# Annual variation in mean body size of a Brambling *Fringilla montifringilla* population

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A sample of 91 male and 49 female Bramblings *Fringilla montifringilla* taken during eight breeding seasons in subalpine heath birch forest in Central Norway revealed significant annual differences in the mean wing lengths of the males. Possible reasons for this annual variation are suggested and discussed: 1. Differences in food availability during the rearing period may result in annual differences in the growth of the primaries. This hypothesis could not be verified. 2. The greater mean wing lengths recorded in some years may be due to an influx of larger birds from the northern or north-eastern part of the range. This hypothesis was rejected. 3. If habitat quality depends closely on the main food source during the breeding season (Geometrid larvae), and if larger birds are more numerous in years when habitat quality is good, a relationship should exist between the mean size of the breeding males and the quality of the habitat. Such a relationship was found and therefore this hypothesis may be considered plausible. 4. The annual differences in mean wing length may reflect differences in the age structure of the population. Since a positive relationship was found between the mean wing lengths of the males and the ratio of adults to yearlings, this hypothesis is probably correct.

It is concluded that the annual variation in the mean body size of the Brambling populations is probably due to intraspecific competition, because the proportion of older and larger-sized birds, with a high social rank, is probably highest in breeding seasons in which habitat quality is optimal and lowest in sub-optimal years.

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## Introduction

The Brambling *Fringilla montifringilla* has a transpalearctic distribution and is considered to be the ecological representative of the Chaffinch *F. coelebs* in the northern birch and coniferous forests (Voous 1960). The species is one of the most abundant passerines in Fennoscandian subalpine forests and, together with the Willow Warbler *Phylloscopus trochilus,* it often composes half to two-thirds of the total passerine community (Hogstad 1976).

A population study of breeding passerines in subalpine heath birch forest in Budal, Central Norway, revealed considerable annual fluctuation in the number of Bramblings present. During the period 1966–1982, the Brambling density varied from 10 to 52 territories per km$^2$, and the population sometimes more than doubled from one year to the next (Hogstad unpubl.). In some years breeding success could be almost nil, about half the Brambling population leaving the study area in the middle of the breeding season (Hogstad 1982), and yet in the following year the population density could be higher than that recorded two years earlier.

As the Brambling is considered to be an irruptive species (Ulfstrand 1963, Newton 1972) and the birds probably change their wintering (Eriksson 1970) and breeding (Newton 1972, Mikkonen 1981, 1983) areas from year to year, the population in Budal presumably consists of a new set of individuals each year. This assumption seems to be confirmed by the fact that none of the 10–30 adult and juvenile Bramblings ringed annually in the Budal study area were recorded in the following seasons. Are there, then, any morphological differences between the birds inhabiting the area in different years? When examining the wing lengths and body weigths of the Brambling samples collected in Budal during the breeding seasons 1972–75 and 1979–82, I found that the birds were larger in some years than in others. In the present study I shall attempt to explain this year-to-year variation in the mean size of the birds in the local Brambling population.

## Study area

The study area is situated in Budal (62°45 'N – 10°30'E), Sør-Trøndelag county, Central Norway. The area is a zone 700–800 m wide, extending from altitude of about

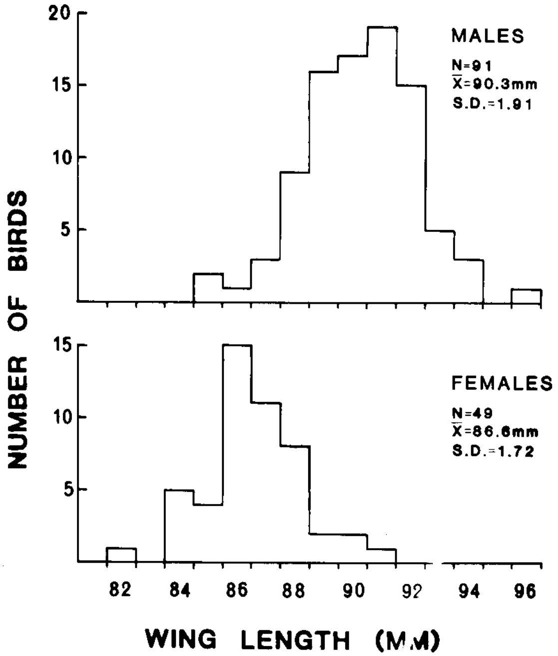

Fig. 1. Wing length frequencies of male and female Bramblings taken in Budal during the breeding seasons of 1972–75 and 1979–82.

750 to 900 m, and consists of homogeneous oligotrophic heath birch *Betula pubescens* ssp. *tortuosa* forest. The general tree height is 3–6 m. The area covers about 3.5 km$^2$.

## Material and methods

The Bramblings were trapped in mist nets (N=64), or shot for gizzard analyses (N=76). Their wing lengths (measured to the nearest mm, when flattened out and straightened, i.e. the maximum lenght; Svensson 1975) and body weights (determined to the nearest 0.2 g with a 30-g spring balance) were recorded. The entire sample consisted of 91 males and 49 females. However, since the body weight of the Brambling, especially that of the females, varies both diurnally and seasonally (see Hogstad 1982), the only weights used in the study were those of males taken before 13.00 hours in June (a period during which little variation in weight occurs).

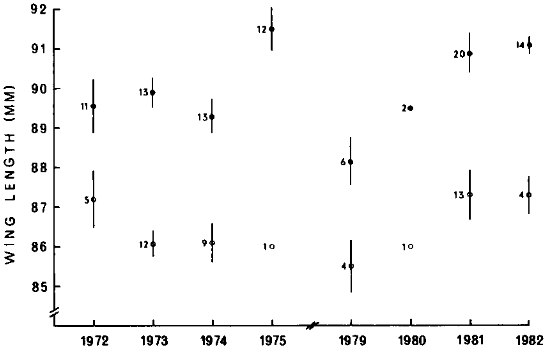

Fig. 2. Mean wing lengths (mm) of male (filled circles) and female (open circles) Bramblings taken during eigth breeding seasons in Budal. The vertical lines indicate the ± SE values.

In addition to the Budal material, wing length were measured on 72 male and 8 female museum specimens of Bramblings collected in Norway and Sweden during the breeding season (20 May – 20 July). All measurements were made by the author.

The Brambling males collected in 1974 (N=13) and 1975 (N=12) (frozen birds) and 1982 (N=14) were classified as yearlings or adults, according to the degree of blackness of the outer webs of their primaries, alula and coverts (see Svensson 1975). However, for some individuals (one from 1974 and 1975, two from 1982) this character provided to be ambiguous and these birds were omitted from the analyses.

## Results

*Wing length.* The mean wing length of the male Bramblings was significantly greater than that of the females (t-test, $P<0.001$; Fig. 1). The difference between the sample means was 3.7 mm. The mean wing length of males varied significantly between years (ANOVA-test, $P<0.01$), but not that of females ($P>0.05$; Fig. 2). The difference between the highest and lowest mean values was 3.3 mm for males and 1.8 mm for females. The mean wing lengths for the males collected in 1975 and 1982 were 91.5 mm and 91.1 mm, respectively. These values were significantly higher than the means for each of the years 1972–74 and for 1979 (t-test, $P<0.05$). The 1980 value is excluded from the comparison because of the small sample size. The mean wing length for males was also high in 1981, but differed significantly only from the means for 1974 and 1979 ($P<0.05$). The low mean recorded for 1979 differed significantly from the values for 1973, 1975, 1981 and 1982.

Although the annual fluctuation in the mean wing lengths of males and females showed the same general pattern (Fig. 3; correlation coefficient $r=0.84$, $N=6$, $P<0.05$), the annual differences in the mean wing lengths of the females were not statistically significant, probably due to the sample sizes being too small.

The mean wing length for males trapped in May differed significantly (t-test, $P<0.05$) from that for males trapped in June (Table 1), which indicates that the males arriving in the heath birch forest early in the breeding season are mostly larger than those arriving later.

*Body weight.* Although the mean body weight of males in June varied between 22.4 in 1972 and 23.2 g in 1975 (Table 2), the annual variation was not statistically significant (ANOVA-test, $P>0.1$). In 1975 and 1982 the mean body weigths were

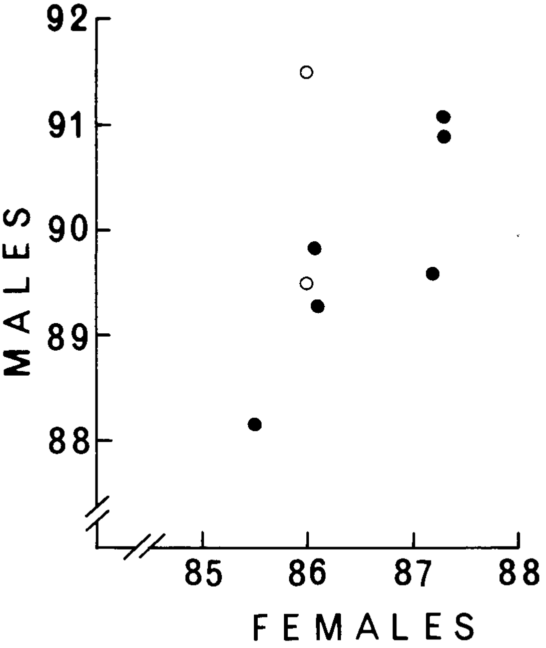

Fig. 3. The relationship between annual mean wing lengths (mm) of male and female Bramblings. The open circles represent measurements of a single female.

significantly greater than in the other study years (22.6 g, SD=0.74; t-test, $P<0.001$ for 1975 and $P<0.05$ for 1982).

The higher mean body weights recorded for males in 1975 and 1982 correspond with the greater mean wing lengths recorded in the same years (see Fig. 2). In 1981, however, the fairly great mean wing length of the males was not accompanied by a correspondingly high body weight.

Table 1. Mean wing lengths of male Bramblings taken in four years during May and June (SD values in parenthesis).

| | May | | June | | Difference in mean wing length |
|---|---|---|---|---|---|
| | N | Mean wing length in mm | N | Mean wing length in mm | |
| 1972 | 1 | 92.0 | 10 | 89.3 | — |
| 1973 | 4 | 90.8 | 9 | 89.6 | 1.2 |
| 1974 | 3 | 89.7 | 10 | 89.2 | 0.5 |
| 1981 | 4 | 92.8 | 16 | 90.4 | 2.4 |
| 1972–74, 1981 | 12 | 91.3 (1.91) | 45 | 89.8 (1.94) | 1.5 |

Table 2. Mean body weights of male Bramblings trapped in different years before 13.00 hours in June.

| Year | N | Weight | SD |
|---|---|---|---|
| 1972 | 9 | 22.4 | 0.42 |
| 1973 | 9 | 22.8 | 0.51 |
| 1974 | 7 | 22.7 | 0.74 |
| 1975 | 8 | 23.2 | 0.37 |
| 1979 | 6 | 22.5 | 1.12 |
| 1980 | 6 | 22.5 | 0.84 |
| 1981 | 15 | 22.5 | 0.87 |
| 1982 | 10 | 23.0 | 0.43 |
| Total | 70 | 22.7 | 0.71 |

The relationship between the mean values for wing length and body weight was not statistically significant ($r=0.53$, $P>0.1$; Fig. 4). However, if we exclude the values for 1981, a year in which the birds had probably exhausted their fat resources due to a long spell of cold weather and consequent poor feeding conditions (Hogstad 1982), the correlation coefficient between wing length and body weight increases to 0.85 ($P<0.02$).

*Relationship between age and wing length.* The mean wing length of adult males was significantly greater than that of yearlings (t-test, $P<0.001$, Table 3). In 1974 the ratio of adult to yearling males differed significantly from the ratio in 1975 and 1982 ($\chi^2$-test, $P<0.05$ for both years).

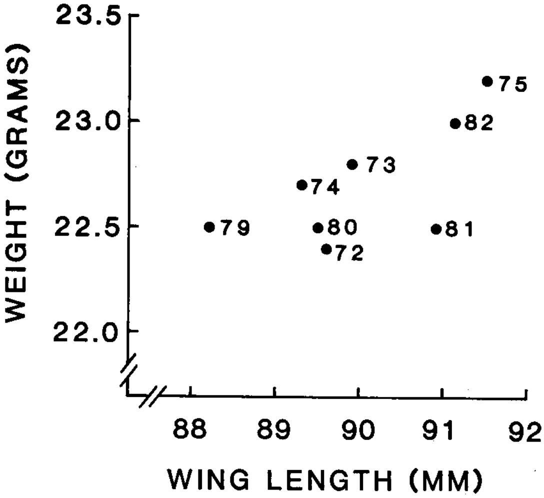

Fig. 4. The relationship between the mean wing length and body weight of male Bramblings taken in Budal in different breeding seasons (indicated by figures), before 13.00 hours in June.

Table 3. Mean wing lengths of adult and yearling Brambling males from Budal.

| Year | Adults | (N) | Yearlings | (N) |
|---|---|---|---|---|
| 1974 | 90.6 | (3) | 88.8 | (9) |
| 1975 | 92.6 | (8) | 89.0 | (3) |
| 1982 | 91.6 | (8) | 90.3 | (4) |
| 1974, 1975<br>1982 | 91.9 | (19) | 89.2 | (16) |

## Discussion

The annual variation in the mean wing length of the Brambling population breeding in Budal may have one of the following reasons. 1. Differences in the feeding conditions during the rearing period; 2. Influxes of larger-sized birds from more northerly populations; 3. A relationship between male size and habitat quality; and 4. Differences in the age structure of the population.

The pros and cons for the above reasons are:

*1. Feeding conditions during the rearing period.* van Balen (1967) suggested that the main factor responsible for the annual differences in the mean wing lengths of both yearling and older Great Tits *Parus major* wintering in Holland was the availability of food during and some weeks after the nestling period. Jakober & Stauber (1980) found that the wing length of adult male Red-backed Shrikes *Lanius collurio* showed significant positive correlation with the body weight of the birds when they were 7–8 days old. They also concluded that wing length was presumably influenced by the feeding conditions during the rearing period.

Berthold (1976, 1977), however, found that the wing lengths of Blackcaps *Sylvia atricapilla* and Blackbirds *Turdus merula* given an experimental, nutrient-poor diet did not differ significantly from those of control birds, i.e. no correlation existed between the feeding conditions during the nestling period and the wing length of the adults. No similar data exist on the relationship between the feeding conditions and body weights of nestling Bramblings and their wing lengths as adults. Since a positive relationship has been found between the Brambling breeding density and the main food source in the Budal study area in different years (Hogstad unpubl.), one might expect a positive correlation between breeding density and the mean wing length of the population present in the following year. However, no such correlation has been found for the Brambling in Budal (r=–0.08, N=7). Nor was a significant correlation found between the weight of adult Bramblings (mean body weight of males trapped before 13.00 hours in June) in any one year and the mean wing length of the males of the Budal population in the following year (r=–0.31, N=7). This is not surprising, however, because Bramblings probably change their breeding areas each year and the food situation in the area in which the birds breeding in Budal were themselves reared is therefore unknown. Thus no firm conclusion can be reached about the importance of feeding conditions during the nestling period for the wing lengths of the birds as adults.

*2. Influx of larger-sized birds from more northerly populations.* The Brambling is probably the most migratory of all the Scandinavian finches. The various populations seem to winter in different areas in different years (Eriksson 1970, Newton 1972, Schlenker 1976), probably because the crop of beechmasts or of the seeds and berries of other trees is seldom abundant in the same area for two years in succession (Svärdson 1957). If the birds living in cooler or drier regions are larger-sized than those in warmer or wetter regions (James 1970), i.e. in the northern or north-eastern part of their range, as has been found to hold for most species (e.g. Snow 1954, Rand 1961, Power 1969, Fonstad & Hogstad 1981), the annual differences in the mean wing lengths recorded in Budal may be explainable in terms of irruptive behaviour of the species. In other words, the larger-sized birds which bred in Budal in 1975, 1981 and 1982 may have belonged to more northerly or north-easterly populations, while the birds recorded in the other study years may have belonged to more southerly populations.

However, wing-length measurements of Bramblings from different parts of Scandinavia, all collected during the breeding season, revealed no clinal increase in wing length with increasing latitude (Table 4). Furthermore, the mean wing length for a sample of Bramblings collected in Finland (c. 65°N, 20 May – 20 June, 18 males=91.1 mm ± 2.2 SD, 7 females=86.2 mm ± 1.1 SD; A. Mikkonen unpubl.) and in the Soviet Union (50 males=90.2 mm, 50 females=85.5 mm; Dement'ev & Gladkov 1970) was almost identical with that recorded for the Norwegian and Swedish birds in the present study.

The distribution of the Brambling is transpalearctic, with a breeding range extending from Norway eastwards to Kamtchatka (Voous 1960, Dement'ev & Gladkov 1970). Despite this vast east-west extent of its breeding range, no subspecies of the Brambling have been recognized (Dement'ev & Gladkov 1970). Since the mean wing length of Bramblings shows no significant clinal variation towards the north or the east of their range, the Scandinavian Brambling population can be considered simply to represent a breeding unit within a larger population. Because of the absence of ringing recoveries from any one breeding area for two or more years in succession (cf. Newton 1972, Mikkonen 1983), it has been suggested that the site-tenacity (Ortstreue) of this species is lacking or poorly developed (Ulfstrand 1963, Mikkonen 1983). If the birds change their breeding area from one year to the next, this irruptive behaviour and the consequent mixing of individuals probably produce a sufficient high rate of geneflow to prevent any clinal variation in wing length.

Therefore, the greater mean wing lengths recorded for the Bramblings in Budal in some years can hardly have been caused by an influx of birds from more northerly populations.

*3. Relationship between male size and habitat quality.* The staple food of the Brambling during the breeding season in the subalpine forest in Budal is geometrid larvae (Geometridae, especially those of *Epirrita (Oporinia) autumnata*), and to a lesser degree weevils (Curculionidae) and leaf beetles (Chrysomelidae). The abundance of all these insects varies annually (Hogstad unpubl.). If habitat quality is directly related to changes in this main food supply, then the quality of the heath birch forest must vary considerably from the year to year. Since the larger males are probably able to dominate over the smaller ones in the competition for food resources (e.g. Dawkins & Krebs 1978), the territories of the larger male Bramblings may be expected to lie in the optimal habitats.

The annual variation in the size of male Bramblings migth therefore be caused by a relationship between habitat quality and male social rank. If larger and more dominant males were more numerous in Budal in years of optimal habitat quality and smaller, lower-ranking, males most numerous in years of sub-optimal habitat quality, then a relationship might be expected to exist between the mean size of the breeding males and the quality of the habitat. Comparison of the mean wing lengths of the males in different years with the abundance of *Epirrita autumnata* larvae (mean number of larvae/100 sweep net catches made in birch trees during June/July) revealed such a relationship (r=0.42, P>0.1, n=8). The larger Brambling males arriving in the study area early in the breeding season may have been socially dominant individuals and the smaller males arriving later may have had a lower social rank (e.g Krebs 1971, Fretwell 1972, Lundberg et al. 1981, Ulfstrand et al. 1981). The hypothesis that bird size is related to habitat quality cannot thus be rejected out of hand.

Table 4. Mean wing lengths (mm) of male and female Bramblings, from different latitudinal zones in Norway and Sweden.

| Latitude °N | Males | | | Females | | |
|---|---|---|---|---|---|---|
| | mean | SD | N | mean | SD | N |
| 58–60 | 91.2 | 1.72 | 6 | — | — | — |
| 60–62 | 91.5 | 1.00 | 4 | 84 | — | 1 |
| 62–64 | 90.3 | 1.94 | 93 | 86.6 | 1.72 | 49 |
| 64–66 | 91.8 | 1.98 | 8 | 88 | — | 1 |
| 66–68 | 90.8 | 2.01 | 34 | — | — | — |
| 68–70 | 91.7 | 1.65 | 18 | 87.2 | 2.64 | 6 |
| 58–70 | 90.7 | 1.96 | 163 | 86.6 | 1.83 | 57 |

*4. Differences in the age structure of the population.* The juvenile birds, or yearlings, of many passerine bird species have shorter wings than the older birds. This has also been found to hold true for the Brambling (Creutz 1961, Stauber, in Jakober & Stauber 1980, Ålbu 1983, present study). In years in which a high proportion of older birds are present in a population, the mean wing length of the population sample will therefore be higher than in years with a high proportion of yearlings. In Finland, the ratio young:adult birds in breeding populations of Chaffinches showed significant annual variations (Mikkonen 1983). During four years the proportion of juvenile Brambling wintering in Neschwitz, in Germany, varied from 22 to 63% (Creutz 1961). The different age distribution of Brambling males found in Budal in 1974 compared with those in 1975 and 1982 strongly suggests the existence of annual differences in the ratio of old to young birds in the population. The annual differences in the mean wing lengths of Bramblings in Budal may therefore reflect annual differences in the age structure of the population.

Thus, of the four reasons suggested for the annual variation found in the mean wing lengths and body weights of the Brambling population in Budal, nos. 3 and 4, i.e. a relationship between body size and habitat quality, and annual differences in the age structure of the male population, would seem to be most plausible and no. 2, i.e. an influx of birds from more northerly populations, to be the least likely. Since the food conditions in the area in which the Bramblings breeding in Budal were themselves reared are unknown, no conclusion can be drawn regarding the relationship between the feeding conditions during the nestling period and adult wing length, i.e. the plausibility of reason no. 1. In conclusion, I suggest that the annual variation in mean body size of the Brambling populations in Budal is most probably caused by intraspecific competition. Due to annual variations in habitat quality (e.g. in food quality and quantity), the proportions of older and larger-sized birds of high social rank is therefore likely to be highest in years in which habitat quality is optimal and lowest in sub-optimal years.

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## Selostus: **Järripeipon ruumiinkoon vuotuinen vaihtelu**

Keski-Norjassa matalassa tunturikoivikossa vuosina 1972–75 ja 1979–82 pesineiden järripeippokoiraiden keskimääräinen siivenpituus vaihteli huomattavasti vuodesta toiseen (kuva 2), mutta 79 naarasyksilöllä ei. Kirjoituksessa esitetään neljä mahdollista selitystä koiraiden koon vuosivaihtelulle. (1) Yksilön kasvuaikainen ravinto voi vaikuttaa sen siipisulkien kasvuun. (2) Joinakin vuosina pohjoisemmilla alueilla tavallisesti pesivät suurikokoisemmat yksilöt saattavat asettua tutkimusalueelle. (3) Suurikokoisempia, sosiaalisesti dominoivampia yksilöitä asettuu alueelle tavallista enemmän, kun habitaatti on pesinnälle suotuisaa tunturimittarien runsaan toukkaesiintymän aikana. (4) Koon vaihtelu heijastaa populaation ikärakenteen muutoksia; vanhat yksilöt ovat pitempisiipisiä kuin nuoret (taul. 3). Todennäköisimpänä selityksenä kirjoittaja pitää lajinsisäistä kilpailua: suurempikokoiset, vanhat koiraat ovat korkeammassa sosiaalisessa asemassa 1-vuotiaisiin koiraisiin verrattuna ja siten suhteellisesti runsaampia hyvinä ravintovuosina.

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