The Nuthatch *Sitta europaea* population of Dalby Söderskog during 15 years: trend and fluctuations

HANS KÄLLANDER

Abstract

Nuthatches *Sitta europaea* were censused each spring 1977–91 in the 36 ha Dalby Söderskog national park, an old, mixed deciduous wood of oak *Quercus robur*, elm *Ulmus glabra* and beech *Fagus sylvatica*, situated less than 10 km ESE of Lund, southernmost Sweden. The number of territories varied between four and 21, that of pairs between four and 20, with one to three unpaired males defending territories in five of the years. The population size in spring co-varied positively with winter temperatures. Over the 15-year period, the population showed

a statistically significant positive trend, increasing by c. 0.7 pairs or territories per year. Similar increases in Nuthatch populations have been reported from Poland, Denmark, Great Britain and Sweden during the same period, and in other Fennoscandian passerines during the last three or four decades, and may be associated with increasing mean winter temperatures.

Hans Källander, Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden.

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Introduction

The European Nuthatch Sitta europaea lives yearround in permanent pair territories (Enoksson & Nilsson 1983, Matthysen 1985) in which large quantities of seeds, especially nuts of beech Fagus sylvatica and hazel Corylus avellana are stored in autumn and used throughout winter (Källander 1993). Both factors, territoriality and food storing, might be expected to lead to smaller population fluctuations in the Nuthatch than in co-existing, non-storing small passerines that do not defend territories in winter, such as Great Tit Parus major and Blue Tit P. caeruleus. To test this idea and to obtain data on the density of Nuthatches in a mature, largely unmanaged, mixed deciduous wood, in 1977 I started yearly censuses of the spring population of Nuthatches in Dalby Söderskog national park. The study was discontinued after 1991 partly because felling operations (the removal of elm Ulmus glabra trees with Dutch elm disease) were altering the habitat and partly because the wood has become part of the Swedish bird monitoring programme (S. Svensson pers.comm.); consequently its bird fauna is censused anyway.

Study area and Methods

Dalby Söderskog is a 36.2 ha mixed deciduous wood dominated by oak Ouercus robur, elm and beech, situated c.10 km ESE of Lund, southernmost Sweden (55°40'N, 13°20'E). Drier parts, dominated by elm and beech, are fairly open, with a scarce to moderate scrub layer mainly consisting of regenerating elm. Wetter areas have either a large proportion of old oak trees or are dominated by oak with an understorey of hazel. The wood was declared a national park in 1918 "to protect a remnant of the mixed deciduous forest typical of the region". Although its management has remained a matter of controversy, the wood has largely been allowed to develop naturally and is characterized by old trees, much dead wood and many fallen trees in various stages of decay (for a detailed history and description of the wood, see Lindquist 1938).

Nuthatches were censused by the mapping method (Anon. 1970) during 5 to 11 visits each spring from mid- or late March until the end of April, sometimes also in early May. Great care was taken to record simultaneously singing males, and the location of all aggressive encounters between neigh-

bouring pairs were plotted on field maps. Nuthatches are easy to census, especially at the time of nestbuilding (usually about mid-April) when the male follows the female closely and often sings close to the nest cavity. In different years between a tenth and two thirds of the nest holes were found and marked on the map. As no other species were censused, I followed individual birds as they moved around their territory and recorded interactions with surrounding Nuthatches. Each day's observations were immediately transferred to a summary map; thereby more time and effort could be directed to areas where uncertainties about the number and location of birds or pairs remained. In the evaluation of the summary maps, in addition to the number of plottings in each cluster, emphasis was laid on the presence of nests, simultaneous singing by males and aggressive encounters between pairs.

To analyse the possible influence of the severity of the winter on the size of the subsequent spring population of Nuthatches, I used two simple temperature indices: the summed mean temperatures of December to February and December to March, measured at the meteorological station in Lund. In addition, I also tested whether the number of days with temperatures below zero had any influence on Nuthatch numbers.

Results

The size of the Nuthatch population

The number of Nuthatch territories in Dalby Söderskog varied from four to 21 during 1977–91, and the number of pairs from four to 20 (Figure 1). Both the number of territories and pairs showed a statistically significant positive trend over the 15-year period, increasing by about 0.7 per year (linear regression, t=3.451, P=0.004 and t=2.970, P=0.011, respectively). Unpaired territorial males were present in five of the fifteen years; in 1985, three of the territorial males were lacking a mate. In addition, in three other years, single non-territorial males were observed on several occasions. Taken together, these observations indicate that mortality is higher in females than males.

Not even in the years when their densities were highest did the Nuthatches use all parts of the wood during the census period in spring. The map positions are too few to calculate reliable home ranges, but the smallest mean territory size, at least in March and April, was considerably less than the 1.7 ha (for 1990) obtained by dividing the wood's area by the number of territories. In 1979, when there were only



Figure 1. The number of Nuthatch territories and pairs in Dalby Söderskog during 1977–91. For those years when the numbers of territories and pairs differ, the latter are shown as open symbols. The regression line (for territories), Y=0.757x+0.741, is statistically different from zero (P=0.004).

Antal revir respektive par av nötväcka i Dalby Söderskog 1977–1991. För de år då antalet revir och par skiljer sig åt, anges det senare med öppna symboler. Regressionslinjen, Y=0.757x+0.741, är statistisk skild från noll (P=0.004).

four pairs, these moved over roughly three to four times larger areas than did pairs in the high density years (based on the plotted positions). Still, in that year, much of the wood remained devoid of Nuthatches and no aggressive encounters were recorded during the censuses.

Population fluctuations in relation to winter temperatures

The number of Nuthatch territories in spring was positively correlated with temperatures during the preceding winter (Figure 2; Spearman rank correlation, r_s =0.756 for Dec-Feb temperatures and r_s =0.568 for Dec-Mar temperatures, n=15, P<0.01 in both cases). The strongest population declines occurred after the three coldest winters, 1978–79, 1981–82 and 1984–85, when the number of territories was reduced by 69, 40 and 53%, respectively. However, the winter of 1986–87 was also cold, but Nuthatch numbers nonetheless increased by a third from 1986 to 1987.

Another measure of the severity of the winter is the number of days with sub-zero temperatures; also this measure showed a statistically significant relationship with the number of Nuthatches in spring



Dalby Söderskog National Park is a mixed deciduous wood dominated by oak, elm and beech. Drier parts usually have a scarce bush layer; a dense bush layer is found in some wetter parts, along a small stream and along the margins of the wood. The wood was formely more open with scattered old trees. Over the last century it has regenerated naturally. The only recent management has been removal of elms afflicted by the Dutch elm disease. There is an abundance of both natural cavities and woodpecker nests suitable for all kinds of hole-nesting birds: Tawny Owls, Jackdaws, Starlings, Redstarts, tits and Nuthatches. Photos: Hans Källander.

Dalby Söderskogs nationalpark är an blandlövskog med främst ek, alm och bok. Torrare delar har ett glest buskskikt, medan täta buskpartier finns i fuktigare partier, längs en liten bäck och längs ytterkanterna. Skogen var förr mera öppen med spridda gamla träd. Under det senaste seklet har den fått växa igen naturligt. Den enda sentida påverkan har varit nerhuggning av almar som drabbats av almsjuka. Det finns gott om både naturliga hål och hackspettbon för alla slag av hålbyggare: kattugglor, kajor, starar, rödstjärtar, mesar och nötväckor.



Figure 2. The relationship between the number of Nuthatch territories and temperatures during the preceding winter. Temperatures are represented by an index for the months December–February, inclusive. The correlation is statistically significant ($r_e=0.756$, P<0.01).

Sambandet mellan antalet nötväckerevir och temperaturen den föregående vintern. Temperaturerna är ett index för månaderna december-februari. Korrelationen är statistiskt signifikant (r. =0.756, P<0.01).

(days Dec-Feb, territories: r_s =-0.806, pairs: r_s =-0.813; days Dec-Mar, territories: r_s =-0.765, pairs: r_s =-0.768; n=15, P<0.01 in all cases).

The fluctuations in relation to population density

To investigate if the fluctuations in Nuthatch numbers showed any relationship with population density, multiple regressions were carried out with the relative change in numbers of territories or pairs as the dependent variable and with the population size in the preceding year and the different temperature measures as independent variables. These analyses revealed that population fluctuations were associated with both winter temperatures and the size of the previous year's Nuthatch population (R²=0.656, ANOVA, $F_{2.11}$ =10.506, P=0.003 for the relative change in number of territories; effect of number of territories in previous year, t=4.387, P=0.001, effect of Dec-Feb temperatures, t=2.947, P=0.013; the results were similar, but with slightly weaker associations, for the relative change in number of pairs and when the other measures of winter severity were used).

Discussion

Population fluctuations

Despite the species' year-round territoriality, the Nuthatch population in Dalby Söderskog varied as much as (nestbox-breeding) Great Tit populations in the same region (C.V._{territories}=36.4, C.V._{pairs}=38.3 vs C.V.=26.3 and C.V.=38.7, respectively, for two Great Tit populations over 9 and 10 years; own unpubl. data). The range of variation in my study was similar to that found for Nuthatches by Nilsson (1978).

As the present study was carried out in a relatively small (36 ha) and isolated wood, one might expect chance effects to have a strong influence on the population fluctuations. Even so, however, the results agree well with previous findings (Källander & Karlsson 1981, Svensson 1981, Nilsson 1987) of a positive relationship between winter temperatures and the size of the Nuthatch population in the subsequent spring. A similar relationship has been documented for a number of passerines in Fennoscandia (e.g. Källander & Karlsson 1981, Svensson 1981, Hildén 1982) and for the whole community of residents and short-distance migrants (Enemar et al. 1994). In his detailed analysis of population fluctuations and mortality in a Nuthatch population c.110 km to the northeast of Dalby Söderskog, Nilsson (1987) found a much stronger correlation ($R^2=0.77$) between mean winter temperatures (December-March) and spring population size than found in the present study ($R^2=0.35$). This may be explained by differences in the size of their Nuthatch populations; Nilsson worked in two different plots together three times as large as Dalby Söderskog and with 50% more Nuthatches, probably making his population less susceptible to random events.

Nilsson (1987) found that much of the variation in Nuthatch numbers that remained after winter temperatures had been taken into account was explained by the size of the beech mast crop in the preceding autumn. Unfortunately, beech mast was not measured in the present study, but bumper crops were produced in the autumns of 1976, 1983 and 1989. However, none of these years was followed by exceptionally large Nuthatch populations. Two possible explanations for this are that either there is an interaction between beech mast and the severity of the winter, such that beech mast has its strongest positive effects in cold winters, or that population density limits the influence of beech mast when Nuthatch populations are large. The absence of any effect of beech mast on winter survival reported by Nilsson (1987; also see Matthysen 1989) or of supplemental feeding in autumn (Enoksson 1990) argues against the former explanation. However, more data on winter survival would be desirable, especially in light of demonstrated positive effects of stored food on the nutritional status of Nuthatches in late winter (Nilsson et al. 1993).

The results of the multiple regression analysis suggest that the effects of population density on relative population change were stronger than those of winter temperature. As the Nuthatches were censused only in spring, density-dependent effects could have acted during any period of the year, for instance through territorial behaviour in autumn, as argued by Enoksson (1990).

The positive population trend

The Nuthatch population in Dalby Söderskog showed a positive trend during the study period, increasing by on average 0.7 territories or pairs per year. Similar, statistically significant increases have been recorded also in other populations during the same period: the British Common Bird Census (Wilson & Marchant 1997), Bialowiecza, Poland (1977–90; Wesołowski & Stawarczyk 1991), the Swedish Breeding and Winter Bird Censuses (Svensson 1994) and the Danish Winter (but not Breeding) Bird Census (Jacobsen 1994, 1994a). In the Danish data, the winter populations were not significantly correlated with those in the following spring, perhaps suggesting that the breeding time census produces less reliable data for the Nuthatch.

Also several other passerines have shown steady increases in recent decades, in many cases since the late 1950s, although the causes may not necessarily always be the same (e.g. Hildén 1988). Enemar et al. (1994) found that residents and short-distance migrants had increased by, on average, 0.76 territories per year between 1953 and 1992 in Fågelsångsdalen ("Bird Song Valley") to the east of Lund. During the same period, mean temperatures in January–March, as measured at the meteorological station in Lund, increased by 3°C.

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Sammanfattning

Nötväckepopulationen i Dalby Söderskog under 15 år – trend och beståndsvariationer

Under åren 1977–91 inventerade jag varje vår populationen av nötväcka *Sitta europaea* i den 36,2 ha stora Dalby Söderskog nationalpark, belägen cirka 10 km ostsydost om Lund. Denna skog har i stort sett fått utvecklas fritt under relativt lång tid och karakteriseras därför av gamla träd, hög andel död ved och talrika liggande stammar i olika stadier av nedbrytning. Skogens torrare delar domineras av bok och alm medan fuktigare partier domineras av ek, inom vissa områden med ett buskskikt av hassel.

Nötväckorna inventerades huvudsakligen under mars-april med en modifierad revirkarteringsmetod, där särskild vikt lades vid samtidig sång, lokaliseringen av bohål samt aggressiva interaktioner mellan paren. Partier av skogen, där oklarhet om antalet fåglar rådde, ägnades extra tid. Nötväckor är relativt lättinventerade, i synnerhet under bobyggnadstiden då hanen följer honan och ofta sjunger nära bohålet.

Antalet nötväckerevir varierade mellan fyra och 21, antalet par mellan fyra och 20. Populationssvängningarna hos den året runt revirhållande och hamstrande nötväckan var därför lika stora som hos den icke-hamstrande talgoxen *Parus major* (se även Nilsson 1978). Under fem av åren fanns en till tre oparade, men revirhållande hanar, vilket antyder att dödligheten är högre hos honorna. Inte ens under toppåret 1990 utnyttjade nötväckorna alla delar av skogen, varför den faktiska revirstorleken understeg de 1.7 ha som erhålls genom att dividera skogens yta med antalet par. Under bottenåret 1979 rörde sig de fyra paren över större områden än så, men en stor del av skogen förblev outnyttjad. Dalby Söderskogs nötväckepopulation uppvisade en positiv trend under inventeringsperioden, med en genomsnittlig ökning med 0,7 revir eller par per år (Figur 1). En liknande positiv trend har registrerats för nötväckepopulationer i Storbritannien, Polen och Danmark och f.ö. bland ett flertal stannfåglar och kortdistansflyttare (Hildén 1988, Wesolowski & Stawarczyk 1991, Jacobsen 1994, 1994a, Enemar m.fl. 1994, Wilson & Marchant 1997).

Storleken på nötväckornas vårpopulation i Dalby Söderskog samvarierade med den föregående vinterns stränghet, mätt antingen som ett temperaturindex för månaderna december-februari eller december-mars, eller som antalet dygn med frost under samma perioder: Ju mildare vinter, desto större vårpopulation av nötväcka (Figur 2). De kraftigaste minskningarna (40-69%) skedde efter de tre strängaste vintrarna, men trots att vintern 1986-87 också var hård, ökade i stället beståndet mellan 1986 och 1987. De relativa beståndsförändringarna visade också ett signifikant samband med antalet par föregående vår. I själva verket var denna täthetsberoende effekt starkare än effekten av vintertemperaturen, men eftersom nötväckebeståndet endast taxerades under våren kan den ha haft sin verkan när som helst under året, t.ex. via revirbeteende under hösten (Enoksson 1990).

Produktionen av bokollon, vilka nötväckorna hamstrar i stor mängd, mättes inte, men tre toppår förekom (1976, 1983 och 1989). Efter dessa höstar var emellertid vårpopulationen inte tydligt högre än förväntat utifrån vintertemperaturen (se Figur 2). Detta är något förvånande med tanke på att hamstrad föda visat sig ha en positiv effekt på nötväckors näringsstatus (Nilsson m.fl. 1993) men stämmer överens med tidigare studier som funnit att vinteröverlevnaden inte tycks påverkas av höstens bokollonskörd (Nilsson 1978, Matthysen 1989).