SHORT COMMUNICATIONS

Do Old Great Tits Forego Breeding?

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There is considerable evidence that young or inexperienced birds are less effective parents than older individuals, but only limited information is available on the reproductive performance of older birds, especially in short-lived species. In Great Tits (*Parus major*) territory size increases with age, reaching a maximum at 4 yr and then decreasing in birds of 5 yr or older (Dhondt 1971). In some cases old Great Tit males (5 yr or more) do not defend a territory or raise young in a first brood, but pair with a female to raise young in her second brood of the season. Perrins and Moss (1974) found that in Great Tit females "The birds of 5 or more years of age seem to be becoming less efficient at breeding, rather than curtailing their breeding effort." They showed, in particular, that older females lay later, have a lower hatching rate, and produce fledglings with a lower chance of survival. The birds of 5–7 yr did somewhat poorer than 1-yr-old females. Webber (1975) showed that at Oxford the annual survival rates of Great Tits increased gradually up to the age of 4 yr and then decreased steadily for birds of 5 or more years. This suggests that all old females will breed, but less efficiently than when younger, and that older males occasionally will miss a reproductive season.

It is generally extremely difficult to document nonbreeding in small passerines. In the populations studied at Ghent (Belgium), however, a large proportion of Great Tits use nest boxes for roosting in winter, so that evidence for the presence of birds can be obtained from routine nightly visits to the nest boxes. I present evidence here that Great Tits of both sexes sometimes forego breeding once they reach 5 years of age. I also verify for the Ghent populations the extent of nonbreeding among first-year birds, as has been shown by Bulmer and Perrins (1973).

In the course of a long-term study of Great Tits at Ghent begun in 1959, all nestlings were ringed and a variable proportion of breeding adults trapped on the nest. Adults were trapped when entering the nest box to feed 1–2-week-old nestlings. Details on study areas and basic information on the study can be found in Dhondt and Eyckerman (1980). Two evening visits to all nest boxes were made each winter, and roosting birds were trapped.

Of the 962 nestlings born between 1959 and 1976 that were recaptured after fledging, 417 were caught at least once on the nest. The analysis presented here used two subsets of these birds. The first data set consisted of 118 birds (74 males, 44 females) from the cohorts 1961–1971 that met two criteria: they were regularly found roosting during winter, and they were trapped on the nest in at least half of the possible years. The first condition gives information on a bird's presence in the study area even if it was not caught on the nest. The second criterion excludes birds that were difficult to trap or were irregular breeders in our nest boxes. The 74 males in this set were trapped 178 times out of a possible 239 (i.e. in 74.5% of the possible instances), and the 44 females were trapped 123 times out of a possible 144 (85.4%); although this difference was statistically significant (*G*-test, Sokal and Rohlf 1969; $G = 6.39$, 1 df, $P < 0.02$), it was an accidental result of the way the sample was drawn together. The relevant question here is, How did trapping rates differ with age or previous captures? If the age structure of the males and females used did not differ, they can be combined into one sample.

The second data set contained 72 males and 44 females, not included in the first group, that were banded as nestlings in the cohorts 1961–1974 and were known to be alive until at least their second breeding season. Some of these were not trapped on the nest until 3 yr old; others were trapped in their first and second breeding seasons but were never found roosting and, therefore, were not included in the first subsample.

My analysis was based on the assumption that the probability of trapping an individual that breeds in a nest box does not vary with age. Van Balen (*in litt.*) pointed out that there always is a proportion of untrapped parents, because the clutch or brood is deserted before trapping is possible. Desertion at an early stage may occur more frequently in very young or very old individuals. To test this hypothesis, I compared the data of two study areas, Maaltepark and Maria-Middelares, in the period 1966–1969 when the entire population was color-banded and known in sufficient detail to identify all birds that attempted to breed. Of 117 breeding pairs that started egg-laying in a first brood, the identity of 115 males and 116 females was known. No young fledged from 19 of the nests, and the identity and minimum age of all but 1 of these unsuccessful adults were known. Of 90 parents of age 1 yr or 5 or more years, 16 (17.8%) were unsuccessful, compared with 21 (14.9%) unsuccessful parents out of 141 aged 2–4 yr. This difference in nest failure between age classes was not statistically significant ($G = 0.34$, 1 df, $P > 0.05$).

Because age does not seem to affect the probability of nest failure, the proportion of individuals actually captured should reflect differences in the proportion of the birds in each age class that breed in the nest

TABLE 1. Proportion of birds that were trapped on the nest (first data set).

Age	Males		Females		All	
1	51/74	0.69	36/44	0.82	87/118	0.74
2	58/74	0.78	39/44	0.89	97/118	0.82
3	33/41	0.80	22/25	0.88	55/66	0.83
4	24/30	0.80	15/15	1.00	39/45	0.87
5–7	12/20	0.60	11/16	0.69	23/36	0.64

TABLE 2. Proportion of birds that were trapped on the nest and were known to be alive until at least the second breeding season, but were not included in the first data set (second data set).

Age	Males		Females		All	
1	32/72	0.44	28/44	0.64	60/116	0.53
2	51/72	0.71	33/44	0.75	84/116	0.72

boxes. In the Ghent study areas, where nest-box density is high, practically all Great Tits use nest boxes for breeding, and very few, if any, breed in natural cavities.

A higher proportion of males and females aged 2–4 yr was trapped on the nest than of younger or older birds (Table 1). Among males none of the differences between age-classes was significant, but among females the birds of 5 or more years were captured in significantly lower proportions than those of 2–4 yr ($G = 4.57$, 1 df, $P < 0.05$). Because the age structure of the two sexes in the sample did not differ ($G = 1.12$, 4 df, $P > 0.50$), I combined them for analysis. Two- to 4-yr-old Great Tits were trapped significantly more often on the nest than were birds of 1 yr ($G = 4.44$, 1 df, $P < 0.05$) or of 5 or more years ($G = 6.66$, 1 df, $P < 0.01$).

The second data set was used to evaluate the probability that birds aged 1 and 2 yr would be captured on the nest (Table 2). Two-year-old males were trapped significantly more often on the nest than when they were 1 yr old ($G = 10.41$, 1 df, $P < 0.01$), but this was not the case for females ($G = 1.34$, 1 df, $P > 0.20$). When I combined both data sets to increase sample size, these results were confirmed: males were trapped more often when 2 yr old ($G = 10.37$, 1 df, $P < 0.01$), but females were not ($G = 2.08$, 1 df, $P > 0.10$).

How far do differences in the proportion of captures with age reflect differences in the proportion of breeders? My data show that nest failure, before parents could be trapped feeding nestlings, was not more frequent among young or very old parents. However, birds that were trapped on the nest once when feeding young were more difficult to trap a second time in the same season (pers. obs.). Individuals that were very difficult to trap altogether were excluded by the way the first data set was constituted. If experienced birds also would become more difficult to trap on the nest because they had been trapped in a previous season, and assuming that all birds breed from the age of 2 onwards, one would expect the proportion of birds trapped to decrease gradually with age. This was not the case (Table 1). I therefore assumed that the proportion of captures reflected the proportion of breeders in all age classes, and, therefore, old birds of both sexes did not breed each year. Similarly, some yearling males did not breed, although all yearling females did.

What proportions of young and old birds breed? Assuming that all birds aged 2–4 yr breed, and knowing that in these age classes 79.3% of the males and 90.5% of the females (see Table 1) were captured, one can calculate the proportion of breeders in the other age classes. These calculations indicate that 75.6% of the males and 76.0% of the females aged 5–7 yr would actually breed. When the calculations were repeated for yearling males, the percentages found were 87% for the first data set, 63% for the second data set, and 76% for the combined data. This is close to the estimate of 66% made by Bulmer and Perrins (1973) for the Wytham Great Tits at Oxford. The difference between the two data sets in the proportion of yearlings breeding was statistically significant: in the first set 64/74 (86.5%) would have bred, compared with 45/72 (62.5%) in the second set ($G = 11.41$, 1 df, $P < 0.01$). This suggests that birds in the two subsets are not equivalent in terms of breeding performance. The main difference between the two groups was that all birds in the first group used nest boxes for roosting from their first winter onwards, whereas birds in the second group did not. This suggests that males that use nest boxes for roosting in their first winter are more likely to obtain a breeding territory and a mate. Great Tits roost during winter in a domicile (Kluyver 1951; pers. obs.). This domicile normally overlaps to a large extent with both the autumn and the spring territory (Dhondt 1971). Furthermore, more dominant individuals have a greater chance of being found roosting in nest boxes during winter than less dominant individuals (Kluyver 1957, Drent 1983). These observations support the conclusion that the more dominant yearling Great Tit males have a higher chance of breeding in their first breeding season. The same may be true for old males because I have observed that some of the old males bred only a second brood, without having defended a spring territory.

These results emphasize previous observations of the effects of old age in Great Tits on weight and winglength (van Balen 1967), territory size (Dhondt 1971), breeding performance (Perrins and Moss 1974), and annual survival rate (Webber 1975). It should be emphasized, however, that only very few individuals reach the age of 5 yr.

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Feeding Habits of the Citreoline Trogon in a Tropical Deciduous Forest During the Dry Season

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The Trogonidae are important frugivores in the tropics, especially in the American tropical forests (Snow 1981). However, with the exception of quetzals (Skutch 1944, Wheelwright 1983) and some data on the diet of the Orange-bellied Trogon (*Trogon aurantiiventris*; Wheelwright et al. 1984), their feeding ecology is poorly known. In the tropical deciduous forest of the Mexican west coast, the Citreoline Trogon (*Trogon citreolus citreolus*) is one of the most abundant resident members of the frugivore guild. To our knowledge there are no reports on its foraging behavior or on the fruit species that it eats. We report here on the fruits eaten by the Citreoline Trogon and on its foraging behavior, during the dry season from 6 to 26 April 1984.

The observations were made in the tropical deciduous and subdeciduous forest in hilly areas and in the riparian vegetation of dry arroyo beds located near the Estación de Biología Tropical de Chamela (Jalisco, México, 19°30'N, 105°03'W, 0–250 m elevation). For a description of the location and vegetation see Solis (1980). Intensive observations were made at a fruiting fig tree (*Ficus pertusa*) on 13 and 16 April. On these dates, data were collected on the frequency of arrivals at the tree, foraging rates, and time spent on each fruit. Timing was done to the nearest 0.2 s with two stopwatches. Ripe fruits of all species eaten by the trogons were measured and weighed, with the exception of *Comocladia engleriana* (Anacardiaceae), the resinous exudates of which cause severe irritation of the skin. Trogons regurgitated *Recchia mexicana* seeds after removing the pulp; we estimated the weight of the consumed pulp and skin of the fruit by subtracting the weight of the seed from the weight of the whole fruit.

Four fruit species were used by the Citreoline Trogon during the observation period (Table 1). Two were drupes produced by small trees (*Recchia mexicana* and *Comocladia engleriana*), one was the berry of a vine (*Trichostigma octandrum*), and one was the syconium of a fig tree (*Ficus pertusa*); the latter two plants were from riparian habitats. The fruiting seasons of these plants (except *F. pertusa*) are restricted to the end of the dry season (February–May; Table 1). Fruiting fig trees were scarce in the study area; in an intensive survey only one *F. pertusa* with ripe fruits was found. *Trichostigma octandrum* berries were locally abundant in large areas of the arroyo beds. Fruiting trees of *R. mexicana* and *C. engleriana* were common but widely dispersed, and each tree had few ripe fruits (100–400 in *R. mexicana*, 30–600 in *C. engleriana*) relative to the thousands of fruits of *T. octandrum* and *F. pertusa*. The weights and characteristics of the fruits of each species are summarized in Table 1.

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