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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, 19^0,04' E; 47^0,41' 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 youngs 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 interbrood 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-egglaying investment, which reduces parental condition and may influence factors determining weather 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 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 döntésfolyamatokon 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 koloniális és magános mesterséges megtelepítése után egyedileg jelölt szülők követésével visgáltuk a szülők reproduktív teljesítményét, valamint a szülők és a születési helyükön maradó utódok túlélését. Eredményeinket az alábbiakban összegezhetjük: (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 reproduktív 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 szezontól (táplálékellátottságtól), illetve életkoruktól függően eltérően bizonyult előnyösebbnek a telepes majd a magános költés, mindkét társas forma fennmaradhatott evolúciós távon az optimális reproduktív tevékenység megválasztásában.

Jelen tanulmány az Acta Oecologica (1993, 14: 447-487), a Journal of Animal Ecology (1994, 63: 265-274), és a Behavioral Ecology and Sociobiology (1994, 34: 113-123) lapokban megjelent dolgozatok összefoglaló szintézise.

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