

Breeding nomadism and site tenacity in the Brambling *Fringilla montifringilla*

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Territory mapping in subalpine birch forest in Ammarnäs, Swedish Lapland, during 1963–1986 revealed that Brambling *Fringilla montifringilla* densities are highest in years with high densities of caterpillars of the geometrid moth *Epirrita autumnata*. The number of stationary males was positively correlated with the number of nests found in the area. Thus, the birds moving into the area do attempt to breed there. In 1983–1986, 999 Bramblings were trapped during the post-breeding period. The proportion of juveniles was significantly higher in years with *Epirrita* peak abundance. The data indicate that the density of breeding Bramblings in Ammarnäs depends on *Epirrita*.

Ringed recoveries and the almost complete absence of recaptures of birds ringed in Ammarnäs in earlier years show that both males and females normally change their breeding sites between years, i.e. they are nomadic. Breeding site fidelity may occur, however, since one male ringed in 1985 returned to Ammarnäs in 1986.

The mean wing lengths of adult females varied significantly between years (1983–1986). As only 60% of these birds could be properly aged it was not possible to discover whether the differences between years were due to a varying proportion of older birds. Older females (+3y) were significantly larger in years with peak food abundance. The mean wing lengths in adult males did not differ significantly between years.

The breeding site strategy of the Brambling is discussed in relation to a theoretical model of breeding nomadism.

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Introduction

The Brambling *Fringilla montifringilla* is one of the most common breeding birds in the Fennoscandian subalpine forests. It is particularly well known for its nomadic winter habits and a large part of the population may change its winter quarters between years (Newton 1972, Jenni 1982). This nomadic tendency seems to prevail during the breeding season (Mikkonen 1983, Hogstad 1985), and it has been suggested that this is due to variation in food conditions between years (Mikkonen 1983, Hogstad 1985). The nomadism of the Brambling is in sharp contrast to the behaviour of the Chaffinch *F. coelebs*, which shows a high breeding site tenacity (Bergman 1939, Anvén & Enemar 1957, Mikkonen 1983).

Andersson (1980) presented a model on breeding site tenacity in bird species that are highly dependent on annually fluctuating food sources for their breeding. Lack of breeding site tenacity between years in adult birds, i.e. "breeding nomadism", should generally be more advantageous than site

tenacity when the food supply varies cyclically, rather than at random. Further, this advantage increases with the interval between good years.

Bramblings respond to high densities of caterpillars of the geometrid moth *Epirrita autumnata*; in the Ammarnäs area, Brambling densities doubled during the *Epirrita* outbreak of 1973 and 1974 (Enemar et al. 1984, and Fig.1). A higher density of Bramblings in years of *Epirrita* abundance has also been reported from Finland (Silvola 1967) and Norway (Hogstad 1969). This insect fluctuates cyclically, with 10 to 12 years between its outbreaks, which are normally preceded by some years of low, but increasing, densities, and last about three years (Andersson & Jonasson 1980). However, it has yet to be shown whether, how, and to what extent, the breeding performance of the Brambling is influenced by the abundance of *Epirrita* caterpillars.

According to the reasoning of Andersson (1980) and assuming that breeding Bramblings are dependent on the cyclically occurring *Epirrita*, one should expect the Brambling to show breeding

nomadism. However, in the model of Andersson (1980), a good year is always followed by a bad year. This is not the case as regards either *Epirrita* (at least two successive good years in each peak), or the population cycle of voles, another prey group causing nomadism in birds. The pattern in voles is normally two good years followed by one or two bad years (Löfgren et al. 1986). Thus, in birds dependent on one of these food sources there is room for more complex strategies than merely nomadism or site tenacity.

Female Tengmalm's Owls *Aegolius funereus* seem to have adapted successfully to the cyclicity of voles by being site tenacious during the peaks, but nomadic between them (Löfgren et al. 1986). As *Epirrita* has a cyclic occurrence similar to that of voles, the strategy of the female Tengmalm's Owl would be plausible for the Brambling as well. In this paper I point out connections between the occurrence of *Epirrita* and breeding in the Brambling, and discuss possible breeding site strategies for this species.

Methods

As a part of the LUVRE project (see Enemar et al. 1984), we have caught and ringed birds at the same locality in subalpine birch forest during the late breeding and post breeding period (31 July – 25 August 1983, 13 July – 15 August 1984, 12 July – 13 August 1985 and 16 July – 21 August 1986) at Lake Tjulträsk near Ammarnäs, Swedish Lapland (65°58' N, 16°07' E). Twenty to twentytwo nets were used every day from 07.00 to 13.00, local summer time. All the birds were aged and sexed according to Svensson (1984) and their wing lengths (maximum method) and weights were determined. Regular calibrations between ringers were made. In spring and early summer, breeding Bramblings can be separated into first-year (2y) and older birds (+3y), but this becomes impossible early in the post-breeding moult, and the birds can merely be aged as +2y. Adult birds in moult were examined according to Ginn & Melville (1983). All individuals recaptured one day or more after ringing were examined again.

Since 1963 the density of breeding birds in the subalpine birch forest in Ammarnäs has been estimated every year by territory mapping in study plots (Enemar et al. 1984).

From 1963 to 1985, 375 nests of Bramblings were found and recorded on nest cards. Most nests

were found by chance, without systematic search, and field activities have been reasonably constant, except for slightly lower activity during the initial four years. Thus, the number of nests found each year may be used as a rough index of the breeding activity that year.

The occurrence of *Epirrita* caterpillars on birch shoots has been recorded in special study plots since 1967, about 1 km from our ringing site. The methods and results up to 1979 are presented by Andersson & Jonasson (1980).

Results

Breeding densities

The number of stationary male Bramblings/km² in 1963–1986 is shown in Fig. 1, together with the mean number of *Epirrita* caterpillars per 1000 birch short shoots in three study plots in the birch forest in 1967–1986. In the *Epirrita* peak of 1973–1975 (peak I), Brambling density was more than twice the normal in two of the three years, though in 1975 the response was less marked. In the peak of 1985–1986 (peak II), there was also a numerical response, though not as pronounced as in peak I. In peak II, the highest density was reached already during the building up phase.

There was a statistically significant positive correlation between the number of stationary males and the number of nests found in each year (Fig. 2).

Trapping

A total of 999 Bramblings were trapped in 1983–1986. The proportion of juvenile (young of the year, 1y) Bramblings trapped during the post-breeding period increased during the period 1983–1986 (1983: 53%, 1984: 62%, 1985: 72%, 1986: 69%). The difference between 1983–1984 (mean = 60%, two years of low food abundance) and 1985–1986 (mean = 70%, two years of peak food abundance) is significant ($\chi^2 = 12.0$, $df = 1$, $P < 0.001$).

The numbers of Bramblings ringed and retrapped in later years are presented in Table 1. It should be mentioned that the relatively low trapping figures in 1985 were partly due to very poor weather (rain on 28 out of 33 days), which frequently prevented trapping during that season. Of the 262 adults and

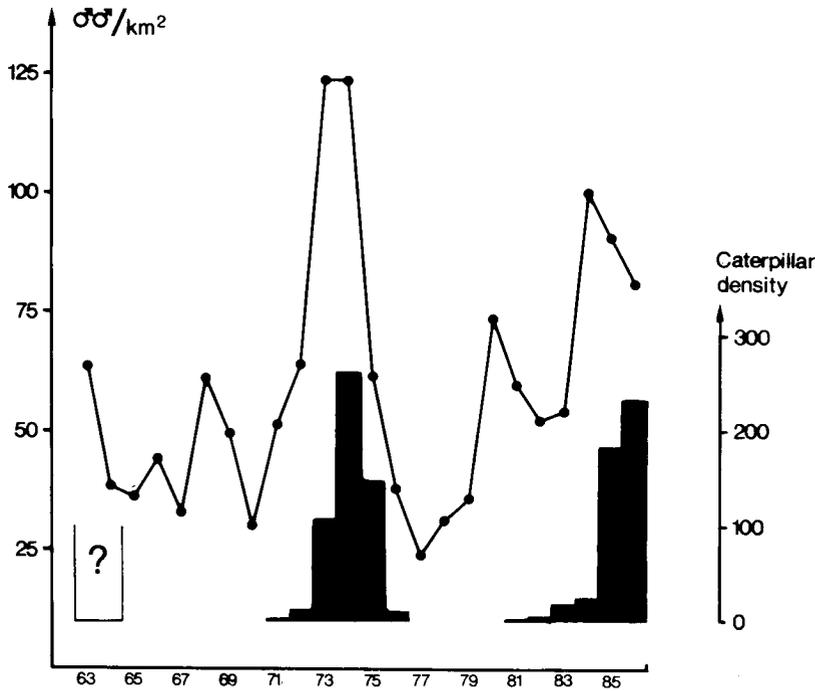


Fig. 1. Density of Bramblings (number of stationary males per km², dots and continuous lines), as determined from territory mapping, and the occurrence of *Epirrita* caterpillars (histogram; number of caterpillars per 1000 short shoots in three study plots) at Ammarnäs, Swedish Lapland in 1963–1986. *Epirrita* caterpillars were present in 1963 and 1964, but the census work on insects did not start until 1967. Data on Brambling densities from Enemar et al. (1984, App.II) and from A. Enemar (pers. comm.). Data on *Epirrita* occurrence from Andersson & Jonasson (1980) and from G. Andersson and T. von Proschwitz (pers. comm.).

434 juveniles ringed in 1983–1985, only one was captured in a later year. For comparison, the corresponding data are presented for the Reed Bunting *Emberiza schoeniclus*, which is not dependent on *Epirrita* and therefore may be expected to show normal breeding site tenacity.

As an estimate of the trapping efficiency, I calculated the mean number of recaptures per ringed bird in the same season for all Bramblings (mean for 1984–1986: adults 0.09, juveniles 0.25) and Reed Buntings (mean for 1984–1986: adults 0.54, juveniles 0.27). This indicates that trapping efficiency for birds from the local breeding population is 6.0 times as high for adult Bramblings as for adult Reed Buntings and 1.1 times as high for juvenile Reed Buntings as for juvenile Bramblings. Using these factors, I calculated the expected number of Brambling recaptures in later years, as shown in brackets in Table 1.

Wing lengths

The mean wing lengths of adult males and females in 1983–1986 are shown in Table 2. It varies significantly between years in females (ANOVA, $P < 0.05$), but not in males ($P > 0.05$). The number of

Table 1. Number of adults and juveniles caught and number of recoveries of birds ringed in earlier years among Bramblings and Reed Buntings at Ammarnäs, Swedish Lapland. Recoveries printed in bold type. Expected retrap figures (see text) for the Brambling shown in brackets.

Brambling	1983	1984	1985	1986
ad.	63	— (4)	—	—
juv.	70	— (1)	—	—
ad.		154	— (4)	—
juv.		250	— (3)	—
ad.			4	1 (2)
juv.			114	— (2)
ad.				93
juv.				210
Reed Bunting	1983	1984	1985	1986
ad.	15	6	—	—
juv.	81	1	—	—
ad.		21	3	1
juv.		78	1	1
ad.			14	3
juv.			54	1
ad.				13
juv.				85

birds measured is lower than the trapping totals (Table 1) because many birds were moulting the outer primaries, so that the wing was impossible to measure. As 40 % of the birds could not be aged

Fig. 2. The number of Brambling nests (y) found during non-systematic search in relation to Brambling densities (x, number of stationary males per km²) at Ammarnäs, Swedish Lapland in 1963–1985. The relationship can be described as follows (with 95% confidence interval): $y = 0.005x^{1.94^{0.53}}$, $r=0.85$, $P<0.001$, $n=23$). Thus, the curve differs significantly from a linear relationship. Data on Brambling densities from Enemar et al. (1984, App.II) and from A.Enemar (pers. comm.).

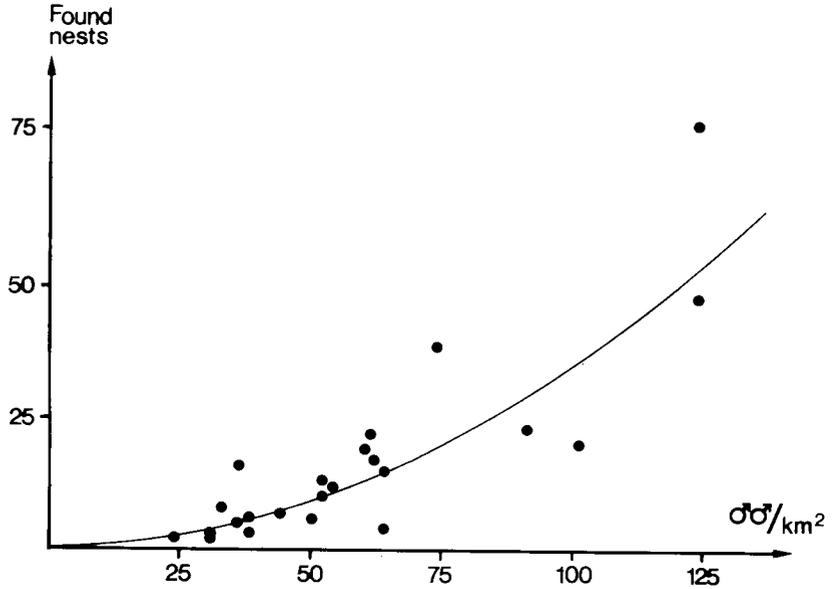


Table 2. Mean wing lengths (in mm) of adult male and female Bramblings during four years at Ammarnäs, Swedish Lapland.

	1983	1984	1985	1986
Males				
Mean	93.0	93.6	93.4	93.8
SD	2.45	2.14	2.17	2.16
n	25	78	31	26
Females				
Mean	87.0	87.5	88.2	88.3
SD	1.86	1.61	1.58	1.92
n	19	78	30	37

(just +2y instead of 2y or +3y), the data for all age groups are pooled.

For those birds that could be aged, the mean wing lengths were as follows: for males, 2y mean = 92.2 mm (SD=2.1, n=43), +3y mean = 94.4 mm (SD=1.7, n=72) and for females, 2y mean = 87.5 mm (SD=1.7, n=26), +3y mean = 88.0 mm (SD=1.6, n=59). The difference between age groups is significant in males (t-test, $P<0.001$) but not in females (t-test, $P>0.05$). I also compared the yearly mean wing lengths within each age and sex group (2y males, 2y females etc.), and found significant differences only in +3y females (ANOVA, $P<0.05$). They were significantly smaller (t-test, $P<0.05$) in 1984 (mean = 87.4 mm, SD=1.2, n=20) than in 1985 (mean = 88.5 mm, SD=1.4, n=15) and 1986 (mean = 88.5 mm, SD=1.8, n=22).

Ringling recoveries

In 1986 we made two Brambling recaptures that gave us information on the choice of breeding sites in different years. The first bird was a male, ringed as an adult (+3y) in Ammarnäs on 5 August 1985. At that time it was well into moult, having a primary score of 16 (out of 45). It was retrapped on 22–23 July 1986 at the very same place, now in the initial stage of the primary moult. If we assume that adult Bramblings moult in the close vicinity of their breeding place (like Willow Warblers *Phylloscopus trochilus*, Bluethroats *Luscinia svecica* and Reed Buntings in the study area, my own obs.) this shows that breeding site tenacity does occur in the Brambling.

The second bird was a female, ringed as full-grown (+2y) at Kilpisjärvi, Finnish Lapland (69°03' N, 20°48' E) on 1 July 1982 and recaptured by us on 18 August 1986, approximately 420 km southwest of its ringing place. When recaptured, this bird was in a late stage of moult, having almost finished its primary moult (primary score 44) but with one secondary newly shed and two still in growth. As it seems unlikely that this moulting bird was on migration, we believe that it was still at its current breeding site.

Looking through ringing reports from Fennoscandia (from Sweden for 1960 to 1975, published in *Vår Fågelvärld* 1964–1971 and by the Swedish Museum of Natural History 1973–1986;

Finland for 1928 to 1967, published in *Memoranda Societatis pro Fauna et Flora Fennica 1929–1969*; and from Norway for 1950 to 1982, Stavanger Museum, published in *Sterna 1952–1985*), I found two further recoveries that indicate a change of breeding area between years. One adult male ringed at Ammarnäs on 27 June 1969 was recovered on 30 July 1970, at Vågstranda, Möre og Romsdal, Norway (62°36' N, 07°20' E), about 580 km to the southwest. The other bird was an adult male, ringed as “migrating” at Korsholm, Jungsund, Finland (63°10' N, 21°35' E), on 10 June 1962 (breeding site probably in Finland that year) and found dead on 20 August 1963, at Dorotea, Sweden (64°18' N, 16°20' E), 280 km to the northwest.

Discussion

Breeding and occurrence of Epirrita

No data are available on the actual breeding success of the Brambling in years with different amounts of *Epirrita*. Yet, the data presented here indicate that the abundance of breeding Bramblings in Swedish Lapland depends on the numbers of *Epirrita*.

1) The density of stationary males increased during both peaks of *Epirrita* (Fig.1), which indicates that Bramblings move into the area when food is abundant (cf. Silvola 1967, Hogstad 1969). These newcomers could be either first time breeders (2y), whereas adult birds are faithful to their previous breeding places, and/or adult birds (+3y) changing breeding sites between the years (cf. Andersson 1980). In an eight year study, Hogstad (1985) found a positive, though not significant, correlation between mean wing length in males and abundance of *Epirrita* larvae. He suggested that in years with a good food supply the population may contain higher proportion of adults (+3y) or that larger and more dominant individuals may breed in the area in these years.

In this study, only 60 % of the adult birds could be aged as 2y and +3y, which makes comparison of the age structure between years uncertain. Contrary to the results of Hogstad (1985), significant differences were found in the yearly mean wing lengths in females, but not in males. Thus, in both sexes the mean wing lengths can vary considerably between years. The possibility cannot be excluded that this is due to different age structures of the population. In this study, +3y females were

significantly larger in the two years of high *Epirrita* abundance (1985–1986), which gives some support to Hogstad's (1985) suggestion that larger individuals move into the area when the food supply is good.

There are many uncertainties in this interplay between breeding densities, population composition and the number of *Epirrita* caterpillars. In 1985 and 1986 the response was much lower than expected (cf. peak I). The breeding density of Bramblings is possibly influenced by other factors as well, e.g. winter mortality, spring and summer weather and the geographical distribution of *Epirrita* outbreaks.

2) Increased density of stationary males was accompanied by an increase in the number of nests found (Fig.2). Thus, the birds that moved into the area did attempt to breed there. Further, the proportion of nests found increased with density. It may be that a higher proportion of the birds breed when densities are high, or the nests may be easier to find at such times. A similar significant non-linear relationship was found in the Dunnock *Prunella modularis* breeding in Ammarnäs in 1963–1982 (A. Enemar pers. comm). That species is not dependent on *Epirrita*, which indicates that the increasing proportion of nests found in the Brambling is probably not due to the *Epirrita* abundance as such.

3) There was a significantly higher proportion of juveniles in the post-breeding population during the two years of *Epirrita* peak abundance than in the preceding years. This is an indication that the breeding success was higher in these years. Different ratios of juveniles to adults in the post-breeding period have also been reported from Finland (Hildén et al. 1982) but there the lower ratio was probably due to very cold weather during the breeding period.

As reported by Hogstad (1982), the diet of Brambling nestlings “consists exclusively of insects, mainly phytophagous species of less agile coleoptera and geometrid larvae”. He also reports that in years with very low insect activity, Bramblings were seen to abandon nests with eggs or nestlings. In conclusion, the breeding success of Bramblings in Ammarnäs seems to be positively correlated with the occurrence of *Epirrita* larvae.

Breeding site strategy

The few recoveries mentioned here show that some Bramblings are nomadic and may breed at sites up to 600 km apart in different years. The occurrence of

nomadism is further stressed by the fact that there were almost no recaptures of birds ringed in earlier years, in both this and other studies (Mikkonen 1983, Hogstad 1985). This is in accordance with the model of Andersson (1980), i.e. a nomadic strategy is to be expected in a species that relies to some extent on a cyclically fluctuating food resource during breeding.

If the Brambling had a breeding site tenacity similar to that of the Reed Bunting, about four recoveries of adult Bramblings could be expected in both 1984 and 1985, but not a single recovery was made. These years showed low numbers of *Epirrita* caterpillars. Interestingly, the only case of breeding site tenacity found so far was for two years with peak food abundance. The one recapture was also near the number expected for that year (Table 1).

In Tengmalm's Owl, the sexes have different breeding site strategies (Löfgren et al. 1986, Korpimäki et al. 1987). Males show permanent breeding site fidelity, probably because their reproductive output is primarily determined by the availability of nest holes, and not food abundance. In the Brambling there is most certainly no shortage of nest sites. Thus, if food abundance is of major importance, male Bramblings should not differ from females in their strategy and, indeed, both sexes were represented among the recoveries showing nomadism.

No return of juveniles was noted in this study or in those of Mikkonen (1983) and Hogstad (1985), which indicates that juveniles do not normally return to breed in their natal area. But as the expected number of recoveries was rather low (Table 1), the behaviour of juveniles is unclear.

Breeding nomadism has been suggested to be the main strategy in the Redpoll *Carduelis flammea* also, another passerine typical of the subalpine birch forest (Enemar & Nyström 1981). During breeding, this species is to some extent dependent on birch seeds, a food supply that also varies considerably between years.

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Sammanfattning: Nomadism och hemortstrohet hos häckande bergfinkar

Revirkartering i subalpin björkskog i Ammamäs, svenska Lappland, under perioden 1963–1986 visade att tätheten av bergfink var högst under år med hög täthet av björkmätarlarver. Antalet stationära bergfinkshanar var positivt korrelerat med antalet funna bon i området (figur 2) vilket indikerar att de bergfinkar som flyttar in i området också går till häckning. 1983–1986 fångades 999 bergfinkar under perioden efter häckningen. Andelen ungfåglar var signifikant högre under år med god larvutgång (figur 1). Tillgången på larver verkar således påverka både häckningstäthet och häckningsframgång hos bergfinken.

Ringmärkningsåterfynden från Fennoskandien och en nästan total avsaknad av återfångster mellan åren i Ammamäs visade att både hanar och honor normalt byter häckningslokal mellan åren, dvs. de är nomadiska (tabell 1). Att hemortstrohet dock kan förekomma visades av en hane som ringmärktes 1985 och återvände till Ammamäs 1986.

Medelvinglängden hos adulta honor varierade signifikant mellan åren (1983–1986; tabell 2). Då bara 60% av honorna gick att åldersbestämma var det omöjligt att avgöra om denna variation berodde på att andelen äldre fåglar varierade mellan åren. Äldre honor (3k+) var signifikant större under år med god larvutgång. Medelvinglängden hos adulta hanar varierade ej signifikant mellan åren.

Bergfinkens häckningsstrategi överensstämmer i stort med en teoretisk modell som förutsäger att nomadism är den mest fördelaktiga strategin för en art som är beroende av ett födoslag med cyklisk varierande täthet.

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