Ornis Hungarica 4:1–8. 1994

Territoriality and population regulation in urban Blackbirds (Turdus merula L.)*

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Ludvig, É., Török, J., Vanicsek, L. and Csörgő, T. 1994. Territoriality and population regulation in urban Blackbirds (*Turdus merula* L.). – Ornis Hung. 4: 1–8.

Population dynamics were studied in an urban Blackbird population in 5 breeding seasons between 1986 and 1992. From nest clusters – which seemed to represent the consecutive breeding attempts of a pair – the number of breeding pairs could be estimated as 72, 81, 72, 74 and 73 in the 5 breeding seasons. Similarly to the breeding population, yearly averages of breeding parameters – clutch size, hatching-, fledging- and breeding success – were also quite stable, consequently their density-dependence could not be detected. The stability of the urban breeding populations – which seem to be saturated – is maintained by the territorial behaviour, while in woodland populations the limited number of suitable nest sites and/or the lower winter survival may lead to the much lower breeding densities.

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1. Introduction

Two main processes can regulate bird populations: either the number of breeding pairs is limited or recruitment rate is density-dependent. Breeding density can be limited by the number of suitable nesting sites (Bellrose *et al.* 1964, Village 1983, Haramis & Thompson 1985) or by territorial behaviour (Watson & Jenkins 1968, Brown 1969, Harris 1970, Watson & Moss 1970, Krebs 1971, 1982, Patterson 1980, Catteral *et al.* 1982, Gautthier & Smith 1987). However, the area of territories can be affected by food supply (Anderson 1981, Village 1982) or the number of breeding pairs (Perrins 1971) as well.

The other limiting process is density-dependence of recruitment rate. Many studies have demonstrated that breeding parameters (clutch size and breeding success) or juvenile and adult survival can be density dependent (Krebs 1970, Dhondt 1971, Kluyver 1971, Perrins 1971, Orell & Ojanen 1983, Ekman 1984, Arcese & Smith 1988, Dhondt *et al.* 1990).

In this paper we studied the role of territoriality and density-dependence of breeding parameters in the regulation of an urban Blackbird population.

* The paper was presented at the "100 Year Old is the Hungarian Scientific Ornithology" meeting, Budapest, 1993.

2. Methods

2.1. Study area, data collection

Our data were collected in a 13 ha urban park (Vérmező) in the centre of Budapest between 1986–1989 and in 1992. The park consists of pathways and lawn areas with a great variety of evergreen and broad-leaved bushes and trees.

The area was searched for new nests once weekster from the beginning of March till the end of June. Each accessible nest was visited at last once a week, so besides clutch size, hatching-, fledging- and breeding success could be determined accurately. If laying date of the first egg was unknown, it could be estimated from the date of hatching assuming that eggs were laid daily and the duration of incubation period was 12 days.

To study territorial behaviour, the location of each individually-marked bird (about 20% of the whole population) was registered on a map at each observation. This procedure was continued even outside the breeding season from October till March when the study area was visited weekly.

2.2. Estimation of the number of breeding pairs

Each year the locations of all nests were registered on a map. Nests built in March and April were regarded as first breeding attempts and were marked with a circle, while those built in May or June were marked with a triangle and a square, respectively (Fig. 1). The marks of nests in which clutch size and breeding success were known, were filled while the others were left open. Nests that were close to each other in space and could be regarded as consecutive breeding attempts by laying date were clumped. The number of nest clusters gave the number of breeding pairs.

Tab. 1. The estimated number of breeding pairs and the yearly averages±S.D. of some breeding parameters in the different breeding seasons.

Year	1986	1987	1988	1989	1992
Breeding pairs	72	81	72	74	73
Clutch size	4.16±0.63	4.14±0.77	4.19±0.67	4.06±0.86	4.03±0.72
n	62	94	97	103	95
Proportion of hatched clutches	0.61	0.58	0.55	0.75	0.63
Proportion of fledged broods	0.62	0.80	0.75	0.58	0.68
Proportion of successful nests	0.38	0.46	0.41	0.43	0.43
n	61	95	93	104	91
Hatching success *	0.89±0.17	0.85±0.21	0.86±0.18	0.85±0.19	0.87±0.18
Fledging success *	0.98±0.08	0.96±0.11	0.96±0.11	0.97±0.11	0.92±0.15
Breeding success *	0.87±0.18	0.81±0.22	0.81±0.24	0.83±0.20	0.80±0.22
n	23	44	38	45	39

* total failures excluded

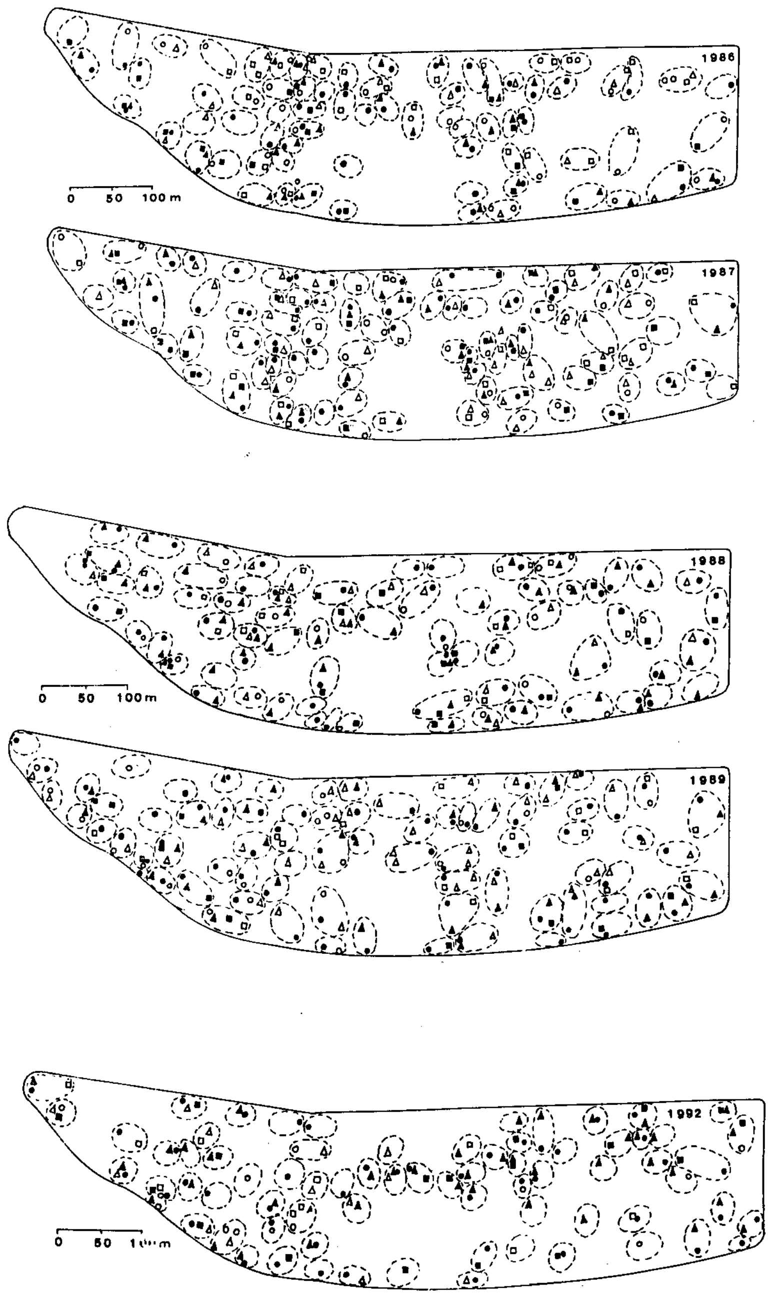

Fig. 1. Spatial distribution of all nests found in 1986, 1987, 1988, 1989 and 1992. Filled circles: complete clutches in March and April, open circles: other nests found in March and April. Filled triangles: complete clutches in May, open triangles: other nests found in May. Filled squares: complete clutches in June, open squares: other nests found in June. From nest clusters 72, 81, 72, 74 and 73 pairs may have bred in the area in the consecutive breeding seasons.

3. Results

165, 196, 171, 176 and 152 new nests were found in 1986, 1987, 1988, 1989 and 1992, respectively. Their spatial distributions are shown in Figure 1. From the nest clusters the number of breeding pairs could be estimated as 72, 81, 72, 74 and 73 in the consecutive breeding seasons. It is remarkable that the spatial distribution of nests was not uniform. However, the pattern of nests was similar each year, which was determined by the spatial distribution of plants suitable for nesting.

Tab. 1 summarises the number of breeding pairs and the yearly averages of breeding parameters. As with the breeding population, the breeding parameters were also quite stable. Consequently density dependence could not be detected in the studied period.

Observations on the individually marked birds showed that adults of both sexes remained close to their breeding territory throughout the year (Fig. 2 a,b). Juveniles were found on a larger area, but towards spring they occurred closer and closer to their future breeding territories (Fig. 3 a,b). It is interesting that the older the birds were the smaller area they occupied in winter.

4. Discussion

According to our results the population density of Vérmező Blackbirds is around 5.4–6.2 pairs/ha, which is similar to densities found in other urban habitats (Tab. 2). In an earlier study on foraging behaviour of Blackbirds in this study area (Török & Ludvig 1988) the average foraging area of males was estimated as 0.18 ha in the earlier rainy periods of the breeding season. Taking this area as the size of territory, 72 pairs can breed in the 13 ha Vérmező, which corresponds well with the estimated size of the breeding population.

The great stability of the population is maintained by the territorial behaviour of individuals. Adults remain in their breeding territory for the whole year or return to the same territory in spring, as was observed in Oxford (Lack 1966) and in Lausanne (Ribaut 1964) as well. Borders of the territories change little and juveniles can get new territories only after the death of adults. Towards spring, territorial behaviour becomes stronger and neighbouring males and sometimes females show aggressive displays and often have serious fights.

Tab. 2. Breeding density and breeding success in some urban Blackbird populations.

Author	City	Area (ha)	Density (pairs/ha)	Breeding success
Snow 1958	Oxford	2.4	4.6–6.7	0.34
Havlin 1963	Brno	22	4.4	0.60
Ribaut 1964	Lausanne	6	4.5–4.7	0.12
Dyrcz 1969	Wroclaw	25	0.96	0.41
Stein 1974	Magdeburg	6.4	6.4	0.19
Osborne & Osborne 1980	Exeter	45	–	0.33
Magrath 1991	Cambridge	16	6.25	–

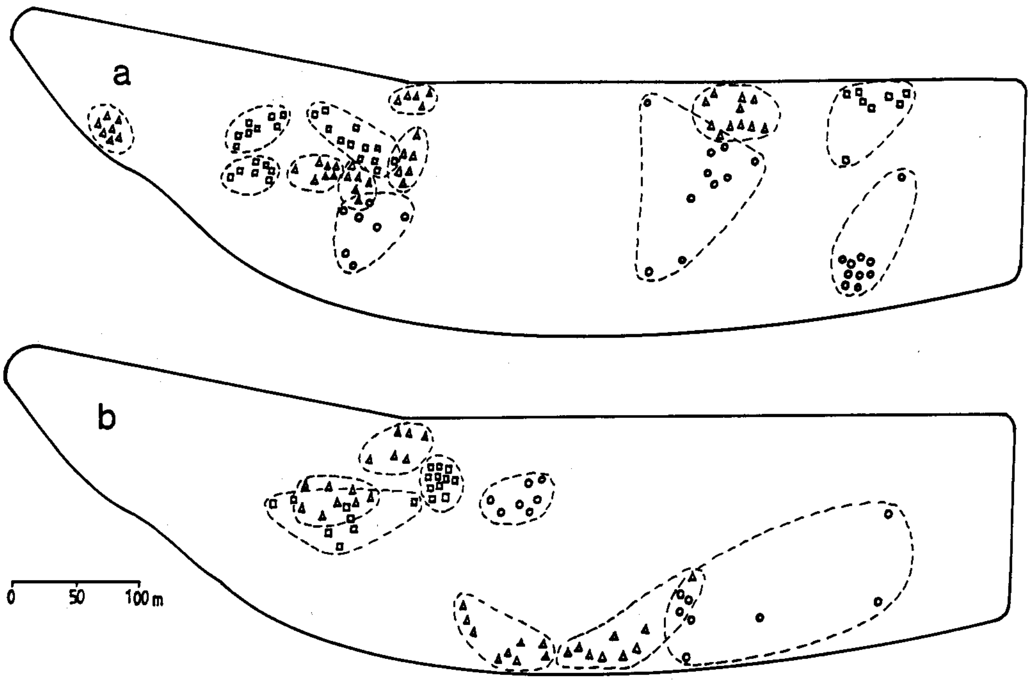

Fig. 2. The occurrence of some individually marked adult males (a) and females (b) during the winter of 1987–1988. Circle: 2 year-old, square: 3-year-old, triangle: 4-year old birds.

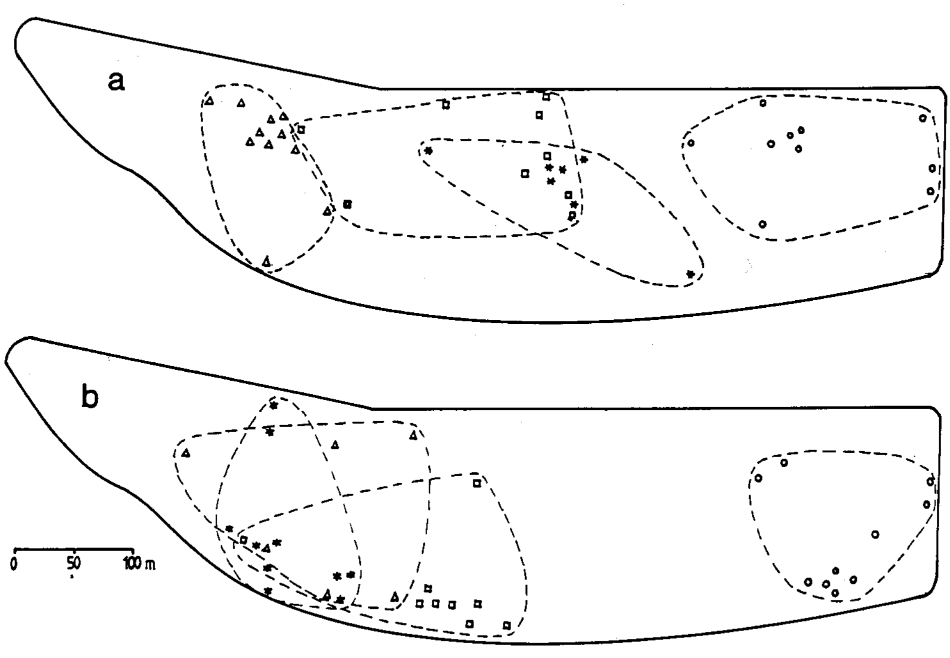

Fig. 3. The occurrence of some individually marked juvenile males (a) and females (b) during the winter of 1987–1988.

Tab. 3. Breeding density and breeding success in some woodland Blackbird populations.

Author	Country	Density (pairs/ha)	Breeding success
Snow 1955	England	–	0.41
Havlin 1963	Czechoslovakia	1.2	0.62
Koródi-Gál 1967	Romania	2.0	0.31
Dyrcz 1969	Poland	0.10–0.14	0.26
Perez *et al.* 1979	France	–	0.30

However, not only territories can limit the number of breeding pairs, but the number of suitable nesting sites also affects breeding density. At the beginning of the breeding season Blackbirds prefer evergreens, which give denser cover. As the number of evergreens is limited, those pairs which could not obtain an evergreen should risk building a nest on bare broad-leaved plants or postpone breeding until leafing. Sometimes more than one nest can be found on evergreen bushes or hedges at the same time showing that pairs try to form the borders of territories so that they contain evergreen plants as well.

Contrary to urban habitats, population density is between 0.1 and 2 pairs/ha in woods (Tab. 3). Consequently density of urban populations is about 5–10 times that of woodland ones. There are several hypotheses for this discrepancy.

Resources, such as food supply or nesting sites may be limited in woods. In urban habitats earthworms are the main food type in the rainy periods, while the diet of Blackbirds becomes more diverse in the drier periods (Snow 1958, Török & Ludvig 1988). In woodland habitats food supply is more diverse (Koródi-Gál 1967, Dyrcz 1969, Török 1981) than in urban habitats suggesting that earthworms may not be so abundant in woods. However, comparison of nestling weights suggests that conditions for rearing young are better in woodland than in urban habitats (Snow 1958). From these contradictory results we cannot decide whether food supply has a significant limiting effect on the population density in woods.

The number of suitable nest sites also may be limited in woods. Blackbirds prefer building their nests on lower bushes (Dyrcz 1969, Perez *et al.* 1979), which can be found usually only in the edges of woods. Thus this phenomenon may lead to the much lower population density in woods.

In Poland the density of urban Woodpigeon populations was 10–38 times higher than the density of rural ones. The main cause of this was a 6 times higher reproductive rate owing to a lower predation rate in towns. However, the breeding success of Blackbirds in woodland habitats was higher than in urban habitats (0.38 on average against 0.33 for urban habitats, see Tabs 2 and 3).

Finally the winter survival may be lower and probably density-dependent for either migrating or resident woodland Blackbirds (Venables & Venables 1952, Batten 1973, 1978) also leading to lower breeding densities.

Summing up, breeding density of Blackbird populations in urban habitats is stable and much higher than in natural ones. Density dependence of breeding parameters could not be detected but the breeding density is limited by the territorial behaviour of the species against woodland Blackbirds, where the lower breeding density can be due to the lower availability of suitable nest sites and/or to their higher and probably density-dependent winter mortality.

Acknowledgements. We thank I. Mohácsi and L. Tóth for their help in the fieldwork. É. Ludvig was supported by a postgraduate scholarship from the Hungarian Academy of Sciences during the field work and by grants from the 'For the Hungarian Science' Foundation of the Hungarian Credit Bank and from the Hungarian National Science Foundation (No. 2222) and by the Evolutionary Ecology Group of the Hungarian Academy of Sciences during data analysis. This work was from the Population Biology Group of the Eötvös University.

Összefoglalás

Territorialitás és populáció szabályozás városi feketerigóknál (*Turdus merula* L.)

A budapesti Vérmezőn fészkelő feketerigók populációdinamikáját tanulmányoztuk 1986–89 között és 1992-ben. Figyelembe véve ugyanazon párok egymást követő fészkeit, a költőpárok száma az öt vizsgálati évben 72-re, 81-re, 72-re, 74-re és 73-ra becsülhető. A fészkelő állomány állandóságához hasonlóan más költési paraméterek is stabilnak bizonyultak, így a fészekaljméret, kelési-, kirepülési- és költéssiker is. Következésképpen az esetleges sűrűségfüggést nem lehetett kimutatni. A vérmezei költőpopuláció stabilitása, mely az állomány telített voltára utal, territoriális viselkedés révén valósul meg. Erdei populációknál viszont a fészeképítésre alkalmas helyek hiánya, és/vagy az alacsonyabb téli túlélés jóval alacsonyabb fészkelési sűrűséget alakít ki.

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