

BEHAVIORAL AND ECOLOGICAL CORRELATES OF TERRITORY QUALITY IN THE EURASIAN NUTHATCH (*SITTA EUROPAEA*)

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ABSTRACT.—I studied the pattern of territory occupation and ownership changes in Eurasian Nuthatches (*Sitta europaea*) in a 38-ha woodland over five years. Approximately 50% of the pair territories in summer were also used for breeding each year. Breeding score (i.e. the number of years a territory was used for breeding) was correlated with order of settlement by juveniles in summer and by female immigrants in spring. Birds that shifted territories generally moved to territories with a higher breeding score. Breeding score is therefore considered an indicator of territory quality. Owners of high-quality territories lost less body mass in winter and survived better than owners of low-quality territories. High-quality territories tended to be larger and to contain gardens and oaks but not conifers. Low-quality territories functioned as population reserves by allowing juveniles to settle in summer and wait for a breeding vacancy in a high-quality territory. Received 17 February 1989, accepted 27 July 1989.

WHENEVER territories vary in quality in a consistent way, individual birds may develop behavior that allows them to maximize territory quality. Individuals may settle preferentially in good territories (e.g. Brooke 1979, Møller 1983) or shift to better sites whenever possible (e.g. Petersen and Best 1987, Beletsky and Orians 1987). The benefit of this selective behavior will be especially high if individuals limit all of their activities to the territory, if they remain for a long time in the territory, and if territory quality does not vary over time. Territory quality can be constant also if territories are defended for future purposes instead of, or in addition to, immediate needs.

The Eurasian Nuthatch (*Sitta europaea* L.) is a small hole-nesting passerine that lives in territorial pairs throughout the year and spends nearly all of its time in the territory (Löhr 1958). First-year birds establish territories in vacant areas within weeks after fledging but may move to another territory at any time of year (Matthysen 1987, 1988). Territory quality may change seasonally because of dietary changes, but territories are probably defended for future purposes as well. These include winter food reserves (Enoksson and Nilsson 1983) but may include nest sites or mates.

The first and most direct method to show the existence of variation in territory quality in bird populations is to demonstrate nonrandom variation in either occupation frequency (Weatherhead and Boak 1986) or reproductive success among territories (Högstedt 1980) or subplots

(Blancher and Robertson 1985, Dhondt 1987). The second method is to correlate habitat characteristics with presumed indicators of quality, such as occupation frequency (Møller 1982, 1983; Brandl et al. 1986; Wiens et al. 1986), site shifts (Petersen and Best 1987), and reproductive success (Holm 1973, Janes 1984, Catchpole et al. 1985, Lanyon and Thompson 1986). A third method is to correlate several independent indicators of territory quality related to both preference for and performance in territories. Examples are positive correlations between survival and breeding success per territory (Högstedt 1981), between occupation frequency and breeding success (Baeyens 1981, Nilsson 1987), and between settling orders in different years (Brooke 1979). This approach requires that territories be identified and followed over several years.

I used the third method, correlation of independent indicators, for a combination of reasons. First, the 5-year study period was insufficient to detect nonrandom variation in territory occupation or in performance because several individuals remained for several years in one territory. Second, correlations with habitat characteristics would require an a priori division of territories into vegetation categories, and this was not possible because of vegetation heterogeneity within and between territories. I attempted to establish whether some territories were preferred over others and to recognize the characteristics of these preferred territories. Further, I tried to establish if owners of these

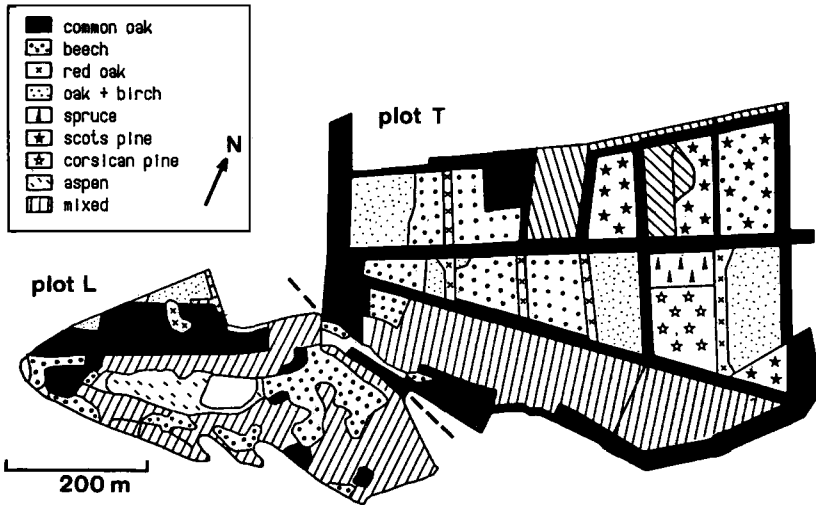


Fig. 1. Vegetation map of the study area. Dashed line (---) shows boundary between subplots.

territories had a higher fitness. Finally, I tried to measure the impact of variation in territory quality on the population level (see also Matthysen 1988).

METHODS

The 38-ha study area is part of a 150-ha woodland complex ("Peerdsbos") to the north of Antwerp, Belgium, and contains two adjacent plots, L and T (Fig. 1). Plot L (10 ha) has parklike vegetation with trees up to 150 yr old and 30–35 m high. The most abundant tree species are beech (*Fagus sylvatica*; 23%), common oak (*Quercus robur*; 14%), sycamore (*Acer pseudoplatanus*; 14%), sweet chestnut (*Castanea sativa*; 13%), yew (*Taxus baccata*; 13%), and aspen (*Populus tremula*; 11%). All are distributed irregularly over the area. In Plot T (28 ha), most trees are <100 yr old and ≤ 25 m high. Tree density is approximately twice that in plot L (180 vs. 100 trees/ha) but average stem circumference is only half (120 vs. 210 cm). Plot T is divided into more or less uniform subplots by lanes bordered with common oak and red oak (*Quercus rubrum*) (Fig. 1). Some subplots are monospecific plantations of common oak, beech, Scots pine (*Pinus sylvestris*), or Corsican pine (*Pinus nigra*). Others contain spontaneous growth of common oak and birch (*Betula* sp.) or mixed stands of common oak, red oak, Norway maple (*Acer platanoides*), and larch (*Larix decidua*). Common oak covers 46% of the plot, followed by birch (10%), beech (10%), Scots pine (9%), and red oak (7%). Part of plot T borders on gardens with parklike habitat, which contains mature trees of various species.

From August 1982 (December 1982 in plot T) until June 1987, I captured, color-banded, and continuously monitored nuthatches during at least biweekly visits

to the area. Birds were captured at temporary feeding stations with mist nets or baited automatic traps, or by sound playback. Juvenile settlement was studied from June in 1985 and 1986, and from mid-July or August in other years. Pair home ranges were mapped as convex polygons (Odum and Kuenzler 1955) every 2–3 months (generally corresponding to summer, autumn, winter, spring, and breeding). The correspondence of home ranges to defended territories was confirmed by general lack of overlap between pairs and by observations of border conflicts and of behavior after release (see Matthysen and Dhondt 1983, 1988).

Juveniles could be aged until late August because adults were in postnuptial molt (Matthysen 1986). Given the extremely sedentary behavior of adult birds (Enoksson 1987, Matthysen and Schmidt 1987), post-molt recruits were also considered as juveniles. Wing length tends to increase after the first complete molt (cf. Alatalo et al. 1984), and only wing measurements from first-year birds were used.

Local survival per territory was defined as the owners' monthly probability of local survival, and *territory fidelity* as the probability that a surviving owner remained in the same territory. To estimate fidelity, each territory was assigned monthly and by sex to one of the following categories: survival (owner remained in the territory), shift (owner moved to another territory), owner disappeared, or no owner present at the beginning of the month. *Local survival* was then calculated as the ratio of months with survival to months with survival or disappearance, and *territory fidelity* as the ratio of months with survival to months with survival or shift. Because nuthatch survival is not sexually biased (Nilsson 1982, Matthysen in press), data for male and female owners were combined. Ter-

territories occupied for <10 months were excluded. For an evaluation of variation in survival and fidelity among territories, the study period was divided into two parts (August 1982 to May 1985, June 1985 to June 1987), and both parameters were correlated between periods.

Territorial vegetation composition was calculated from a map of territories with contiguous boundaries. This map was drawn using information from all seasons. I excluded a few marginal territories that were occupied in 1 or 2 yr only and that were, in other years, incorporated into surrounding territories.

RESULTS

Territory occupation and stability.—Pair territories were defended year-round and changed little in position, even if one pair member was replaced. Several territories were occupied continuously but by different owner combinations. If both owners of a territory disappeared, it remained vacant at least until the next summer, as this was the only time when pair vacancies were filled (see Matthysen 1987). Locations of territories corresponded generally with previous boundary positions. This tradition in boundaries may have been due largely to limits set by surrounding and more continuously occupied territories. Vacant territories were generally not incorporated by surrounding territories. Territory size increased little from summer to breeding (Matthysen unpubl.).

When I compared territory locations in the summers of 1983 and 1986 with complete territory maps, ca. 57% ($n = 24$) of the 1986 territory surfaces were included in the same (or corresponding) territory in 1983. Although this figure seems low, only 9.3% (on average) of the 1986 territory surfaces constituted part of a different territory in 1983. Thus, although territory positions were variable between years, they remained within a rather well-defined area. Observations from other years and different seasons support the stability of territory positions and suggest that correspondence between years could be raised considerably with additional observations. I recognized 30 different territories that were occupied for least one summer by a nuthatch pair.

I tested territorial preference by trying to establish correlations between independent parameters of preference. I included occupation frequency, order of settlement in vacant territories, and shifts between territories.

Occupation frequency.—Nuthatch population size decreased by 30–60% from summer to breeding each year. Consequently, only 50% of the summer territories were used for breeding in a particular year. The number of years a territory was used for breeding (i.e. breeding score) was very unevenly distributed (Fig. 2). Clearly, some territories were preferred over others; however, given the site fidelity of adult owners, there may have been a strong effect of individual life span. Breeding score was influenced directly by settling patterns and territory shifts during the study period. Correlations between breeding score and settling order or direction of shifts are useful only if breeding score was recalculated for the years that preceded the comparison. I defined high breeding score as 4–5 yr of breeding over the total study period, and low score as 0–3 yr. Summer occupation score was defined in an analogous way as breeding score.

Settling order.—Territories not occupied in the breeding season were rapidly taken by pairs of juveniles in early summer (Matthysen 1987). Juveniles settled significantly earlier in territories with a higher past breeding score (Fig. 3). The one territory that deviated in both years (L7, see Fig. 3) was twice occupied at the beginning of the breeding season. In both years however, the breeding pair disappeared before the end of breeding.

After the summer, the only recruits found were individuals that replaced owners that disappeared or, at least in a few cases, evicted owners. Most male immigrants settled between December and February, most females from February to April (Matthysen 1988). Immigrants did not settle more than expected in territories with high breeding score, if expected values were calculated from the number and average winter occupation of territories in each class (χ^2 test, males and females both, $P > 0.5$). Settling date was correlated significantly with breeding score in females (Spearman rank correlation $r_s = 0.52$, $n = 24$, $P < 0.01$) but not in males ($r_s = 0.25$, $n = 14$, $P > 0.1$). When I included only those territories where females settled after a vacancy of at least 1 month, the correlation improved considerably ($n = 16$, $r_s = 0.84$, $P < 0.01$). I could not test the relationship between settling date and past breeding score because most female immigrants appeared in the first 2 yr of study. Female settling order was

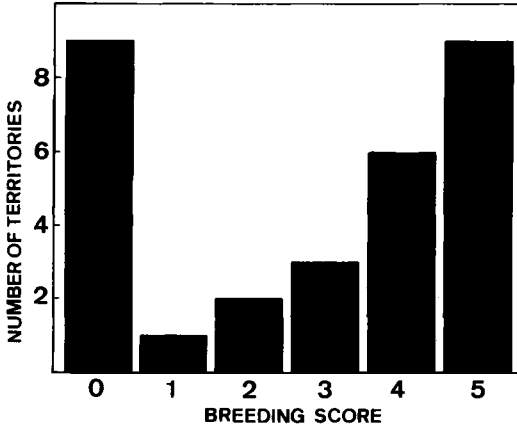


Fig 2. Frequency distribution of breeding score (number of breeding seasons each territory was occupied).

also correlated with juvenile settling order in summer in the same territories ($r_s = 0.9, n = 7, P < 0.01$).

Territory shifts.—Thirty-five individuals or pairs moved from one territory to another, generally without any overlap between successive territories (Fig. 4). All were first-year birds except one male. Shifts occurred throughout the year. Most frequently they were in response to the disappearance of owners and were, with a few exceptions, between adjacent territories. One female returned to her original territory a few months after moving. One male was evicted from his territory and moved to another. Both were excluded from the analysis. The remaining 32 shifts fit three categories (cf. Matthysen 1988): (1) shifts toward vacant territories by pairs ($n = 5$) or by solitary birds ($n = 1$); (2) shifts of birds leaving their partner to move to a neighbor (divorce; $n = 9$); and (3) shifts of “widowed” birds to a neighbor ($n = 17$). Territory fidelity was significantly correlated with territory quality in two parts of the study period (see Methods; $n = 24, r = 0.49, P = 0.02$). Birds generally moved from territories with a lower to a higher past breeding score (18 of 26 cases including 6 with equal score, binomial test, $P < 0.01$). Territory shifts were related to total breeding score and summer occupation score, with the same general tendency (Fig. 4).

Clearly, territories are not occupied randomly. Because breeding score was correlated with the independent parameters of settling order

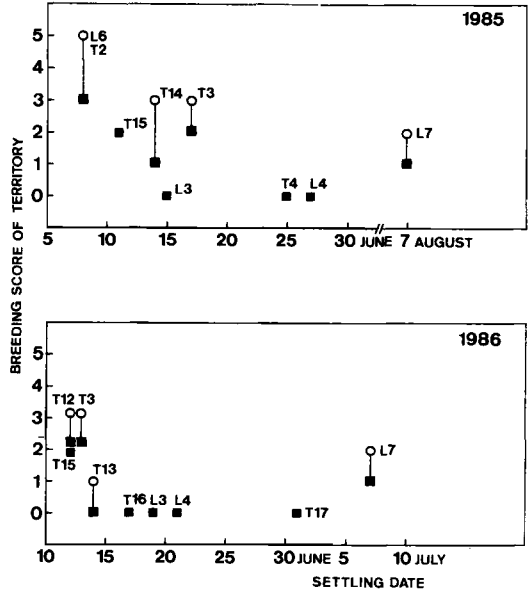


Fig. 3. Settling date by juveniles in summer in relation to past (■) breeding score (number of breeding seasons in which a territory was occupied in previous years) and total (○) breeding score. Spearman rank correlations with past breeding score: 1985, $r_s = 0.71, P > 0.05$; 1986, $r_s = 0.62, P > 0.05$.

and territory fidelity, and could be estimated easily for all territories, I used it as an estimate of territory quality in the following analyses.

Territory quality, size, and vegetation.—Mean territory size in summer (July–August) was significantly smaller in plot L ($n = 8, \bar{x} = 0.68$ ha) than in plot T ($n = 10, \bar{x} = 1.21$ ha; $t = 5.14, P < 0.001$). Mean territory size (documented over a minimum of 3 yrs) was correlated with breeding score in both plots (plot L: $n = 8, r = 0.70, P = 0.05$; plot T: $r = 0.64, n = 13, P = 0.02$). I tested for a positive effect of age by comparing the same territories inhabited by adult and juvenile pairs in different summers, but no difference was found ($n = 10, \text{mean difference} = 0.17$ ha, $t = 0.9, P > 0.2$). Owners generally shifted from smaller to larger territories (areas in summer were larger in 18 cases, smaller in 6, equal in 1; binomial test, $P = 0.01$). Settling order of juveniles in summer was correlated significantly with territory size in plot T ($n = 10, r_s = 0.76, P = 0.01$) (insufficient data for plot L).

Vegetation composition was quantified by measuring the surface of vegetation types on a

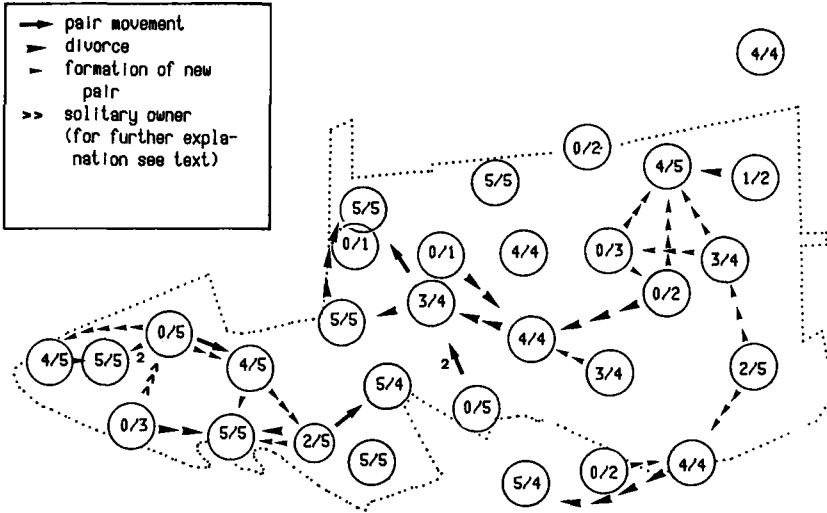


Fig. 4. Shifts between territories (circles) in relation to breeding and summer occupation score, indicated within each territory by 0-5.

map with contiguous territory borders (see Methods). Because of differences in vegetation, plots L and T were considered separately. In plot T, breeding score was negatively correlated with amount of conifers, positively (but not significantly) correlated with beech, but not correlated at all with oak (Table 1). Conifers and beech were negatively self-correlated ($n = 14$, $r = -0.53$, $P = 0.06$). When the conifer effect was removed, all correlations with beech or oak disappeared (partial correlations, see Table 1). Settling order in summer was negatively, but not significantly, correlated with amount of conifers (Table 1). No significant differences were found between pre- and post-shift territories (all comparisons $P > 0.3$, binomial tests).

I tabulated the most important and frequently used vegetation types in each territory and I incorporated gardens of which the exact contribution to territory size was unclear. Generally, a shift in vegetation types occurred with

declining territory quality, from oaks and gardens in high-quality territories to beeches and other deciduous trees in intermediate territories to conifers in low-quality territories (Table 2). Three territories with zero breeding score and occupied in only one or two summers contained vegetation characteristic of more preferred territories (oak, garden, and beech). These three were rather small (<0.9 ha), and two were even less than 0.4 ha with a plot average of 1.2 ha. With the exclusion of these territories, there is a significant association between territory rank and presence of oak and garden (positive) and conifer (negative) (Table 2).

In plot L, only oak and beech were sufficiently present in homogeneous stands for a quantitative analysis (see Fig. 1). Neither was positively correlated with breeding score ($r = -0.15$ and -0.03 , $n = 8$), nor did they differ between pre- and post-shift territories (oak increased in 5 of 11 cases, beech in 3 of 11; 2 had no change).

TABLE 1. Correlations between vegetation composition and parameters of territory quality in plot T. Unless otherwise indicated (values in parentheses), $P > 0.1$.

Parameter	<i>n</i>	Conifers	Beech	Oak
Breeding score	14	-0.55 (0.05)	0.52 (0.06)	0.22
Partial correlation ^a	14	—	0.32	0.01
Settling order in summer ^b	8	-0.29	-0.17	0.31

^a Effect of conifers removed.

^b Spearman rank correlation.

TABLE 2. Presence of vegetation types in territories in plot T. Territories are ranked by descending quality (breeding and summer occupation scores). When territories T16, T17, and T7 were excluded (see text), territory preference was significantly related to the presence of oak (Mann-Whitney test, $U = 8$, $P = 0.03$), garden ($U = 1$, $P = 0.02$), and conifers ($U = 9$, $P = 0.03$).

	Breeding score	Summer score	Oak	Garden	Beech	Mixed deciduous	Oak-birch	Conifers
T1	5	5	+	+			+	
T5	5	5	+	+				
T2	5	5	+					
T9	4	5		+		+		+
T6	4	4+			+	+		
T8	4	4+			+	+		
T3	3	4+			+			
T14	3	4+					+	+
T12	3	4				+		
T15	2	5						+
T13	1	2						+
T4	0	5	+					
T10	0	3						+
T11	0	2					+	+
T16	0	2		+				
T17	0	1	+					
T7	0	1			+			

Body size and condition.—Juveniles living in high-quality territories in summer were not significantly larger than birds in other territories (wing length, tarsus length, bill length and depth; all comparisons $P > 0.1$, $n = 54 \delta$ and 45 ♀). I found no uniform trends. For example, male wing lengths are smaller in high-quality territories, and female lengths are larger.

Mean body mass of juveniles in low-quality territories decreased ca. 1 g from summer to spring, while there was little change in juveniles in good territories and in adults (Fig. 5). This was confirmed by individual mass changes of juveniles captured in summer (July–August) and recaptured in early winter (November–December) (mean change = -0.86 vs. -0.24 g; $t = 3.3$, $df = 32$, $P < 0.01$).

Local survival.—Local survival was not correlated in the two parts of the study period ($r = 0.13$, $n = 24$, $P > 0.2$). Local survival (calculated before settlement) was not correlated with settling order by juveniles in summer (1985: $n = 9$, $r_s = 0.06$, $P > 0.1$; 1986: $n = 6$, $r_s = 0.08$, $P > 0.1$). However, local survival was positively correlated with settling order by female immigrants ($r_s = 0.72$, $n = 16$, $P < 0.01$), and birds generally moved towards territories with higher local survival (25 of 31 cases; binomial test, $P < 0.01$).

DISCUSSION

Some territories—even if they remained temporarily vacant between successive settlements—were occupied consistently before others, and more frequently than others. The most logical explanation of my finding is that some territories are more valuable to nuthatches, that the birds can recognize variation in quality, and that they adjust their settling behavior accordingly. I demonstrated variation in quality and then I used breeding score as an estimate of quality for correlation with other variables (cf. Brooke 1979, Møller 1982, Nilsson 1987). It can be argued that breeding score is related not only to settlement patterns but also to longevity of individual owners, because adult birds are faithful to their territories. This is a problem especially if the study period (in this case 5 yr) is short compared with the owners' occupancy. Annual mortality of adult nuthatches is ca. 50% (Matthysen in press), and very few birds remained on one territory for >3 yr. Regardless, the significant relationships between breeding score and several independent measures of preference suggest that the confusing effect of longevity is small (or that variation in longevity is also related to territory quality). This justifies the use of breeding score as a parameter for

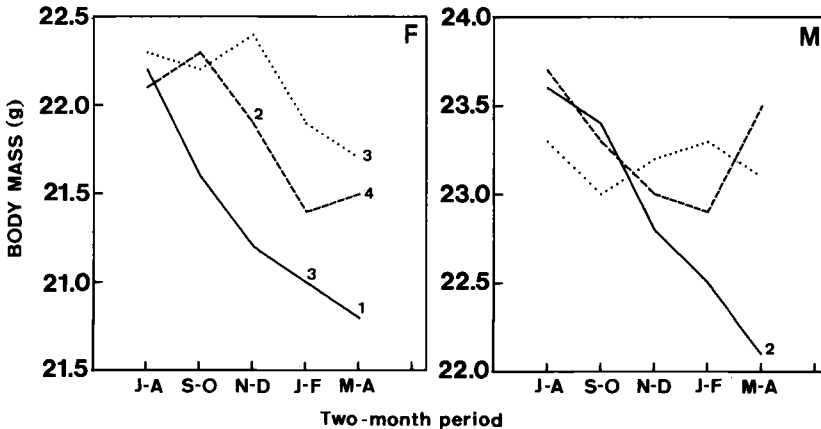


Fig. 5. Bimonthly average body mass of juveniles in good (·····) and poor (—) territories, and of adult birds (---). Sample sizes <5 are indicated; F = females, M = males.

territory quality. A general advantage of this method is that variation in territory quality can be demonstrated directly as it is perceived by the owners, without any assumptions on proximate or ultimate aspects of quality. The method can also be used for territories that are otherwise not comparable (e.g. in different habitats). A disadvantage is that the relationship between territory quality and survival cannot be examined with breeding score.

The quantitative vegetation analysis showed only that territory quality decreases as beeches are replaced by conifers. The qualitative comparison yielded results consistent with data on breeding density in different habitats (e.g. Löhrl 1967, Foyer 1976, Smith et al. 1987), general habitat distribution (avoidance of conifers; Lack 1971, Yeatman 1976), and geographical distribution (correlated with oak; Källander et al. 1978). The correlation between territory preference and size may be both a consequence and a cause of variation in quality. The latter is possible only if territory boundaries (i.e. sizes) are fixed. For example, boundary defense may be linked to topographical features (Reid and Weatherhead 1986). This condition would be more likely in plot L, which is small and elongated with a high border-to-surface ratio and a central clearing. Alternatively, territory quality may influence size directly. Asymmetries in expected benefit may result in more vigorous defense or more frequent patrolling in better territories. Birds in better territories can expect to remain there longer and may adjust territory size to future needs (Stamps and Tollestrup 1984,

Enoksson 1988). Conversely, birds on small low-quality sites with little long-term value may minimize defense costs while waiting for a better vacancy.

Some territories never used for breeding were small but contained vegetation elements typical of better territories (oak, garden, and beech). These territories may not represent permanent places in the system, but rather temporary settlements where the available area does not permit a longer stay. Such "marginal settlements" may be comparable to nonterritorial residents (Matthysen and Dhondt 1983, Matthysen 1989b).

One explanation for selective preference is that owners of more preferred territories have a higher fitness derived from higher territory quality (Petersen and Best 1987, Beletsky and Orians 1987). Evidence for territory-related variation in local survival is equivocal because there was no consistent variation when two parts of the study period were compared. Local survival was correlated with direction of shifts and with immigrant settling order, but the same individuals were involved both in settling and in the calculation of survival over the whole study period. The differential body mass changes of juveniles in different territory classes constitute supportive evidence for the correlation. In an earlier analysis (Matthysen 1988), I also found a correlation between settling order in summer and local survival, calculated over a 3-month period. This result was not confirmed in the present analysis, where I calculated survival monthly and used data from two summers instead of one. I have no data on breeding success

in different territories, but Nilsson (1987) found more brood failures in territories less frequently occupied by Eurasian Nuthatches. Age may have been a confounding factor because older birds usually have the better territories. My data on juvenile body-mass changes suggest that at least variation in local survival is not due to an age effect.

In general, territory-related variation in success can be caused by either territory or individual quality. Then, better territories would be inhabited by better individuals, but this was not confirmed from data on body size. This is not surprising in nuthatches, where settling is strongly influenced by fledging date (Matthysen 1987). Further, both settling and subsequent shifts depend on the unpredictable appearance of vacancies that are filled rapidly. Nilsson (1987) found longer-winged males on territories with oak, but this was also probably an age effect.

Ultimately, differences in success must be related to vegetation or other characteristics of the territory. Nilsson (1976) found higher breeding success in oak compared with beech habitat, and variable success in spruce. Nuthatches prefer oaks to beeches when they forage within their territory (Matthysen unpubl.). Oaks and other rough-barked trees may be easier to climb and better shelter for arthropods (Löhrl 1967, Jackson 1979). In Britain, there are more arthropod species on oak than on beech or Scots pine (Kennedy and Southwood 1984). Less mature trees, and probably conifers also, may be less attractive because they lack cavities (Löhrl 1967). Gardens may be preferred for vegetation structure, variation in tree species, or an abundance of extra food.

Vegetation characteristics may influence several aspects of territory quality. For example, broods in territories with conifers fledge earlier (Matthysen 1989a), and juveniles survive better, in beech territories in years with a good beech crop (Matthysen in press). Perhaps no simple relationship between vegetation and preference for territories should be expected.

Territory quality of juveniles in summer is correlated mainly with settling date (cf. Brooke 1979, Møller 1983, Lanyon and Thompson 1986). However, most postbreeding vacancies are of intermediate to low quality compared with adult territories, and most juveniles can benefit by shifting to another territory. This explains the low territory fidelity in juveniles (<30% from summer to breeding; Matthysen 1988). Some

owners were apparently evicted from their territory by immigrants, but there was no evidence that this happened between neighbors. Shifts seem to be mainly a passive process of birds moving into neighboring vacancies that appear by chance (Baeyens 1981, Drent 1987). Information on quality of surrounding territories can be obtained by occasional trespassing (Bartels 1984). As expected, most intruders were found in territories with a higher quality than their own (24 of 36 cases including 9 with equal breeding score; binomial test, $P < 0.001$).

Many territories in the study area rarely or never supported a breeding pair. Nevertheless they had an important role in the population by allowing juvenile birds to settle while they waited for a better vacancy. If such low-quality areas were unavailable, juveniles would probably be forced either to leave the breeding habitat or to live on adult territories (Ekman 1988). On the other hand, variation in territorial quality increases the benefits of site fidelity in high-quality sites and probably favors year-round territory defense.

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