TERRITORIAL AND NONTERRITORIAL SETTLING IN JUVENILE EURASIAN NUTHATCHES (*SITTA EUROPAEA* L.) IN SUMMER

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ABSTRACT.—Eurasian Nuthatches (*Sitta europaea*) are territorial in pairs throughout the year. Juvenile birds can settle in summer by taking up vacant territories in pairs, by pairing with unpaired adults, or by becoming nonterritorial residents. During five consecutive years, I studied settling behavior of juveniles and their recruitment in a breeding population. Three types of nonterritorial settlement are included: satellite birds with a territorial pair, and solitary or paired birds with home ranges that overlapped several territories. All nonterritorial residents either disappeared or became territory owners before spring. Settling behavior was not correlated with body size, but transient juvenile females weighed less in summer than resident juvenile females. Compared with territorial juveniles, nonterritorial residents that became territorial after summer survived equally well, were in an equally good winter condition, and subsequently bred in relatively high-quality territories. Despite this apparent equal success, the number of individuals in both categories in relation to density implies a preference for territorial settlement. The importance of summer territoriality for surviving the first months of life and the risk of not finding either a territory or a mate for breeding may explain these patterns. *Received 28 October 1988, accepted 13 April 1989.*

RECENTLY, a number of studies have attempted to explain nonbreeding social organization in birds (see Kalela 1958, Pulliam and Millikan 1982, Barnard and Thompson 1985 for reviews). Although most of these studies have focused on short-term factors that influence group size and territoriality (e.g. Davies 1976, Barnard and Thompson 1985, Tye 1986, Ekman 1988), there is an increasing awareness of the importance of long-term effects such as pair bonding, site fidelity, and prospects of future dominance or territory ownership, especially in nonmigratory populations (Buskirk 1976; Woolfenden and Fitzpatrick 1978; Smith 1978, 1984; Ekman 1988; Enoksson 1988).

An important component of social organization in resident populations is the way juvenile birds are recruited into the adult population (e.g. Smith 1984, Birkhead and Clarkson 1985, Ekman 1989, Matthysen in press 1). Newly fledged juveniles must survive and acquire a breeding site and mate. Both survival and acquisition of mate and site are influenced by social status (Brown 1969, Krebs 1971, Ekman 1988, Nilsson and Smith 1988). These problems can be overcome by acquiring an all-purpose territory as soon after fledging as possible (Dixon 1956, Löhrl 1958, Birkhead and Clarkson 1985). This possibility is, however, usually limited by a finite number of vacancies. Juveniles may also settle as subordinates in already occupied areas or marginal habitat, and delay territory ownership until quality vacancies appear. Within a population, different nonterritorial behavior types can be observed (Smith 1984, Birkhead and Clarkson 1985) with apparently equal payoffs (e.g. Smith 1984). The benefit of choosing a given option is measured ultimately by the probability of acquiring a breeding territory and mate.

Eurasian Nuthatches (*Sitta europaea*) are territorial in pairs throughout the year (Löhrl 1958). Juveniles of this species can settle in territories in early summer (Löhrl 1958, Matthysen 1987), but different types of nonterritorial settlement have been observed. These include settling as subordinates within pair territories (*satellites*, Enoksson 1988) and as solitary or paired individuals in border areas between territories (Matthysen and Dhondt 1983). I describe variation in juvenile settling behavior as observed over 5 yr, and I compare the success of territorial and nonterritorial individuals in terms of local survival, condition, and territory quality when first breeding.

METHODS

I studied nuthatch social organization and demography in a 38-ha woodland area near Antwerp, Belgium. The area is covered by secondary, mainly deciduous forest dominated by oak (*Quercus robur*), beech

(*Fagus sylvatica*), birch (*Betula* sp.) and scots pine (*Pinus sylvestris*). Details on the study area and methods can be found elsewhere (Matthysen 1990).

I captured nuthatches with mist nets and baited traps at temporary feeding sites throughout the year. Feeding sites were supplied with sunflower seeds only during trapping sessions or a few days before each session. Feeding tables were generally emptied within a few hours by nuthatches, tits, or squirrels (*Sciurus vulgaris*), and the surplus food probably had little influence on the birds' behavior or survival. Trapping was most intensive in summer when juveniles were banded.

Individuals were sexed, color-banded, weighed, and measured when captured (80% of the measurements were made by one person). Because wing length of nuthatches increased from their first (i.e. hatching) year to their second year (Matthysen unpubl. data), individual mean wing length was calculated from measurements in the first year only. Birds captured while roosting in nest boxes had significantly higher body mass than those captured during the day and were excluded from the weight analyses. Juveniles were aged in summer (until the end of August) by the absence of postnuptial molt (Matthysen 1986a). Because dispersal by adult nuthatches is limited (Enoksson 1987, Matthysen and Schmidt 1987) and all postsummer immigrants of known age proved to be juveniles, all other immigrants after August were assumed to be juveniles. The origin of most recruits was unknown except for a few birds banded as nestlings in nest boxes (eight individuals from nine broods banded).

The presence of all individuals was checked at weekly intervals throughout the year, with more frequent visits from June to September and less frequent visits in winter. In 1982, 1983, and 1984, no observations were made before the second half of July. From August to November 1982, only a part of the area (10 ha) was covered. The 1982 observations have been described in detail (Matthysen and Dhondt 1983) and we incorporate the quantitative results here.

Home ranges of all individuals were mapped every two or three months using all observations and trapping data. *Transient* or *nonresident* birds were defined as individuals observed in the area for a short time only (< 10 days), over large distances (>500 m) within the area, or both. Most *resident* individuals were identified as territorial individuals, which defended an exclusive area (Emlen 1957, Pitelka 1959), on the bases of exclusive use of their home range (except for a mate), conflicts with neighbors, dominance over and aggression towards intruders, their response to playback, and their use of vocalizations (see Matthysen and Dhondt 1988). I defined *nonterritorial residents* as individuals who did not have exclusive use of their home range and were subordinate to territorial individuals within all parts of their home range.

The study area contained 30 different territories. The positions of territories remained more or less stable even when the owners were replaced or when some territories were temporarily vacant. Territory quality was related to the number of years each territory had been occupied. This measure was correlated with local survival per territory, with winter condition and with preference by recruits (Matthysen 1990).

RESULTS

Description of settling behavior.—From early June onwards, new pairs began to establish territories in vacant parts of the area. All of these recruits were juveniles, except for three pairs that consisted of a juvenile female and an adult male immigrant. Assuming that fledging dates in other areas were similar to those in the study area, the earliest juveniles could have been independent from their parents for no more than a few days when settling. Most pairs established themselves before the beginning of July, and all before mid-August. Each summer 8–12 territorial pairs were added to the population, which approximately doubled its size (Table 1). Fights occurred between juvenile birds in June and July, apparently for possession of a territory. Juveniles were not observed to settle by taking over parts of adult birds' territories, nor did juveniles evict adult owners in summer.

Fourteen juveniles settled by pairing with a solitary owner who had lost its mate ("sex-vacancy," Matthysen 1986b; Table 1). Three paired with an adult owner as early as June. The previous history of these replacement birds was generally unknown, especially in June and July. Replacement birds with known history included previous neighboring territory owners and nonterritorial residents, but most were probably immigrants.

Eighteen males and 11 females settled as nonterritorial residents (Table 1); 10 were not banded. They were less conspicuous than territory owners and sometimes detected only by captures or observations at feeding sites. Nonterritorial residents were supplanted by territory owners at feeding stations in 11 of 13 observed conflicts. In the remaining 2 cases, a nonterritorial resident supplanted another (unknown) individual.

All nonterritorial residents captured before the end of the molt were juveniles; most were unbanded. One had been banded as a nestling ca. 200 m from where it was observed as non-

TABLE 1. Summer settling behavior of juvenile birds. All individuals are included only once, even if they later switched to another category. In 1982 only a part of the area was observed.

Settling behavior	1982	1983	1984	1985	1986	Total
		Territorial				
Settled as pair[a]	2	18	15	22	24	81
Males	1	8	7	11	12	39
Females	1	10	8	11	12	42
Paired with owner	2	3	4	2	3	14
Males	1	1	2	1	1	6
Females	1	2	2	1	2	8
		Nonterritorial				
Satellite	1	0	0	0	1	2
Males	1	0	0	0	1	2
Females	0	0	0	0	0	0
Solitary[b]	5	3	4	1	3	16
Males	3	2	3	1	3	12
Females	2	1	1	0	0	4
Paired[c]	1	5	4	0	1	11
Males	0	2	2	0	0	4
Females	1	3	2	0	1	7
Total	7	8	8	1	5	29
Males	4	4	5	1	4	18
Females	3	4	3	0	1	11
Territory density (pairs/ha)						
Breeding	—	35	40	28	34	—
Postbreeding (August)	—	54	56	55	63	—

[a] Includes 3 juvenile females paired to immigrant adult males.

[b] Includes 4 possible satellite males.

[c] Includes 3 females that settled with an already present solitary nonterritorial male.

territorial resident. A few individuals were captured in or near their home range as nonterritorial residents in June and early July. The settling dates of other individuals are unknown, except for some who settled in late September or October. All nonterritorial residents that settled in summer either disappeared or acquired a territory before March of the next year.

Nonterritorial residents were classified in three categories (Table 1). The largest group was solitary individuals (12 of 18 males, 4 of 11 females) with home ranges that overlapped several territories or parts of them. A second group was paired birds ($n = 7$ pairs), whose ranges overlapped several territories. Individuals of both categories never associated with territory owners except coincidentally at feeding sites or in conflict situations. Nonterritorial pairs were sometimes observed in conflict with territorial pairs or reacting to playback, but their home ranges were not used exclusively. The third group was satellites (Enoksson 1988) that lived within a territory and associated with the owners without overt conflicts. Two satellite males were observed with the territorial pair in 80% of all observations (6 of 7, and 6 of 8 observations, respectively). Four other males (possibly satellites) also stayed within one territory, but did not associate with the local owners. A few nonterritorial residents switched their home range and apparently their behavior during their stay. They include two solitary males that were later joined by one nonterritorial female, one paired male that settled solitarily elsewhere after its mate disappeared, and one male that twice shifted its home range and was apparently paired in the second home range (Fig. 1).

The number of nonterritorial residents per year (1-8 individuals) was positively correlated with preceding breeding density ($r = 0.91$, $n = 4$, $P = 0.09$) but not with territory density in summer ($r = -0.16$, $n = 4$, $P > 0.1$). The location of resident nonterritorial home ranges was related to territory quality (Fig. 2). Two satellite males and four possible satellites all lived in high-quality territories (occupied continuously for 5 yr) while this category of territories represented only 37% of occupied summer territories ($\chi^2 = 10.4$, df $= 1$, $P < 0.01$). Other non-

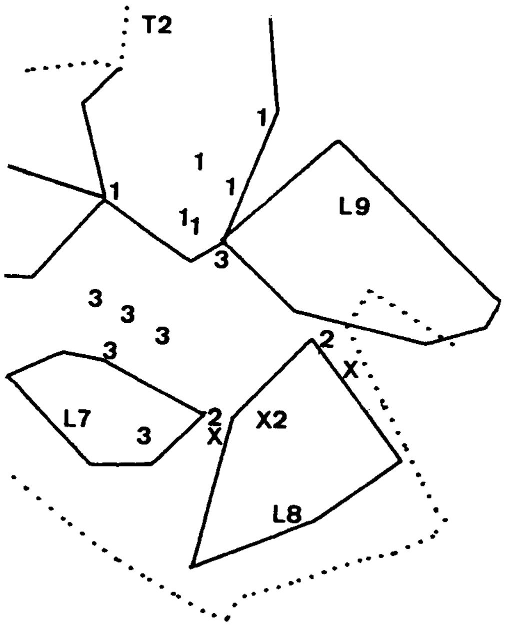

Fig. 1. Behavior of nonterritorial resident male M136 (1986–1987). 1 = possible satellite (within territory T2) in July and August; 2 = paired nonterritorial in September (X = nonterritorial female F148); 3 = solitary from November to January. M136 replaced a territorial male in territory L7 in January. Solid lines indicate territorial boundaries; dashed lines, the study area border.

territorial residents were not associated with a particular territory, and high-quality sites were scattered throughout the area, so it would be difficult to prove a preference for settling near high-quality territories. However, nonterritorial residents were markedly absent from the northeastern part of the area which lacked high-quality territories.

Body size and condition.—No difference in body size (wing length, mass, tarsus length) was found between the nonterritorial residents (all assumed to be juveniles) and territorial juveniles (all comparisons: $t < 1.2$, $P > 0.1$; sample sizes: $n = 10$ and 7 for nonterritorial males and females; $n = 78$ and 76 for territorial juveniles). Resident birds did not differ from transient individuals in wing length or tarsus length, but they were significantly heavier even if corrected for tarsus length (Table 2). In June and August (the months with sufficient data), the only significant mass difference was for female birds in August. The difference in females changed from 0.2 g in favor of nonresidents in June to 0.9 g in favor of residents in August (Table 2).

Settling date of territorial juveniles was not correlated with body size ($n = 18$ for both sexes in 1985 and 1986 combined; correlations with mass, tarsus length, and wing length: all $r < 0.3$, $P > 0.1$), except for a correlation between male wing length and settling date ($r = -0.49$, $P = 0.04$). This correlation was due entirely to the effect of two small males who settled after

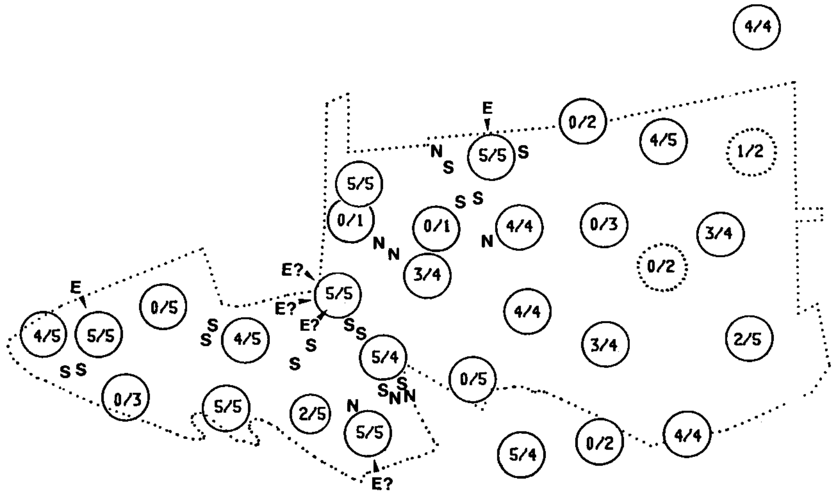

Fig. 2. Approximate home-range positions of nonterritorial residents in relation to territory quality. Circles indicate positions of territories stable throughout the study period. Values within circles are the number of summers and breeding seasons for which each territory was occupied during the 5-yr study. E = satellites; E? = possible satellites; S = solitary nonterritorial resident; N = pair of nonterritorial residents.

TABLE 2. Comparison of body size and condition (body mass divided by tarsus length) in resident juveniles and transient birds. Sample sizes are in parentheses; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

		Residents	Nonresidents	*t*
Wing length (mm)	M	86.4 (64)	86.1 (15)	0.79
	F	83.5 (57)	84.1 (15)	1.6
Tarsus length (mm)	M	18.05 (75)	17.86 (18)	1.79
	F	17.83 (67)	17.76 (16)	0.64
Body mass (g)	M	23.1 (74)	22.2 (17)	3.5***
	F	21.9 (66)	21.2 (16)	2.3*
Condition	M	1.28 (74)	1.24 (17)	2.5*
	F	1.23 (66)	1.19 (16)	1.98*
Mass (June)	M	22.0 (11)	21.4 (7)	1.4
	F	20.3 (7)	20.5 (6)	−0.5
Mass (August)	M	23.5 (63)	22.9 (8)	1.6
	F	22.3 (45)	21.4 (11)	2.6**

mid-July (remaining sample: $n = 16$, $r = 0.04$, $P > 0.3$).

Seven individuals that remained as nonterritorials until November or later did not change in mass from summer (July to September) to winter (November to February) (mean difference = +0.01 g; range: −0.25 to +0.55 g). Territorial juveniles lost on average 0.40 g (range: −2.1 to +0.8 g, $n = 25$). Although this difference was not significant (Mann-Whitney test, $U = 49.5$, $z = 1.73$, $P = 0.08$), variation in weight change was significantly smaller in nonterritorials (Bartlett test, $\chi^2 = 4.5$, df = 1, $P < 0.05$).

Recruitment.—Recruitment of territorial juveniles into the breeding population was higher among early settling individuals (80% vs. 12%, Table 3), but this effect was not equal in the sexes (Three-way *G*-test, interaction term $G = 6.8$, df = 1). There was a highly significant effect among males ($G = 20.3$, df = 1, $P < 0.001$) but not among females ($G = 1.9$, df = 1, $P > 0.01$).

The effect of social status (territorial vs. nonterritorial) on juvenile local survival changed with time (Three-way *G*-test, interaction term $G = 25.6$, df = 7, $P < 0.001$), so I tested the difference for each month separately. There was a significant difference in August only (Fig. 3) when territorial individuals had a higher survival rate.

Eight nonterritorial birds (6 males and 2 females = 28% of nonterritorial residents) eventually became owners of a pair territory. In all cases, these territories overlapped with, or bordered on, their previous home range (see Fig. 1 for an example). All replaced a local owner and paired with its mate, except one nonterritorial male who replaced a solitary male and acquired a mate later. Two settled in September, one in October, one in November, two in January, and two in February. The quality of their territories was high (mean breeding occupation = 3.2 yr) compared with those of other juveniles (mean in December = 2.5), but the difference was not significant ($t = 1.0$, $n = 8$ and 94, $P = 0.3$). Six nonterritorial birds (4 males and 2 females) eventually bred in the study area. Three of these had shifted to a different territory from the one in which they first became territorial. Their territories were also of high quality (mean breeding occupation = 4.7, mean for other breeding juveniles = 4.0) but they were not significantly different ($t = 1.5$, $n = 6$ and 84, $P > 0.1$).

DISCUSSION

Variation in settling behavior.—The early development of juvenile territoriality in Eurasian Nuthatches has not been reported in other species, probably because it is understudied (Matthysen 1987). In some group-living species, juveniles also settle early, possibly to increase dominance status (Nilsson and Smith 1988). Settling seems to occur much earlier in the study population than in one studied by Löhrl (1958), probably due to differences in population density and availability of vacancies (Matthysen 1987, 1990).

Nonterritorial juveniles have several options. The behavior of satellite birds differs from all other juveniles in that they associate with territory owners. Satellites have been described in a Swedish population (Enoksson 1987, 1988) where more than one satellite (of different sexes) exist within a territory. They may be analogous to subordinate juveniles within social groups in

TABLE 3. Survival (%) of early (before 15 June) and late settlers among territorial juveniles. Sample sizes are in parentheses.

		Early	Late
Males	1985	100 (4)	0 (3)
	1986	100 (4)	0 (5)
Females	1985	33 (3)	0 (4)
	1986	75 (4)	40 (5)
Total		80 (15)	12 (17)

Pygmy Nuthatches (*Sitta pygmaea*) (Norris 1958, Sydeman et al. 1988) and several species of tits (e.g. Brawn and Samson 1983, Ekman 1988, Nilsson and Smith 1988) or to subordinate birds that settle with solitary territorial Pied Wagtails (*Motacilla alba;* Davies 1976, Davies and Houston 1981). It is unknown whether satellite Eurasian Nuthatches contribute to territorial defense as in the Pied Wagtails (Davies and Houston 1981) or tits (Brawn and Samson 1983).

Solitary nonterritorial birds apparently remained in the immediate neighborhood of high-quality territories while waiting for a vacancy. None of those observed tried to expand its home range into a territory. The exact nature of nonterritorial pair behavior is not clear. These individuals may either represent pairs that tried to establish a territory but were unable to acquire absolute dominance in their home range, or nonterritorial individuals that settled independently in the same part of the area. The latter is clearly the case with some solitary males which settled in summer and were joined by a female in early autumn.

The success of the nonterritorial individual depends on the probability of acquiring a territory and mate in the future. Hence, immigrant birds in winter and spring very rarely settled as nonterritorials because the chance of finding either a territory, a mate, or both in time presumably was limited (see Matthysen 1988 for seasonal recruitment patterns). Postsummer immigrants either joined widowed territory owners or displaced paired owners (Matthysen unpubl. data).

Only a few individuals live as satellites compared with the number of solitary individuals. High-quality territories may be a prerequisite for satellites to be tolerated by owners, just as satellite wagtails are tolerated only in situations with abundant food (Davies and Houston 1981). Satellite Eurasian Nuthatches occurred more frequently in a Swedish population (Enoksson 1987, 1988), which may have been due to experimental addition of food. Enoksson did not report solitary nonterritorials, perhaps because observations began after the summer period. Löhrl (1958) also observed nonterritorial resident Eurasian Nuthatches and reported juvenile females within pair territories that did not associate with the owners, and solitary males that lived in marginal, unoccupied areas. Solitary or paired nonterritorials with small home ranges were observed also in year-round territorial Magpies (*Pica pica*), where most nonterritorials live in large flocks (Baeyens 1981, Birkhead and Clarkson 1985, Eden 1987).

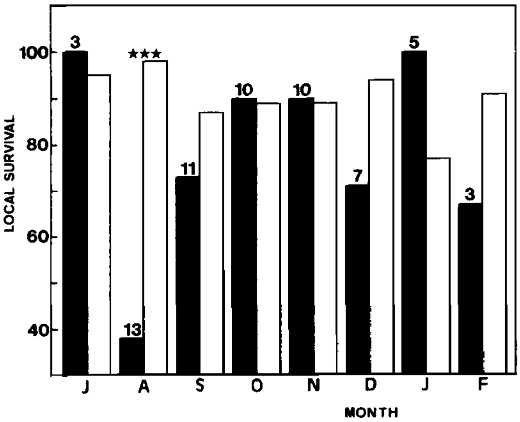

Fig. 3. Local survival by month of nonterritorial residents (filled bars; sample sizes are indicated) and territorial juveniles (empty bars; all sample sizes > 40). *** = $P < 0.001$ ($\chi^2 = 25.2$, df = 1); all other comparisons $P > 0.1$.

Success of different strategies.—Local survival was equally high in territorial juveniles and nonterritorial birds except in August. The winter condition of nonterritorial birds was at least as high as that of territorial juveniles, with a significantly lower variance in mass change. The lower local survival in August may at least partly reflect dispersal instead of mortality (Löhrl 1958, Gatter 1974). The good winter condition of nonterritorial residents reflects their presence in or near high-quality territories, because mass loss in territorial juveniles correlates with territory quality (Matthysen 1990).

Transient birds appeared to suffer from their nonresident status; the transient females were significantly lighter than resident females in August but not in June. The fact that female but not male transient birds were lighter may be explained by the subordinate status of females, even if males do not defend their territories against female intruders (Matthysen 1986b). A difference in competitive ability between the sexes could also account for the small number of females (4 of 16) among solitary nonterritorial residents.

Nonterritorial residents that remained in the study area until spring bred in relatively high-quality territories. Presumably they had already settled near high-quality territories. Territory quality (measured by occupation frequency) apparently influences the owners' local survival, may also influence their breeding success (Matthysen 1990), and is an important contributor to the future reproductive success of juveniles.

Nonterritorial residents have expected benefits at least as high as territorial juveniles after August, but relatively few birds settle in this manner. Limitation of suitable sites is one reason, but it cannot be the sole reason because several sites used with success in some years were not occupied in other years. In the summer of 1985, following the lowest breeding density in 5 yr, only one nonterritorial resident was observed. The density effect suggests that nonterritorial settlement occurs only if most of the territorial vacancies are filled. This may imply a trade-off between additional territorial and nonterritorial settlement, which ultimately depends on the quality of the remaining sites (ideal free distribution, Fretwell 1972). There may be a high premium on territorial behavior in the crucial first weeks or months of life, whereby survival chances of nonterritorial residents would be reduced even in or near high-quality territories. Nevertheless, we expected at least some territorial juveniles to switch to a nonterritorial strategy after August, but this was never observed. Perhaps the main disadvantage of being a nonterritorial resident is the risk of not acquiring a territory and mate in time for the next breeding season.

Phenotypic correlates of settling strategies.—Fledging date is undoubtedly a crucial factor that determines juvenile nuthatches' settling behavior. It allows early young to take up a territory before potential competitors arrive. The fact that most territorial juveniles banded in June continued to occupy their territory during summer confirms their competitive advantage over later juveniles. This asymmetry may be a consequence of differences in age, experience, or familiarity with the territory. Early settlers were also able to settle in high-quality territories (Matthysen 1990), which explains why they survived better, at least among males.

The importance of age to social status may explain why little or no differences in body size were found between territorial and nonterritorial juveniles, or between residents and nonresidents. The difference in body mass probably reflects the consequences rather than causes of social-status differences. The origin and previous history of territorial and nonterritorial juveniles remains largely unknown. Additional studies with more nestlings banded before independence would determine whether juveniles are more successful in settling in or near their parents' territory, and whether some satellites are the territory owners' offspring, as reported in group-living Pygmy Nuthatches (Norris 1958) and Tufted Titmice (*Parus bicolor;* Laskey 1957).

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