Reproductive effort of colonial and solitary breeding tree sparrows *Passer montanus* L.

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**Abstract.** A total of 250 nestboxes were arranged in five plots in a suburban area of Budapest, Hungary (19°04'E, 47°41'N). In each plot, 25 were placed at 50 m intervals to simulate solitary breeding and 25 3–5 m apart to simulate colonial breeding. Length of nest building period, feeding frequency, nestling mortality, nestlings' diet, productivity and parental condition were compared for colonial and solitary breeding tree sparrows *Passer montanus*. Parents with long nest-building periods, including the majority of first-year females, produced fewer young than parents which built over short periods. Parents fed nestlings more frequently and nestlings had lower mortality in second than first broods; whether or not a third brood was reared was determined by the costs invested in first and second broods. Females that laid a third clutch had reared fewer young in first and second broods and were heavier than females that reared many young in two broods. Colonial birds had higher feeding frequencies, more similar diets and suffered lower nestling mortality than solitary parents for first broods, but they fed less frequently, diets were less similar, and nestling mortality was higher in second and third broods. It is suggested that colonial breeders benefited from the social stimulation of simultaneous feeding in first broods, but the advantage of synchronicity in feeding declined in second broods and the sparser breeding spacing of solitary parents was more advantageous for feeding in second and third broods. Birds that changed nest spacing between broods had fed nestlings less frequently and had higher nestling mortality before changing than birds which retained their spacing. Parents which changed from colonies to solitary nests fed more frequently with lower nestling mortality in the next brood than parents which retained colonial nests for their second (and third) brood. Solitary parents did not show such a relationship. The rearing of three broods caused higher weight loss in colonial than solitary parents.

**Introduction**

Recent studies of the costs and benefits of colonial breeding in birds have focused on the adaptive advantages of coloniality arising from food acquisition (Crook 1962; Horn 1968; Ward and Zahavi 1973; Krebs 1978; Waltz 1983) and predator avoidance (Kruuk 1964; Hoogland and Sherman 1976; Veen 1977; Götmark and Andersson 1980). 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 and Hunt 1985). Infanticide and intraspecific nest parasitism have also been associated with colonial breeding (Hoogland and Sherman 1976; Moller 1987). Some authors have suggested that shortage of nesting habitat rather than direct benefits of group living are responsible for coloniality (Lack 1968; Snapp 1976; Shields and Crook 1987).

Comparative studies on reproductive effort of colonial and non-colonial breeders of the same species may help to elucidate the adaptive significance of coloniality. Tree sparrows breed both colonially and solitarily in various suburban and agricultural habitats (Pinowski 1968; Summers-Smith 1988). They nest in groups, commonly in the nests of white storks *Ciconia ciconia* and birds of prey, in the earth 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 rearing multiple broods. Body mass and feeding frequency have commonly been used to estimate the reproductive effort of passerines; we also included nest-
building activity as a reproductive investment in the tree sparrow. We simulated colonial and solitary breeding situations by placing nestboxes densely and sparsely. Our study focused on nest-building activity, feeding frequency and nestlings' food composition in relation to (i) breeding performance, (ii) parental condition and (iii) colonial and solitary breeding.

Methods

Five study plots were chosen in a suburban park of Budapest (19° 04'E, 47° 41'N, Cemetery Park) and 50 nestboxes were distributed in each of the study plots; 25 boxes were placed 3-5 m apart to simulate colonial breeding and 25 sited approximately 50 m apart to simulate solitary breeding. The distance between neighbouring study plots was 500 m. Shrubs and trees of various species and ages including locust trees Robinia pseudoacacia, poplar Populus italica, horse-chestnut Aesculus hippocastaneum and lilac Syringa vulgaris were scattered through the parks. Arable land and locust trees 20–30 years old surround the park.

The nestboxes were checked at 3- or 4-day intervals from the middle of March until the end of August during the 7-year study period (1986–1992). When the appearance of first nest material, laying of the first or last egg, hatching or fledging of nestlings from the nest occurred during the period 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 (Svenson 1975) when birds were captured during the breeding season. Tree sparrows often desert nests if they are caught and marked during nest building or incubation (Pinowski et al. 1973), so trapping during breeding was restricted to the nesting period. As the tree sparrow can be aged with certainty only by marking the nestlings, we used only recruited offspring banded as nestlings in some analyses. Young were individually colour-ringed during the late nestling period.

The study of 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 nest-building period was divided into six time units: 1-3, 4-6, 7-9, 10-12, 13-15 and 16-18 days, taken from the first appearance of nest material to the laying of the first egg.

Some authors (Turner 1965; Krebs 1978; Ward and Zahavi 1973) have suggested that synchronous activities are advantageous for colonial parents both during the nest-building and feeding periods. Hence we recorded simultaneous visits at neighbouring nests and single nests by male and female by visual observation. Visits were recorded for 1 h in 1-3, 7-9 and 13–15 day units of the nest-building period and in 1-3 and 4-7 days of interbrood intervals, after the young had fledged. Feeding visits were observed for 1 h in early and late feeding periods. When neighbouring pairs (or one member each from neighbouring pairs) were present at the same time on the trees where nestboxes hung, simultaneous visits were recorded. When both sexes were present on the tree where their nestboxes hung, between-sex synchronicity was noted. We recorded the number of occurrences of synchronous stay; the length of visits was not considered. Neighbouring nests were chosen at random; the distance between nests was a maximum 5 m in colonies.

Traffic of parents during the nestling period was determined using photocell devices with an automatic recorder. Devices were fixed to the entrances of nestboxes for 24 h during early and late nestling periods, at 5-8 and 9-12 days after the young hatched. Objects resembling photocell devices were placed at the nestboxes before nesting, so that when actual devices were used they did not affect the birds' behaviour. Automatic recorders and software developed for the Commodore 64 computer tabulated the number of visits per hour. As the parents flew in and out of the nestboxes during the feeding activities, the number of passes through the entrance was divided by two for calculation of feeding frequency during the nestling period. This was assumed to be an accurate measure of feeding frequency because tits, which might have visited the nests of tree sparrows, were incubating eggs or feeding young, so they were busy in their own broods. When we recorded simultaneous feeding activities, 17 visits to colonial nests and 8 visits to solitary nests from tree sparrows which were not the owners were observed visually during the total observational period. Assuming that such a low visit frequency from foraging tree sparrows in our study area applies throughout the feeding period, the results obtained with photocell devices would not be influenced by these activities.

Two neighbouring nests were chosen for 60 colonial and 60 solitary pairs to study dietary diversity and similarity. Nestlings' food was collected by the neck-collar method in the early (5-8 days) and late (9-12 days) feeding period. A total of 74 food types were distinguished mainly by the families of insects, and diversity of food composition was calculated by 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 brood failures and brood reduction], and number of fledglings were used as parameters for the analyses of breeding performance. Weights of the parents were measured with Pesola spring balances in the late feeding period. To avoid differences due to daily fluctuation, parents were measured between 08-00 and 10-00 hours. To prevent desertion, parents were not weighed either in egg-laying or incubation periods, so weight loss through the breeding period could not be recorded. However differences in the weights in the end of first, second and third broods could be shown.

Statistical analyses were carried out using the SPSS statistical package. Unless using the χ² test, percentage data were arc sine transformed for parametric testing. Some birds might be involved more than once in the same test, and individual observational periods were not used as independent measures for calculations.

Results

Length of nest building, interbrood intervals and synchronicity of nest visits

Differences were found in the distribution of length of the nest-building period between colonial and solitary parents (Table 1, χ² = 55.92, P < 0.001). The building of most colonial nests took 13–15 days, measured from when the first nest material appeared in the nest until the laying of the first egg, while the majority of solitary parents built their nest in 7–9 days. A higher proportion of females in colonies than in solitary nests were first-year recruiting birds (χ² = 14.13, P < 0.001). Parents that built over a long period produced fewer fledglings than parents which built over a short period (ANCOVA F₁,238 = 3.47, P = 0.008). First-year recruiting females built for longer and reared fewer young than older females (F₁,238 = 4.90, P = 0.026 and F₁,238 = 6.43, P = 0.015).

The time after 15 April was divided into 5-day intervals, and data on first egg-laying recorded in these intervals are presented in Fig. 1. First eggs were laid in 48% of first colonial nests within a single interval (5–10 May). The highest proportion of the first solitary nests where first eggs were recorded within a single interval was 27%. This difference and the comparison of distribution of percent frequency (χ² = 23.76, P < 0.01) reflect higher synchronicity of egg-laying in colonies than in solitary nests. There was a low difference in the highest propor-