological release.

There are a number of indications that, in Europe, many urban woodland parks have much higher breeding densities of some bird species compared to countryside woods of comparable type and age (Tomiałojć, 1976, 1998, 1999; Tomiałojć & Profus, 1977; Luniak & Muslow, 1988). As a result, separate guild and total bird densities in the urban habitats are often much higher (Tomiałojć & Profus, 1977; Tomiałojć, 1998). Similar patterns were revealed in a study of open-land green areas (Sorace, 2002). As to feeding spectra, types of nesting, and migratory habits, urbanization tends to select for omnivorous and granivorous, cavity nesting, and resident (or partially resident) species, respectively (Tomiałojć & Profus, 1977; Bezzel, 1985; Konstantinov, 1996; Chace & Walsh, 2006). It does not imply, however, that abundances of separate species belonging to these groups (e.g., cavity-nesters), their combined densities, and/or species richness do not suffer considerable losses in urbanizing areas (see Marzluff, 2001).

The main question in the "density compensation context" is the following: Are unexpectedly high breeding bird densities in some urban green areas, especially woodlands, the result of (1) release from "negative" species interactions (competition, predation, nest parasitism, parasitism) due to species impoverishment or decrease in their intensity, (2) release from persecution by man (which often seems to be more typical of rural areas, especially for waterfowl and diurnal raptors), (3) higher resource (especially food) abundances or/and availabilities in urban compared to natural landscapes, (4) favorable abiotic (e.g., climatic) conditions in urban landscapes, (5) restricted dispersal of juvenile and/or adult individuals (higher levels of natal philopatry and/or site fidelity compared to more extensive and less encapsulated woodlands) due to the "fence effect" created by sharp habitat boundaries between green islands and built-up matrix, or (6) combined effects of the factors mentioned? Theoretically, the hopes to find indications of interspecific competitive release in woodland and woodland-edge birds inhabiting urban parks and forests seem to be good.

MOSCOW CITY AND ITS FOREST ISLANDS

The city of Moscow, currently occupying an area of about 880 km^2 inside the Moscow Circular Highway (MCH) and about 200 km^2 outside the MCH (as 7 "peninsulas"), contains many "green islands" of different sizes, origins, and combination of habitat types. The city has expanded mostly in a concentric pattern, and its growth has been especially rapid during the past 100 years. Since 1912 and 1960, Moscow increased in area by ca. 6 and 3 times, respectively (see Isakov & Kazanskaya, 1978), excluding numerous "satellite" towns and urbanizing territories. In this paper, the terms "urban" and "suburban" in reference to a green area are used to denote its location (mostly inside or mostly outside the city, respectively) and the types of surrounding landscapes rather than to reflect its position along the gradient of urbanization (e.g. as Marzluff et al., 2001b proposed) based on the percent area built, building density, and human density.

Within MCH, woodlands currently cover more than 100 km^2 (Samoilov & Morozova, 1998a). Among them, there are 14 especially large ones ranging from 1.4 to ca. 33 km^2 in size (see Fig. 1). The latter area is part of the National Park "Losinyi Ostrov" jutting into the peripheral and middle circular zones of the city. In fact, it is an extensive suburban forest (separated from the "countryside" part of the national park by MCH) located within the official city boundaries. Hereafter, it is not considered "urban woodland". Some other large woodlands of the city (Bitsevskiy Forest Park, Serebryanoborskoe Lesnichestvo) also still adjoin suburban green areas being separated from them by MCH. However, at a slightly larger scale, such peripheral forests are part of more extensive green islands (e.g., the whole territory of the National Park "Losinyi Ostrov") completely or mostly surrounded by urban or urbanizing areas.

Until the mid-XIX to early XX centuries, many of the lands currently covered by urban woods were country-seat parks (some of which modified several times in style) and/or hunting grounds belonging to rulers or rich families. During the XIX century, an increasing number of them became partly accessible for public recreation (Polyakova & Gutnikov, 2000; Chernyavskaya et al., 2004). Nationalized in 1917 and then managed (or continued to be managed) as areas of recreational, historic, and some (e.g., the Main Botanical Garden of the Russian Academy of Sciences and the Experimental Forest of the K.A. Timiryazev Agricultural Academy) also of scientific values, they were gradually surrounded with the expanding city during the XX century. The history of their vegetation over the past nine decades was the combination of "natural" forest succession and anthropogenic pressure, including forest management. Human impact varied considerably depending on time, woodland island, and patch within the woodland island.

Currently, mature and old-growth birch- (*Betula pendula, B. pubescens*), pine- (*Pinus silvestris*), lime- (*Tilia cordata*), and oak-dominated (*Quercus robur*) stands prevail in urban woodlands (Rysin, 1998; Samoilov & Morozova, 1998b; see also Polyakova & Gutnikov, 2000; Nosova, 2001) (Figs 2-14). Most old-growth pine-dominated stands have a substantial admixture of deciduous species (mainly *T. cordata*, *Acer platanoides*, *Q. robur*, and *Betula*) in the lower tree sublayer (Fig. 10) and seem to transform gradually into deciduous forests in the process of succession (Rysin, 1998). The patches dominated by aspen (*Populus tremula*) occur in several large woodlands, but their total area is insignificant. However, this species is a common component of mixed stands dominated by other trees. In many large forest islands, there are narrow strips and small patches of swampy common alder (*Alnus glutinosa*) stands situated along the streams. In contrast, spruce-dominated (*Picea abies*) patches occur in few sites (Fig. 13).

The presence and abundance of non-native tree and shrub species vary considerably between woodland islands and their different parts. In the interior parts of many woodland islands, such species are absent or very sparse. At the same time, separate shrub species, both native (e.g., *Corylus avellana*) and alien (e.g., *Swida sanguinea*, *Amelanchier* spp.), reach unusually high abundances and heights in some of the woodlands. There are some patches with unusual combinations of plant species forming different layers, e.g., mature larch (*Larix* spp.) plantations with the luxuriant understory composed of *Tilia cordata*, *Corylus avellana*, and other deciduous trees and shrubs (Fig. 3).

Many interior parts of mature and old-growth forests have multi-layer vegetation, well-developed understory, insignificantly or moderately disturbed herb cover, some amount of dead timber (as dead standing and fallen trees), substantial or high densi-

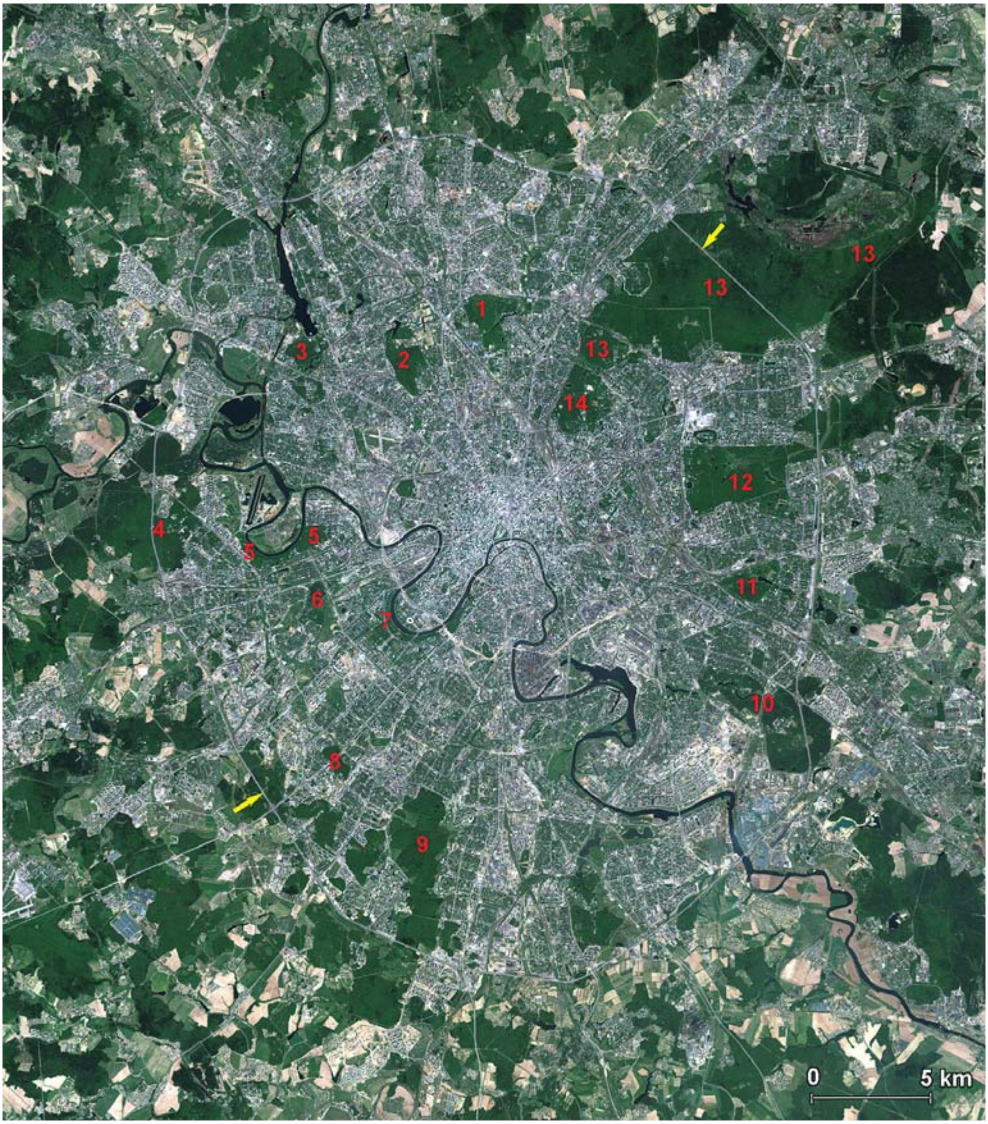

Fig. 1. Landsat-7 image of Moscow City taken in May 2001. Arrows indicate the Moscow Circular Highway. Numbers indicate the woodlands mentioned in Table, text, or list of references: 1 – Natural and Historic Park "Ostankino" (hereafter NHPO), 2 – Experimental Forest of the K.A. Timiryazev Agricultural Academy, 3 – Pokrovskoe-Glebovo-Streshnevo Forest Park, 4 – Serebryanoborskoe Lesnichestvo, 5 – Fili-Kuntsevskiy Forest Park, 6 – Volynskiy Forest, 7 – Vorobyovy Gory, 8 – Yugo-Zapadniy Forest Park, 9 – Bitsevskiy Forest Park, 10 – Kuz'minskiy Forest Park, 11 – Kuskovskiy Forest Park, 12 – Izmailovskiy Forest, 13 – National Park "Losinyi Ostrov", 14 – Park "Sokol'niki".

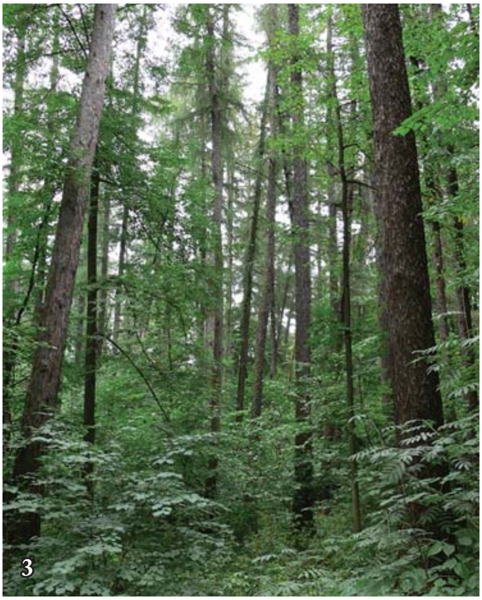

Fig. 2. Lime-pine stand in the interior part of the Experimental Forest of the K.A. Timiryazev Agricultural Academy, 24 July 2007.
Fig. 3. Larch stand in the interior part of the Experimental Forest of the K.A. Timiryazev Agricultural Academy, 24 July 2007.

ties of natural cavities in trees, and no or few nest-boxes. However, within most habitat patches of urban woodlands, the tree layer or each distinguishable upper tree sublayer is more or less evenly aged. The herb layer is usually dominated by species typical of non-urban stands of the same types, e.g., in most mesic broadleaved forests by *Carex pilosa, Ranunculus cassubicus, Galeobdolon luteum, Aegopodium podagraria, Anemone ranunculoides, Stellaria holostea,* and *Equisetum pratense*. Even though they are visited by pedestrians, some sites currently look like they would be developed in protected natural areas. They provide good (including some unique) opportunities to study, e.g., nest-site selection and related aspects of breeding ecology in cavity- and open-nesting forest birds.

At the same time, the Moscow woodlands differ in their structure and age from those located in the city surroundings. Some of the most interesting urban deciduous forests have no direct counterparts in the countryside. Many tree stands situated in the outskirts of the city are younger and/or, in some respects, more shaped by past and present forest management than the urban ones. This pattern creates difficulties for comparing bird abundances among urban, suburban, and countryside woodlands, because any differences found may be attributed to differences in habitat structure rather than to the urban–countryside gradient itself.

Some characteristics of eight large forest islands in which the author conducted any bird censuses are given in Table 1. Most of the field work was carried out in an area of the Natural and Historic Park "Ostankino" (NHPO) covering the territories of the

Table 1. Some characteristics of eight large wood islands (with mature and old-growth tree stands) in which any bird censuses were conducted during this study

Woodland (No)	Wooded area (km^2)	D (km)	P	Most abundant species in the upper tree layer	Prevailing types of tree stands
Natural and Historic Park "Ostankino" (1)	2.8	1.2	6.0	*Quercus robur, Betula* spp., *Pinus silvestris*	Mostly oak- and birch-dominated; also pine, mixed coniferous-deciduous (birch, pine, oak, lime) and grey alder stands
Experimental Forest and adjacent wooded patches of the K.A. Timiryazev Agricultural Academy (2)	2.8	1.1	3.7	*P. silvestris, Betula* spp., *Q. robur, Tilia cordata, Larix* spp.	Mostly pine-, oak-, birch-dominated and different mixed stands; also larch stands
Fili-Kuntsevskiy Forest Park (5)	2.2	0.9	7.2	*T. cordata, Q. robur, P. silvestris, Betula* spp., *Ulmus* spp.	Mostly lime-dominated, also mixed (lime, pine, birch, oak in several combinations); also oak- and birch-dominated stands
Kuskovskiy Forest Park (11)	1.5	0.9	2.2	*Betula* spp., *Q. robur, T. cordata*	Birch-dominated; also oak-dominated and mixed deciduous (oak, birch, lime in different combinations) stands
Pokrovskoe-Glebovo-Streshnevo Forest Park (3)	1.4	0.9	3.7	*P. silvestris, Betula* spp., *T. cordata, Acer platanoides, Q. robur, Alnus glutinosa*	Mostly mixed (pine, lime, Norway maple, birch), pine-, birch-dominated and common alder stands
Vorobyovy (Leninskie) Gory including the Botanical Garden of the Moscow State University (7); without Neskuchnyi Sad	1.0	0.35	21.4	*T. cordata, Q. robur, Betula* spp., *Populus balsamifera(?), A. platanoides, Salix fragilis, Ulmus* spp., *A. glutinosa*	Mixed deciduous, mostly lime-, birch- and oak-dominated stands
Volynskiy Forest including Matveevskiy Forest (6)	0.9	0.6	2.7	*Picea abies, Betula* spp., *P. silvestris, T. cordata, A. platanoides*	Spruce- and birch-dominated, mixed coniferous-deciduous (pine, spruce, birch) and deciduous (mostly lime and birch) stands; also crack willow and grey alder riparian stands
Yugo-Zapadniy Forest Park (8)	0.7	0.55	2.8	*Betula* spp., *P. silvestris*	Birch-dominated stands; also pine-dominated patches

No – woodland number in Figure 1; D – approximate diameter of the largest circle which can be completely placed inside the most extensive part of the woodland; P – ratio of the area of the circle having the perimeter equal to that of a given woodland to the actual area of this woodland (to reflect the relative proportion between edge length and woodland area). The woodland area, edge length and D were measured from satellite and aerial images.

Main Botanical Garden of the Russian Academy of Sciences, the adjacent valley of the Jauza River, Park "Ostankino", Estate Regular Garden "Ostankino" with Sheremetev's Palace, and the north-western sparsely built-up part of the Russian Exhibition Centre. It is one of the largest (ca. 4.6 km^2) and best surveyed by ornithologists "green islands" in the northern part of Moscow City. Currently, its wooded parts cover 2.8 km^2, the total length of their edges is about 17 km. Mature and old-growth oak-dominated stands prevail (> 60% of the forested area). Their core part (located in the territory of the


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Fig. 4. Old-growth oak-dominated forest in the Main Botanical Garden of the Russian Academy of Sciences, NHPO, 5 May 2006.
Fig. 5. Old-growth oak-dominated forest in the Main Botanical Garden, NHPO, late April 2001.
Fig. 6. Old-growth oak-dominated forest in the Main Botanical Garden, NHPO, 30 May 2008.
Fig. 7. Fili-Kuntsevskiy Forest Park, lime-dominated stands on the right side (left on the photo) of the Moskva River, 10 August 2007.
Fig. 8. Old-growth lime stand in Fili-Kuntsevskiy Forest Park, 10 August 2007.
Fig. 9. Birch stand in Kuskovskiy Forest Park, 23 July 2007.
Fig. 10. Mixed pine-dominated stand in Pokrovskoe-Glebovo-Streshnevo Forest Park, 7 August 2007.
Fig. 11. Vorobyovy Gory, deciduous stands on the right side of the Moskva River, 1 August 2007.
Fig. 12. Lime-dominated stand in Vorobyovy Gory, 1 August 2007.
Fig. 13. Spruce stand with an admixture of birch in Volynskiy Forest, 22 July 2007.
Fig. 14. Birch stand in Yugo-Zapadnyi Forest Park, 12 July 2007.


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Main Botanical Garden), unmanaged during the past decades, is especially interesting (Figs 4-6). The upper canopy (tree heights up to 30 m, mostly 18-26 m) of the forest is composed of 80-300-year-old oaks with an admixture of birches, aspens, and limes. Several large spruces also occur. There are many standing, broken, and fallen dead trees. The lower canopy is composed of *Betula, Sorbus aucuparia, Populus tremula, Quercus robur, Salix caprea*, *Padus avium*, and *Acer platanoides*. The shrub layer consists of two sublayers. The upper one (cover up to 95%, height up to 12 m) is dominated by massive *Corylus avellana*. The lower sublayer is composed of *Lonicera xylosteum*, *Euonymus verrucosa* and saplings of *Sorbus aucuparia, Padus avium*, and *Acer platanoides*. The herb cover is like that in other mesic broadleaved forests (see above). The rest of the NHPO woodland is composed of old-growth and mature birch-, pine-, and lime-dominated and mixed stands, grey alder (*Alnus incana*) and willow (*Salix* spp.) belts along the river, small patches of planted spruces, firs, and larches. Other biotopes in NHPO are ponds, small rivers, plantations of cultured species, lawns, waste grounds with ruderal vegetation, and small built-up patches.

MATERIAL AND FIELD METHODS

All published information about birds inhabiting wooded areas of Moscow City was taken into account. Bird species composition of the NHPO was studied during the periods 1929-1935 (Krotov, 1941), 1949-1963 (e.g., Bel'skiy & Chmutova, 1951; Bel'skiy, 1954, 1965), and 1990-2008 (Morozov, 1996 and unpublished). Some observations were also conducted in 1975-1980 (Blagosklonov, 1977; Berezin, 1980), the autumn of 1987, and the winter 1987/1988. The history and complete bibliography until 1996 are given in Morozov (1996). Author's data and information from other sources (e.g., Groot Koerkamp, 2007) for the period 1997-2008 are added here. Because each of the three faunistic surveys lasted for 7 years or more, the probable effects of separate "unusual" years and stochastic fluctuations in the local presence/absence of rare species on their results are believed to be minimized. A number of other woodlands in the city were visited between 1999 and 2008 to perform observations.

Unfortunately, most density estimates for passerines and woodpeckers in Moscow available from the literature were obtained with different modifications of the line-transect method. The method provides the opportunity to cover extensive areas but produces indices rather than true or nearly true density estimates for most species and distort numerical proportions between species because of species-specific differences in census accuracy (see Tomiałojć, 1983; Hilden & Järvinen, 1989; Cherenkov, 1998). Intense nest searching, territory mapping, and other profound census methods were used in few studies and only in those focused on separate species or species groups (e.g., Grabovskiy, 1983; Voronetskiy & Leonov, 2003; Zakharov, 2003).

Most of my own data on breeding bird densities were collected in the interior, oak-dominated part of the NHPO woodland (see above and Figs 4-6). In this forest, a 30-ha study plot was established in which the census work and population studies of several model species were performed in the years 1992-1997 and 1999-2008. The shape of the plot was similar to a square. The plot included a 22-ha fenced area having the status of a protected oak forest in the territory of the Main Botanical Garden. Although the fence contained holes and was mostly symbolic rather than of real prohibitive significance, the fenced area and its surroundings were penetrated by people much less frequently than the rest of the woodland. It was not uncommon, even late in spring and in summer, to spend the whole day in the fenced area and to meet no or few pedestrians there. There were no nest-boxes in the plot and its vicinity at least during the past three decades. The breeding bird assemblage was censused by territory mapping in 1992-1994 and 1999-2001. Special attention was paid to collecting simultaneous records of singing birds (Tomiałojć, 1980).

The study plot was too large to census during one visit. For this reason, from mid-April, it was subdivided conventionally into 2-3 parts and covered by census work during two or (in few instances) three visits, usually on consecutive days, which together formed one "complete visit". The number of complete visits varied from 15 (1992, 1993) to ten (1994, 2000) and nine (2001). Some additional registrations made in passing during other field work (see below) are believed to compensate partly for the lower numbers of visits in 2000 and 2001. The complete visits had been distributed more or less evenly from early or mid-April to the end of June or early July. All but two complete visits were made in the morning. In May and early June, census work often started 0.5-1 h before local sunrise.

Before sunrise, the author moved quickly, trying to cover an area as large as possible to census *Turdus philomelos* (see Tomiałojć & Lontkowski, 1989) and *Erithacus rubecula*. Birds of other species were recorded casually. After sunrise, this area was censused again more accurately. For *Accipiter gentilis*, woodpeckers, *Corvus cornix, Pica pica*, and *Turdus pilaris*, a number of pairs were estimated mostly by nest searching. See Morozov (1994a, b) for more details. The numbers of "paper territories" delineated on species maps in the first census year (see Morozov, 1994a) were re-evaluated and substantially corrected (increased for most species) later on the basis of the improved knowledge about the bird assemblage.

Some model species were censused by species-specific methods within the whole plot or some part of it also in the years 1995-1997 and/or after 2001. For example, *T. philomelos* was censused in the plot also in the years 2002-2007. Yearly, two complete visits (the first between 31 May and 9 June, the second between 21 and 27 June) were made early in the morning before sunrise and/or in the evening, mostly at twilight, to map the singing males of this species. The results of both visits were supplemented with the information about nests to obtain a single maximum estimate of territorial males. This approach was comparable to that applied at the final step of interpreting *T. philomelos* maps in 1992-1994 and 1999-2001 when, in fact, few early-morning visits in semi-darkness giving maximum numbers of simultaneously singing males (unexpectedly, often those made in June) formed a basis for final estimates of the territory numbers. In any separate year, some *T. philomelos* nests were found as a result of searching focused on the species, whereas the others were performed during other field works. The first ones began to prevail in the annual samples since 2003. However, even in reference to the second category, I tried to distribute searching efforts more or less evenly across vegetation layers and substrates to decrease probable biases due to uneven detectability of nests placed in different sites.

In the 11.8-ha permanent part of the plot (hereafter called subplot), the actual number and distribution of territories of *Parus caeruleus* were studied by mapping the positions of individually marked birds and nest-searching in the years 1993-1996 and 1999-2004. For this purpose, from 27 (1992) to 65 (2003) individuals of this species were captured and color-ringed within the subplot in late March to early April in 1992-1995 and 1999-2004. A number of *Parus major* and *Sitta europaea* were also color-ringed in some of the years. Birds were captured by semi-automatic and automatic traps with a captive *P. caeruleus* individual as a lure. A playback of species' songs and sunflower seeds were also used to attract birds to the traps.

During April and early May, the subplot was regularly visited to map *P. caeruleus* individual territories, to reveal the composition of the breeding pairs, and to find as many nest holes of the species as possible. Few additional observations were made later in May. As an exception, for few of the years, one or few adults were additionally captured for ringing later, at the holes with fairly large nestlings. Territories were delineated mostly on the basis of extreme positions of singing or calling males. Locations of territories, their number, and their owners were determined precisely but not their sizes and configurations. Every year, some individuals of both sexes (mostly females) having territories in the subplot remained unmarked. In springs 1996 and 1997, no trapping work was conducted, and only those birds ringed in the previous years were individually recognizable. For more details of the work in 1992 and 1993, see Morozov (1994b). After the 2000 breeding season, a 4-year experiment on nest-hole exclusion was conducted in the subplot to determine whether *P. caeruleus* was limited by the availability of holes in the forest (see below).

Since 1999, less regularly in 1993-1996, the majority of active nests (i.e. those which were recorded during building or as containing nest contents) found in the 30-ha plot and its vicinity were monitored until either fledging of the young or any unsuccessful outcome. In *P. caeruleus* and *P. major*, any biases due to uneven detectability of holes of different origin and location are believed to be small or moderate, because the majority of holes were revealed through observing (following) adult birds visiting them. During 1999-2004, most of the (presumably) occupied holes found in April and early May at the egg-laying, nest-building or earlier stages were begun to be checked since 2-25 May that usually corresponded to incubation, hatching or nestling stages. Starting from this, the holes were checked every 3-5 days (sporadically, 1-2 or 6-7, rarely more days) from the ground for the presence or absence of any activity. Some checks lasted about one hour or even longer. If no activity was observed by a ground checking and no damages of hole were seen, a nest-hole was inspected directly (when possible) in the following days. Nest-holes were approached by using a ladder, spurs, and other equipment for climbing.

Small mirrors, a small lamp, and bendable wire were used to inspect the hole interior. In most cases, predation was ascertained indirectly on the basis of egg/nestling injuries, remains, or disappearance often combined with characteristic hole damages made by woodpeckers (Fig. 15). Several times, *Dendrocopos major* were directly observed robbing nest-holes. The majority of fledged nest-holes (accessible for a human observer) were also at least once inspected directly, usually at the stages of late incubation, feeding nestlings, or after fledging the young.

The active nests of thrushes *Turdus* spp. were usually checked every 1-5 days in 1999-2004 and every 4-7 days in 2005-2007 (sometimes at longer intervals in both periods and at shorter intervals in the second period). For no serious reason, especially in the first five years of this work, I avoided to disturb parent birds approaching close to the nests and especially to flush them (especially laying eggs or incubating females) from the nests. When I checked the nest, at first, I tried to ascertain from a considerable distance (using binoculars) that it is active by looking at its condition, the presence of the parent bird (that is typical of *T. philomelos* even at the late nestling stage), and/or old nestlings (Fig. 16). If such a check gave no reliable information, nest vicinities could be visited more than once during a day or the following day. The nests supposed to be inactive were approached and inspected directly. A mirror attached to the top end of long woody pole or telescopic plastic rod was used to inspect nest contents in highly located nests (up to 7-8 m) supposed to be inactive on the basis of ground checking.

Fig. 15. Damage in a woodpecker-made (Lesser Spotted Woodpecker *Dendrocopos minor*) hole occupied by Blue Tits *Parus caeruleus* for nesting in 2006, NHPO oak forest. The nest of tits was depredated between 31 May and 2 June, by Great Spotted Woodpecker *Dendrocopos major* which made its hole at about the nest level.

Because of the procedure mentioned above, clutch size and partial nestling loss were established for few nests in most years of the study. However, the precautionary measures were decided to be of prior importance to minimize the observer-induced risk of nest desertion by birds at early stages of nesting and especially the risk of nest predation by corvids watching the human observer or/and searching for nests with the help of alarm calls produced by parent birds. Even for *T. philomelos*, the most numerous thrush, the number of active nests found in any separate year (from 7-12 in 1999-2002 to 22-37 in 2003-2007) was too low to calculate the nesting success by the Mayfield method. Fortunately, it was possible to use almost all completely built nests of this species (with the cup made of rotten wood) and some nests of other thrushes found either after nesting failure or successful fledging to estimate nesting success.

The nests of *T. philomelos*, even strongly damaged and thrown down by predators, were preserved sufficiently well during at least the nearest weeks and usually told the story about the outcome of the breeding attempt. The signs used to estimate the outcome of the nesting attempt were nest damages (often made by some corvids, e.g., *Corvus cornix*, see Fig. 17), egg shells and remains of interior contents, nestling remains, traces

16

17

Fig. 16. Incubating Song Thrush *Turdus philomelos* well-seen from a long distance, NHPO oak forest, 11 May 2007.

Fig. 17. Destroyed nest of Song Thrush in the NHPO oak forest, 7 May 2004. The nest was built up during the first days of May and depredated in the immediately following days. The manner of depredation is typical of several corvid species but, in this area, Hooded Crow *Corvus cornix* is the most probable robber. Many nests of thrushes depredated in such a manner were found in spring but few in summer (see text for detail).

of blood, plumes and other remains of the parent bird attacked by predator, the presence and abundance of scales after nestlings in the cup, how much the cup (made of rotten wood) rubbed out, nestling droppings and their distribution in the cup, in and outside the nest, and so forth (Fig. 18). To evaluate seasonal change in nesting success, breeding attempts were subdivided into those where the nest was completely built before 1 June, and after this date, according to calculations based on the following assumptions: median clutch size (when unknown), (4)–5 eggs; egg-laying periodicity, 1 egg per day; both incubation and nestling stages (when unknown precisely), 12 days. For some nests found in summer, classification into any of the two groups could not be estimated. Both for open- and hole-nesting species, nesting attempt was considered to be successful if at least one young bird fledged. The other details of collecting data on nest-site characteristics and nesting success will be published elsewhere.

As a by-product of intensive work on few model species, it was possible to estimate accurately the number of territories or active nests for several more species (e.g., *Dendrocopos* spp., *Phylloscopus sibilatrix, Sitta europaea*) in some of the years when the whole breeding bird assemblage was not censused (mostly after 2001).

Also, the model and some other species were censused with species-specific modifications of the line-transect method outside the 30-ha plot in NHPO and/or in several other Moscow woodlands in the years 1999-2005. For example, in 2004 *T. philomelos* and

Fig. 18. A successful nest of Song Thrush a few days after fledging, NHPO oak forest, 30 May 2007.

T. merula were censused in 7 other large wood islands of the city mentioned in Table. In each of the woodlands, the permanent transect(s) of unfixed width and from 2.4 to 8.1 km in length (depending on woodland configuration and area) crossing its interior part was censused (at an average speed of 3-4 km/h, using a bicycle) twice between 3 June and 1 July, mostly in the early morning before sunrise and in the evening, mostly at twilight. Approximate mapping of singing birds permitted to combine the results of 2 censuses to obtain a single, maximum estimate for a given transect. This approach was similar to that applied for *T. philomelos* in the NHPO plot (see above). It is believed to provide close-to-true estimates for this species.

In 2000-2004, tits and some other species were censused along permanent transects of unfixed width established outside the 30-ha plot in NHPO oak-dominated woodland (3 transects, in sum 3.3-km long) as well as in deciduous stands of Vorobyovy Gory (3.2-km long) and Fili-Kuntsevskiy Forest Park (3.9-km long). Each transect was censused in the morning (2)–3 times during the breeding season, viz. in the second half of April, early May, and late May–early June. The results of these censuses were needed, apart from estimating densities itself, as a control for the experiment on nest-hole exclusion in the NHPO subplot.

LONG-TERM CHANGES IN THE COMPOSITION OF BREEDING BIRD SPECIES IN A LARGE WOODLAND PARK IN THE PROCESS OF CITY EXPANSION: SPECIES IMPOVERISHMENT OR ENRICHMENT?

In an attempt to answer this question, I examined long-term changes in bird species composition in the NHPO area between the periods 1929-1935, 1949-1963, and 1990-2008. The results are summarized focusing an attention on woodland and woodland-edge species.

During the first two surveys, NHPO was a suburban area (mostly occupied by deciduous and mixed forests bordering with a rural landscape) outside the built-up part of the city. By the late 1980s, it was already located deeply inside the built-up area and "isolated" from other urban green islands. Currently, the distances to the centre and to the nearest official boundary of the city are 7.5 and 5.8 km, respectively. Thus, formally, NHPO is located in the middle circular zone of Moscow. However, the shortest distance to the extensive forested area of the National Park "Losinyi Ostrov" jutting deeply into the city is 2.2 km (Fig. 1).

Among negative factors emerged in woodland birdlife between the second and third surveys, the establishment of urban population of *Corvus cornix*, a major nest predator, must be specially noted. Over more than the past three decades, Moscow City has supported huge and dense population of this species established in the 1960s and early 1970s (Blagosklonov, 1981; Konstantinov et al., 1982; Grabovskiy, 1983; Konstantinov & Zakharov, 2005). In some built-up areas mostly composed of well-spaced blocks of flats separated by woody vegetation, nesting densities of *C. cornix* reached 6 pairs/10 ha, locally up to 8-10 pairs/10 ha (Panfilova, 2007; author's data). The nesting density in the inner parts of large forest islands in the past 15 years was not so high (less than 1.0-1.5 pairs/10 ha), but nest predation pressure of this species in the second half of spring seemed to be heavy there (as everywhere in the city) because of the presence of a high number of non-breeding individuals (Morozov, 2004 and unpublished).

Altogether, 134 bird species have been recorded in NHPO (except those seen or heard only in flight above vegetation) over the past 80 years. During the periods 1929-1935, 1949-1963, and 1987-1997, the total number of bird species observed in NHPO was 78, 78, and 100, respectively. The total number of species found during at least one of the two "suburban" periods (plus one more species recorded in the 1940s) and the whole currently lasting "urban" stage (1987-2008) having a similar duration was 93 and 114, respectively. Even in long-term studies, however, the total number of species recorded (including rare visitors) all the year round or during non-breeding periods strongly depends of the observer's efforts and chance. The number of breeding species is a more "reliable" measure in this respect.

Similarly, 93 species bred or presumed to breed in NHPO over the past 80 years. During the periods 1929-1935 and 1949-1963, the total number of significantly or presumably breeding species was 47 and 50, respectively. The 1990-1997 survey revealed 61 species corresponding to the criteria (according to Hagemeijer & Blair, 1997) of "confirmed" or "probable" breeding; eleven more species were "possible" breeders. The total number of species breeding significantly or presumably during at least one of the two suburban periods was 59-60. During the period 1990-2008, the number of species corresponding to the criteria of "confirmed" or "probable" breeding was 72; eight more species were "possible" breeders. Among woodland and woodland-edge pigeon, woodpecker and passerine species known to breed in the Moscow Region, at least once since the beginning of the XX century, only 14 (*Columba palumbus, Streptopelia turtur, Picus viridis, P. canus, Dryocopus martius, Dendrocopos medius, Picoides tridactylus, Ficedula albicollis, Turdus viscivorus, Parus ater, P. cyanus, Remiz pendulinus, Acanthis flammea, Emberiza rustica*) were never reported to stay in NHPO as breeders or presumable breeders.

Certainly, some species turnover has occurred between suburban and urban stages. Fifteen species were reported as breeders in at least one of the two periods during the suburban stage (1929-1935 and 1949-1963) but were not observed as breeders or probable breeders during the urban one (1990-2008): *Falco tinnunculus, Coturnix coturnix, Actitis hypoleucos, Columba oenas, Caprimulgus europaeus, Jynx torquilla, Lullula arborea, Alauda arvensis, Corvus monedula, Sylvia curruca, Regulus regulus, Saxicola rubetra, Parus montanus, P. cristatus, Emberiza citrinella*. Some of them (*Sylvia curruca, Regulus regulus, Saxicola rubetra, Emberiza citrinella*) continued to be recorded in some years of the past two decades as irregular "possible breeders" with extremely low numbers.

The following 28 species have been recorded for the first time as breeders or probable breeders during the "urban" stage: *Tadorna ferruginea, Anas platyrhynchos, Bucephala clangula, Accipiter gentilis, A. nisus, Falco subbuteo, Gallinula chloropus, Charadrius dubius,* *Tringa ochropus, Larus canus, Sterna hirundo, Columba livia, Dendrocopos leucotos, Hirundo rustica, Garrulus glandarius, Nucifraga caryocatactes, Corvus corax, Troglodytes troglodytes, Prunella modularis, Phylloscopus trochiloides, Ficedula parva, Luscinia svecica, Turdus merula, Fringilla montifringilla, Carduelis chloris, Pyrrhula pyrrhula, Coccothraustes coccothraustes, Emberiza schoeniclus*. Among them, at least 20 species became regular breeders (or probable breeders) by or during the period 1990-2008. Four species that can be classified as rare (irregular or single-year) breeders (*Larus canus, Prunella modularis*) or probable breeders (*Nucifraga caryocatactes, Fringilla montifringilla*) appeared in NHPO for the first time in the 2000s. The short-term "colonization" of NHPO by *Nucifraga caryocatactes* in the 2000s (including two breeding seasons) seems to be related to a numerical "splash" in this species in the Moscow Region that lasted several years.

Forty four and 51 woodland and woodland-edge species bred or presumably bred in NHPO at the suburban and urban stages, respectively. Thirty six, 38, and 45 species belonging to these categories were recorded during the periods 1929-1935, 1949-1963, and 1990-1997, respectively. Thus, some species enrichment occurred in woodland-related birds. Ten species disappeared as breeders and probable breeders, but 17 "colonized" the area between the suburban and urban stages. It must be emphasized that some of the species (e.g., *Garrulus glandarius, Prunella modularis, Turdus merula*) became numerous breeding birds of wood parks and other urban green areas in some parts of Western and Central Europe many decades ago (Cramp, 1988; Flade, 1994; Hagemeijer & Blair, 1997; Tomiałojć & Stawarczyk, 2003) but still remain to be "true" forest species in Central European Russia. At least five of the ten species lost were rare or innumerous breeders at the suburban stage. Moreover, among them, the disappearance of *Jynx torquilla, Lullula arborea*, and *Parus cristatus* from NHPO between suburban and urban stages seemed to be predetermined by large-scale population trends rather than by "local reactions" of these species to the city growth (Morozov, 1996). In addition, the almost complete disappearance of old spruces and forest management activity during the 1930-1940s (Bel'skiy & Chmutova, 1951) could negatively affect *Regulus regulus, Parus montanus*, and *P. cristatus*.

Nevertheless, forested parts of NHPO experienced less considerable "unfavorable" habitat changes between and during suburban and urban stages than the open biotopes did. On the contrary, ageing of tree stands, decrease of recreation and management pressures, and the accumulation of dead wood in the interior part of the forest, mostly in the territory of the Main Botanical Garden, seem to have made NHPO increasingly attractive for woodland birds during the past 5-6 decades. However, many NHPO "colonists", viz. *Accipiter gentilis, Falco subbuteo, Dendrocopos leucotos, Garrulus glandarius, Corvus corax, Troglodytes troglodytes, Phylloscopus trochiloides, Ficedula parva, Turdus merula, Carduelis chloris, Coccothraustes coccothraustes*, have remained, became, or are becoming more or less regular breeders also in other extensive forest islands throughout the city. It is noteworthy that this list contains species from different trophic groups, including insectivores as well as a number of open-nesters.

The group of species closely related to agricultural landscape including some woodland-edge ones suffered the most considerable losses in the process of city growth.

Coturnix coturnix, *Alauda arvensis*, *Saxicola rubetra*, reported to breed in one or both suburban periods disappeared probably because of habitat loss. Two woodland-edge species, *Falco tinnunculus* and *Emberiza citrinella*, for which fields and meadows are important foraging habitats also "deserted" the area. *Emberiza citrinella* was among the most common breeding species at the suburban stage, but then, the population of this species declined dramatically as in some other "green areas" in Moscow (e.g., Flint & Teikhman, 1976; Avilova & Eremkin, 2003) and St-Petersburg (Mal'chevskiy & Pukinskiy, 1983). Local population crash has been observed also in *Pica pica* (initially also associated with countryside landscapes), which was the common species in NHPO up to the early 1990s but currently is represented by few breeding pairs.

No waterfowl species were recorded to breed during the suburban periods. The appearance of six species (currently regular breeders except *Larus canus*) was conditioned by making a number of artificial ponds in NHPO in the mid-XX century. "Colonizing" the area by *Tadorna ferruginea*, *Anas platyrhynchos*, *Bucephala clangula* and *Gallinula chloropus* was a part of the establishment of their urban populations throughout the city in the second half of the XX century (Avilova & Eremkin, 2001; Avilova et al., 2001, 2003). In NHPO, *Bucephala clangula* nests both in nest-boxes and natural tree cavities thus being also partly related with mature stands.

Two more forest islands of considerable size having compact configurations viz. the Experimental Forest of the K.A. Timiryazev Agricultural Academy with the adjacent woods (see Table) (Moravov & Smolin, 1960; Avilova & Eremkin, 2003; Avilova et al., 2007 and references therein) and Izmailovskiy Forest (> 10 km^2 in size) (Promptov, 1932; Flint & Krivosheev, 1962; Flint & Teikhman, 1976) were covered by several short-term (1-3 years) surveys at the suburban and urban stages. To summarize, the results of these surveys are not in conflict with those of the NHPO study. However, in the Experimental Forest the present-day number of breeding and presumably breeding species seems to be lower than that in the early XX century (55 vs. 63 species recorded including some large-size or/and shy ones) but higher than in 1958 (41). In some publications, a tendency (not found in NHPO, see above) to species impoverishment in the mid-XX century was specially noted (Flint & Teikhman, 1976; Avilova & Eremkin, 2003; Avilova et al., 2007). It is a reasonable suggestion that species impoverishment (including components not related to habitat disturbance and loss) which actually occurred in some extensive woodland areas during the transitional period between suburban and urban stages, later gave way to species enrichment (which included returning some species as breeders) resulting from synurbization processes (e.g., Konstantinov et al., 1990; Voronetskiy, 2000; Avilova et al., 2007; Friedman et al., 2008). The alternative is that the differences in the number of breeding species recorded could be an artifact related to short durations of separate surveys.

It may be tentatively concluded on the basis of the Moscow example that surrounding extensive (> 2.5-3 km^2) forest islands having more or less compact shapes with an expanding city by itself does not inevitably result in impoverishment of their avifaunas or decrease in the number of woodland species, at least at the temporal scale of 5-10 decades. Heavy recreation pressure throughout a forest island (especially if it has a configuration of a narrow strip) and habitat destruction and loss seem to be more important causes of species "extinctions" (e.g., Belyaev, 1937, 1938; Ptushenko, 1976; Il'ychev, 1990; Konstantinov et al., 1990; Khrabryi, 1991). It must be emphasized that the conclusion implies the "late suburban stage" as the starting point of observations and thus does not take into account large-size and shy birds, e.g., some raptor, owl, and forest tetraonid species, highly sensitive to urbanization and usually disappearing even from more distant vicinities of cities and urban agglomerations.

BIRD SPECIES COMPOSITION AND DENSITIES IN LARGE URBAN WOODLANDS

The information over the period 1992-2008 can be summarized as follows. The breeding bird assemblages in the interior, less disturbed parts of large woodlands with no or few nest-boxes were usually dominated by some of the following three species: *Fringilla coelebs, Parus major*, and *P. caeruleus*. In some of the sites, their individual species' densities regularly and substantially exceeded 10 pairs (territorial males)/10 ha. Both *Parus* species were numerous mostly in old-growth oak- and lime-dominated stands having high numbers of natural holes in the trees. In most years and woodlands, *P. major* dominated numerically over *P. caeruleus*, often by more than 1.5 times. This pattern was typical also of the built-up matrix of the city as well as of suburban and countryside areas.

In the interior part of NHPO and, seemingly, few other large woodlands, *Erithacus rubecula, Turdus philomelos*, and in few years, possibly *Ficedula hypoleuca* and *Phylloscopus sibilatrix* densities also achieved or slightly exceeded the level mentioned above. For the latter two species, however, the values between 5 and 10 pairs/10 ha in preferred habitats seemed to be more typical even in "peak" years. Obtaining accurate density estimates for *Ficedula hypoleuca* by standard mapping method was strongly complicated because of considerable numbers of presumably bachelor males occupying temporary territories for short periods. In *Phylloscopus sibilatrix*, local densities fluctuated drastically from year to year (in the 30-ha plot in NHPO oak-dominated forest, the number of territories in the years 1992-1994 and 1999-2004 varied from no in 2003 to 26 in 1994; the maximum year-to-year change was from three territories in 1993 to 26 in 1994) that was found in this species in some non-urbanized areas as well (e.g., Wesołowski & Tomiałojć, 1997). In some woodland habitats, also *Sylvia atricapilla* regularly or at least in few years reached a density in the range of 5-10 pairs (territorial males)/10 ha. It must also be noted that, regularly in the second half of spring, *Corvus cornix* was very numerous in most large woodland islands, including their interior parts, but mainly as a result of the influx of non-breeding flocking individuals searching for food.

In those woodland edges or interior open woods (especially provided with nest-boxes and bordering with the open green areas) which have high numbers of natural holes in trees, *Passer montanus* and *Sturnus vulgaris* usually have added as dominants.

Nest-boxes with small entrance hole diameters supplied sporadically (mainly in the last 7-8 years after the long-term break in such activity) and usually placed in a line pattern along some parkland roads were occupied mostly by *Passer montanus* and *Ficedula hypoleuca*. Also, *Corvus cornix* and *Turdus pilaris* were locally numerous breeders in some semi-open, mainly peripheral, woodland sites. *Passer domesticus* was observed in a considerable number only in a very narrow peripheral belt in those woodland edges which border closely human constructions and contain artificial food sources. This species bred at high densities in much smaller and heavily recreated wooded parks and cemeteries, including those situated in the central part of the city.

Also, the following woodland and woodland-edge species were regularly or periodically recorded during the breeding season in many large forest islands: *Accipiter gentilis, Falco subbuteo, Strix aluco, Asio otus, Dendrocopos major, D. leucotos, D. minor, Anthus trivialis, Oriolus oriolus, Garrulus glandarius, Corvus corax, Troglodytes troglodytes, Hippolais icterina, Sylvia borin, Phylloscopus trochilus, Ph. collybita, Ph. trochiloides, Muscicapa striata, Ficedula parva, Phoenicurus phoenicurus, Luscinia luscinia, Turdus iliacus, Aegithalos caudatus, Sitta europaea, Certhia familiaris, Chloris chloris, Carduelis spinus, C. carduelis, Carpodacus erythrinus, Pyrrhula pyrrhula,* and *Coccothraustes coccothraustes*. Only few of them, e.g. *Phylloscopus trochilus*, were known to achieve locally the densities of 3-5 territorial males/10 ha in some years. Some more species belonging or partially belonging to the same habitat groups occurred, in low densities and some very irregularly, in few or single large woodlands: *Accipiter nisus, Falco tinnunculus* (currently most pairs in the city nest outside woodlands and woodland edges), *Tringa ochropus, Columba oenas, Cuculus canorus, Dryocopus martius, Jynx torquilla, Picoides tridactylus, Nucifraga caryocatactes, Corvus frugilegus* (currently almost disappeared from the city as a breeder), *C. monedula* (most pairs nest in human constructions outside woodlands and woodland edges), *Prunella modularis, Sylvia curruca, Regulus regulus, Parus montanus, P. ater, Loxia curvirostra*. Currently, *Dendrocopos medius* and *Ficedula albicollis* are trying to "colonize" Moscow woodlands, seemingly as a result of range expansion.

Yearly, the number of species breeding (viz. having at least half a breeding territory) within the 30-ha plot in the NHPO oak-dominated forest varied from 23 to 30 in the periods 1992-1994 and 1999-2001. Among them, 16 species have occurred annually. In total, 43 species were recorded to occupy permanent territories in the breeding season within the plot between 1992 and 2008. No data obtained by the same method in non-urban broadleaved woods are available from the surroundings of the city for comparison. The plots established in broadleaved but compositionally and structurally differing forests located in protected natural areas in distant parts of Europe seem to be richer in breeding bird species (e.g., Tomiałojć et al., 1984; Tomiałojć & Wesołowski, 1996; Kosenko, 2007). For example, yearly, from 24 to 30 breeding species, 18 of them as annual breeders, were recorded within a substantially smaller (14.4-ha) plot in an oak-dominated forest with an admixture of birch, spruce, and pine in the Bryansk Region ca. 440 km to the south-west of Moscow in 1993-1995 and 2004-2006 (Kosenko, 2007). However, the differences in species richness resulted mostly from the absence in the NHPO plot (1) of three “western” species (*Dendrocopos medius, Ficedula albicollis, Parus palustris*) still remaining to be very rare in the Moscow Region (Ptushenko & Inozemtsev, 1968; Kalyakin & Voltzit, 2006), (2) of several species which need a considerable admixture of conifers in tree stands (*Picoides tridactylus, Regulus regulus, Parus ater, P. cristatus, Pyrrhula pyrrhula*), and (3) of a number of low-density non-passerine and non-woodpecker species.

It may be stated that, in some broadleaved woods of Moscow, total bird densities in the breeding season are currently higher compared to those obtained by territory mapping in non-urban extensive woods of comparable types elsewhere in temperate forest zone of Europe (usually less than 90-100 pairs/10 ha, see Tomiałojć et al., 1984; Tomiałojć & Wesołowski, 1990; Flade, 1994; Tomiałojć, 1998, 2000; Kosenko, 2007). In old-growth and mature oak woods of NHPO, as well as in old-growth lime stands covering the riverside slopes in Vorobyovy Gory and Fili-Kuntsevskiy Forest Park, the total densities exceeded 110-120 pairs/10 ha in the late 1990s–2000s. These values are intermediate or close to those found in some small Western and Central European woods and urban parks (up to 150-200 pairs/10 ha or even much higher) censused by the mapping method. It must be emphasized that sufficiently high total densities have been approached in the Moscow woodlands in spite of the absence or low densities of some of those species which have very high densities in a number of Central and/or Western European urban wooded areas and non-urban fragmented woods used for comparison, viz. *Columba palumbus, Corvus frugilegus, C. monedula, Prunella modularis, Turdus merula, Troglodytes troglodytes* (see Tomiałojć et al., 1984; Tomiałojć & Wesołowski, 1990; Flade, 1994; Tomiałojć, 1998, 2000; Wesołowski, 2007a and references therein).

High total densities in old-growth oak- and lime-dominated woodlands (with no or few nest-boxes) in Moscow is mostly a result of high densities of some non-excavators (secondary hole-nesters) viz. birds which breed in holes but are not able to excavate holes themselves and thus entirely depend on the presence and availability of natural tree cavities, holes made by other animal species, or their artificial substitutes (nest-boxes or cavities in human constructions) for nesting. In several large woodlands in Moscow, some other species and guilds composed of ecologically similar congeners, e.g., *Turdus* spp., also developed fairly high breeding densities.

ARE THERE ANY INDICATIONS OF RECENTLY ACTING INTERSPECIFIC COMPETITION AMONG ECOLOGICALLY SIMILAR CONGENERS?

Numerical trends and breeding ecologies of several model species belonging to both guilds mentioned above have been studied mostly in NHPO. The main results and considerations directly concerning the theme of this chapter are briefly reviewed below. Details are omitted here and will be published elsewhere.

Early-breeding non-excavators. It has been considered for a long time that a shortage in suitable cavities restricts the numbers of secondary hole-nesters in an area.

Indeed, the provision of nest-boxes was shown to result in an increase in non-excavator breeding densities in most studies (Lack, 1954; von Haartman, 1957, 1971a; Perrins, 1979; Newton, 1994). However, in Europe the majority of studies were performed in man-modified woodlands where natural holes could be in short supply. Moreover, the strongest numerical response to the provision of nest-boxes was recorded in *Ficedula hypoleuca* which strongly prefer them over natural cavities when the latter are available in excess (van Balen et al., 1982; Lundberg & Alatalo, 1992). Several studies conducted in the last decades indicated the presence of unoccupied natural holes appropriate for breeding in some North American and primeval European forests (e.g., Waters et al., 1990; Walankiewicz, 1991; Newton, 1994; Wesołowski, 2007b).

Most of the knowledge of the breeding ecology of non-excavators in Europe comes from nest-box studies. Investigations on birds nesting in natural holes and, especially, the sites where long-term studies of this kind have been conducted are scarce (van Balen et al., 1982; Nilsson, 1986; Wesołowski, 1989, 2007b; Walankiewicz, 1991 and references therein). Some authors argued there are a number of reasons to expect considerable differences between nest-boxes and natural holes and cautioned that nest-box data can be unrepresentative for a broad set of natural conditions (Nilsson, 1986; Walankiewicz, 1991; Newton, 1994; Wesołowski & Stańska, 2001; Mitrus, 2003; Wesołowski, 2007b). Moreover, selective pressures (e.g., nest predator vs. parasite loads) acting on birds nesting in natural holes and nest-boxes may be different (Wesołowski & Stańska, 2001). Studying the breeding ecology of non-excavators in woodlands without artificial nest-sites is of prime importance.

Among nine small-sized, secondary hole-nesting species currently found in the Moscow woodlands, *Sturnus vulgaris, Parus major, P. caeruleus, P. ater, Sitta europaea, Passer montanus,* and *P. domesticus* may be called early breeders. These species normally start breeding before the arrival of *Ficedula hypoleuca* and *Jynx torquilla*, thus having a broader choice of unoccupied cavities. Also, both facultative (secondary) hole-nesters, *Phoenicurus phoenicurus* and *Erithacus rubecula*, are relatively late breeders. In the absence of nest-boxes, four hole-nesting species achieved very high local densities in large oak- and/or lime-dominated woodlands of Moscow: *Parus major, P. caeruleus, Passer montanus*, and *Sturnus vulgaris*.

The latter two species tending to collect food outside dense tree stands were more or less numerous breeders along forest edges and in open wood patches only. The highest local densities resulted from their "semi-colonial" nesting (right next to simultaneous nesting of several pairs in same trees) were approached in the riverside old-growth lime-dominated stands of Vorobyovy Gory and Fili-Kuntsevskiy Forest Park. In both localities, *Sturnus vulgaris* collected considerable (probably, most) part of the food at the opposite side of the Moskva River in semi-open spaces of the Luzhniki Sports Complex and in the agricultural areas of Nizhniye Mnevniki, respectively. In other words, high local densities in these two species were partly explained with the edge-effect (see Haila, 1988; Tomiałojć, 1998) viz. including surroundings of the woodlands in birds' home ranges. Both species were scarce or absent in the interior parts of large forest islands having compact shapes. For example, the maximums recorded for *P. montanus* and *S. vulgaris* in the 30-ha plot in NHPO were five pairs in 1992 and one pair in 2001, respectively. By contrast, breeding densities in both tit species were high or very high both in peripheral and interior parts of some woodlands (as well as in the built-up areas containing woody vegetation).

Parus caeruleus and *P. major* are species with strongly overlapping habitat preferences, diets, nest-site, and roosting hole requirements (Dhondt, 1989). In nest-box studies, conclusive evidence were obtained that they can compete for nest-sites and roosting holes in winter. The larger *P. major* seems to be superior in the interference competition for holes but is a less effective competitor in utilizing caterpillar food supply in the breeding season than *P. caeruleus* (Perrins, 1979; Dhondt & Eyckerman, 1980; Minot & Perrins, 1986; Török, 1987; Dhondt, 1989; Török & Toth, 1999 and references therein).

Both species, especially *P. caeruleus*, obviously increased their breeding numbers in Moscow City during the past 4-5 decades. Until the 1960s–1970s, *P. caeruleus* was no numerous breeder in NHPO (Krotov, 1941; Bel'skiy, 1954; Blagosklonov, 1977). It was a fairly scarce species in the city (Strokov, 1962; Blagosklonov, 1977) and the Moscow Region (Ptushenko & Inozemtsev, 1968). During the 1970s-1990s, its numbers and local breeding density gradually increased by an order of magnitude. In 1993-1995 and 1999-2004, the density in the interior part of the NHPO oak forest ranged from 16 to 33 territories/10 ha (see below). *P. major* densities in the same site in the same years except 1995 were at least 1.2-2.0 times higher. Similar values were recorded for both species by line transect censuses made in late April and early May 2000-2004 in the riverside old-growth lime-dominated stands of Vorobyovy Gory and Fili-Kuntsevskiy Forest Park. These figures approach the highest ones known for nest-box areas in continental Europe and Britain (Perrins, 1979; Wesołowski et al., 1987; Cramp & Perrins, 1993; Flade, 1994; Solonen, 2001). The breeding populations of both tit species in Moscow are partially migratory but the proportions of migrant birds and their winter quarters are unknown. Among individuals breeding in the NHPO forest, some are continued to be seen there, either sporadically or periodically, during autumn and winter. It is unknown how much time sedentary individuals breeding in Moscow woodlands spend in the built-up areas of the city during the non-breeding period.

The numeric rise in both species in Moscow City could hardly be explained by local factors such as the provision of nest-boxes and artificial feeding of birds in winter in some urban green areas. It seemed to result from population growth and synurbization processes at broader scales (Konstantinov et al., 1990, 1996; Friedman et al., 2008). This increase alone gives rise to the assumption that in mature, broadleaved woodlands, cavities suitable for nesting were not in short supply and competition for them (both inter- and intraspecific) did not limit the densities of early-nesting non-excavators. The hypothesis does not exclude the possibility that in some woodlands of the city, including broadleaved ones, an increase in tit local densities could (partially) be caused by an increase in natural hole abundance due to ageing of tree stands. Population studies conducted in the NHPO oak forest cast more light on the question.

In many regions and habitats, woodpeckers are important hole providers for non-excavators (for a review, see Wesołowski, 2007b). Three woodpecker species regularly bred in NHPO over the period 1992-2008: *Dendrocopos major* (in 1992-1994 and 1999-2007, 1-4 active nests within the 30-ha plot yearly, mean 1.9) (Fig. 19), *D. minor* (0-2, mean 0.8), and *D. leucotos* (0-2). In the first two species, the number of individual pairs whose breeding territories included some part of the plot seemed to be higher (yearly at least four and two, respectively) than the number of active nests within the plot. Also, *Dryocopus martius* yearly appeared in autumn (probably more than one individual) and stayed until early spring. However, only 9% of *Parus major* (n=121) and 3% of *P. caeruleus* (n=263) active nests found during 1993-1997 and 1999-2006 were situated in woodpecker-made holes (mostly in those excavated by *D. major* and *D. minor*, respectively). The majority of tit pairs bred in non-excavated holes supplied by timber decay, branch detachment, natural cracking or breakage processes (Fig. 20). Nest-holes of these two species were often situated close to each other. Six times during 1999-2004, active nests of both species were found to be simultaneously located in different holes of the same tree. The shortest distances between their entrances were 1.0, 1.4, and ca. 1.7 m (Morozov, 2003 and unpublished).

In the years 1993-1995, 1999, and 2000, *P. caeruleus* density within the 11.8-ha subplot varied from 15.7 (1994) to 30.1 (2000) territories/10 ha (mean 22.0 territories/10 ha). Among them, the proportion of territories occupied by the bachelor males (those which remained unmated in early May when most pairs completed egg-laying) ranged from 5% (1994) to 38% (1993). The density of breeding pairs varied between 11.9 (1993) and 27.1 (2000) per 10 ha, being on average 18.4 pairs/10 ha. It was found in some studies that in the sites of joint occurrence, *P. caeruleus* prefer cavities with smaller entrances inaccessible for *P. major* which dominate in the competition for holes (Dhondt


19


20

Fig. 19. Great Spotted Woodpecker near its nest-hole, NHPO oak forest, 17 June 2007.
Fig. 20. A natural hole in the living oak occupied by Blue Tits, NHPO oak forest, late May 2000.

& Eyckerman, 1980; Minot & Perrins, 1986; Kempenaers & Dhondt, 1991). In NHPO oak forest, *P. caeruleus*, being slightly earlier breeders, nested on average in smaller-sized holes with smaller entrances than *P. major*. However, considerable overlap in nest-site use was observed, and many cavities were occupied by both species in different years. Some holes in the plot were used for breeding during more than three years by the same or different (including *Ficedula hypoleuca*) species.

After the breeding season 2000, a 4-year manipulative experiment was conducted in the subplot to determine whether *P. caeruleus* was limited by the availability of holes in the forest densely populated by both tit species. The entrances in a number of cavities used for nesting or actively advertised by bachelor males in the previous breeding season (except those which were not found within the mapped territories or were unattainable for the author) were blocked with broken branches or artificial plugs in the post-breeding time. In autumn 2000, I excluded 29 nest-holes occupied by *P. caeruleus* in the breeding seasons 1999 and 2000, and they could not be used by birds in 2001. Twenty three "new" cavities occupied by the species in the 2001 breeding season were blocked in the same way after the fledging period (or, few, lost due to tree fall) by the beginning of the breeding season 2002 in addition to those excluded in autumn 2000 (the blocked nest-holes of 1999 and 2000 remained unblocked). The procedure was repeated in the post-breeding and autumn periods for 28 and 24 holes occupied in the breeding season 2002 and 2003, respectively (Fig. 21).

Fig. 21. Blue Tit nest-hole (at a height of 17 m) of 2003 blocked in November 2003 with an artificial plug, NHPO oak forest, April 2004. Some holes out of reach from a ladder and by climbing like this one were blocked from the nearest trees by using a long telescopic plastic rod.

Blocking holes did not result in any considerable decrease of *P. caeruleus* densities (27.1-33.1, mean 29.0 territories/10 ha in 2001-2004) or increase in the proportion of bachelor males within the subplot (1.5-9%). By contrast, the share of unmated males reached the minimum during the experiment (in 2002). The density of breeding pairs (territories except those occupied by unmated males) during 2000-2004 was higher than in the 1990s and remained relatively constant (25.0-30.1, mean 27.3 pairs/10 ha) (Fig. 22). Few conflicts for holes were observed between the two species of tits (and between any of *Parus* spp. and *Sitta europaea*), and the number of such conflicts did not increase during the study period including the years of the experiment.

Among early breeding non-excavators, *S. europaea* is another species common in the interior parts of the large forests. However, in contrast with the two tit species, it had low density everywhere in Moscow and its vicinity. Old-growth, unmanaged oak-dominated stands with *Corylus avellana* seem to be among the most attractive habitats for this species in the region. Nevertheless, from two to four (mean 2.9) pairs only occupied territories in the 30-ha plot in NHPO in the years 1992-1994 and 1999-2004. The values 0.7-1.3 pair/10 ha are suggested to be close to the upper breeding density limit for the region but are several times lower than those found in deciduous woodlands in Central and Western Europe (Wesołowski & Stawarczyk, 1991; Cramp & Perrins, 1993; Flade, 1994). The numeric stability in the plot could hardly be explained by nest-site shortage and interspecific competition for them because *S. europaea* is one of the earliest breeders

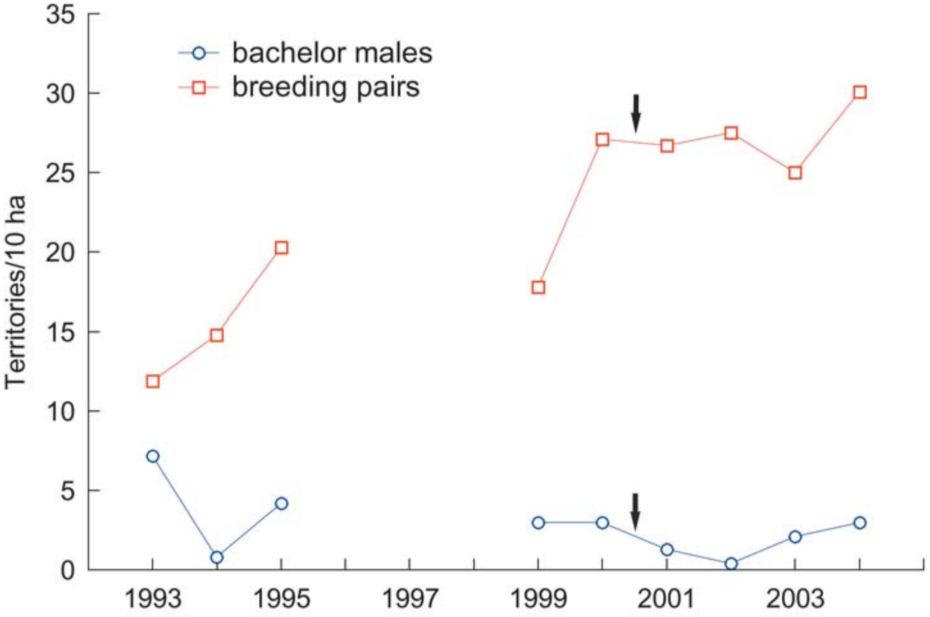

Fig. 22. Year-to-year changes in the density of Blue Tit territories in the 11.8-ha subplot in the interior part of the NHPO oak forest. Arrows indicate the start of the 4-year long experiment on nest-hole limitation.

even among the early nesting non-excavators. The low variability was rather explained by the larger sizes of territories (ca. 8-10 ha) occupied by the pairs of this species in the NHPO oak forest (as, seemingly, everywhere in Moscow and its surroundings) all year round, including the breeding season which, in turn, could be related, for example, to feeding conditions in the non-breeding period.

It can be summarized that *P. caeruleus* and *S. europaea* were not strictly limited by the availability of nest-sites in the relatively unmanaged part of the NHPO oak-dominated forest at least in 1999-2004. There are no data to reach the same conclusion for *P. major* which, however, developed extremely high density in the forest without any nest-boxes (although in the absence of stronger competitors for holes such as *Sturnus vulgaris*). Interestingly, the conclusion that secondary hole-nesters are not strongly limited by the availability of non-artificial nest-sites was made earlier for the primeval deciduous forests in eastern Poland (Walankiewicz, 1991; Wesołowski, 2007b). It must be emphasized, however, that combined densities of early breeding non-excavators in the Polish wood were much lower than those in the NHPO interior forest.

Turdus philomelos and T. merula. Among six European species belonging to this genus, at least four (*T. iliacus, T. merula, T. pilaris, T. philomelos*) can be supposed to compete sometimes and at some places, because their breeding habitats, feeding substrates, foraging techniques, and diets overlap considerably (Cramp, 1988). At the same time, *T. pilaris*, the species breeding both in colonies and solitarily and showing strong nest defense against predators, is supposed to provide a "protective umbrella" for other bird species. *T. iliacus* is one of those species which seem to associate actively with *T. pilaris* in the breeding season in different regions (e.g., Slagsvold, 1979, 1980; Gubin et al., 1990; Morozov, 2001), including Moscow City and its vicinity (Morozova, 1984; Samoilov & Morozova, 1987). *T. philomelos* and *T. merula* are also known to locate nests in an areas with *T. pilaris* colonies when breeding in the same habitats. In the breeding time, *T. pilaris* tend to collect food outside the forest (e.g., Gubin et al., 1990) that can reduce a possible competition for it with the congeners.

Some aspects of *Turdus* species' ecology in Europe are well-studied, but the possible role of interspecific competition in their coexistence in the breeding season is rarely discussed (but see Dyrcz, 1969; von Haartman, 1971b; Gubin et al., 1990; Cherenkov et al., 1995; Wesołowski & Tomiałojć, 1997; Wesołowski, 2003). Five species regularly inhabit urban landscapes at least in some parts of the breeding ranges (Cramp, 1988; Snow, 1988; Luniak et al., 1990; Flade, 1994; Hagemeijer & Blair, 1997; Hewlett, 2002; Tomiałojć & Stawarczyk, 2003; Kelcey & Rheinwald, 2005). Currently, four of them are regular breeders in Moscow woodlands. In the breeding season, *T. pilaris* and *T. iliacus* inhabit mostly woodland edges, open woodland, and forest gaps. Their densities in the core parts of large forest islands are low. For example, zero (in most years) to 2 pairs of *T. pilaris* and zero to 7-8 (in 2007; usually less than five) pairs of *T. iliacus* bred yearly in the NHPO 30-ha plot during the periods 1992-1994 and 1999-2007. By contrast, *T. philomelos* and *T. merula* prefer the inner parts in the large woodlands of the city, although they can also be found in some small forest islands with low recreation pressure.

T. merula is one of the best known examples of extending the distribution of urban population(s) within the species' breeding range (Tomiałojć, 1985; Luniak & Mulsow, 1988; Luniak et al., 1990; Stephan, 1999; Luniak, 2004). Being initially a forest bird, it began to colonize urban green areas in western Germany in the first half of the XIX century. The expansion of urban population(s) continued in the western and central European parts of the range during the second half of the XIX and the XX centuries. Synurbization in this species has also been observed in the Caucasian/Anatolian region and central Asia, which are inhabited by two other subspecies. At the same time, in Europe, non-urban population(s) irregularly expanded northeastwards and eastwards. As a result, the species approached southern Karelia in the north (Mal'chevskiy & Pukinskiy, 1983; Khokhlova, 2007) and South/Central Ural in the east (Ryabitsev, 2001). The geographical expansion was preceded and/or accompanied by a numerical rise in some earlier populated regions (Mal'chevskiy & Pukinskiy, 1983; Cramp, 1988; Luniak & Mulsow, 1988; Tomialojc & Stawarczyk, 2003). Until the 1990s, no urban populations were known in the northeastern part of the species' breeding range in Europe, including central European Russia.

The ecology and behavior (preconditioned by physiology) of urban *T. merula* populations differ from those of non-urban ones in the same region (Luniak & Mulsow, 1988; Luniak et al., 1990; Partecke et al., 2004, 2005, 2006a, b). A fundamental ecological feature of populations from relatively undisturbed, extensive forest blocks in Europe (including those in the forest zones of European Russia sampled by the mapping method, see Morozov, 1992; Cherenkov et al., 1995; Kosenko & Kaigorodova, 2000; Kosenko, 2007) is their low breeding densities even in preferred habitats (up to 3-4 territories/10 ha). By contrast, small or fragmented woods in Western and Central Europe often support much more dense populations (5.0-24.0 territories/10 ha). Very high densities (locally up to 40-70 territories/10 ha) were found in urban conditions viz. in green areas of some Western and Central European cities (Luniak & Mulsow, 1988; Luniak et al., 1990; Tomiałojć, 1993, 1998; Flade, 1994; Mason, 2003; Luniak, 2004).

During the late XIX and the XX centuries, in the Moscow Region, *T. merula* was a more or less common but unevenly distributed and low-density species (Ptushenko & Inozemtsev, 1968; Il'ychev et al., 1987). It was not a rarity in large woodlands located in the vicinity (e.g., Ptushenko & Inozemtsev, 1968; Korneeva, 1979; Korol'kova, 1980; Konstantinov et al., 1990; Cherenkov et al., 1995; Voronetskiy & Poyarkov, 1996), the outskirts, and the peripheral zone of Moscow City (Promptov, 1932; Flint & Krivosheev, 1962; Flint & Teikhman, 1976; Korol'kova, 1977; Samoilov & Morozova, 1987, 1998b), although, at different periods, it was reported to disappear or decline in some of them (Belyaev, 1937; Korol'kova, 1977; Savokhina, 1989). A tendency to the development of an urban population emerged in the 1990s, when the numerical rise in some large forest islands and the attempts to colonize smaller-sized woodlands of the city were recorded (Eremkin & Ochagov, 1998; author's data).

In NHPO, *T. merula* was not found to stay in the breeding season in 1929-1935 (Krotov 1941), 1949-1963 (Bel'skiy & Chmutova, 1951; Bel'skiy, 1965), and 1992-1993.

From 2-3 to 5-6 males established permanent territories yearly in the core part of the oak forest in 1994-1997. Thrush nests were not specifically searched for in this period. Probably for this reason, (successful) breeding was first confirmed in 1997. In the years 1999-2001, the density in the 30-ha plot approached 3.3-4.5 territories/10 ha (Fig. 23) and currently seems to remain at approximately the same or a higher level. The number of territorial males in the breeding season in the whole NHPO woodland in the period 1999-2007 was estimated to be at least 40 yearly. The establishment of the local population in this area seemed to be an active colonization according to the terminology used by Tomiałojć (1985). However, such a high breeding density is still exceptional compared with those in the other woodlands in Moscow. For example, surveys conducted early in the morning and in the evening from 3 June to 1 July 2004 in seven large forest islands confirmed the presence of the species only in three of them viz. in the Experimental Forest of the K.A. Timiryazev Agricultural Academy, Volynskiy Forest, and in Kuskovskiy Forest Park. In the latter forest, the species was censused by the same method also in 2005. From two to three singing males were only censused along transects and found within the whole area in each of the latter two woodlands. In the whole area of the Experimental Forest of the K.A. Timiryazev Agricultural Academy, their number was probably in the range 3-10, but only 1-2 singing males were counted within the 100-m wide (50+50) strip along the 2.9-km long transect crossing the interior parts of the forest. For each of these three woodlands, the density estimate was less than 0.5 males/10 ha.

It must be noted that wintering of single or few *T. merula* individuals (of unknown origin), which was observed very rarely and irregularly in the region before the 1990s (Ptushenko & Inozemtsev, 1968; Il'ychev et al., 1987), currently is still uncommon (Kalyakin & Voltzit, 2006), i.e. the species remains migratory in the city and its vicinity. At the same time, some signs of synurbization were recorded in NHPO such as relatively small escape distances and the use of anthropogenic objects as an addition to natural materials for nests (in four nests in four different years from 2002 to 2008 out of 15 nests inspected for nest materials during this period). This was also observed in *T. philomelos* and *T. iliacus* in the core part of the forest.

T. philomelos, the "true" forest species, also colonized green areas in a number of Western and Central European cities and towns (e.g., Flade, 1994; Hagemeijer & Blair, 1997; Hewlett, 2002; Tomiałojć & Stawarczyk, 2003), although the degree of ecological and behavioral differences between its urban and non-urban populations seems to be smaller than that of *T. merula*. In many urban areas, these species have co-existed at considerable densities for a long time. In some parts of Europe, the trend to populate urban green areas in *T. philomelos* has tended to reverse in the second half of the XX century (Hagemeijer & Blair, 1997; Tomiałojć & Stawarczyk, 2003).

In human-shaped landscapes in Western Europe, especially Britain, *T. philomelos* locally reaches densities up to 15-34 territories/10 ha. However, in Central and East Europe, including the forest zones of European Russia (e.g., Morozov, 1992; Cherenkov et al., 1995; Cherenkov, 1998; Kosenko & Kaigorodova, 2000; Kosenko, 2007), the species usually occurs at densities less than 8.0-8.5 territories/10 ha (Cramp, 1988; Flade, 1994; Hagemeijer & Blair, 1997; Tomiałojć & Stawarczyk, 2003); those habitats which support more than 9 territories/10 ha are "high-density" ones.

During the past two decades and in the more distant past, *T. philomelos* has been a common breeder in the Moscow Region (Ptushenko & Inozemtsev, 1968; Il'ychev et al., 1987; Kalyakin & Voltzit, 2006) and in the large forests in the outskirts and the peripheral zone of Moscow City (e.g., Belyaev, 1937; Flint & Krivosheev, 1962; Flint & Teikhman, 1976; Korol'kova, 1977; Il'ychev et al., 1987; Samoilov & Morozova, 1987; Ravkin, 1988; Savokhina, 1989; Konstantinov et al., 1990; Morozov, 1996; Avilova & Eremkin, 2003; Kalyakin & Voltzit, 2006). In June 2004, it was found in all eight urban forest islands censused in early morning and evening time (see "Material and field methods"). The lowest densities (calculated as the number of singing males recorded within the 100-m wide (50+50) strip along a transect) were recorded in deciduous, mostly lime-dominated stands on the riverside slopes in Vorobyovy Gory (1.2 males/10 ha, n=5 singing birds censused) and Fili-Kuntsevskiy Forest Park (1.4 males/10 ha, n=4). Over most of their lengths, both woodlands have configuration of a relatively narrow (120-400 m wide) strip. Within the extensive part of Fili-Kuntsevskiy Forest Park (see D-value in Table) also dominated by lime (in some parts with a considerable admixture of pine, birch, and oak), the density was much higher (5.7-6.1 males/10 ha, n=13). The densities of singing males were considerable (7.6-7.9/10 ha) in the interior parts of Volynskiy (n=17), Pokrovskoe-Glebovo-Streshnevo (n=14), and Kuskovskiy (n=12) forests. A high local value was recorded in the centre (ca. 10-ha area) of Kuskovskiy Forest Park (ca. 15 males/10 ha, n=6). The number of males in the whole woodland in June 2004 was conservatively estimated to be 7-12 for Yugo-Zapadnyi Forest Park, 10-14 for Vorobyovy Gory, more than 20 for Kuskovskiy, Pokrovskoe-Glebovo-Streshnevo and Volynskiy Forests Parks, and more than 30 for Fili-Kuntsevskiy Forest Park and the Experimental Forest of the K.A. Timiryazev Agricultural Academy.

In NHPO, *T. philomelos* was reported to be a low-density breeder in 1929-1935 (Krotov, 1941) and the mid-XX century (Bel'skiy & Chmutova, 1951) but became numerous by the early 1990s. A high breeding density (8-10 territories/10 ha) found in the core part of the woodland in 1992-1994 continued to increase and approached 15-23 territories/10 ha in 2004-2007 (Fig. 23). The annual number of territorial males in the breeding season in the whole NHPO woodland was conservatively estimated to be more than 40 in 1992-1994 and more than 70 in the last years. By now, the establishment and considerable rise of *T. merula* local population in the core part of the NHPO woodland (during 1992-1997 and 1999-2001, Spearman rank correlation R_s=0.89, p=0.001, n=9) did not result in a negative numerical response in local density of *T. philomelos*. By contrast, the latter species tended to increase its breeding density (during 1992-1994 and 1999-2007, R_s=0.93, p<0.001, n=12) which was already sufficiently high in 1992-1995. Again, as for *Parus major* and *P. caeruleus*, it must be noted that the same directions of long-term numerical trends and non-compensatory year-to-year changes in *T. philomelos* and *T. merula* were found earlier in the primeval forest in eastern Poland (Tomiałojć & Wesołowski, 1990; Wesołowski & Tomiałojć, 1997; Wesołowski, 2007a). However, in the main types

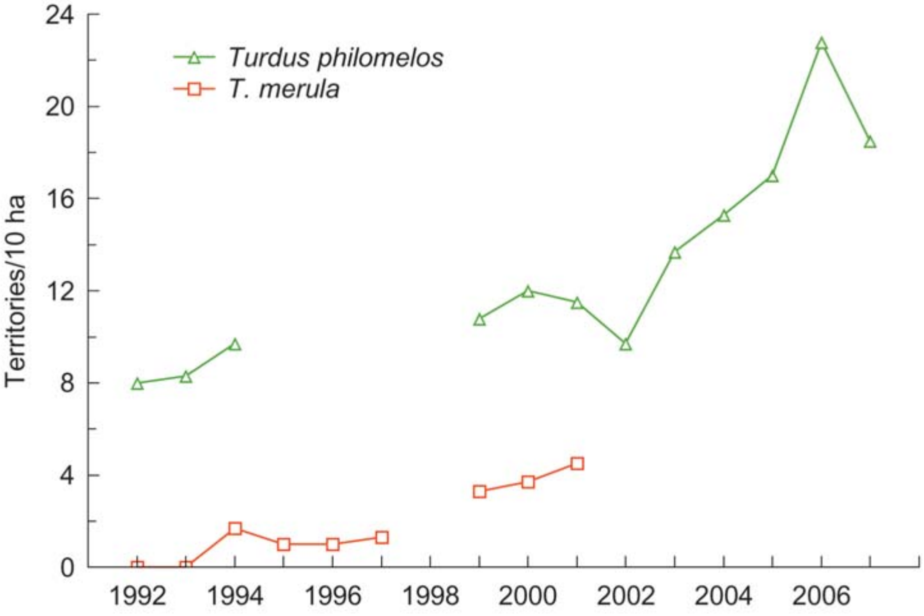

Fig. 23. Year-to-year changes in the population densities of two species of thrushes in the 30-ha plot in the interior part of the NHPO oak forest.

of that forest, the combined density of *T. philomelos* and *T. merula* during the study period was lower than that recorded in the core part of the NHPO woodland since 1999.

To summarize, there is no ground to suspect density compensation among woodland species due to competitive release or competitive exclusion between or during suburban and urban stages. On the contrary, two pairs of ecologically similar congeners increased their densities during the same or overlapping periods.

NEST PREDATION

The release from predation is one more synecological mechanism that is widely believed to possibly be responsible for a considerable numerical rise. Well-reasoned arguments were provided that comparatively low breeding bird density, both overall (contrary to those which might be expected on the basis of comparatively high species richness) and in separate species, is a "pristine" feature of European temperate forests. In the large block of primeval forests, undersaturation seems to occur more frequently among bird species, and in a number of them, individuals occupy much larger territories for reproduction than in secondary woods. These patterns seem to be shaped by a heavy pressure of diverse assemblage of predators, especially nest predators (rather than by resource shortage and strong competition for them), which results in low productivity of birds and strong selection for dispersion of their nests (large territory sizes). By contrast, high breeding densities observed in some man-transformed woodlands can be the secondary phenomenon preconditioned by a (partial) release from predation pressure (Tomiałojć et al., 1984; Tomiałojć & Wesołowski, 1990, 2004; Walankiewicz, 1991; Tomiałojć, 1998; Wesołowski, 2003, 2007a).

As a rule, researchers which discussed the theme of predation pressure in urban and urbanizing areas emphasized one of the following two opposite ideas. The first one is that the assemblages of predators are strongly impoverished in many urban landscapes. Usually, some major natural predators are absent in cities, whereas domestic cats and dogs are much less "efficient" in this role. In the absence of main predators (both nest predators and predators on adults), many generations in a number of bird species have comparatively high nesting success, annual productivity, and adult survival, resulting in the development of high or very high breeding densities (Tomiałojć & Profus, 1977; Tomiałojć, 1979, 1982, 1994, 1998, 1999; see also Gering & Blair, 1999; Kosiński, 2001; Marzluff, 2001; Antonov & Atanasova, 2003; Kuranov, 2008). The hypothesis is valid for any areas with impoverished assemblages of natural predators.

The results of some (mostly artificial nest) studies seem to contradict the generalization that predation pressure in cities is lower than outside of cities (e.g., Groom, 1993; Sasvári et al., 1995; Russo & Young, 1997; Jokimäki & Huhta, 2000; Haskell et al., 2001; Sorace, 2002; see also the brief review in Chace & Walsh, 2006). The opposite idea is based on the fact that in many urban and urbanizing areas, some major native (e.g., some corvids as nest predators) and/or exotic predators as well as predatory domestic animals can permanently occur or temporarily crowd at extremely high densities. Any part of such an area available and "transparent" for these predatory species can operate as an ecological trap for birds trying to breed there.

Obviously, the two ideas are not in conflict in the sense that different scenarios can be observed in a same area at different times. Also, conclusions can depend strongly on the sub-areas and habitats taken into account within a given urban landscape. By using *Turdus merula* and *Columba palumbus* as the examples, Tomiałojć (1994, 1999) argued that results of short-term studies taken out of historic context can fail to give an adequate picture, especially if they are automatically combined or averaged with the data of the same sort from other sites. In Western and Central Europe, many urban populations of both species reproduced for a long time in the absence of main predators, especially nest predators. At that time, they suffered low nesting losses and reached high production of young. However, in many cities, the favorable period finished with colonization by *Pica pica*, *Corvus cornix/corone*, locally also *Martes foina* and *M. martes*. Since then, very high nesting losses, some even higher than those in non-urban areas, started to be reported. At the same time, in some studies (e.g., Witt, 1989, 2005; Gooch et al., 1991), no evidence of decline in nesting success and/or numbers was found in a number of open-nesting species in response to a marked rise in abundance of an important nest predator.

The picture observed in the interior part of the NHPO woodland did not distinctly correspond to any of the two opposite ideas. Nest destroying by humans and nest desertion by parent birds were numerically unimportant in the plot. In some cases, the activities of *Lasius niger* (Hymenoptera, Formicidae) in dead wood seemed to be the cause of nest failure in hole-nesting birds. As in many other areas and species (Nice, 1957; Ricklefs, 1969; Nilsson, 1984; Martin, 1992, 1993; Wesołowski & Tomiałojć, 2005), nest predation was the major cause of nest loss. Nesting success in both hole- and open-nesting model species calculated as the proportion of nests which fledged at least one young was not very high or very low compared to other sites and regions from which the information about the same or ecologically similar congeneric species is available.

Nest predators. The species composition of the mammalian (Karaseva et al., 1999) and avian predators inhabiting Moscow City is quite-well known. The author spent a large amount of time (including many night hours) in and near the NHPO plot in the breeding season, especially in the years 1999-2007, when population studies were conducted. As a result, the knowledge about the composition of the predator assemblage in the NHPO woodland was substantially improved.

To summarize, *Accipiter gentilis* (one pair bred yearly in the woodland outside or within the plot), *A. nisus* (one pair bred outside the plot at least in some years, migrants in spring almost yearly), *Dendrocopos major* (more than 8-10 pairs in the woodland yearly; about its density within the plot see above), *Garrulus glandarius* (1-2 pairs almost yearly), *Corvus cornix* (numerous; see below), *C. corax* (one pair bred in the interior forest outside the plot since 1996), *Sciurus vulgaris* (up to seven individuals simultaneously seen in the plot), and *Mustela nivalis* (occurred at least in the years of high rodent density) were those nest predators which occurred in the interior part of the woodland more or less regularly from year to year. However, *C. corax* was never seen to search for or rob the nests of small- and medium-sized passerines and, with very few exceptions, even to visit the subcanopy space of the plot. Also, *Apodemus agrarius, A. sylvaticus*, and *Clethrionomys glareolus* must be included in this list as potential predators on the smallest passerines' nests. In some years or during several years, *Asio otus* (1-2 individuals were recorded to stay in the plot in the diurnal time; up to 4-5 broods in peripheral parts of the NHPO woodland), *Strix aluco* (one pair in the woodland), and *Nucifraga caryocatactes* (1-3 individuals in 2003 and 2004) were recorded to stay in the plot or to visit it in the breeding season. *Rattus norvegicus* was common at the periphery of the NHPO woodland, especially near the ponds and other water sources, but only few times over the whole study period, single individuals were seen in the interior part of the forest. Stray dogs are common resident breeders in the woodland (as everywhere in the city) but were not observed to show any goal-directed predatory interest to the accessible nests of small- and medium-sized passerines. Domestic cats were very rare visitors in the inner forest.

Pica pica (which was both a breeder and a visitor from the woodland periphery) and *Erinaceus* sp. (*europeus* or/and *concolor*) were common in the plot up to the early and mid-1990s, respectively, but then disappeared because of the crash of their local populations. The important nest predators typical of temperate woodlands but lacking as residents during decades in the NHPO plot are wild canids, *Martes martes* and other mustelids, except *Mustela nivalis*, glirids, and *Apodemus flavicollis*. It can be concluded that, currently, the local assemblage of nest predators is not species-poor, but several principal predators are absent. In general, the conclusion is valid for most other large woodlands of the city.

Parus caeruleus and P. major. In both species, few or no pairs had the second brood in a year, at least so in the interior part of the forest. In 1993-1997 and 1999-2006, most nesting attempts (at least nest building observed) in both species were made in the holes situated in living (*P. caeruleus*: 67%, n=263; *P. major*: 64%, n=121; but among them many in dead parts of living trees) and dead (*P. caeruleus*: 27%; *P. major*: 14%) oak trees. The majority of active nests were placed in the holes located at heights above 5 m (*P. caeruleus*: 80%, n=261; *P. major*: 78%, n=121). More than half of the nests in *P. caeruleus* (58%) but less than half in *P. major* (40%) were located higher than 10 m. Twenty one percent and 16% of their active nests, respectively, were situated above 15 m. Predation caused most of the failures where a cause was known or presumed. *Dendrocopos major* seemed to be the main predator or at least among the 2-3 most important predators on tit nests in the plot.

Annual samples of nest-holes monitored in the 30-ha plot and its vicinity during 1999-2004, especially those found at the early nesting stages, were small. To increase sample sizes, the data were pooled for 2-year (1999-2000, 2001-2002, and 2003-2004), 3-year (1999-2001 and 2002-2004), and 6-year periods. The nesting success was calculated for the samples larger than 15 nests in three different ways: (1) as the proportion of successful nests in a sample consisting of nests with a (presumably) known outcome in which incubation commenced (i.e., those began to be regularly checked since any time after the onset of incubation including the end of the nestling period), (2) as the proportion of successful nests in a sample consisting of nests with a (presumably) known outcome found at the stages of cleaning the holes before building therein (especially typical of *P. caeruleus*), nest building, laying, or early incubation, (3) as the probability of nest survival during incubation and nestling stages calculated by the Mayfield (1961) method. Using this latter method, the length of the period from the end of egg-laying to fledging was assumed to be 33 days in both species. The first method strongly overestimates nesting success (Mayfield, 1961, 1975). The second one is expected to underestimate the success considerably since a number of initially occupied holes are deserted by birds before the onset of egg-laying. The details of data processing will be provided elsewhere (Morozov, in preparation). Here, using different calculation methods for each year or period of years, I tried to show the upper and the lower possible limits of nesting success estimates rather than to compare the methods.

To summarize, the estimates of *P. caeruleus* nesting success in the plot and its vicinity calculated by the three methods ranged within 43-87% for annual samples (n=19-36 nests; the total number of exposure days with the use of the Mayfield method ND=347-726), 50-80% for the 2-year periods (n=31-69 nests; ND=916-1311), 58-74% for the 3-year periods (n=56-91; ND=1629 and 1642), and 62-72% for the whole 6-year period (n=125-181 nests; ND=3271). Twelve estimates calculated for single years and periods by the Mayfield method were 56-87% (n=21-160). The nesting success estimate of 43% (for 2004, n=21) obtained by the second (conservative) method was the only value less than 50%. For 18 of the 35 samples (larger than 15 nests), the nesting success estimates calculated by different methods were higher than 70%.

For the 11.8-ha subplot taken separately, the estimates of nesting success in *P. caeruleus* calculated using the second method for the periods 1999-2000, 2001-2002, and 2003-2004 were 75% (n=20), 74% (n=39), and 45% (n=42), respectively. The respective figures obtained by the Mayfield method were 74% (n=35; ND=656), 79% (n=49; ND=1098), and 60% (n=39; ND=773). Thus, excluding nest-holes did not result in a decrease in nesting success in the first two years of the experiment (see above) compared to 1999-2000.

The estimates of *P. major* nesting success in the plot and its vicinity calculated by the three methods ranged between 47 and 86% for the 2-year periods (n=19-34; ND=377-566), 57-84% for the 3-year periods (n=16-51; ND=739 and 765), and 64-78% for the whole 6-year period (n=39-88; ND=1504). All of the six estimates calculated for different periods by the Mayfield method were around 80% (n=21-77). The nesting success estimate of 47% (for 2001-2002, n=19) obtained by the second (conservative) method was the only value less than 56%. For 12 of 16 samples (larger than 15 nests), the nesting success estimates calculated by the different methods were higher than 70%.

The proportions of successful nests in both species during 1999-2004 were among the common ones within the range of values reported for small-sized cavity-nesting birds breeding in nest-boxes or natural holes in non-tropical regions (see Nice, 1957; Nilsson, 1984, 1986; Li & Martin, 1991; Walankiewicz, 1991; Wesołowski & Tomiałojć, 2005 and references therein). The majority of the NHAO figures can be considered moderate or relatively high but not unusually high.

Turdus species. In the earliest three *Turdus philomelos* nests found in the plot, egg-laying started on 16-17 April (2004), 22-24 April (2000), and 24 April (2001). The latest brood fledged in the beginning of August (2000). No individual marking of birds was conducted, but some of them seemed to produce two broods during the breeding season. Those who lost their first nests had enough time for renesting attempts. In the study plot, spruce *Picea abies*, which is strongly preferred by this thrush as nesting tree (Siivonen, 1939; Bochenski, 1968; Ptushenko & Inozemtsev, 1968; von Haartman, 1969; Mal'chevskiy & Pukinskiy, 1983; Cherenkov, 1996), was very scarce in the understory and represented by only few trees in the upper canopy. Moreover, almost all young spruces in the plot had very sparse crowns and were rarely used for nesting (Fig. 16). In late April and May, *T. philomelos* built their nests mostly at the bases of *Corylus avellana* shrubs (61%, n=261 for the combined data over the period 1999-2007) at heights below 1.7 m (Figs 17, 24, 25). Fallen twigs, branches, trunks, and pieces of oak bark stuck fast in the lower parts of the shrubs served as an (additional) support for such nests. Fifteen percent of the nests were placed in *Corylus* or low trees belonging to the same layer at heights of 1.7-5.7 m, and 13% were situated in niches in tree trunks and snags, in stumps, sites of tree trunk break, and pockets of loose bark provided by dead trunks at heights of 0.5-7.3 m. About half (52.5%) of all found nests built in April and May (n=261) were located at heights up to 1 m, and 13% were situated at heights up to 30 cm.

With the leaf development during May, an increasing proportion of *T. philomelos* nests were placed higher in the *Corylus* layer, mostly either among (often nearly horizontal or sloping) trunks, crossing branches and twigs of this shrub (Fig. 26), and low

Fig. 24. A nest of Song Thrush at the base of *Corylus avellana* shrub with a large piece of oak bark serving as an additional support, NHPO oak forest, 6 June 2002.
Fig. 25. Incubating Song Thrush on the nest located at a height of 1.3 m at the base of *C. avellana*, NHPO oak forest, 11 May 2007.

trees (*Sorbus aucuparia, Padus avium, Salix caprea*), or against tall (usually oak) trunks supported by branches/twigs (usually concealed with the foliage but sometimes not, see Fig. 27). Most nests built in June–early July were located in such structures (54% and 21%, respectively; n=68 for the combined data over the period 1999-2007) at heights of 2.0-8.5 m. Much fewer nests were built at the bases of *C. avellana* shrubs at heights below 1.7 m (13%) and few were built in stumps, sites of tree trunk break, and pockets of loose bark provided by dead trunks (4%). Only 12% of all nests built in summer were located at heights up to 1 m, and 3% were built at heights up to 30 cm (n=68).

Yearly during the period 1999-2007, the outcome of breeding (successful or not) was ascertained for 13 to 48 *T. philomelos* nests built before 1 June (mean 29, median 24 nests). From 8% (n=37) in 2004 to 57% (n=14) in 2002 of the spring nests produced fledged young. Excluding these extreme values, nesting success varied from 19.5% (n=41) in 2007 to 39% (n=23) in 2001. Mean and median nesting success for the 9-year period was 29% and 23%, respectively. The value calculated from the pooled data from all these years was 26.5% (n=260). At first sight, the nesting success seems to be moderately low, but the estimates include numerous nests which (being completely built) failed, mostly because of predation, during the pre-laying or egg-laying stages. In NHPO, just in these stages,

Fig. 26. A nest of Song Thrush placed at a height of 4.7 m among crossing, nearly horizontal branches of *C. avellana*, NHPO oak forest, 18 July 2003.

Fig. 27. A nest of Song Thrush located at a height of 5.2 m on a short bough against the trunk of a dead oak, NHPO oak forest, 24 June 2002.

the daily survival rate of the nests seemed to be especially low (Morozov, unpublished). By contrast, a traditional approach to estimate nesting success is to use those nests in which egg-laying was successfully completed (e.g., Snow, 1955; Mayfield, 1961, 1975). In other words, nest-building and egg-laying stages were not taken into account in most studies of nesting success. Compared to them, the NHPO values given above underestimate nesting success and should be corrected for nest survival probability during the egg-laying stage. However, in some studies used for comparison, the nesting success was estimated by starting from the onset of egg-laying (e.g., Cherenkov et al., 1995; Wesołowski & Tomiałojć, 2005).

The estimate of nest survival during the egg-laying stage in NHPO was calculated by the Mayfield (1961) method starting with the assumption that this stage lasts four days. Because of very low the numbers of active nests found before or during egg-laying in any separate year, I was compelled to combine the data of all years. The estimate of nest survival calculated for the egg-laying stage from this sample (n=62 nests monitored, among them 17 depredated in the egg-laying stage, ND=178 exposure days during egg-laying) was 67%. From this, the mean/median success of nests with completed clutches was presumably in or close to the range 34-43% (estimates for the separate years should also be corrected for survival during egg-laying in those years).

Possibly, it is even more important that the absolute majority of failures among "spring" nests occurred at the early stages of breeding. In other words, most birds which lost their nests seemed to conserve much energy and time for renesting attempts. Only 25% of the monitored nests built before 1 June which survived (or, in several cases, were presumed to survive) to hatching were lost during the nestling stage, all due to predation, whereas the others produced fledglings (n=56; 1999-2007 data combined).

The outcome of breeding was established for much fewer nests (zero to 14 in separate years, mean 7, median 5) built in June–early July compared to those that appeared in spring. However, it seemed from the combined (1999-2007) and some separate year (from 2003 to 2006) data that summer nests survived better. In the combined sample of nests built in summer, 50% (n=66) produced fledglings. In 2003, 2004, 2005, and 2006, the estimates were 50% (n=14), 80% (n=10), 46% (n=13), and 38% (n=13) vs. 37.5% (n=24), 8% (n=37), 32% (n=47), and 23% (n=48) for the nests built before 1 June, respectively. The estimate of nest survival during the egg-laying stage calculated by the Mayfield method from the combined sample (n=17 nests monitored, among them one depredated in the egg-laying stage, ND=54 exposure days during laying) was 93%. From this, the success for pooled sample of nests (1999-2007) with completed clutches was presumed to be around 59%. Only 10% of those monitored nests built in June–early July which survived to hatching were lost during the nestling stage, all because of predation, whereas the others produced fledglings (n=29; 1999-2007 data combined). Thus, nesting losses in *T. philomelos* declined from spring to summer. The seasonal change in nest survival was supported by the results of an artificial nest study conducted in 2001-2004 (Morozov, in preparation).

The rise in *T. philomelos* nesting success from spring to summer mostly resulted from the decline in *Corvus cornix* predatory activity in the interior forest. In NHPO, *C. cornix* and *Sciurus vulgaris*, especially the former, seemed to be responsible for most of the nest failures in *T. philomelos* in spring (Morozov, unpublished). It was mentioned above that Moscow City supports a huge and dense population of *C. cornix*. Certainly, some observations of high breeding losses in open-nesting passerines due to predation of this species were made, especially in small-sized and "transparent" green areas of the city (e.g., Morozova, 1984). During the past 15 years, *C. cornix* did not reach very high breeding densities in the interior parts of large forest islands including NHPO. No (in 1994, 1999, 2000, 2003-2007) to four (in 1992) active nests were recorded within the 30-ha plot. Nevertheless, its predation pressure there in the second half of spring was very heavy because of regular penetrating of non-breeding individuals searching for food (Morozov, 2004 and unpublished). By late May–early June, *C. cornix* combed the ground (Fig. 28), all vegetation layers, and substrates, checking and usually destroying active (see Fig. 17) and even old nests found.

Every year, *C. cornix* gatherings and flocks foraging in the forest markedly increased in size during the second or third ten-day periods of May (probably, because of an influx of individuals from the surrounding areas of the city). The process corresponded to the appearance of the alternative prey viz. old-age caterpillars, especially Green Oak Leaf Roller Moth *Tortrix viridana*, developing on oak foliage. The caterpillars were collected by crows very intensively (Fig. 29). Being flushed from tree crowns, hundreds *C. cornix*

Fig. 28. A Hooded Crow foraging in the interior part of the NHPO oak forest, 5 May 2006.
Fig. 29. Hooded Crows collecting caterpillars from oak foliage in the NHPO forest, 18 May 2007.

individuals were sometimes seen simultaneously circling the forest (Morozov, 2004). Paradoxically, the decline in *C. cornix* pressure on bird nests in the subcanopy space seemed to begin already during this "crowding period" (11-20 days) in the second half of May–early June. Then, presumably just after the decline in caterpillar food supply in oak crowns, *C. cornix* left the inner forest. Thus, their foraging pressure was restricted to the period from the mid- or the second half of April (soon after snow melting) to the mid- or early June. Later in summer, in many years, even starting from its beginning, *C. cornix* penetrated the core part of the forest very rarely.

A similar picture was observed in the interior parts of many other large woodlands (0.7-3 km^2 in size) having compact configurations, both containing many oak trees with caterpillars or not. Few decades ago, a decline in *C. cornix* predation pressure on bird nests since the second half of June was reported for a suburban forest in the National Park "Losinyi Ostrov" (Shurupov, 1984). It reflected the seasonal change in preferred foraging habitats from wooded to open ones. However, in the inner parts of Losinyi Ostrov and some largest (> 10 km^2 in size) peripheral forest parks of the city, *C. cornix* were currently almost absent, at least far apart from the built-up surroundings, even during late April and May. By contrast, in small wooded parks as well as peripheral or narrow parts of large forest islands of the city, especially those where recreation pressure was high, they foraged all the year round in high or considerable numbers and probably continued to rob bird nests during summer.

On average, *T. philomelos* nesting success in NHPO plot seemed to be moderate in spring but sufficiently high in summer compared to other regions and habitats from which similarly processed data on either this species or ecologically similar congeners (mostly *T. merula*) were published (see Snow, 1955, 1988; Dyrcz, 1969; Groom, 1993; Tomiałojć, 1993, 1994; Grégoire et al., 2003; Wesołowski & Tomiałojć, 2005 and references therein). It must be noted that it is questioned whether some of the highest estimates (about 60%) given in several old publications are comparable because of the different methods of data collecting and processing (see Snow, 1955; Mayfield, 1961, 1975). In the Białowieża primeval forest, which supports an almost entire assemblage of natural nest predators, the nesting success for the whole breeding season, calculated by starting from the onset of egg-laying, varied from 26 to 34% across years/habitats (overall 28%). The NHPO overall estimate for the "spring" nests (26.5%) was similar, but that for the "summer" ones was much higher (50%) than the Białowieża overall value. On the other hand, the only study on *T. philomelos* in the Moscow Region conducted (by using similar precautionary measures during nest checking and comparable data processing procedure) in a 49.7-ha plot with highly mosaic mixed stands within an extensive forest block ca. 25 km south-west of the city gave estimates of nesting success similar to the NHPO overall/mean values. In 1990-1992, the species' density in this plot estimated by territory mapping was 6.8-9.6 pairs/10 ha (Cherenkov et al., 1995). Most nests (97.5%, n=197) were placed in spruces. The forest was not penetrated by *Corvus cornix* but otherwise supported a much more complete set of natural nest predators (including *Martes martes*) than urban woodlands. The proportion of nests which produced fledglings amounted to 27-34% (n=27-32, totally 87) in patches dominated by deciduous tree species and 51-53% (n=19-26, totally 66) in those dominated by conifers (chiefly spruce). The nests were not subdivided according to months but it looked like that the patches dominated by deciduous trees were "forcedly preferred" for nesting early in the breeding season, possibly because food (lumbricids) was more readily available. Later in the season, an increasing proportion of pairs made (re)nesting attempts in the patches dominated by conifers where the nest predation rate was much lower (Cherenkov, 1996).

Because of the scarcity of *T. iliacus* and the low number of nests found yearly (from zero to six) in *T. merula*, little can be said about their nesting success in the NHPO plot. (Several nests of both species found in 2008 were included here.) It may only be noted that the estimate for *T. iliacus* based on the pooled data (41% of the nests with ascertained outcomes found during 1992-1994 and 1999-2008 produced fledglings, n=27, among them 24 built before 1 June) was not in conflict with the conclusion that on the average the conditions for thrushes in the interior part of the NHPO woodland were not unfavorable in terms of the nest predation pressure and nesting failures. Only one of seven monitored nests which survived to hatching (all but one built before 1 June: four at the bases of *Corylus avellana* shrubs, one on the ground under *Corylus*, and two in stumps) was lost (because of predation) during the nestling stage, whereas the others produced fledglings. The majority of *T. iliacus* nests built before 1 June (68%, n=25) were placed, as for *T. philomelos*, at the bases of *Corylus* shrubs (Figs 30, 31).

Fig. 30. A nest of Redwing *Turdus iliacus* at the base of *C. avellana* at a height of 0.5 m, NHPO oak forest, 12 May 2008.
Fig. 31. The same nest of Redwing, 12 May 2008.

By contrast, there were reasons to suppose moderately low nesting success for *T. merula*. The proportion of successful nests in the species reported in the literature for urban areas varied from ca. 5 to 50-60% (it was questioned whether some figures about and higher than 60% reported in several old publications were comparable because of different methods of data collecting and processing). The lowest of these values was not "reached" in suburban and rural landscapes, where success ranged from 12-14 to ca. 50% (Snow, 1955, 1988; Dyrcz, 1969; Groom, 1993; Tomiałojć, 1994; Grégoire et al., 2003 and references therein). In the Białowieża primeval forest with its high and diverse predation pressure, the nesting success estimated by starting from the onset of egg-laying varied from 21 to 42% across years/habitats (overall 33%) among the samples consisting of pooled data (Wesołowski & Tomiałojć, 2005). However, much greater variation (from 8 to 48%) was found at a finer habitat scale for sequences of years (Tomiałojć, 1994). In a small sample of 22 nests with ascertained outcomes found in the NHPO plot during 2000-2008 (among them, at least 18 were built before 1 June), 27% produced fledglings. Among five monitored nests which survived to hatching (all built before 1 June at the bases of *Corylus*), two were depredated during the nestling stage, and three produced fledglings. A special, intensive search for nests of *T. merula* was not conducted. Among those known or suggested to be built before 1 June, 56% (n=18) were located at the bases of *Corylus* shrubs (Figs 32, 33), whereas 44% were situated in niches or pockets of loose bark provided by standing or fallen tree trunks and stumps. A very low number of

32

33

Fig. 32. A nest of Blackbird *Turdus merula* at the base of *C. avellana* at a height of 0.4 m, NHPO oak forest, 18 May 2007.
Fig. 33. A nest of Blackbird at the base of *C. avellana* at a height of 26 cm, nestlings a few days before fledging, NHPO oak forest, 2 June 2008.

nests found compared to considerable species' density in the plot is supposed to result from locating most of the others in closed and poorly acceptable sites, presumably in niches and cavities of tree trunks and snags (discs of flat root-systems of uprooted trees known to be an important sites for nest location in this species in some old-growth forests (Tomiałojć, 1993) are almost absent in the NHPO plot). Another, hypothetic possibility (indirectly supported by few or no records of *T. merula* females and fledged broods in the plot in some years) is that the proportion of mated males was low in this recently established local population of the species.

CONCLUSIONS

There seem to be no reasons to talk about species impoverishment or decrease in the number of forest species in large woodland islands in Moscow City, except for components related with habitat loss or heavy disturbance, at least at the temporal scale of 5-10 decades. The exclusion concerns shy and/or large-sized species, which have disappeared mostly at early suburban stages. Species enrichment rather than impoverishment has occurred in the only long-studied large woodland island in the transitional period between suburban and urban stages. In this area, neither tied pairs of congeners nor ecologically similar woodland forms could be seen among "colonists" and "extinct" species in which any of the latter had more than few breeding pairs annually and thus could potentially be strong "density restrictors" for their competitors during the suburban stage. In other words, there is no ground to suspect density compensation caused by species "extinctions" or competitive exclusions between or during suburban and urban stages. On the contrary, two pairs of ecologically similar congeners developed high local densities during the same or overlapping periods.

In the interior part of the model woodland, the nesting success in a number of years was fairly high or moderate in some hole- and open-nesting species compared to other sites and regions, from which information about them or ecologically similar congeners is available. The fact that the percentage of successful nests in *Turdus philomelos* was moderate or moderately high in some years came as a surprise, because Moscow City has supported a huge and dense population of *Corvus cornix*, a major predator on open nests, over more than the past three decades. As in many other large woodlands of the city, the assemblage of potential nest predators in the forest studied has not been species-poor, but several important natural predators (e.g., *Martes martes*) have been absent as residents. Thus, partial release from nest predation could be among the mechanisms responsible for the high local densities which have currently been observed in some passerine birds in this and some other Moscow woodlands. On the other hand, the nesting success in the study species was not too high compared to that known for them or ecologically similar congeners from other regions to suggest that it could be the only determinant of this pattern.

Certainly, these findings are tentative and must not be extrapolated to other urban habitats and landscapes in this or other regions. A wide set of urban sites and avian species must be studied in detail in Moscow City and the Moscow Region to test them for validity and generality.

Unexpectedly high breeding densities developed by some bird species in urban and other man-modified green areas seem to be a widespread phenomenon. It is incredible, however, that a single most important factor (e.g., food or predation) is responsible for producing it in different species and operate everywhere. For example, the pattern parallel to that found in NHPO was reported in the 25-ha deciduous woodland in the Parc de La Colombiére of Dijon City in France: no indications of species impoverishment compared to countryside forest but unexpectedly high total density. The Dijon situation was supposed to result from the absence of main predators and high availability of food resources for species breeding in the park but foraging outside it in the rural outskirts of the city (Tomiałojć, 1998). In regions with relatively harsh winters, a high abundance of artificial food combined with an excess of cavities appropriate for roosting in winter and nesting may cause strong positive response of some *Parus* spp. in the form of increasing settlement in an area (see van Balen, 1980; Hansson, 1986; Orell, 1989; Hõrak, 1993). One of the most important topics for future research is the interplay between different factors shaping local populations and assemblages in an urban landscape, especially probable synergistic (multiplicative) effects revealed recently at the population level in several non-urban studies on mammals and birds (Krebs et al., 1995; Karels et al., 2000; Zanette et al., 2003; Clinchy et al., 2004). Considerable progress can hardly be achieved without conducting a number of long-term studies at different spatial scales and manipulative field experiments, which still remain very rare in urban studies.

Ecological and evolutionary processes can be affected by markedly different species interactions and selective pressures in non-urban and urban landscapes. By now, very little is known about synecological consequences of synurbization, e.g., possible differences in interspecific competitive abilities between urban and non-urban populations of the same species. The parallel numerical trends and very high densities found in some ecologically similar congeners in urban green areas seem to be in some conflict with the competitive paradigm with its inevitably successful search for ecological segregation and resource partitioning among sympatric congeneric species. Possibly, some causal aspects of similar positive responses of those species to urbanization can be better understood in terms of the realization of similar ecological and evolutionary potentials by phylogenetically related taxa (Chernov, 2008).

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