

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

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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, Catterall *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.

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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 \pm 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 \pm 0.63	4.14 \pm 0.77	4.19 \pm 0.67	4.06 \pm 0.86	4.03 \pm 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 \pm 0.17	0.85 \pm 0.21	0.86 \pm 0.18	0.85 \pm 0.19	0.87 \pm 0.18
Fledging success *	0.98 \pm 0.08	0.96 \pm 0.11	0.96 \pm 0.11	0.97 \pm 0.11	0.92 \pm 0.15
Breeding success *	0.87 \pm 0.18	0.81 \pm 0.22	0.81 \pm 0.24	0.83 \pm 0.20	0.80 \pm 0.22
n	23	44	38	45	39

* total failures excluded

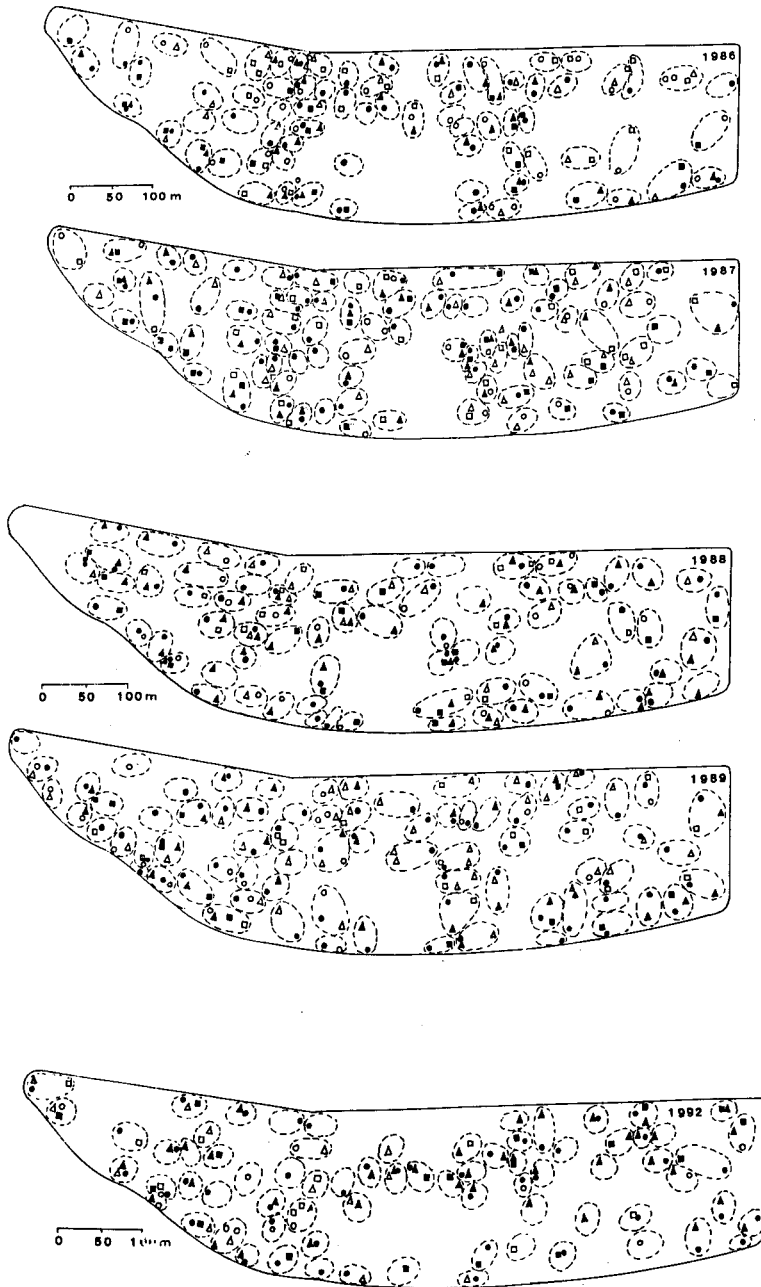


Fig. 1. Spatial distribution of all nests found in 1986, 1987, 1988, 1989 and 1992. Filled circles: complete clutches in March and April, open circles: other nests found in March and April. Filled triangles: complete clutches in May, open triangles: other nests found in May. Filled squares: complete 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	–

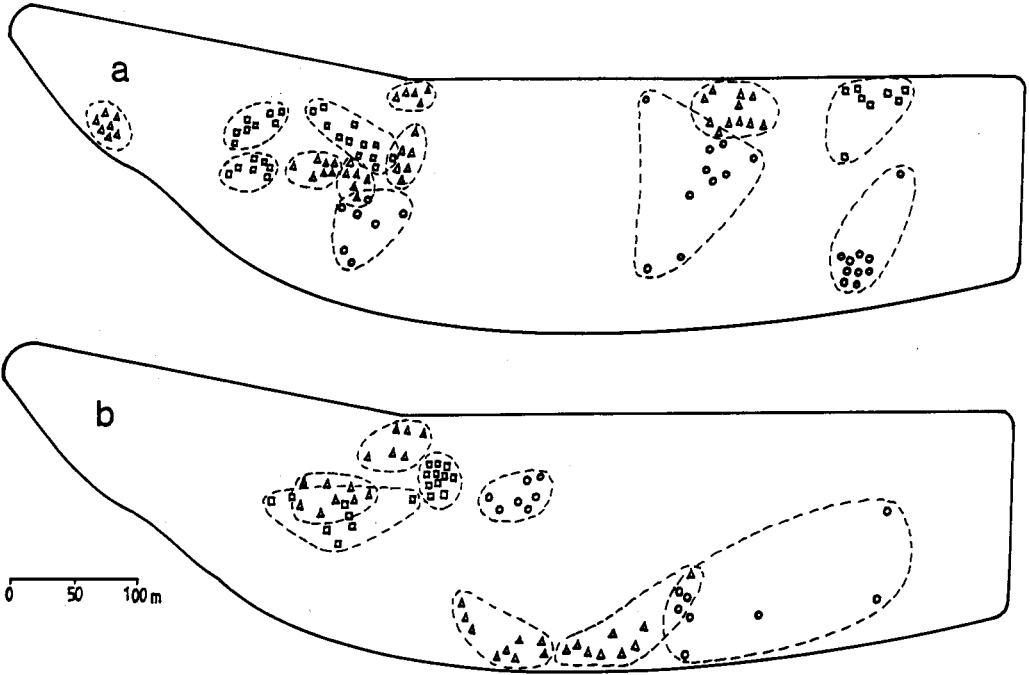


Fig. 2. The occurrence of some individually marked adult males (a) and females (b) during the winter of 1987–1988. Circle: 2 year-old, square: 3-year-old, triangle: 4-year old birds.

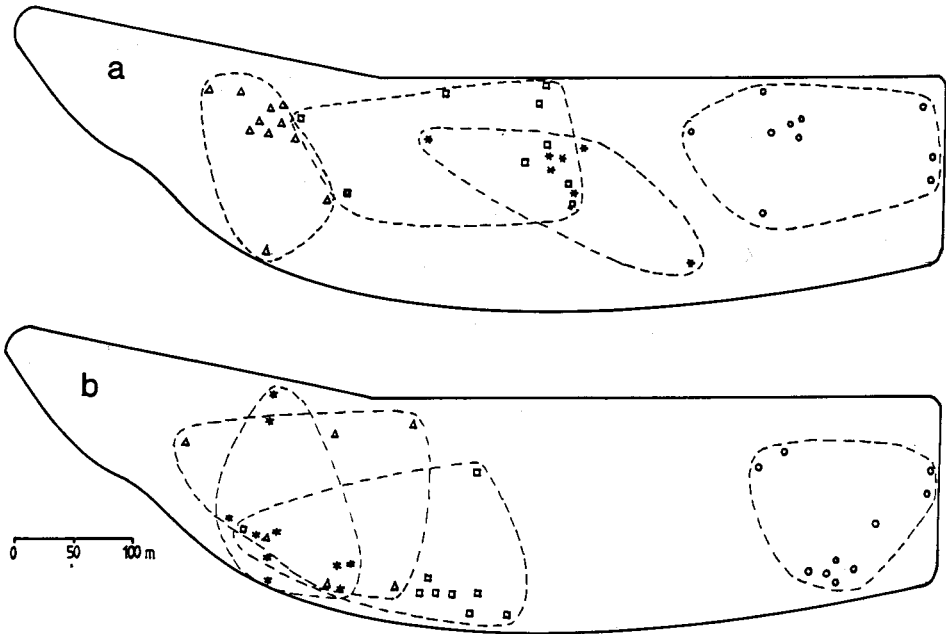


Fig. 3. The occurrence of some individually marked juvenile males (a) and females (b) during the winter of 1987–1988.

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 <i>et al.</i> 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.

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Összefoglalás

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

A budapesti Vérmezőn fészkelő feketeterigók 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 fészkekajlméret, kelési-, kirepülési- és költéssiker is. Következésképpen az esetleges sűrűségfüggést nem lehetett kimutatni. A vérmezei költőpopuláció stabilitása, mely az állomány telített voltára utal, territoriális vi-

selkedés révén valósul meg. Erdei populációknál viszont a fészkeképzésre alkalmas helyek hiánya, és/vagy az alacsonyabb téli túlélés jóval alacsonyabb fészkelési sűrűséget alakít ki.

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Alternative reproductive tactics as viable strategies in the Tree Sparrow (*Passer montanus*)^{*}

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Some bird species have both colonial and solitary breeding behaviour. One such species is the Tree Sparrow (*Passer montanus*), which is suitable for studying the adaptive significance of coloniality and the reasons why alternative breeding tactics can be maintained as viable strategies. We simulated both colonial and solitary breeding situations with dense and sparse spacings of artificial nestboxes and focused on the breeding performance and the returning rate of Tree Sparrows favouring dense or sparse nesting situations.

This paper is a synthesis of results published in *Acta Oecologica* 1993, 14: 447–487; *Journal of Animal Ecology* 1994, 63: 265–274; *Behavioral Ecology and Sociobiology* 1994, 34: 113–124. Evidence proved that colonial and solitary breeding may be maintained as viable reproductive strategies. It is possible for birds to choose different sociality on the basis of breeding experience and to attempt to improve their performance by changing nesting situation. Three principal factors seem to induce the retention of alternative breeding tactics as viable reproductive strategies. (1) Multibreeding. Species should be able to breed two or three times within a breeding season. (2) Food environment should become richer and/or more diverse as the season progresses. (There is an adaptive adjustment in Tree Sparrow to increase food supply: parents rear more fledglings in second and third broods than in first broods.) (3) Difference in breeding experience between young and old parents. Older parents which have acquired experience prefer solitary nesting behaviour.

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1. Introduction

Recent studies on the costs and benefits of colonial breeding in birds have focused on the adaptive advantages of food acquisition (Crook 1962, Horn 1968, Ward & Zahavi 1973, Krebs 1978, Waltz 1983) and predator avoidance (Kruuk 1964,

Hoogland & Sherman 1976, Veen 1977, Götmark & Andersson 1984). However, costs of colonial breeding including increased competition for mates, nesting sites and food, increased risk of predation, disease and transmission of ectoparasites have also been identified (Alexander 1974, Wittenberg & Hunt 1985). Infanticide and intraspecific nest parasitism have

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also been associated with colonial breeding (Hoogland & Sherman 1976, Moller 1987). Some authors have suggested that shortage of nesting habitat rather than direct benefits of group living is responsible for coloniality (Lack 1968, Snapp 1976, Shields & Crook 1987).

Comparative studies on reproductive performance of colonial and non-colonial breeders of the same species may help to understand the adaptive significance of coloniality. Tree Sparrows breed both colonially and solitary in various suburban and agricultural habitats (Pinowski 1968, Summers-Smith 1988). They commonly nest in groups in the nests of White Storks (*Ciconia ciconia*) and birds of prey, in the ground holes of Sand Martins (*Riparia riparia*) and Bee-eaters (*Merops apiaster*) or in the roofs of dwellings in villages in the Carpathian Basin. Tree Sparrows rear two or three broods during a breeding season. Hence this species is suitable for studying not only the difference in reproductive effort between colonial and solitary nesting birds, but also the costs and benefits of having more than one brood in a year. Body mass and feeding frequency have commonly been used to estimate the reproductive effort of passerines; in addition we also considered nest building as a reproductive investment in the Tree Sparrow. We simulated colonial and solitary breeding situations by placing nestboxes densely and sparsely.

Our principal questions were: (1) Do Tree Sparrow prefer solitary or colonial breeding? (2) What are the reproductive consequences of sociality in terms of numbers of fledglings and recruits? (3) How social preference and breeding success change over the season and in subsequent breeding years?

In addition, our study focused on nest building activity, feeding frequency and nestlings' food composition of the Tree Sparrow in relation to (i) breeding performance, (ii) parental condition, and (iii) colonial and solitary breeding.

2. Study area and methods

Five study plots were chosen in a suburban park of Budapest (Cemetery Park, 19°04' E; 47°41' N) and 50 nestboxes were distributed in each of the study plots, with 25 boxes 3–5 m apart to simulate colonial breeding and 25 sites approximately 50 m apart to simulate solitary breeding. The distance between neighbouring study plots was 500 m.

Shrubs and trees of various species and age including locust-trees (*Robinia pseudoacacia*), poplar (*Populus* sp.), horse-chestnut (*Aesculus hippocastaneum*) and lilac (*Syringa vulgaris*) were scattered throughout the parks. Arable land and 20–30 years old locust trees surrounded the park.

The nestboxes were checked every third or fourth day from middle of March until the end of August during the 7 years of the study (1986–1992). If the appearance of the first nest material, laying of the first or last egg, hatching or fledging of nestlings occurred between two subsequent checks, the day halfway between visits was recorded. Adults were caught at their nestboxes and at winter roosts, and individually marked with different combinations of colour rings. Sexes were determined by the occurrence of a cloacal protuberance or a brood patch (Svensson 1975), when birds were captured during the breeding season. Tree Sparrows often

desert nests if caught and marked during nest building or incubation (Pinowski *et al.* 1970), hence trapping during breeding was restricted to the nestling period. As Tree Sparrows can be aged with certainty only by marking the nestlings, we used only recruited offspring banded as nestling in some analysis. Young were individually colour ringed during the late nestling period.

The examination on reproductive effort began in the breeding season of 1987. The length of the nest building period was observed for 20 colonial and 20 solitary marked pairs each year. The length of the nest building period was divided into six time units: 1–3, 4–6, 7–9, 10–12, 13–15, or 16–18 days, starting from the first appearance of nest material to the laying of the first egg.

Some authors (Turner 1965, Krebs 1978, Ward & Zahavi 1973) have suggested that synchronous activities are advantageous for colonial parents both during the nest-building and the breeding periods. Hence we recorded simultaneous visits at neighbouring nests and which sex attended the nest by visual observation. Visits were recorded for an hour in 1–3, 7–9 and 13–15 day units of the nest-building period, respectively, and in 1–3 and 4–7 days of interbrood intervals after the young had fledged. Feeding visits were observed for an hour in early and late feeding periods. When neighbouring pairs (or one member from neighbouring pairs) were present at the same time on the trees where nestboxes hung simultaneous visits were recorded. When both sexes were present intersexual synchrony was denoted. We recorded events of synchronous stay, while the length of visits was not considered. Neighbouring nests

were chosen at random; the distance between nests was a maximum of 5 m in colonies.

Movements of parent during the nestling period was determined using photocell devices with an automatic recorder. The devices were fixed to the entrances of nestboxes for 24 h during early and late nesting periods, 5–8 and 9–12 days after the young had hatched. Objects resembling photocell devices were placed at the nestboxes before nesting, so when the objects were changed to actual devices, they did not affect the birds' behaviour. Automatic recorders and software, developed for the Commodore 64, tabulated the number of visits per hour. As the parents flew in and out of the nestboxes during feeding activities, the number of passes through the entrance was divided by two to calculate the feeding frequency during the nestling period. Assume, that an accurate measure of feeding frequency was obtained because the Tits, which might have visited the nests of Tree Sparrows incubated eggs or fed young during this period, so they were busy with their own broods. When we recorded simultaneous feeding activities, 17 visits to colonial nests and 8 visits to solitary nests from Tree Sparrows other than the owners were observed visually during the total observational time. Assuming such a low visit frequency from foreign Tree Sparrows through the feeding period, the results obtained with photocell devices might not be influenced by these activities.

Two neighbouring nests were chosen for 30–30 colonial and 30–30 solitary parents to study diet diversity and similarity. Nestlings' food was collected using the neck-collar method in early (5–8 days) and late (9–12 days) feeding periods. Sev-

enty-four food types were distinguished mainly by insect families and diversity of food composition was calculated using the Shannon-Weaver (1949) index, and similarity of diets was calculated using the index suggested by Hurlbert (1978).

Nestling mortality (1-number of fledged per number of hatched young) including both total failures and brood reduction, and number of fledglings were used as parameters for the analysis of breeding performance. Weights of parents were measured with Pesola spring balances in the late feeding period. To avoid differences due to daily fluctuations, parents were measured between 8.00–10.00 a.m. To prevent desertation, parents were not weighted either in the egg-laying or the incubation period, so weight loss through a breeding period could not be recorded. However, differences in weights in the end of the first, second and third broods could be obtained.

Statistical analysis were carried out using SPSS/PC+ statistical program package. Unless using chi-square test, percentage data were arcsine-transformed for parametric tests. Some birds might be involved more than once in the same test, and individual observational periods were not used as independent measures for calculations.

3. Results

A synthesis of results were published in details in *Acta Oecologica* 1993, 14: 447–487; *Journal of Animal Ecology* 1994, 63: 265–274; *Behavioral Ecology and Sociobiology* 1994, 34: 113–123.

3.1. Seasonal and lifetime trends in solitary nesting preference

The seasonal and lifetime trends in solitary breeding preference reflect optimal nest choice as illustrated by the following points:

(1) The majority of females chose colonial nesting for first broods and produced more offsprings and reared more recruited young per brood than females that chose solitary nesting.

(2) Both colonial and solitary females with low reproductive performance shifted nesting situation between first and second and third broods, however,

(3) a higher rate of colonial than solitary breeders changed nesting situation.

(4) Hence a higher proportion of shifting parents benefited from changing: pairs leaving colonies produced more offspring in solitary nests than pairs that retained colonial nesting, and pairs leaving solitary nests produced less offspring in colonies than pairs retaining solitary nesting.

(5) The majority of returning females chose colonial breeding and retained it through the season in the first breeding year, however,

(6) females whose productivity was low in colonies, bred in solitary nests next year. Solitary females of low productivity moved to colonies to breed next year. These changes were recorded between the first and second as well as second and third years of their return.

(7) Colonial females benefited from changing between years, because their productivity was higher and they reared more recruited young per brood in solitary nests than females which retained colonial nesting. Conversely, solitary females benefited from retaining their nesting

situation since reproductive results of shifting females was lower in colonies next year.

(8) The rate of shifting females increased in colonies and decreased in solitary nesters in subsequent breeding years, and, as a consequence, the majority of females bred in solitary nests in the second and third years of their return.

3.2. Productivity at different ages

The reproductive cost hypothesis implies a trade-off between current and future reproductive success and that investment in reproduction will reduce the parents' chances of surviving or reduce their productivity in the next reproductive effort (Williams 1966, Charnov & Krebs 1974, Stearns 1976, Ricklefs 1981). We provide evidence on the existence of a reproductive cost in Tree Sparrows that survived longer than two successive breeding seasons. Females which survived three, four or five breeding seasons produced fewer offsprings in their first and second breeding years than recruited females which bred only in the first and the second year at their birth place. The mean total productivity of subsequent breedings was lower for parents which bred through three, four or five years than for the parents which bred only in two successive years. There appears to be a compromise between present and future reproductive rate, i. e., low performance in early breeding activities results in good survival prospects in Tree Sparrows.

3.3. Different effects of weather conditions on colonial and solitary broods

Daily mean temperature affected the productivity of both colonial and solitary

parents in the first broods and that of colonial parents in the second broods. Daily mean humidity affected the breeding performance of colonial parents in the first and the second broods. No effect was recorded for third broods. Parents which produced fewer fledglings than average in previous broods produce more than average numbers of fledglings in second and third broods. We suggest that multibreeding with small clutches is an adaptive adjustment by Tree Sparrows to the effects of fluctuating weather conditions. In first broods, when adverse weather conditions affect both colonial and solitary breeders, colonial nesting is more advantageous; in second broods, when weather condition affect only colonial broods, solitary nesting is more advantageous for rearing offspring. This hypothesis is supported by our findings that parents that produced fewer than average offsprings in first broods reared more fledglings than average in second broods, and triple colonial breeders, whose productivity was below the mean in first plus second broods produced more young than average in their third broods.

Reduced brood size and multibreeding are advantageous for Tree Sparrow because: (1) there is no risk of high losses in reproductive periods when the survival rate of the eggs and young is extremely low because of the deleterious effects of ambient conditions. (2) The lower investment in a smaller brood means that the parents are capable of repeated breeding, where they can replace previous losses. (3) Laying fewer eggs and rearing fewer young helps the parents to maintain their reproductive efforts even in third broods. (4) Offspring reared together with fewer siblings may be heavier when leaving the

nest and greater body weight increases their chance of survival.

3.4. When to rear a third brood

The majority of first year females had long nest-building periods, long inter-brood intervals, and reared only two broods during a breeding season. Their weight measured during the late nesting period of the second brood was lower than that of immigrant and older returning parents. We suggest that the longer nest-building period and interbrood interval reflect a longer time needed for egg production by first year females than by older birds. Nevertheless, the longer time spent with nest building may be considered as a longer pre-egg-laying investment, which reduces parental condition and may influence factors determining whether to breed two or three times within a breeding season.

In our study the physical deterioration with increased feeding effort is indicated by: (1) Parent which reared few nestlings (2-3) in their first brood fed second, large broods (4-5 nestlings) more often than parents which reared many young in both their first and second broods. (2) Parents which did not rear a third brood, fed their young more often in both first and second broods than triple breeders. (3) Triple breeders which reared few nestlings in their first and second broods combined, fed their third broods more often than parents that had reared many young in their two previous broods. (4) Triple breeding parents fed less in their third brood than in their second brood.

The positive relationship between body weight and feeding frequency in the first brood showed that parents in better

condition invest more in reproduction at the start of the season. Exhaustion was already indicated after the second brood, where feeding frequency correlated negatively with weight of females that did not rear a third brood, and that of males that had fed many nestlings in first and second broods combined. Both females and males were lighter after the third brood when they had reared a large number of fledglings. Double brooding females were lighter after the second brood when they had reared many young in first and second broods, than if they had raised few young.

Starting a third brood depends on the exhaustion of reserves during the first and second broods in Tree Sparrows. Mothers which were light during the second brood did not raise a third one. They raised more young in their first and second broods than females that were heavier and laid a third clutch. We did not find that later second broods influenced the initiation of a third brood; thus lower costs invested in first and second broods are presumed to induce a third breeding.

3.5. Reproductive effort in colonial versus solitary breeders

We found three differences in first broods between colonial and solitary breeders, which were reversed in second and third broods:

(1) Colonial parents fed at a higher frequency than solitary parents in the first brood but at lower frequencies in second and third broods.

(2) Colonial nestlings suffered lower mortality than solitary nestlings in the first brood, but higher mortality in second and third broods.

(3) Similarity of diet was higher in colonial than in solitary nests during first broods, but was lower in colonies in second and third broods.

We found four activities to be more synchronous in colonies than in solitary breeders: (i) The majority of first year females bred in colonies and showed high rates of simultaneous activities in the colony, even during the nest building period. (ii) We found a higher synchrony in colonial parents in laying the first egg, a difference which disappeared, however, in second and third broods. (iii) We found a high rate of simultaneous feeding between neighbouring colonial parents, but this declined notably in second and third broods. (iv) The similarity in diets of neighbouring colonial nests was highest in first broods, with a decreasing similarity in second and third broods, which reflected the decline of synchrony in feeding activity.

An increased food supply during second broods results in a higher feeding frequency and lower nestling mortality both in colonial and solitary nests. However, the sparse spacing of solitary parents is more advantageous than the dense spacing of colonial parents. The increase of food richness presumably results in a decline in social stimulation among foraging colonial parents. However, they gather food at greater distances from the nests than solitary pairs. This was supported indirectly by solitary parents that fed at a higher frequency and with a greater dietary similarity in both second and third broods.

The advantage of solitary breeding was demonstrated by colonial parents that changed from colonial to solitary sites between two broods. They fed at a higher frequency and the nestlings suffered lower

mortality in the second and third broods (the latter change after the second brood), than parents which remained in colonies. Solitary parents that changed breeding situation fed at lower frequencies and had a higher nestling mortality in their first broods than parents remaining in solitary nests, but neither feeding frequency nor nestling mortality differed from the second broods of parents that remained solitary nesters.

Reproductive effort differed between colonial and solitary breeders in first and second broods, while rearing of three broods caused higher weight loss in colonial than solitary parents. Finally, we suggest that double breeding Tree Sparrows benefit from both colonial and solitary nesting since each choice is advantageous in one of the broods. To choose and retain solitary nests through a breeding season is more advantageous for parents which rear three broods, because they lose fewer nestlings in their third brood and stay in better condition than colonial breeders.

4. Discussion

It is possible for birds to choose different sociality on the basis of breeding experiences and to attempt to improve their performance by changing nesting situation. Switching pairs seem to be in poorer condition before changing and as the move from colonial to solitary breeding is advantageous both by within and between years changing, the future gains, which is predicted by the females is justified in solitary spacing. Although colonial nesting is more advantageous than solitary nesting in first broods, the majority of

females retain colonial breeding through the season in their first year.

The majority of first year females which successfully reared many fledglings with relatively low costs, did so in colonies, only a few females bred solitary. First year females, which suffered higher costs, bred solitary in higher proportion, and when breeding performance was low with high costs, first year females changed their nesting situation next year.

The majority of old females benefited from breeding solitarily and increasing breeding performance with decreasing costs reflects an increasing proportion of solitary breeders in old females. As a consequence, rate of colonial breeders declined steeply in subsequent years.

The final question is why alternative breeding tactics may be maintained as viable reproductive strategies, and which species is able to choose between colonial and solitary breeding throughout life.

Three principal factors seem to induce the retention of alternative breeding tactics. The first factor is multibreeding. Species should be able to breed two or three times within a breeding season. The second factor is a change of food resources during the breeding season. Food environment should become richer and/or more diverse as the season progresses. (There is an adaptive adjustment in Tree Sparrow to the increased food supply: parents rear more fledglings in second and third broods than in first broods.) The third factor is the difference in breeding experience between young and old parents.

In first broods, colonial breeding is advantageous for young parents because they acquire experience from companions. In second and third broods, when they are

able to collect food from a predictable food environment, solitary breeding is advantageous because they have already acquired the necessary experience and want to avoid competition. Older parents which have acquired knowledge about the feeding and nesting environment and have successfully reared large broods in solitary spacing, prefer solitary nesting behaviour.

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Összefoglalás

Alternatív szaporodási taktikák a mezei verébnél

A madárpopulációk aktív válogató-választó képességük révén döntéshozatalokon keresztül tartják fenn életüket. A választás lehetősége úgy maradhatott fenn stabil stratégiaként, ha az alternatív megoldások evolúciós távon megerősítést nyertek. Az eltérő megoldások túlélési értékét és evolúciós léptékű fennmaradását tanulmányoztuk a fenti címmel jelzett kutatási programban.

Hogyan lehetséges két merőben eltérő szociális magatartás és a reprodukció összekapcsolódása, illetve ennek alternatív változása a magánosan és telepesen egyaránt költő madárfajokon? - merült fel az alapvető kérdés. A magyarázatot a mezei verebeken (*Passer montanus*) végzett vizsgálatokkal kíséreltük megtalálni. E faj kolonialis és magános mesterséges megtelepítése után egyedileg jelölt szülők követésével vizsgáltuk a szülők reprodukív teljesítményét, valamint a szülők és a születési helyükön maradó utódok túlélését. Eredményeinket az alábbiakban összegezzük: (1) A költési idő kezdetén, mikor a táplá-

lék kevés, a madarak többsége, főként a fiatal, először költők, telepesen fészkelnek, mert a táplálék fellelése csoportosan hatékonyabb. (2) A rossz reprodukív teljesítményt nyújtó szülők változtatnak a fészkelés módján, a telepesek magánosak lesznek a második költéskor, és fordítva. A változtatás azonban csak a magánossá válóknak lesz előnyös, mert csak ez növeli teljesítményüket. Ugyanis az utódtáplálás ekkor már magánosan hatékonyabb. Harmadik költésre a madarak többsége magánosan fészkel. (3) Évek egymásutánjában az idősödő szülőpárok preferálják a magános költést (már a költésidő elején is), mert szaporodási teljesítményük nagyobb, mint telepesen. Következtetésünk: a madarak költési tapasztalatuk birtokában képesek javítani szaporodási teljesítményüket, és mert a költési szезontól (táplálékellátottságtól), illetve életkoruktól függően eltérően bizonyult előnyösebbnek a telepes majd a magános költés, mindkét társas forma fennmaradhatott evolúciós távon az optimális reprodukív tevékenység megválasztásában.

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The degree and causes of destruction of endangered Great Bustard (*Otis tarda*) nests in Hungarian populations^{*}

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The degree and causes of destruction of Great Bustard nests were studied in eastern Hungary in 1990–1993. 29.5% of 95 known clutches hatched successfully, 17.9% were predated, 49.5% were unsuccessful due to other reasons mainly including the nest desertion and success of 3.1% was unknown. The main egg predators were Hooded Crow, fox and dog. Buffer zones of various sizes were created around some nests during mowing. It appears that areas of at least 900m² of standing vegetation around nests gave the best chance of successful hatching in spite of the predation risk and disturbance. It seems likely that the degree of incubation has an effect on nest desertion.

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1. Introduction

It is well known that the Hungarian Great Bustard population has undergone a considerable decline. In 1941, 8557 individuals were counted (Fodor *et al.* 1971). In the last few years only about 1100 birds have been censused (Fatér unpublished data).

Nowadays, a large part of the population lives in agricultural areas. Cultivated crops may be attractive resources. For example, lucerne can provide a good animal food supply in the reproductive season (Farágó 1988). However, nesting in cultivated lands is dangerous to the species,

because agricultural work, such as the harvesting of lucerne, destroys a considerable number of nests. Ena *et al.* (1987) found that 50% of nests in Spain were destroyed, mainly by farm machinery. In Hungary this destruction was estimated to be 70% (Sterbetz 1980).

This great population decline prompted the Hungarian Ornithological and Nature Conservation Society to start a Great Bustard protection project. In the present study we report some results of this project. Answers were sought to two main questions: i) What is the degree of destruction of endangered clutches? ii) What factors contribute to such nest destruction?

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

2. Material and methods

The nests studied were in Borsod-Abaúj-Zemplén, Heves, Jász-Nagykun-Szolnok and Hajdú-Bihar counties in Eastern Hungary (Fig. 1), from 1990-1993. 82% of the nests were found during agricultural work performed by farm machinery.

When it was possible the previously informed workers left a "buffer zone" around the nests during harvesting. Such nests were checked and if a bird did not come back to the nest for a long time or the situation was very dangerous, the eggs were substituted by artificial ones and placed in an incubator. Later, females which were sitting on artificial eggs received hatching real ones. This procedure often shortened the incubation period, because eggs of other nests, which hatched

earlier, were often put under females. We did not find that females left the clutch because of this changing of eggs. Breeding results were recorded.

We also studied the causes of breeding failure: egg predation, desertion, death of female.

We assume egg predation when broken eggs were found or the nest was empty before the end of the incubation period. The term "desertion" is used only if the female ceased to incubate in spite of having eggs (even artificial ones), except in cases when we had evidence of the death of the bird.

To study the relationship between the potential reasons and success of nests, we measured the following parameters at each nest: distance from the margin of the vegetation unit, diameter of the vegetation unit, size of buffer zone, vegetation type,

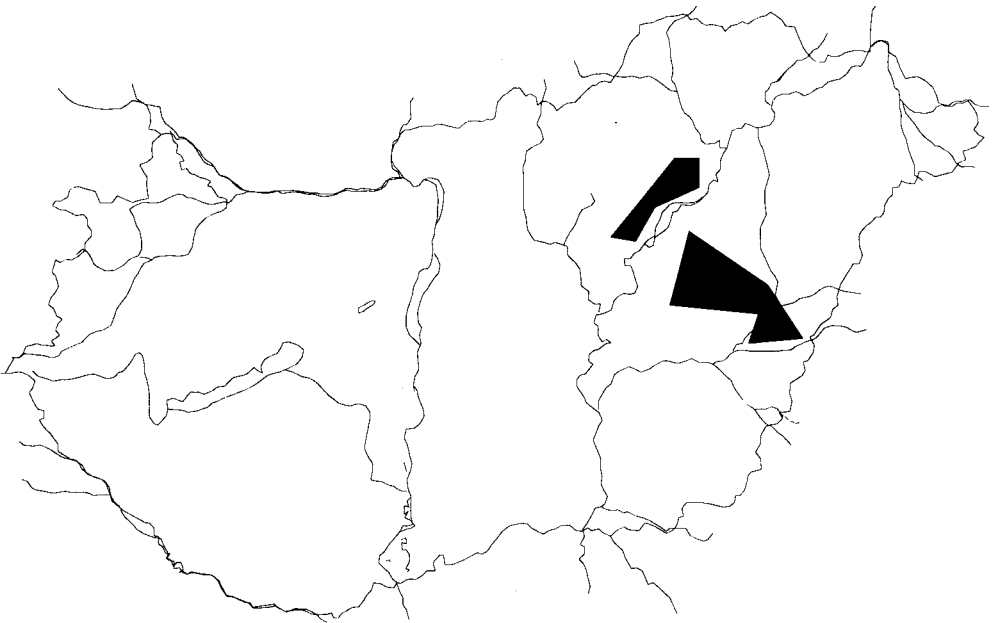


Fig. 1. Map of Hungary showing the location of the study areas.

intensity of vehicle traffic on the nearest track, intensity of pedestrian traffic on the nearest track, number of known rousings, human presence within 1km.

These parameters may be related to predation risk and disturbance. Therefore the features of predated and abandoned clutches were compared with the characteristics of successfully hatched clutches.

We assumed that the incubation investment had an effect on nest desertion. Therefore we compared the degree of incubation (at the time of nest finding) of clutches hatched successfully in the field with clutches which were abandoned immediately. The degree of incubation (in days) was calculated from the known hatching times and the results of water tests (Sukhanova *et al.* 1992). The average incubation period was considered to be 26 days (Faragó 1983, Johnsgard 1991).

Statistical analysis used were the chi-square test and the Fisher's exact test (Vargha 1990).

3. Results

3.1. Breeding result

Altogether 95 nests were found in four years. 55.8% of nests were in lucerne, 28.4% in pasture land or hay fields, 12.6% in cereals and 3.2% in other vegetation.

Only 29.5% of these hatched successfully, 17.9% were destroyed by predators and 49.5% of breeding attempts were unsuccessful due to other reasons including clutch desertion. In 3.1% of cases the success was unknown.

3.2. Predation

The Hooded Crow (*Corvus corone cornix*) was the predator in 9 nests where we found the eggs destroyed. This was verified by field observations. Large animals such as foxes and dogs were responsible for 7 missing clutches and one dead female was found near her destroyed eggs.

Tab. 1. Effect of the studied parameters on egg predation and nest desertion.

Parameter	Predated vs. successful nests	Deserted vs. successful nests
Distance from the margin of the vegetation unit	ns	ns
Diameter of vegetation unit	ns	ns
Size of buffer zone	p<0.05	p<0.05
Vegetation type	ns	ns
Distance to the nearest used track	ns	ns
Intensity of vehicle traffic on the nearest used track	ns	ns
Intensity of pedestrian traffic on the nearest used track	ns	ns
Distance to the nearest settlement	ns	p<0.05
Number of known rousings	ns	ns
Human presence within 1km	ns	ns

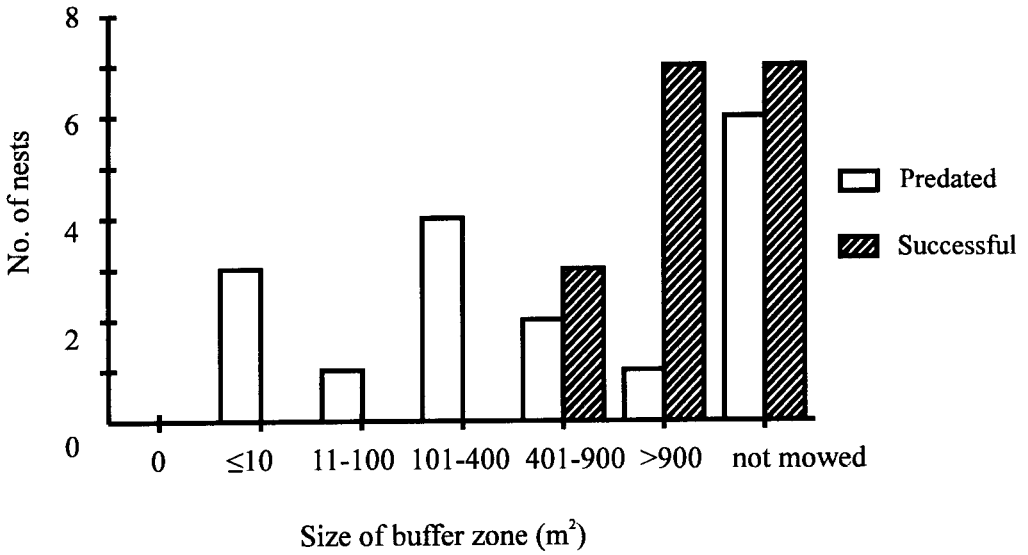


Fig. 2. Frequency distribution of predated and successful Great Bustard nests in different size of buffer zones.

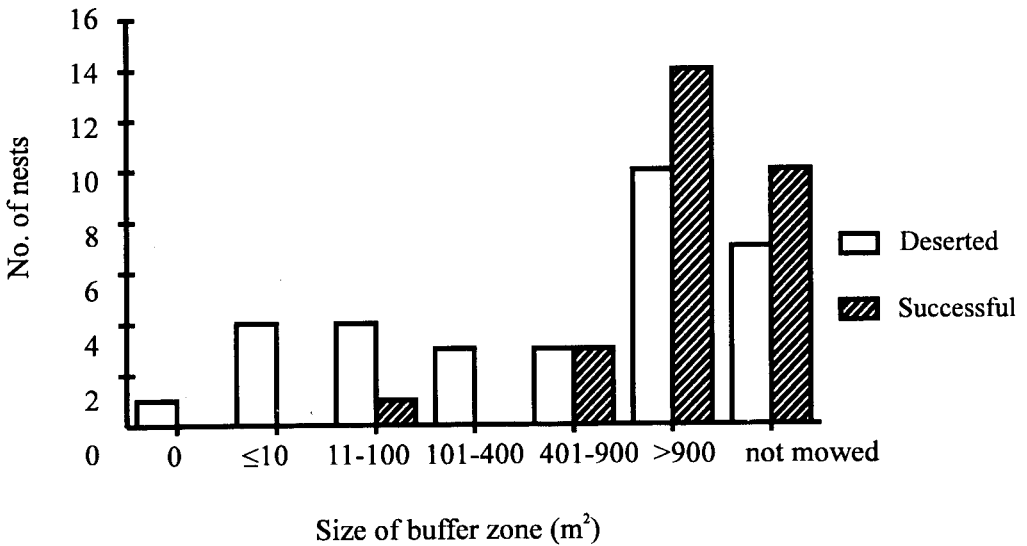


Fig. 3. Frequency distribution of deserted and successful Great Bustard nests in different size of buffer zones.

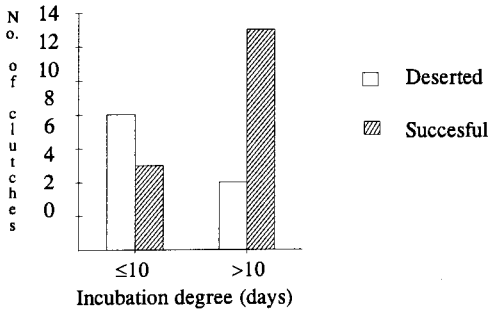


Fig. 4. Incubation degree of immediately deserted and successfully hatched Great Bustard clutches at the time of finding.

Comparing the parameters of predated and not substituted successful clutches we found significant differences only in the size of the buffer zone ($\chi^2_{1\text{corr}}=4.48$; $p<0.05$) (Tab. 1). The majority of successful nests had buffer zones larger than 900m^2 or were in unmowed vegetation (Fig. 2).

3.3. Nest desertion

We have no evidence of disturbance by conspecifics. The cause of nest desertion was the death of a female in one case, when the bird was killed by a mowing machine.

A significant difference was found between the deserted and successful nests in the size of buffer zones ($\chi^2_{1\text{corr}}=5.90$; $p<0.05$) and in the distance of the nearest settlement ($\chi^2_1=4.76$; $p<0.05$) (Tab. 1). The majority of successful nests were in buffer zones larger than 900m^2 or in unmown vegetation (Fig. 3). Contrary to our expectations, the successful nests were closer to settlements.

Difference was found between the incubation degree (at the time of finding) of successful and immediately deserted clutches ($\chi^2_{1\text{corr}}=2.99$; $p<0.05$). The ma-

ajority of successful nests were found later than 10 days incubation (Fig. 4).

4. Discussion

However, we know only a lesser part of really existing nests on the studied area (approx. 170 females) we think that the proportion endangered by human activities is considerably larger. Certainly, conservation measures played important role in success of 29.5% of nests. Distribution of discovered clutches in different vegetations shows that the most dangerous habitats were lucerne and grassland due to mowing.

In cases of both predation and nest desertion, the size of the buffer zone seems relevant. A great proportion of studied nests went through mowing which produced a vegetation island around it. Later gathering work takes place close to nests which can also be found easily by predators. It is likely, that the effects of disturbance and predation risk prevail through the size of the vegetation island – although nests were often on the margin of it – and most of the other parameters lose their importance. However, successfully hatched clutches were closer to settlements, sizes of their buffer zones were larger. According to our opinion this fact also verify the previous statement.

Considering the difference between the incubation degree of deserted and successful clutches, and that we have experienced the desertion of just hatching eggs only on one occasion, it seems likely that increasing incubation investment could reduce the probability of nest desertion.

The results provide an opportunity to draw practical conclusions. It appears that

the ideal required size of buffer zones, which gives chance the nests to reach the hatching, is bigger than 900m². This size is guaranteed only, when the borders of it have been marked out before mowing. According to our experiences incubating females often tolerate the short time presence of 1–2 persons from a distance of 20–30 meters. This procedure necessitate accurate observations about nesting birds which sometimes very difficult. Therefore exact information of agricultural workers is very important. On the other hand, the postponement of harvesting for a few days could reduce the probability of nest desertion.

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Összefoglalás

A fészkek-pusztulások mértéke és oka magyarországi túzok (*Otis tarda*) populációkban

Kelet-Magyarországi vizsgálati területünkön a túzok fészkek pusztulásának mértékét és okait tanulmányoztuk 1990–1993 között. Kilencvenöt ismert fészekből 29,5% kelt ki sikeresen, 17,9%-t ragadozók fosztottak ki, 49,5% más okok miatt volt sikertelen, elsősorban a fészkek elhagyása miatt. Az ismert fészkek

3,1%-nak sorsa ismeretlen maradt. A fő predátorok a szürke varjak, rókák és kutyák voltak. Egyes fészkek körül különböző méretű puffer (nem bolygatott) zónák lettek kialakítva a kaszálás során. Eredményeink szerint legalább 900m² érintetlen vegetáció szükséges a fészkek sikerének biztosításához a predáció és zavarás ellen. Valószínű, hogy a kotlottság mértékének is hatása van a fészkek elhagyására.

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Is information transfer always advantageous when food patchily distributed? A simple ESS model

Z. Barta and T. Szép

Barta, Z. and Szép, T. 1994. Is information transfer always advantageous when food patchily distributed? A simple ESS model. – *Ornis Hung.* 4:25–30.



One of the potential benefits of colonial breeding may be using information on the location of food gained from other members of the colony. Obtaining this information without searching may improve the foraging efficiency especially when food occurs in rich patches whose locations are unpredictable both in space and time. A question is arising: is this efficiency really improved by the information transfer? Using the game theory we modelled the problem by two strategies: (1) Searcher looks for food actively and (2) Follower reaches the food patch by following Searchers. Investigating the equilibrium between these strategies we concluded that information transfer may increase the individuals' average foraging efficiency when the Searchers gain benefits from the exchange too.

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1. Introduction

Thirteen percent of bird species breed in colonies (Lack 1968) even though this behaviour has many disadvantages including the increased possibility of ectoparasite or disease infection (Brown & Brown 1986, 1988, Wittenberger & Hunt 1985) and intensive competition for food, nest sites, nest materials and mates (Wittenberger & Hunt 1985). One of the likely benefits from coloniality may be the possibility of using information on the location of food from other members of the colony to improve foraging efficiency (Krebs 1974).

The food of many colonial birds is located in rich patches which are distributed

in an unpredictable fashion both in space and time (Ward & Zahavi 1973, Krebs 1974). Under these conditions finding a food patch is very costly. However, if a bird can obtain information on the location of food without searching then the saving in time and energy may be spent in increasing its foraging efficiency.

The most widely accepted way of acquiring information is through the mechanism of information centre (Ward & Zahavi 1973, Mock *et al.* 1988). This hypothesis supposes that a previously unsuccessful individual can follow its successful colony mates to their previously discovered foraging site. Furthermore it is assumed that the unsuccessful birds parasitize the successful ones and that the parasites gain a net benefit while the

parasitized one suffers a slight or no cost (Krebs 1978, Evans 1982, Mock *et al.* 1988). Beauchamp & Lefebvre (1988) studied this situation using the ESS approach (Maynard Smith 1982). They found that the information gainer strategy (following strategy) can be evolutionary stable if it is difficult to find a new food patch and enough food remain in the patch after the initial discovering. However, the average feeding rate in their ESS was smaller than that would be in the case of non-following strategy. They supposed that the lower variance of feeding rate associated with the following strategy and other forms of information transfer (e.g. local enhancement or network foraging) could still explain why the birds breed colonially. Almost all of the previous studies supposed that an individual follows its colony member just after a long unsuccessful foraging trip. For example Beauchamp & Lefebvre (1988) used fixed maximum searching time for all individuals in their model. However, one can expect that some of the colony members will cheat, namely will not spend a long time searching if they have the possibility to follow other successful birds.

In this paper, using a very simple ESS model, we investigate whether these two strategies of searching and following can exist together and furthermore whether the information transfer at a breeding colony, in spite of the cheating, can alone explain the maintenance of coloniality.

2. The model

We modelled the information exchange by two strategies – Searcher and Follower. The former looks for food and the latter

waits at its nest for a successful individual and then follows it (Barta & Szép 1992). After the finding of food, both of them return to the discovered patch.

Tab. 1 shows the payoff matrix of the game. The elements of the matrix were considered to be energy intake rate which a forager experiences when it feeds with others of the given strategies. We did not distinguish between cases when the Searcher forages alone or with other Searchers. On the other hand Followers were assumed to always feed with Searchers. When a Follower plays against another Follower its intake rate was presumed to be zero since nobody searches for food. Assuming that following is more advantageous than searching, we set the energy intake rate of Follower against Searcher (c) larger than the payoff of Searcher against another Searcher (a). Let p be the proportion of Searchers in the population. Under these conditions the proportion of strategies reaches an equilibrium point where

$$p = b/(c-a+b) \quad c-a+b \neq 0 \quad (1)$$

Since 'c' was assumed greater than 'a' only a mixed ESS is the solution of this game ($p < 1$).

Tab. 1. The payoff matrix to player 1 of the game between two different foraging strategies. Searcher looks for food and Follower follows their successful colony members. Letters denote energy intake rate.

		Player 2	
		Searcher	Follower
Player 1	Searcher	a	b
	Follower	c	0

Consider a population that consists of both Searchers and Followers. The payoff to Searchers is:

$$W_S^E = pa + (1-p)b \quad (2)$$

and that to Followers is

$$W_F^E = pc \quad (3)$$

When the population is in equilibrium then these payoffs are equal:

$$W_S^E = W_F^E = W^E \quad (4)$$

where W^E denotes the fitness of an average individual in the population (Maynard Smith 1982). Let us consider another population that consists of Searchers ($p=1$) only. Information transfer of food location is not allowed in this population. Now the payoff of Searchers is:

$$W_S^S = a \quad (5)$$

3. Results

Comparing the payoffs of Searchers in these populations we can evaluate the effect of information exchange on the foraging success of individuals. We can distinguish three cases on the basis of how the presence of Followers influences the payoff of Searchers.

First when the food is limited, the attendance of Followers decreases the intake rate of Searchers ($a > b$). Under these conditions the relation of payoffs is:

$$pa + (1-p)b < a \quad (6)$$

Hence the individuals in the mixed population benefit less than they would do if they live in a pure Searcher population (Fig. 1a).

In the second case the food is assumed to occur in very dense but short life-span patches which is the case of many colonial bird (Ward & Zahavi 1973). Consequently it is unlimited so the Followers do not influence the energy intake rate of Searchers ($a = b$). Now the compared payoffs have the following relationship:

$$pa + (1-p)b = a \quad (7)$$

namely the information transfer does not affect the foraging success of average individuals (Fig. 1b).

Thirdly, the presence of Followers improves the foraging efficiency of Searchers ($a < b$) when the connection between the payoffs is:

$$pa + (1-p)b > a \quad (8)$$

So the information transfer can only improve the success of birds in this case (Fig. 1c).

The effects of either kin selection or reciprocal altruism is a further possibility to increase the average foraging efficiency for an individual. They may drive the proportion of Searcher (p) from its equilibrium point toward the maximum (Fig. 1a).

4. Discussion

An evolutionary biologist should assume (i) regular changes of the roles of searching and following or (ii) an ESS mixed from these two strategies so that the in-

formation transfer at a central place can exist. In the case of the first assumption the individuals can benefit from information transfer (Barta & Szé \acute{c} p 1992), however, the conditions of maintaining the regularity by kin selection or reciprocal altruism are often not realized under the circumstances of large crowded colonies (Waltz 1982, Mock *et al.* 1988, Galef 1991).

On the base of the presented model, when mixed ESS exists in the population, the information transfer can only improve the foraging efficiency of individuals if both Searchers and Followers gain advantages

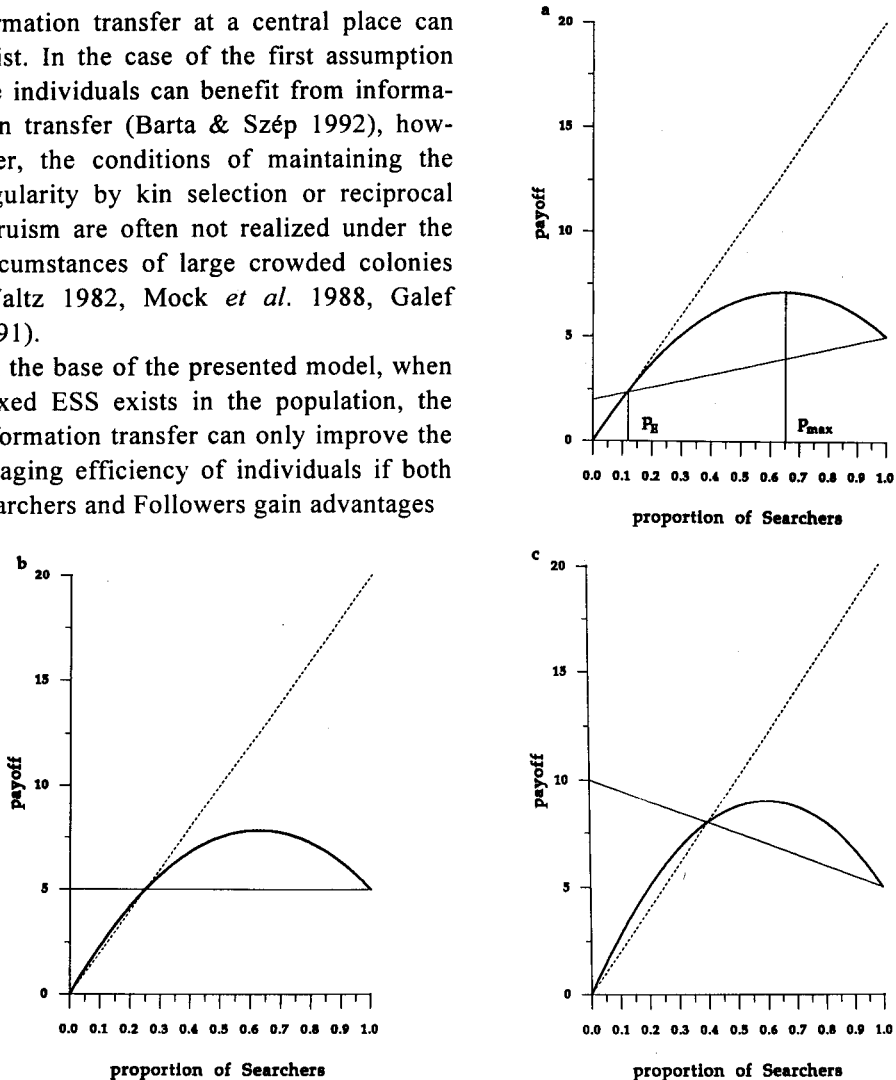


Fig. 1. Graphic presentation of the foraging game. Solid line indicates payoff of Searcher, dotted line marks payoff of Follower and heavy line shows the payoff of an average individual. The payoff of an average individual in a pure Searcher population is equal to 5. Arbitrary parameters of the games are given in brackets.

a. The Followers decreased the payoff of Searchers. The population can reach the maximum average payoff due to the effects of kin selection or reciprocal altruism which may drive p from p_E to p_{max} . p is the proportion of Searchers, p_E is the equilibrium proportion of Searchers and at p_{max} an average individual reaches maximum payoff ($a=5$, $b=2$, $c=20$).

b. The Followers did not influence the payoff of Searchers ($a=5$, $b=5$, $c=20$).

c. The Followers increased the payoff of Searchers ($a=5$, $b=10$, $c=20$).

from the exchange. However, these benefits of Searchers may be caused by factors outside of information transfer, e.g. social foraging (Götmark *et al.* 1986) and anti-predation advantages (Mock *et al.* 1988). Therefore, one may conclude that the information transfer alone may not be able to maintain the colonial nesting in the common cases (e. g. large crowded colonies). In other words, the widely used condition of patchily distributed food for the advantage of information transfer may not be sufficient, and it would be needed to amplify with the benefits of Searchers. When we do not assume benefits for Searchers, the information transfer could decrease the foraging success of individuals (Vickery *et al.* 1991, Caraco & Giraldeau 1991).

The most widely cited field studies of information transfer are those of Brown (1986, 1988) and Greene (1987). Both studies were able to demonstrate the improvement of information exchange on foraging efficiency of colony members. In the osprey colony studied by Greene (1987) close relatives lived together so the kin selection may be responsible for the benefits of information transfer. On the other hand, the degree of relatedness in cliff swallow colonies was very low (Brown 1986). Brown (1986) supposed that both Searcher and Follower cliff swallows benefit from information transfer which may be supported by their food sharing call (Brown *et al.* 1991). One of the possible benefits may be that the Searcher can more easily find the food patch with the aid of Followers on its subsequent trip. This is so of the swallows, since the food patch (aerial swarms of insects) can easily move away during a short time (Emlen & Demong 1975, Brown *et al.* 1991).

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Összefoglalás

Előnyös-e mindig az információ átadás foltszerű táplálék esetén? Egy egyszerű ESS modell

A telepes fészkelés egyik lehetséges előnye a teleptársak által gyűjtött, a táplálék helyéről szóló információ felhasználása. Ennek az információnak keresés nélküli megszerzése növelheti az egyedek táplálkozási hatékonyságát, különösen, ha a táplálék ritka, de gazdag foltokban fordul elő, és a foltok helye időben jószolható. Egy kérdés merül fel: tényleg növeli-e az információ-átadás a táplálkozási hatékonyságot? A játékelmélet eszközeit használva két táplálkozási stratégiával modelleztük a problémát: (i) a Kereső aktívan keres a táplálékfoltok után, (ii) a Követő a Keresőt követve éri el a táplálékfoltot. A két stratégia között beállt egyensúlyt vizsgálva, az a következtetés vonható le, hogy az információ-átadás csak akkor növeli a táplálkozási hatékonyságot, ha a Keresőknek is előnyös az átadás.

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Autumn migration dynamics of the Sedge Warbler (*Acrocephalus schoenobaenus*) in Hungary

J. Gyurácz and T. Csörgő

Gyurácz, J. & Csörgő, T. 1994. Autumn migration dynamics of Sedge Warbler (*Acrocephalus schoenobaenus*) in Hungary. – *Ornis Hung.* 4:31–37.



More than 3500 Sedge Warblers were trapped at "Actio Hungarica" camps of the Hungarian Ornithological and Nature Conservation Society in 1990. The migration dynamics of the Sedge Warbler is described in this paper. There were significant differences in the timing of migration between the three stopover sites under study. The median dates were: 17 August at Ócsa (47°19'N, 19°13'E), 19 August at Fenékpusztá (46°44' N, 17°14' E), and 16 August in Sumony (45°58'N, 17°56'E). Adults usually migrate earlier than juveniles. The birds were equally likely to be recaptured at each stopover site, but stopover time differed between stopover sites. The northern populations come from Southern Scandinavia and the Baltic region and migrate in largest numbers at the end of August and in early September in the Carpathian Basin.

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1. Introduction

The *Acrocephalus* Project of EURING (European Union for Bird Ringing) was started in 1981. The Hungarian Ornithological and Nature Conservation Society joined this international research program, which was started to assess the breeding areas, migratory routes dynamics and stopover sites of different migrating populations of *Acrocephalus* warblers. This work is important to the research of alternative evolutionary strategies of related species as well as to practical nature conservation (Csörgő 1991, Koskimies & Saurola 1985, Spina & Bezzi 1990).

The best-known migration dynamics

of European Sedge Warblers is that of the British populations. Their migration is fast and it considerably depends on the presence and quantity of the reed aphid (*Hyalopterus pruni*) considerably (Bibby *et al.* 1976, Bibby & Green 1981, Gladwin 1963, Insley & Boswell 1978, Ormerod 1990, Pepler & Pepler 1972, Shennan 1986, Sitters 1972). We also have information on migrating birds from France (Bibby & Green 1983), Yugoslavia (Gergely 1986), Finland (Koskimies & Saurola 1985) and Italy (Spina & Bezzi 1990). Dynamics (Gyurácz & Csörgő 1991), direction (Csörgő 1991, Csörgő & Ujhelyi 1991) and the age differences in migration (Gyurácz & Csörgő 1991) were examined in Hungary. Little is known

about the important stopover sites of Sedge Warblers in Central and South-East-Europe. Hungary took the initiative in the research of bird migration in Bulgaria (Burgas), Rumania (Istria), Croatia (Pag), Serbia (Ludas), but the data is yet to be processed.

This paper analyses the spatial differences in autumn migration dynamics of European Sedge Warblers and the age dependence of migration in Hungary.

2. Study area and methods

The birds were caught and ringed in the "Actio Hungarica" camps of the Hungarian Ornithological and Nature Conservation Society in 1990.

The three study sites were: Ócsa (47°19'N, 19°13'E), Fenékpuszta (46°44'N, 17°14'E) and Sumony (45°58'N, 17°56'E). The nets stood both in homogeneous reed beds (in standing water) and in dry bushes at Ócsa and Sumony, while they were only in the reed bed of Lake Balaton at Fenékpuszta. The study was carried out between 15 July and 15 September at Ócsa, between 15 July and 23 September at Fenékpuszta and between 28 July and 9 September at Sumony. Thus, we could compare the three study sites between 28 July and 9 September. The nets were 12 m long and 2,5 m high. The area of nets erected was constant in each area, the overall surface of nets was 1980 m² at Ócsa, 300 m² at Fenékpuszta, and 900 m² at Sumony. The birds were extracted from the net in every hour, with the first net-check at dawn, and the last one after dark. All birds were ringed, sexed, and aged according to Svensson (1984). Of the 3895 Sedge Warblers ringed in 1990,

309 were ringed at Ócsa, 3185 at Fenékpuszta, and 401 at Sumony.

The migration diagrams were calculated from the number of ringed and recaptured birds per day. We calculated the percentage of adults, and juveniles for five-day periods (pentads). The "minimum" stopover time of a bird was calculated from the first capture and the last recapture dates. We only considered birds that were ringed and recaptured at the same study site in 1990.

3. Results

There were significant differences in the timing of migration between the three stopover sites in respect of the same migration period, from 28 July to 09 September. The median date was 17 August at Ócsa, 19 August at Fenékpuszta, and 16 August at Sumony. The differences were: Ócsa-Fenékpuszta $z=7.64$, $P<0.01$, Ócsa-Sumony $z=3.27$, $P<0.05$, Fenékpuszta-Sumony $z=7.28$, $P<0.01$ (Mann-Whitney U-test, Fig. 1)

The migration dynamics of juveniles and adults did not differ significantly at Ócsa (median pentad_{ad}=04-08 Aug, $S^2_{ad}=62.88$, median pentad_{juv}=09-13 Aug, $S^2_{juv}=26.21$, $F=2.39$, $d.f.=9$, $P>0.05$), nor did at Fenékpuszta (median pentad_{ad}=04-08 Aug, $S^2_{ad}=40.19$, median pentad_{juv}=19-23 Aug, $S^2_{juv}=28.40$, $F=1.41$, $d.f.=9$, $P>0.05$), and nor did at Sumony (median pentad_{ad}=09-13 Aug, $S^2_{ad}=42.77$, median pentad_{juv}=19-23 Aug, $S^2_{juv}=20.43$, $F=2.09$, $d.f.=9$, $P>0.05$, Fig. 2).

In total, 429 individuals were recaptured at least one day after ringing. At Ócsa 44 (14% of total birds ringed), at Fenékpuszta 367 (12%) and at Sumony 18

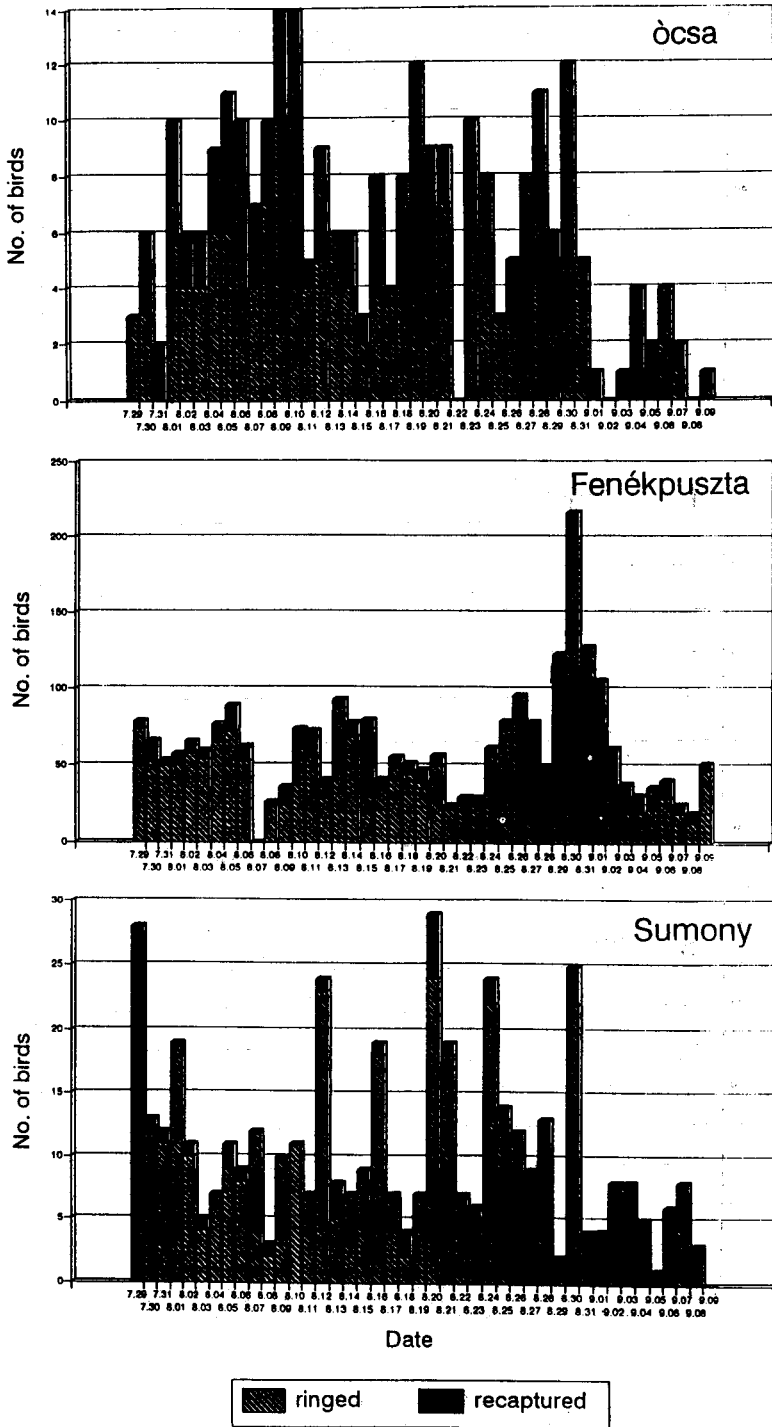


Fig. 1. The timing of migration of the Sedge Warblers at the three study areas.

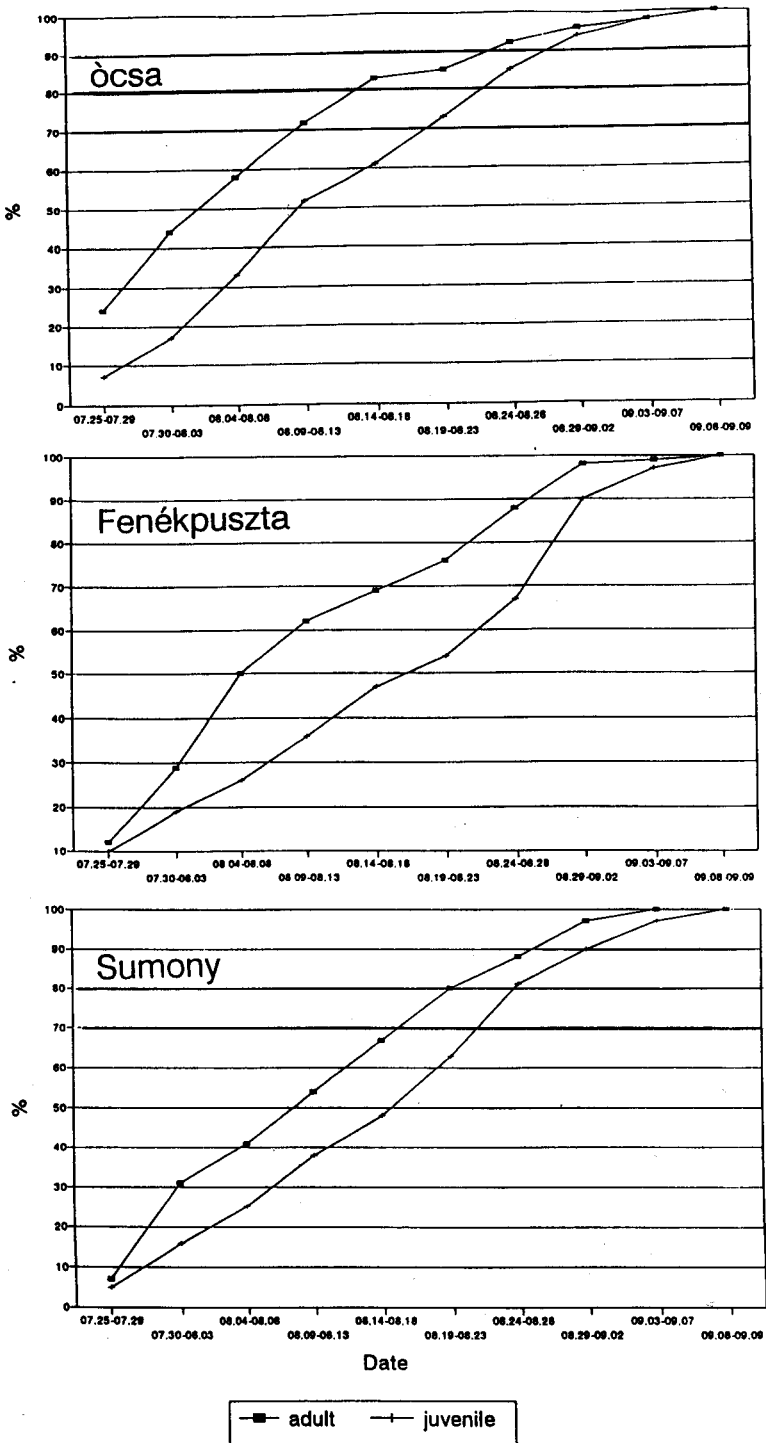


Fig. 2. Migration curve of adult and juvenile Sedge Warblers at the three study areas.

(5%) birds were recaptured. The birds were equally likely to be recaptured in each stopover site ($\chi^2=4,33$, d.f.=2, $P>0.05$).

Stopover time (birds not recaptured were excluded from the calculations) differed between stopover sites. The average length of stopover was 7.72 ± 6.08 days at Ócsa (N=44), 5.66 ± 4.46 days at Fenékpusztá (N=367), and 7.50 ± 5.2 days at Sumony (N=18). There was a significant difference between Ócsa and Fenékpusztá (one-way ANOVA, $F=5.31$, d.f.=4.26, $P<0.05$).

4. Discussion

The majority of Sedge Warblers usually pass through Hungary at the end of August and in early September. Hungarian results are in accordance with the foreign findings. The migration is fast and continues for a long time, similar to that of West-European populations (Pepler & Pepler 1972, Sitters 1972). Mainly birds from Southern Scandinavia and the Baltic region migrate through the Carpathian Basin in addition to smaller numbers of Central European populations in the second half of August and in early September. The median capture date was 15 August for adults and 24 August for juvenile birds arriving from northern areas of Hungary (Csörgő & Ujhelyi 1991). The peak of the migration of Sedge Warblers is in early August in Finland (Koskimies and Saurola 1985). According to Bibby *et al.* (1976), the migration of more southern populations starts gradually earlier, because of the early senescence of reed. This statement relates to local breeding populations, too, which migrate earlier than more northern populations (Zwicker 1982).

The peak of the Sedge Warbler migration avoids Ócsa, therefore this area is not an important stopover area for migrating northern populations. Most Sedge Warblers were ringed at Fenékpusztá. The reason for this is that the reed belt of Lake Balaton is very narrow at the mistnetting site, and it packs the birds together, that otherwise would move in the wide reed bed, an area not studied. There were not researches during migration in similar extensive reed beds, for instance at Lake Fertő and Lake Velence in Transdanubia, or at the fish ponds of Hortobágy in Eastern Hungary. We do not know what is the role of these large reed beds as of the migrating Sedge Warblers in Hungary. Reed beds can be found in the Great Hungarian Plain at the same latitude as Fenékpusztá and Sumony. We suppose that these reed beds also have an important role in the migration of the northern populations of Sedge Warbler.

The direction of migration averaged 182° , almost exactly southward to the birds arriving from the Baltic region to Hungary (Csörgő & Ujhelyi 1991). It is possible that a smaller part of the Baltic population of Sedge Warbler migrates East of the Carpathians and has a stopover site in Dobruzsa near the Black Sea (the first Estonia-ringed Sedge Warbler was found at Istria in 1992). The role of the reed beds in the migration of European Sedge Warblers is still unknown in South and East-Europe. The simultaneous application of the orientation cage (Spina & Bezzi 1990) is necessary at more sites for exact assessment of the migration directions in Hungary. The comparative analysis of morphological features (wing length, wing shape) of birds trapped at different latitudes would be important in order to know the sites of origin of the migrating populations.

The adults leave the breeding area about one or two weeks earlier than juveniles do (Gyurácz & Csörgő 1991, Insley & Boswell 1978, Koskimies & Saurola 1985, Spina & Bezzi 1990). This difference may have morphological, physiological and evolutionary reasons. (1) The adults have longer wings than juveniles. The longer wing makes faster flight possible for adults (Albu 1983). The juveniles' shorter wings increase the ability of manoeuvring, so they help in feeding. The adults compensate for the decreased ability of manoeuvring by experience (Alatalo *et al.* 1983). (2) The wing and tail of juveniles grow even after leaving the nest and as they are inexperienced as well as less efficient than adults in gathering food, they need a longer period for developing fat reserves before migration (Koskimies & Saurola 1985). (3) This species occupy territories in the wintering area (Moreau 1972). The earlier arriving birds may be able to occupy better territories and can increase their fitness. The earlier arrival does not always imply a shorter migratory route. The reason for this may be that they reach the sufficient fat level earlier (arriving-time hypothesis: Ketterson & Nolan 1983). Huszel (1991) examined an *Empidonax* species in North-America and argues that the dependence of migration on age can also be explained by competition for wintering territories. The juveniles cannot occupy territories in the wintering area, therefore earlier migration is not advantageous for them. (4) The decrease in food abundance influences migration of the juveniles in the breeding area.

The conservation of the breeding habitats, stopover sites and wintering areas of Sedge Warbler populations is very

important because the sizes of breeding populations have decreased all over Europe during the last decades (Haland 1982, Marchant *et al.* 1990, Spina & Bezzi 1990). The preservation of reed beds in Hungary is necessary not only for the protection of Hungarian breeding populations, but for the protection of Scandinavian and Baltic populations over Hungary.

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Összefoglalás

A foltos nádiposzáta (*Acrocephalus schoenobaenus*) őszi vonulásdinamikája Magyarországon

A Magyar Madártani és Természetvédelmi Egyesület "Actio Hungarica" madárgyűrző táborában (Ócsa, Fenékpusztá, Sumony) 1990-ben gyűrzött több mint 3500 foltos nádiposzáta adatai alapján vizsgáltuk a faj vonulásának dinamikáját. A vonulás csúcs ideje (a befogott madarak 50%-hoz tartozó időpont) alapján megállapítottuk, hogy Fenékpusztán és Sumonyban augusztus végén, szeptember elején is intenzív a vonulás. Ennek oka, hogy ebben az időszakban vonulnak át legnagyobb számban a Dél-Skandináviából és a Balti-tenger térségéből származó populációk Magyarországon. Ócsán ezt kevésbé lehet tapasztalni, mert ott nem, vagy csak kis számban pihennek meg az északi madarak. Az öreg madarak előbb vonulnak mint a fiatalok. A megpihenő madarak átlagos tartózkodási ideje Fenékpusztán volt a legrövidebb.

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Short communications – Rövid közlemények

Breeding site fidelity of Great Tits (*Parus major*) in a Central-European alder forest

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Many passerine birds are faithful to the same area, because familiarity with previously occupied sites may enhance reproductive success and survival (Slagsvold & Lifjeld 1990). Dispersion, however, seems to be an advantageous evolutionary strategy through the avoidance of inbreeding (Perrins 1990).

Our aim in this study is to demonstrate the breeding area fidelity of Great Tit in a Hungarian black alder (*Alnus glutinosa*) forest. The study was conducted in the Ócsa Landscape Conservation Area (47°15'N; 19°15'E) from 1986 to 1990. A nestbox area was created with 100 nestboxes in the early spring of 1986. The movement of ringed individuals was followed within and between breeding seasons. The description of the study area and the methods are given in Báldi (1991), Báldi & Csörgő (1994).

We used data in which the same individuals were recaptured in the nestboxes or were mistnetted before the entrance of

the nesting holes. In addition, we included those records of pairs in which either the male or the female was captured, though we caught both individuals in an other breeding attempt.

During the study there were altogether 57 observations (Tab. 1). The differences between within year and between years dispersal distances seems to be great in both sexes, although not significant, possible due to the small sample size (procedure ONEWAY from the SPSS/PC+ (Norusis 1986); degree of freedom=56, F ratio=3.458, $p=0.0683$). Both sexes' dispersion distances proved to be similar (degree of freedom=56, F ratio=0.004, $p=0.950$).

Our findings corroborate the results of other authors. Harvey *et al.* (1979) found that 75% of Great Tits moved less than 100 m in England. Winkel & Frantzen (1989) studied dispersal of Great Tits in Germany. They found that 78% of males and 67% of females chose nesting hole in

different year within 100 m. We argue, that the breeding area fidelity of the Great Tits is irrespective of habitats, since similar dispersal distances were achieved in different habitats.

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Tab. 1. Breeding area fidelity of the Great Tit in a Hungarian alder forest. (N: number of individuals; %: percent of movements within 100 m; X: average distance between breeding holes).

		N	%	X (m)	SE	Range(m)
Males	Within year	5	80	50.4	29.3	30–108
	Between years	12	75	67.2	44.7	0–175
Females	Within year	21	95	49.9	26.7	30–108
	Between years	19	68	75.4	53.7	0–210