

# Fluctuation of a breeding population of Brambling *Fringilla montifringilla* during 33 years in a subalpine birch forest

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The breeding density of a Brambling *Fringilla montifringilla* population studied during 1966–1998 in a subalpine birch forest area covering 3.5 km<sup>2</sup> in central Norway varied between two and 52 territories/km<sup>2</sup> with a mean of 28.4. The population fluctuated synchronously with the abundance of larvae of the geometrid moth *Epirrita autumnata* ( $r_s = 0.82$ ,  $P < 0.001$ ) with population peaks in 1975–1976, 1985–1986 and 1996. The birds were largest (wing length as index of body size) in peak years. Although nest predation did not markedly influence the breeding success of Bramblings, it was negatively correlated ( $r_s = -0.42$ ,  $P < 0.05$ ) with the density of small rodents, probably because of increased predation by mustelids in years after the population crash of rodents. In summers with long periods of cold, rainy weather, several pairs abandoned their nests with eggs or nestlings when the abundance of *E. autumnata* was low, but not when it was high. It is suggested that the Brambling, due to its widespread movements and lack of breeding site tenacity, may be less adapted to varying environmental conditions and resources than other breeding species in the subalpine passerine community, and that Bramblings breeding in subalpine forests are dependent on *E. autumnata*.



## 1. Introduction

The Brambling *Fringilla montifringilla* belongs to the Siberian faunal type and is distributed extensively from Scandinavia to eastern Siberia. The species is considered to be the ecological counterpart of the Chaffinch *F. coelebs* in northern birch and coniferous forests (Voous 1960). However, in contrast to the Chaffinch, Bramblings have no breeding site tenacity and select nesting sites within their breeding range according to yearly variations in the weather, the time of snow melting and food conditions (Mikkonen 1983). Consequently, the breeding density of Bramblings vary considerably from year to year, and in subalpine birch forests density seems dependent on

the abundance of larvae of the geometrid moth *Epirrita autumnata* (e.g. Silvola 1967, Hogstad 1969, Enemar et al. 1984, Lindström 1987). In the present article, I complete studies on the fluctuation in the breeding density of a Brambling population in a Norwegian subalpine birch forest during 1966–1998, focusing especially on variation in the annual abundance of moth larvae, weather and nest predation.

## 2. Study area and methods

The fieldwork was carried out in a homogeneous subalpine forest of Downy Birch *Betula pubescens tortuosa* in Budal (62°45'N–10°30'E), central

Norway. The forest is unmanaged and extends from 750 to 900 m above sea level, and the general tree height is 3–6 m. The study area covered 3.5 km<sup>2</sup>.

The density of the breeding bird community was estimated during 1966–1998 by the territory mapping method in accordance with international recommendations (Anon. 1970), within one permanent study area of 30 ha (100 × 3000 m). The field work mostly took place from the last week of May when Bramblings establish in the area, to mid July when they leave. In 15 years (1972–1975, 1979–1982, 1984–1985, 1990 and 1994–1998) Bramblings were trapped in mist nets and their wing lengths (as an index of body size) were measured to the nearest mm when flattened out and straightened, i.e. the maximum length (Svensson 1992). The fresh egg weights of totally 95 newly completed clutches were found in the years 1972–1998 (except 1978 and 1982) by using a balance with accuracy 0.1 mg.

Because the breeding density of Bramblings in subalpine birch forests has been considered dependent on the abundance of larvae of the geometrid moth *Epirrita autumnata* (e.g. Hogstad 1985, Lindström 1987), I have estimated the density of larvae in the study area. In 1972–1998, larvae of the moths *E. autumnata* and *Operophtera brumata* were collected with a sweep-net from branches on the lowest four metres of birch trees. However, although the two populations fluctuated synchronously (Hogstad 1997), *O. brumata* made a small fraction of the moth larvae in Brambling gizzards (cf. Hogstad 1988) and has therefore been omitted from the analyses. Each year, 5–15 collections, each of 100 sweeps, were taken in the first days of July, i.e. when the larvae were in their two last instars, 4 and 5 (body length 20–27 mm, see Hogstad 1996).

Predation on the nest content varied considerably. Nest predators present in the area were Ravens *Corvus corax* (one pair), Hooded Crows *Corvus corone cornix* (one or two pairs), Pine Martens *Martes martes*, Stoats *Mustela erminea* and Weasels *Mustela nivalis*. The densities of the last two species varied from year to year, based on the number of their tracks seen on the snow during the winter/spring, and were highest when small rodents were at peak numbers. Accurate density indices of these mustelids could not be assessed

due to their cryptic way of life (cf. Marcström et al. 1990). Heavy nest predation by mustelids has been demonstrated for tree-nesting birds in years with low densities of small rodents, their primary prey (e.g. Järvinen 1985, Sørensen et al. 1990). Since the disturbed lining of several nest cups emptied of eggs may indicate that mammalian predators had visited the nests, I have related the nest predation of Bramblings to rodent density in the years 1972–1998. The relative density of small rodents was estimated based on tracks seen on the snow during winter and spring and from observations during the following breeding season; 0 = no tracks, no rodents observed; 1 = few tracks, rodents rarely observed; 2 = new tracks seen almost daily, rodents regularly observed; 3 = many tracks, rodents frequently observed. The most common rodents were the Norway Lemming *Lemmus lemmus*, the Bank Vole *Clethrionomys glareolus* and the Field Vole *Microtus agrestis*.

The date of birch coming into leaf (defined as the stage when the petioles are just visible; 1–30 = 1–30 June) was used as an index of phenological development in the years 1972–1998 (Slagsvold 1976). Meteorological data (amount of precipitation and mean monthly temperature in May and June) are from Berkåk meteorological station, about 25 km from the study area and 450 m above sea level. Statistical tests are two-tailed. Parameters preceded by ± sign are standard deviations.

### 3. Results

#### 3.1. Breeding density

The Brambling density varied between 2 and 52 territories/km<sup>2</sup> with a mean of  $28.4 \pm 14.5$  (N = 33) and a coefficient of variation (100 SD/mean) of 51% (Fig. 1). The relative density (percentage of Brambling pairs of the total passerine community) varied from 1.5% to 31.7% with a mean of  $19.0\% \pm 8.0$ . Three population peaks occurred during the study period: in 1975–1976, 1985–1986 and 1996. Except for the peak in 1985–1986 with a density of 36 territories/km<sup>2</sup>, the peak densities were about 50 territories/km<sup>2</sup>.

A correlation analysis between Brambling density and environmental factors gave significant values for the density of moth larvae (Spear-

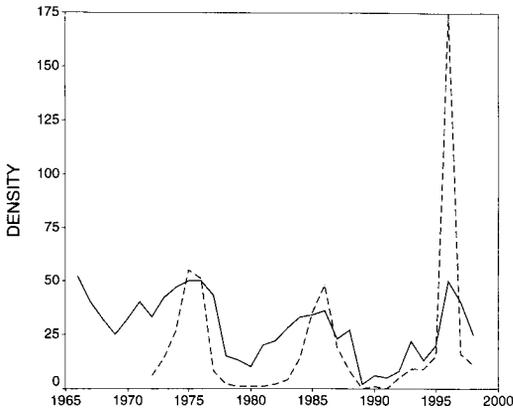


Fig. 1. The fluctuation of the breeding density (territories/km<sup>2</sup>) of the Brambling during 1966–1998 (solid line) and the density of *Epirrita autumnata* larvae (stippled) in birch trees (mean number of larvae per 100 sweeps with a net) during 1972–1998.

man rank correlation,  $r_s = 0.82$ ,  $N = 27$ ,  $P < 0.001$ ; Fig. 1), birch phenology ( $r_s = 0.41$ ,  $N = 27$ ,  $P < 0.05$ ), and precipitation in June ( $r_s = -0.42$ ,  $N = 33$ ,  $P < 0.05$ ). Thus, the variation in the density of larvae is of primary importance for the Brambling density in Budal.

The Brambling density was positively correlated with the annual mean wing length of the birds (males:  $r_s = 0.56$ ,  $N = 14$ ,  $P < 0.05$ ; females:  $r_s = 0.48$ ,  $N = 15$ ,  $P = 0.07$ ), indicating that the birds were largest in the years with high breeding density. Although the annual fluctuation in the mean wing lengths of males and females showed the same general pattern ( $r_s = 0.61$ ,  $N = 14$ ,  $P = 0.05$ ), only males tended to be significantly correlated with the density of *E. autumnata* (males:  $r_s = 0.51$ ,  $N = 14$ ,  $P = 0.06$ ; females:  $r_s = 0.38$ ,  $N = 15$ , n.s.).

### 3.2. Clutch size and incubation

The clutch size varied from four to seven eggs, with a mean of  $5.6 \pm 0.73$  ( $N = 95$ ). Clutches of five and six predominated, together comprising 85% of 95 clutches (Fig. 2). The mean fresh egg weight of newly completed clutches varied between 2.11 and 2.17 g (mean  $2.14 \text{ g} \pm 0.02$ ), and was positively related to the size of the female (wing length; Pearson correlation  $r = 0.70$ ,  $N = 10$ ,  $P = 0.02$ ).

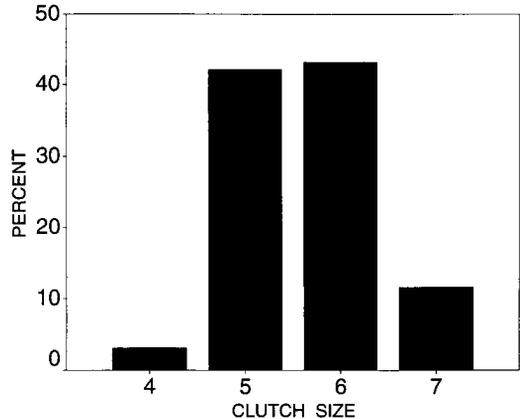


Fig. 2. Percentage frequency distribution of clutches of different sizes ( $N = 95$ ).

The eggs were generally laid at one-day intervals before 08:00. However, in years with periods of cold, rainy weather, laying could be interrupted for one to five days. About 80% of the nests (43 nests examined from laying to hatching) hatched within 24 h and the remainder within two days. Thus, incubation apparently begins with the last egg or occasionally the one before. Females incubated (time from last egg to last hatching) for 11–12 days, with a mean of 11.4 days (11 d:  $N = 23$ , 12 d:  $N = 15$ ). However, if the incubation time of five nests, which, due to spells of adverse weather, lasted 13 days ( $N = 3$ ) and 14 days ( $N = 2$ ), respectively, are included, the mean incubation time increases to 11.6 days. The nestling time was 12–14 days, with a mean of 13.2 days (12 d:  $N = 4$ , 13 d:  $N = 28$ , 14 d:  $N = 11$ ).

### 3.3. Brood failure

Three summers (1978, 1979 and 1981) with extremely cold and rainy weather gave low breeding success in Bramblings. Several pairs abandoned their nests with eggs or nestlings. In 1978, about half the Brambling population (density 15 territories/km<sup>2</sup>) left the area during the second half of June and no fledglings were observed. In 1979, two nests with eggs incubated five and seven days, respectively, and one nest with two days old nestlings, were found abandoned. In 1981, four nests, two with six eggs incubated 7–10 days and two

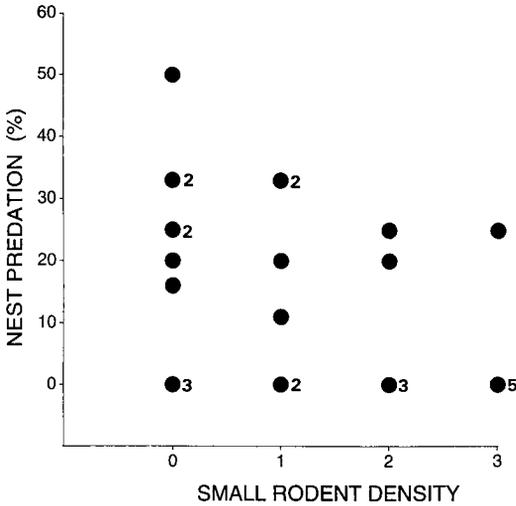


Fig. 3. The relationship between the annual relative density of small rodents and the nest predation of Bramblings during 1972–1998. (Figures denote sample size within each dot).

with 2–6 days old nestlings, were abandoned. In these summers, low temperature combined with several days of rain or snow lowered the insect activity (based on sweep-net catches, see Hogstad 1982) and probably decreased the availability of insects as food for the birds. Correspondingly, Bramblings caught in 1981 had no visible subcutaneous fat, in contrast to birds caught in 1980, and it seemed likely that the birds had exhausted their fat reserves during the lasting cold weather and bad feeding conditions (see Hogstad 1982). Also in 1996, there were several days with cold and exceptionally rainy weather in the nestling period, but no effect on the breeding success of Bramblings was observed. However, in contrast to 1978, 1979 and 1981, the density of moth larvae was high in 1996 (Fig. 1).

### 3.4. Nest predation

Nest predation (the proportion of nests emptied of eggs or nestlings) varied considerably between years, and correlated negatively with the relative density of small rodents ( $r_s = -0.42$ ,  $N = 27$ ,  $P < 0.05$ ; Fig. 3). In the same years, other factors like density of larvae ( $r_s = 0.18$ ), Brambling density ( $r_s = 0.17$ ), or weather conditions in June as mean

temperature ( $r_s = 0.21$ ) or precipitation ( $r_s = 0.32$ ) were not found significant.

## 4. Discussion

As found in other studies (e.g. Silvola 1967, Hogstad 1969, Enemar et al. 1984, Lindström 1987) the present study clearly demonstrates the relationship between the Brambling density and the abundance of *E. autumnata*. Although not quantified, the density of Bramblings in the Budal area was markedly lower in 1965 than in 1966. Furthermore, the moth larvae occurred in large numbers in 1966 and in low numbers in the following year (Hogstad 1968). Thus, apparently four concurrent population peaks of the Brambling and moth larvae occurred, approximately each tenth year. The dependency of the Brambling on the geometrid larvae was most obvious in the cold, rainy summers in Budal, as the breeding success of the birds was poor when *E. autumnata* larvae were uncommon, but as normal when they were abundant.

The summer of 1981 was exceptionally cold and rainy in Finland, too, and in Lapland the Bramblings produced very few young though Redstarts *Phoenicurus phoenicurus* and Bluethroats *Luscinia svecica* managed as well as normal (Hildén et al. 1982). Also in Budal, the breeding success of Willow Warblers and Bluethroats apparently were normal in the rainy summers (O. Hogstad unpubl.), in contrast to that of Bramblings. As mass occurrences of *E. autumnata* occur at regular 9- or 10-year intervals, and are relatively synchronous throughout Fennoscandia (Tenow 1972), the abundance of the larvae was most likely low in Finnish Lapland in 1981 as it was in Swedish Lapland (Svensson 1996).

I have suggested earlier, based on nine breeding seasons, that the two most abundant species in the passerine community in the Budal study area, the Brambling and the Willow Warbler *Phylloscopus trochilus*, fluctuated inversely with each other ( $r = -0.95$ ,  $N = 9$ ,  $P < 0.001$ ) and exhibited partial interspecific territoriality (Hogstad 1975, see also Angell-Jacobsen 1980). However, also working in the Budal area, Fonstad (1984) demonstrated that the reduced territorial overlap was most likely due to habitat preferences. After 33

breeding seasons, no significant relationship has been found between the density fluctuations of the two species ( $r = 0.17$ , n.s.). However, the fluctuating pattern of the relative densities of the species was still found to be negatively correlated (Fig. 4;  $r = -0.40$ ,  $N = 33$ ,  $P = 0.02$ ). The reason for the negative relationship between the two species may be that the Brambling responded numerically ( $r_s = 0.82$ ) to the fluctuation in the abundance of larvae while the Willow Warbler did not ( $r_s = 0.07$ ,  $N = 27$ , n.s.; O. Hogstad unpubl.). Thus, it is not likely that the breeding density of the Brambling is influenced by interspecific competition.

Although nest predation varied from one year to another, it was scarcely a decisive factor for the fluctuation pattern found in the Brambling in Budal. A long term study in Finnish Lapland revealed that about 43% of 479 Brambling nests were destroyed (Saari et al. 1999). In Budal, mustelids seems to be more effective nest predators on Bramblings than avian predators. The density of Stoats and Weasels increases with increasing small rodent densities (Hogstad 1995, see also Korpimäki et al. 1991). When the population of voles, their primary prey, decreased, the mustelids probably were forced to turn to alternative food (cf. Erlinge 1981, Angelstam et al. 1985), such as eggs and nestlings of passerines (Järvinen 1985, Hogstad 1995).

Significant differences found in the yearly mean wing lengths of Brambling males in Budal (Hogstad 1985) and females in Ammannäs, Swedish Lapland (Lindström 1987), may be due to different age structures of the population. As the Bramblings were largest in years with a high density of *E. autumnata*, it may be suggested that older, larger birds move into the area in years with a good food supply.

It seems remarkable that the Brambling suffered from the bad weather to a greater degree than other bird species of the same size and eating apparently similar food. When put under the stress of severe weather and poor food availability, the females probably have to channel most of their food into maintaining their body temperature rather than into breeding activities. The interruptions in laying during cold, rainy weather may also be due to the physical condition of the females. A similar laying pattern is found in *Parus* species (S. Haftorn unpubl.) that also experience

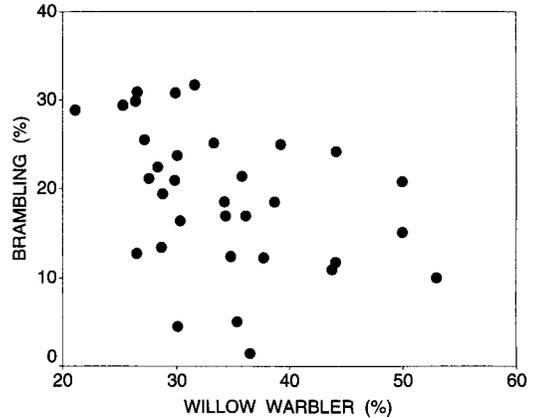


Fig. 4. The relationship between the annual relative densities (percentage of pairs of a species within the total passerine community) of the Brambling and the Willow Warbler in Budal during 1966–1998.

high mortality of nestlings in bad weather.

The clutch size of the Brambling (mainly varying between 5.5 and 6 eggs) is, moreover, larger than that of other European finches (14 species, mean 4.7 eggs; Cramp & Perrins 1994). The mean clutch size of the closely related Chaffinch *F. coelebs*, which has a strong breeding site tenacity (Mikkonen 1983), is 4.7 eggs (Haartman 1969).

Although the breeding success of Bramblings is influenced by adverse weather and to some degree by nest predation, the most important factor for those breeding in subalpine birch forests is apparently the abundance of *E. autumnata*. When breeding far north where the summers are short and the environmental predictability is low, birds have to be adapted to the climatic conditions. Contrary to most passerines, the Brambling has no breeding site tenacity (Mikkonen 1983, Lindström 1987) and seems adapted to select nesting sites at any place within their breeding range according to food conditions and the time of snow melting, i.e. a trend towards an opportunistic strategy. This may be a favourable strategy when resources are abundant, but is unpredictable in time and space.

Thus, the Brambling apparently suffers from bad weather to a greater degree than other species (e.g. Hildén et al. 1982, this study), and may even leave the breeding ground in subalpine areas without producing young (this study). In a study from Eastern Finnish Lapland, Bramblings got no off-

spring at all in several years during 1970–1997 (Saari et al. 1999). It may be suggested that the vulnerability of the species results from its widespread movements disrupting local adaptations (e.g. Horn 1983). However, when food is in good supply, i.e. when *E. autumnata* larvae are abundant, the breeding success of the Brambling was normal even under severe climatic conditions. It may therefore be suggested that Bramblings breeding in the subalpine birch forest responded to the food supply and not directly to weather conditions as such. I therefore conclude that, to produce young in subalpine birch forests where environmental conditions and resources vary greatly, the Brambling is entirely dependent upon the occurrence of *E. autumnata* larvae.

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## Selostus: Järripeipon populaatiobiologia Keski-Norjan subalpiinisessa koivu-vyöhykkeessä 1966–1998

Kirjoittaja tutki järripeipon pesimäbiologiaa Norjassa 33 vuoden aikana kerätyn aineiston avulla. Järripeipon populaatiotiheys vaihteli kahdesta parista 52 pariin neliökilometrillä, ollen keskimäärin 28.4 paria. Näin ollen lajin vuosien välinen tiheysvaihtelu oli suurta (CV = 51 %). Vastaavasti järripeipon osuus tutkimusalueella pesivien varpuslintujen kokonaismäärästä vaihteli 5–31.7 %, ollen keskimäärin 19.0 %. Erityisesti tunturimittari toukkien määrä vaikutti positiivisesti järripeippotiheksiin. Järripeipot munivat neljästä seitsemään munaa, keskiarvon ollessa 5.6. Kylminä, sateisina vuosina muninta saatoi keskeytyä jopa viiden päivän ajaksi. Naaraat hautoivat munia keskimäärin 11.4 päivää ja poikaset viipyivät pesässä keskimäärin 13.2 päivää. Poikkeuksellisen kylminä ja sateisina kesinä järripeipojen pesimämenestys oli erittäin huono. Esimerkiksi kesällä 1978 noin puolet järripeippopopulaatiosta poistui alueelta jo kesäkuun toisella viikolla, eikä lentopoikasia havaittu alueella lainkaan. Pesien hylkäämisiä tapahtui erityisesti sellaisina vuosina jolloin tunturimittareiden esiintyminen oli niuk-

kaa. Järripeipojen pesiin kohdistuva predaatio vaihteli huomattavasti (0–50 %) vuosien välillä. Pesäpredaation suuruus korreloi negatiivisesti pikkujyrsijätiheyden kanssa. Havainto viittaa siihen, että huonoina pikkujyrsijävuosina lintujen pesiin kohdistuu suurempi predaatiopaine. Kirjoittaja ehdottaa, että nomandisena lajina järripeippo on sopeutunut muita lajeja heikommin vaihteleviin ravinto-olosuhteisiin. Kirjoittaja toteaa, että hänen tutkimusalueella järripeipon pesimämenestys on riippuvainen tunturimittarien esiintymisestä.

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