Density-dependent reproductive output in relation to a drastically varying food supply: getting the density measure right

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When a limiting resource (e.g. food) varies drastically between years, and population density is measured in the conventional way as individuals per area, demographic processes such as productivity and survival may erroneously be considered density-independent. We tested the hypothesis that if the variation in a limiting resource is not taken into account in the density measure, this may lead to erroneous conclusions about the density-dependence of demographic variables. We studied the food-related variation in productivity of bramblings *Fringilla montifringilla*, an insectivorous passerine bird, using 19 years of standardised insect censusing, bird censusing and mist-netting of birds in subalpine birch forest in Swedish Lapland. The yearly variation in our measure of brambling per capita productivity (numbers of juveniles per adult trapped) was explained to 30–40% by the larvae abundance of the moth *Epirrita autumnata*. Taking larvae density into account, no other environmental variable (inferred predation pressure, breeding phenology, and summer temperature) was significantly related to variation in reproductive output. There was no effect of brambling population density on per capita productivity, that is, when density was measured the conventional way, productivity seemed density-independent. However, per capita productivity was significantly and negatively correlated to the food-related population density (population density divided by larval density), supporting the hypothesis that not including a limiting resource into the density measure may indeed lead to erroneous conclusions about the density-dependence of demographic variables.

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Identifying the processes governing demographic variables such as reproduction, dispersion and survival of animals helps to understand why animals vary in numbers. Such knowledge is important in its own right, but is also fundamental for successful management of populations (Sutherland 1996, Sillett and Holmes 2002). The key factors and processes identified to affect population dynamics are food supply, social behaviour, predation, pathogens, habitat quality (including sites for reproduction), environmental disturbance and weather. These factors often interact in complex ways and their relative importance varies between organisms (Begon et al. 1996, Newton 1998, Sinclair and Krebs 2002).

Some of these factors influence demographic variables in a density-dependent way. Since there is a risk of confusion when using the word "density-dependence" (Berryman et al. 2002), we define density-dependence as a response that is negatively related to population density ("negative feedback" sensu Berryman et al.

2002), for example, a lower per capita productivity with increasing population density. The underlying, often implicit, explanation to density-dependence is that the less of a limiting resource per capita, the poorer each individual does. The traditional measure of population density used when testing for density-dependence is simply the number of organisms within a study area. However, if the critical resource, e.g. food, varies drastically between years, and this variation is not recorded and properly accounted for, density-dependence may go undetected (Newton 1998). Accordingly, density-independence may be reported where density-dependent processes prevail. With a large variation in e.g. food abundance, the most relevant density measure is the number of breeding birds per amount of food, and not the conventional measure, number of breeding birds per area. Newton (1998) did not find a single study that analyzed density-dependent reproduction taking a varying food supply into account (but see Elmberg et al. 2003 for a recent study), and concluded that this may have lead to an under estimate of the frequency and strength of density-dependence in nature (Newton 1998, p. 120).

We measured the reproductive output of a small passerine bird, the brambling *Fringilla montifringilla*, over 19 years, at the same time measuring the abundance of its main prey, the larvae of the cyclically appearing autumnal moth *Epirrita autumnata*. First, we are able to show that larvae abundance is a limiting factor for brambling reproductive success. Second, we test the hypothesis that when a limiting resource varies drastically between years and population density is measured conventionally as individuals per area, reproductive output is likely to be considered density-independent, but when variation in food abundance is taken into account, density-dependence may still prevail (Newton 1998).

Methods

The study site

The study was carried out in subalpine birch forest immediately north and east of Lake Tjulträsk, Ammarnäs, in Swedish Lapland (about 66°N, 16°E), as a part of the LUVRE project (Enemar et al. 1984, 2004). The altitude varies between 540 m a.s.l. (the trapping site near Lake Tjulträsk) and 720 m a.s.l. (the upper boundary of the census area). The area is dominated by near-primeval subalpine birch forest, with rich under-growth of herbs, although the habitat is drier and less rich near the upper border of the study area. All biological data were collected within 5 km of each other. Although the bird and *Epirrita* census work started in 1963 and 1967, respectively (Enemar et al. 1984, 2004), the data referred to here is from a shorter

period, 1984–2002, because post-breeding trapping of birds (used to estimate reproductive output) was carried out only in these later years.

The study organisms

Larvae of *Epirrita autumnata* are found mainly on birch trees (*Betula*). Within the alpine and arctic regions of northernmost Europe there are regular outbreaks at a given site on average every decade (variation 5–15 years, Tenow 1972, Ruohomäki et al. 2000, Selås et al. 2001), when large areas of forest may be completely defoliated. Each outbreak lasts about 3–4 years and in the intervening years, larvae densities are hardly measurable (Tenow 1972, Selås et al. 2001). In addition, the outbreaks seem to be well synchronised over large areas of northernmost Europe (Tenow 1972, Ruohomäki et al. 2000, Selås et al. 2001). After a growth period of 2–3 weeks, the larvae pupate in the ground litter a few centimetres below surface, where they are no longer available for bramblings. Ruohomäki et al. (2000) report that pupation takes place before midsummer. At Ammarnäs, however, pupation is about a week later, with some larvae still visible in the first week of July. The exact timing depends on the earliness of spring (G. Andersson and T. von Proschwitz, pers. obs.).

The brambling is a 20–25 g passerine bird that breeds in northernmost Europe and eastwards throughout Asia (Cramp and Perrins 1994). In subalpine birch forest in northern Sweden, it comprises about 20% of the bird community, being on average the second most common bird after the willow warbler *Phylloscopus trochilus* (Enemar et al. 1984). Bramblings are insectivorous in summer and the preferred prey is *Epirrita* larvae (Hogstad 1988). Outside the breeding season it is to a large extent granivorous, aggregating in areas with large beech *Fagus silvatica* mast crops (Newton 1972, Cramp and Perrins 1994).

Bramblings arrive at Ammarnäs in late May or in the first days in June (Sandberg 1996), normally one to two weeks before leafing and many birds also commence egg laying before leafing. Bramblings defend breeding terri-tories, but territories and song posts are often grouped close together, creating small "colonies" (Mikkonen 1985). Juveniles leave the nest in late June and early July, but the timing varies with the earliness of spring and some birds fledge considerably later (R. Sandberg, pers. comm.). Population density of bramblings in northern Europe covaries between years with the density of *Epirrita* larvae (Silvola 1967, Hogstad 1969, Ytreberg 1972, Enemar et al. 1984, 2004, Lindström 1987, Hogstad 2000). This is probably possible because bramblings show little or no breeding site tenacity between years (Lindström 1987). The effect of *Epirrita*

larvae on the reproductive output of bramblings is poorly known, although a four-year study in Swedish Lapland indicated that more young were produced in years with higher densities of *Epirrita* larvae (Lindström 1987).

Estimating *Epirrita* density

G. Andersson, T. von Proschwitz and J. Jonasson have carried out standardised yearly counts of *Epirrita* larvae in the Ammarnäs study area since 1967 (Andersson and Jonasson 1980, Selås et al. 2001). The number of larvae on 1000 short shoots of birch was counted within each of four 50×50 m plots of birch forest. The counts were repeated six times during the last two weeks of June each year. *Epirrita* density was calculated for each year by using the average of the six counts for each plot, then taking an average for the three plots situated within 2 km from our trapping site (excluding a fourth plot ca 20 km away). For more details of the *Epirrita* sampling, see Andersson and Jonasson (1980) and Selås et al. (2001).

Estimating brambling population density

A "derived density index" (Enemar et al. 1984, 2004) for bramblings was calculated for each year by combining data from two different census techniques: (1) territory mapping with 10 visits per year in four plots of known size (total area $= 0.42$ km^2), and (2) repeated line transects within an approximate area of 9 km^2. During line transects, all birds heard or seen were counted. While the former value would include only territory holders, the second would include some unknown (but probably small) proportion of females and non-breeders. The derived density index is calculated by multiplying the actual density of territories recorded in the four study plots with the proportion that the bramblings formed of all birds recorded during line transects, and is expressed as territories km^{-2} (Enemar et al. 2004). In 2000 and 2002, only two of the plots were censused (the two largest, in total 0.24 km^2). For these years, the derived density index was calculated assuming that these two plots contained the same proportion of all study plot birds as they did on average the other 17 years. The index is linearly correlated with territory density as recorded in the territory mapping ($r_{18} = 0.97$, P < 0.001). The line transect data are unadjusted for detection probability, and are possibly underestimates of brambling abundance.

The logic behind the derived density index, used in other studies on the bird community in this area (Enemar et al. 1984, 2004), is to get more accurate values for more sparsely occurring species. Although the brambling is a common bird, we have used this index to standardise density estimates given here with those in different publications from the same data set. From now on we will refer to the derived density index as "population density".

Standardised trapping of birds

Daily trapping of birds was carried out each summer 1984–2002, as a way of estimating population density independently of the censuses and to record the reproductive output of the population. Trapping seasons started on average on 16 July (range 15–18 July) and ended on average on 18 August (range 13–21 August). In 1988, trapping continued until 31 August, but birds trapped after 21 August were excluded from the analysis. The length of the trapping season each year was determined before the field season started and depended on the availability of personnel, not on the availability of birds. The average length of the trapping season was 34 days (range 27–37 days). Twenty-two mist-nets were erected between 07:00 and 13:00 local time, in the same positions throughout the study. On some days each year, trapping was carried out in the afternoon, usually because rain had prevented trapping in the morning. Catching was cancelled on average 3 days per year (range 0–8 days).

All birds were ringed and aged as either juveniles (first calendar year, Euring code 3), or adults (second calendar year or more, Euring code 4) according to Svensson (1984). Some of the adults could be aged as either second-year birds (second calendar year, Euring code 5) or older than second-year birds (third calendar year or more, Euring code 6). However, the proportion of birds aged 5 or 6 was low and varied between years, and we therefore refer to all birds with Euring codes 4–6 as adults.

The first ten days of ringing normally coincided with the period when juvenile bramblings became independent. From this period onwards, the juvenile brambling replaces all its body feathers and some of its wing coverts (Svensson 1984). This post-juvenile moult was scored according to a six-grade scale (Bensch and Lindström 1992), where a bird in moult stage 1 (MS1) has not yet started body moult (and outer primaries are not yet fully grown). At MS2, the outer primaries are fully grown and new body feathers start to appear on the upper throat. A bird in MS5 has dropped all the feathers about to be moulted, but some of the new feathers are still growing on the flanks. In MS6 no more feathers are growing.

Inferred predation pressure, phenology and temperature

We have no data on nest predation or chick mortality on bramblings. As a measure of potential (inferred) predation pressure on bird nests in the area, we used data on predation on pied flycatcher *Ficedula hypoleuca* nests. We used the proportion of depredated nests among total nests started in a nest box study going on since 1964. The main predators on pied flycatcher nests in the area were small mustelids, the weasel *Mustela nivalis* and stoat *M. erminea*. These animals also eat the nest-contents of open-nesting species such as bramblings (Hogstad 2000).

The start of the breeding season varied between years, but there are no good data for the yearly variation in brambling egg-laying in Ammarnäs. Instead we used the yearly average trapping date for juvenile bramblings in moult stage 2 (MS2, at this stage the birds have just become independent). The length of the period between hatching and this early stage of post-juvenile moult, ca 25 days (Bensch and Lindström 1992), is likely to vary little between years. Therefore, we assume this moult stage provides a good index of the yearly variation in timing and duration of brambling breeding.

Temperature was recorded in the village of Ammarnäs, ca 6 km east of our study site, between 1984 and 2000. Due to the closing of the weather station in Ammarnäs, temperature data for 2001–2002 were obtained from Boksjö (ca 40 km SSV of Ammarnäs, with similar climatic conditions). We used the averages for June and July, respectively, as a measure of overall temperature. Data were obtained from the Swedish Meteorological and Hydrological Institute.

Statistics

Averages are presented with $\pm$ sd. To allow for parametric tests, per capita production data were square root transformed, predation data were square-root arcsine transformed, and *Epirrita* density and food-related population density data (population density divided by the *Epirrita* density) were $\log_{10}$-transformed. Non-transformed values for per capita reproduction are presented in graphs for clarity. All non-transformed basic values are presented in Table 1.

First and second order autoregressive models were fitted for each variable to estimate the partial auto-correlation function (PACF1 and PACF2), in order to look for autocorrelation between years. We used a crude significance limit of $\pm 2/\sqrt{N}$, where N is the length of the time series (Chatfield 1999). PACF1 was significant for *Epirrita* density, and PACF2 were significant for *Epirrita* density and July temperature. Therefore, the residuals from the PACF2 for these two variables were used in statistical tests, in order to correct for the autocorrelation between years. It should be noted that when taking the second order autocorrelation in the *Epirrita* density into account, all correlations including this factor are somewhat weakened since two years fall out of the final analysis. In addition, it is two outbreak years (1984–1985) that fall out. Accordingly, while correcting for autocorrelation improves the statistical procedure, important biological information is lost. Therefore, in some key analyses we have included the correlation statistics

Table 1. Yearly data for the brambling population and for environmental variables used in the present study. Inferred predation rate is the proportion depredated pied flycatcher nests (in nest boxes) in the area. The phenology of juvenile independence is expressed as the average day for juveniles trapped in early moult (day 1 = 1 July). For more details, see Methods.

Year	Population density	No. adults trapped	No. juveniles trapped	Ratio juveniles/ adult	*Epirrita* larvae density	Inferred predation rate	Phenology of juvenile independence	Average $T°_{June}$	Average $T°_{July}$
1984	112.3	154	249	1.62	23.67	0.000	36.8	10.1	11.8
1985	103.5	46	114	2.48	184.70	0.007	35.2	10.9	13.0
1986	100.3	93	220	2.37	235.07	0.020	40.6	12.8	12.5
1987	76.0	92	131	1.42	6.90	0.421	41.4	9.7	11.3
1988	86.6	85	28	0.33	0.07	0.555	39.3	11.9	14.4
1989	110.3	73	86	1.18	0.07	0.101	37.7	9.9	10.9
1990	63.0	17	29	1.71	0.10	0.152	37.0	11.1	12.8
1991	55.4	80	84	1.05	0.90	0.211	36.4	8.9	13.8
1992	79.5	47	90	1.91	15.27	0.536	42.3	10.6	10.4
1993	126.2	133	149	1.12	31.97	0.437	38.4	7.8	12.4
1994	101.5	44	109	2.48	23.80	0.350	33.2	8.0	13.7
1995	80.6	57	202	3.54	28.83	0.076	38.4	9.6	11.1
1996	61.9	42	44	1.05	5.50	0.152	35.0	9.2	11.9
1997	70.6	57	39	0.68	2.23	0.283	41.5	11.4	15.0
1998	73.7	43	16	0.37	0.53	0.323	32.8	9.4	13.2
1999	76.1	42	73	1.74	1.27	0.114	37.0	11.1	12.2
2000	45.1	68	70	1.03	1.40	0.263	34.0	9.0	13.0
2001	94.0	65	73	1.12	9.50	0.333	42.7	9.9	11.6
2002	124.7	119	114	0.96	4.37	0.390	36.0	12.6	13.5

for both corrected and uncorrected data. In graphs, only the uncorrected values are shown in order to present the full information. Statistical analyses were carried out using SPSS 11.0 (SPSS Inc.).

Results

Variation in environmental variables and larvae density

Average temperatures in June and July varied between $+7.8°$ and $+12.8°C$, and $+10.4°$ and $+15.0°C$, respectively (Table 1). The average density of *Epirrita* larvae varied with more than three orders of magnitude, between 0.07 and 235.07, with three peaks within the study period (Fig. 1). The *Epirrita* density did not vary significantly with average temperatures in June the same year ($r_{15} = -0.084$, P = 0.75; for a longer time series and an in-depth analysis of this moth population, see Selås et al. 2001). The proportion of pied flycatcher nests depredated each year varied between 0 and 0.56.

Brambling population densities

The yearly population density of bramblings varied between 45.1 and 126.2. Population density did not correlate significantly to the *Epirrita* density ($r_{15} = 0.185$, P = 0.48). This relationship is upset particularly by one year, 1989, when population density was high despite a very low abundance of larvae. Brambling population density was not significantly correlated to our phenology measure ($r_{17} = 0.095$, P = 0.70), or to population density of the year before ($r_{16} = 0.280$, P = 0.26) or to the *Epirrita* density of the year before ($r_{14} = 0.005$, P = 0.98).
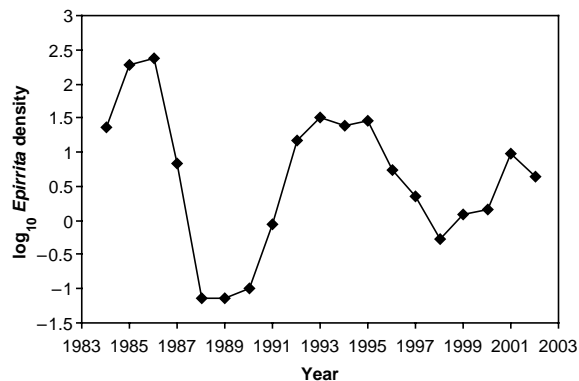

Fig. 1. The annual variation in the density of *Epirrita* larvae in the study area. The larvae have a cyclical appearance with outbreaks about every ten years.
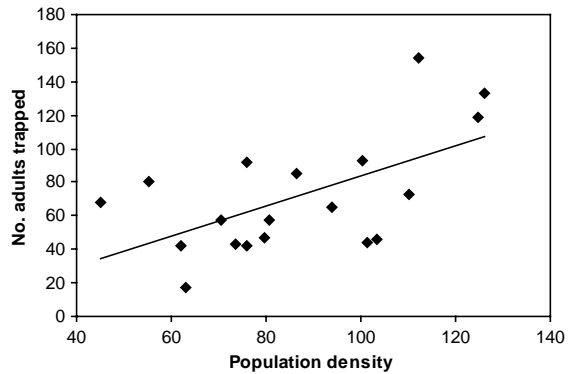

Fig. 2. The number of adults trapped was positively correlated to the population density, as estimated by line transects and territory mapping ($r_{17} = 0.596$, P = 0.007).

Juvenile production

We trapped between 17 and 154 adults (mean 71 ± 35), and between 16 and 249 juveniles per year (mean 101 ± 66). The number of adults trapped in a given year was significantly and positively correlated to the brambling population density as estimated by the censuses (Fig. 2). This suggests that our trapping totals reflected local population size and can be used as an independent measure of breeding bird density. We used the number of adults trapped (not the population density estimated from censuses) as the density measure when calculating productivity to avoid including the same variable (and therefore the same measurement errors) in both the dependent and the independent variable of a regression. The standard deviation in trapping date for juveniles in moult stage 2 did not correlate to the *Epirrita* density ($r_{15} = 0.207$, P = 0.42), indicating that the number of larvae did not influence the length of the breeding season (Newton 1999).

The total number of juveniles trapped each year was positively correlated to the *Epirrita* density ($r_{15} = 0.472$,
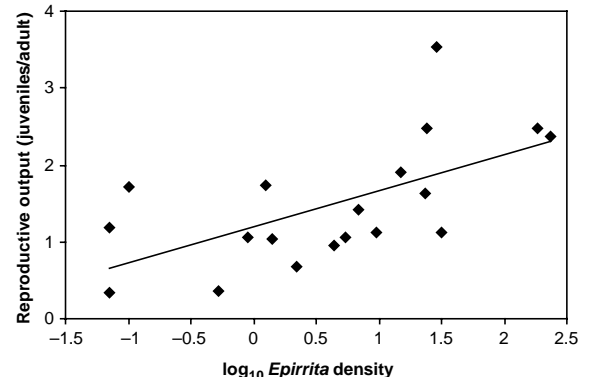

Fig. 3. The per capita reproductive output (juveniles per adult trapped) was positively correlated to the density of *Epirrita* larvae ($r_{15} = 0.541$, P = 0.025).

P =0.056). Also our measure of per capita productivity, juveniles per adult trapped, was positively correlated to the *Epirrita* density (Fig. 3). When ignoring the auto-correlation in the *Epirrita* density between years, the number of juveniles trapped, and juveniles per adult trapped, correlated even stronger to the *Epirrita* density ($r_{17} = 0.698$, P <0.001 and $r_{17} = 0.629$, P =0.004, respectively). Hence, up to about 40% of the variation in the per capita reproduction estimate was explained by the abundance of a single prey species.

When entering population density, June and July temperature, phenology, inferred predation pressure, and the *Epirrita* density into a stepwise regression with the enter probability of 0.05 to explain the variation in number of juveniles per adult trapped, only the *Epirrita* density emerged as significant (Table 2). The same pattern emerged when *Epirrita* density and July temperature was not corrected for autocorrelation between years.

Density-dependent vs density-independent reproductive output

There was no correlation between our per capita productivity measure (number of juveniles per adult trapped) and population density (as estimated from the censuses) the same year (Fig. 4). Hence, with density measured in the conventional way as number of individuals (in a given study area), reproductive output in bramblings seems density-independent. However, for each year we also calculated a measure of breeding density in relation to food abundance ("food-related population density"), that is, population density per larvae. We chose to put the food measure in the denominator in order to get the classical negative correlation between productivity and density, should a density-dependent relationship be present. The absolute values of food-related population density varied between 0.43 and 1576 and we therefore carried out the critical regression on $\log_{10}$-transformed values of both produc-
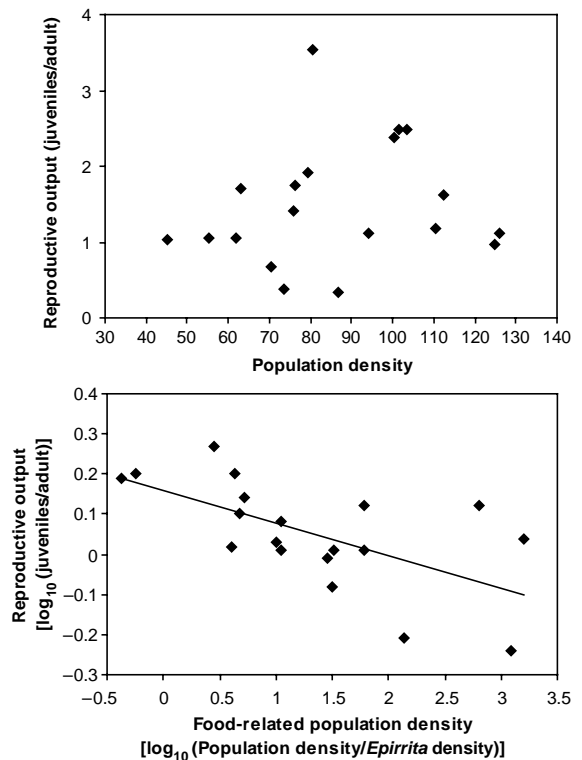

Fig. 4. Upper graph: per capita reproductive output (juveniles per adult trapped) in relation to population density ($r_{17} = 0.163$, P =0.50), indicating a density-independent reproductive output. Lower graph: when per capita reproductive output is analyzed in relation to food-related population density, reproductive output is clearly density-dependent ($r_{17} = -0.630$, P =0.004). Inversing the density measure to $\log_{10}$(population density/ *Epirrita* density) results in the same strong, but positive, relationship ($r_{17} = 0.630$, P =0.004).

tivity and food-related population density. There was a significant negative correlation between food-related population density and per capita production over the 19 years (Fig. 4), that is, the more birds per food item, the lower the reproductive output per bird. Using the alternative (inverse) food-related population density measure, $\log_{10}$(*Epirrita* density/population density), that is larvae per individual, does not influence the relationship between productivity and density. Hence, when the large yearly variation in food abundance was taken into account, there was a clear density-dependence in breeding output among the bramblings.

Discussion

To be able to find the most relevant density measure sensu Newton (1998), that is, resource per capita, one must first identify the limiting resource(s). It is then possible to test whether the inclusion of a resource in the density measure does indeed influence whether the

Table 2. The relationship between brambling per capita reproductive output (juvenile bramblings per adult trapped) and the investigated environmental variables, as estimated by stepwise linear regression with an entry probability of 0.05. The values of *Epirrita* density and July temperature have been corrected for second order autocorrelation, and therefore the analysis is only carried out for 17 years.

Variable	F	df	Partial corr.	P
Full model				
Epirrita density	6.2	1, 15	0.541	0.025
Not included				
July temperature			−0.403	0.12
Inferred predation rate			−0.332	0.21
Phenology			−0.098	0.72
June temperature			−0.041	0.88
Population density			−0.006	0.98

demographic variable studied can be considered density-dependent or not.

Epirrita larvae as a critical resource

In our study system, the abundance of *Epirrita* larvae was the single most important factor explaining yearly variation in reproductive output in the brambling. The density of this single prey species explained up to 40% of the yearly variation in per capita productivity. Such a strong influence of a single prey species on productivity is probably unusual among insectivorous birds. Many raptors and owls depend on one or a few species of rodents, but insectivorous birds normally eat a multitude of species (Cramp and Perrins 1994). Insect outbreaks are known to correlate positively to several parameters among bird predators: 1) breeding density, either in the same season or in the following year (McArthur 1958, Morris et al. 1958, Enemar et al. 1984, 2004), 2) clutch size (McArthur 1958, Zach and Falls 1975, Perrins 1991), and 3) the likelihood of repeat clutches (Zach and Falls 1975). Data on juvenile production during insect outbreaks are scant (Lindström 1987, Holmes et al. 1991), but high breeding densities in years following outbreaks have been interpreted as an effect of more birds returning because of high productivity during the outbreak years (Tomialojc and Wesolowski 1990, Holmes et al. 1991).

Hogstad (2000) suggested that bramblings are "entirely dependent upon the occurrence of *E. autumnata* larvae" for reproduction. While these larvae are clearly very important, young are nevertheless also produced in years with extremely low *Epirrita* densities. This is essential given the short lifespan of bramblings compared to the long periods with almost complete absence of *Epirrita*. A more correct picture of the situation may be that in the outbreak years, reproduction can be raised considerably above bare values (Holmes et al. 1986).

There was no independent effect of our inferred predation pressure on reproduction when taking *Epirrita* density into account, but we do not really know whether our measure of inferred predation pressure is relevant for bramblings. It seems reasonable though, since weasels in our study area are known to switch to bird nests when there are low rodent numbers (as measured by standardised rodent trapping; N. E. I. Nyholm, unpubl.), and weasels are known to eat eggs and chicks of bramblings (Hogstad 2000). Thus, we cannot exclude predation rate as a factor influencing brambling productivity, but any effect is probably small (Hogstad 2000).

Temperature (in July) seemed to have only a weak, if any, effect on the reproductive output of bramblings. June temperatures had no effect at all. Hogstad (2000) found that summers with cold and rainy weather caused breeding failure among bramblings, at least in years with poor food abundance. Enemar et al. (2004) found in their analysis of a 37-year study period that the population density of bramblings was positively correlated to the average temperature in July the year before. To judge from the lack of a positive effect of temperature on productivity in our study, the latter result probably depend on also other variables being positively correlated to temperature, such as adult and juvenile survival between years (Enemar et al. 2004).

In summary, among the investigated environmental factors, food abundance (*Epirrita* density) was the single most important factor explaining brambling reproductive output. It is therefore both justified and important to take food abundance into account when analysing density dependence of brambling reproductive output.

Density-dependent vs density-independent reproductive output

When density was analysed in the conventional way by equalling population density to number of breeders (implicitly per area), per capita productivity was apparently density-independent. However, there was a significant negative correlation between food-related population density and per capita production. Thus, when taking the large variation in food abundance between years into account, there was a clear density-dependent effect on reproductive output. Accordingly, our results support the hypothesis put forward by Newton (1998) that when variation in food abundance between years is taken into account, density-dependence might still be present in what otherwise seems to be a density-independent relationship.

Also other bird species in the area are known to feed on *Epirrita* larvae, but we do not know to what extent. We are aware of that the total predation pressure of all species should ideally have been taken into account in our food-related density measure. Notwithstanding that it is almost impossible to calculate because the comparative feeding data are not available, there are reasons to believe that it would not change the general picture. First, in no other species than the brambling did *Epirrita* density a given year correlate significantly to population density (Enemar et al. 2004), indicating that bramblings have the tightest relationship with this prey species. Second, the population sizes of the three potentially most important *Epirrita* predators, two thrush species *Turdus pilaris* and *T. iliacus* (because of their large size), and the willow warbler (very numerous), varied positively, albeit weakly, in parallel to brambling population density (Enemar et al. 2004). Third, and more importantly, the between-year variation in *Epirrita* density is far higher than the variation in the total bird numbers. Therefore, the relationship between food-related density

and brambling productivity is unlikely to change when including the effect of all potential predators.

Elmberg et al. (2003) analysed the per capita production of young in dabbling ducks in relation to both duck density, and duck density per food available. In general they found only weak evidence for density-dependent productivity and including food in the density measure did not change this picture. The reason for the latter result may be that food is simply not generally a limiting factor for the ducks in their study area (the latter concluded by Elmberg et al. 2003). Accordingly, it may not have been the relevant factor to include in the density measure. Further, the variation in food abundance over their twelve study years (CV 36–56%, the highest value being seven times higher than the lowest) may not have been large enough for an effect of a varying food supply to be detected. In our study, the CV in *Epirrita* density was 214%, the highest value being 3300 times higher than the lowest.

The same general principle of including a limiting factor in the density measure should of course hold for other environmental factors than food. Nest site availability is another potentially important limiting factor on reproduction. Jones and Leopold (1967) found that the per capita production of young by wood ducks *Aix sponsa* was negatively correlated to the number of pairs per available nest box, probably as an effect of intraspecific interference (many pairs inspecting and sometimes laying in the same box). Jones and Leopold (1967) did not make the conventional test relating productivity to bird density per se. We therefore reanalyzed the data of their Table 1 and found that using the conventional density measure, there was a negative, but insignificant correlation between productivity and density ($r_6 = -0.314$, $p = 0.14$), that only improved marginally when including nest box availability in the density measure ($r_6 = -0.430$, $p = 0.08$). The variation in nest box numbers again was small (the highest value being five times higher than the lowest), which may explain the small effect it had to include this factor in the density measure.

We conclude from our study on bramblings and *Epirrita* that the inclusion of a limiting environmental variable into the density measure may drastically influence the conclusion drawn concerning the density-dependence of important demographic variables.

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