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Large brood sizes of pied flycatcher, sparrowhawk and goshawk in peak microtine years: support for the mast depression hypothesis

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Abstract The mast depression hypothesis (MDH) proposes that cyclic population fluctuations of microtines and other herbivores are an effect of cyclic seed cropping of plants. This is because high seed crops, termed masts, are produced at the expense of chemical defence against herbivores. It has generally been assumed that bird-hunting raptors produce high numbers of offspring when microtine prey are abundant because of reduced competition from generalist predators. However, this may also be caused by higher production of herbivorous insects, and thus insectivorous bird prey, because of lower contents of chemical defence compounds in some plant species, such as bilberry *Vaccinium myrtillus* and cowberry *V. vitis-idaea*. In Aust-Agder county, southern Norway, the mean brood size of pied flycatcher *Ficedula hypoleuca*, sparrowhawk *Accipiter nisus* and goshawk *A. gentilis* was higher in peak vole years than in other years. The effect was not due to variation in nest predation, as only successful nesting attempts were included in the analyses. For the pied flycatcher, the annual proportion of large broods (> 6 fledglings) was positively correlated with the vole trapping index. No correlation was found between the offspring production of goshawks and the proportion of voles in their diet. During a 3-year light-trapping study of nocturnal moths prior to our study, four moth species whose larvae ate *Vaccinium* were commonest in the vole peak year. All these results are consistent with the MDH.

Key words Breeding success · Hawks · Mast depression · Pied flycatcher · Voles

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Introduction

The well-known 3- to 5-year population cycles of microtine rodents in the boreal zone of Europe and North America have been assumed to influence the populations of a large number of bird species. One obvious effect of microtine outbreaks is increased breeding success of microtine-hunting owls and raptors (Hagen 1969; Newton 1979; Mikkola 1983). However, breeding success is also highest for bird-hunting species, such as the merlin *Falco columbarius*, the gyrfalcon *F. rusticolus* and the goshawk *Accipiter gentilis*, when microtines are abundant (Hagen 1952, 1969; Bergo 1992). Since microtines are of minor importance as food for these raptors (Hagen 1952; Höglund 1964; Sulkava 1964; Langvatn 1977; Wikman and Tarsa 1980; Widén 1987), improved breeding success in peak microtine years may be a result of increased food supplies because of reduced competition from generalist predators (Hagen 1969).

The idea of relaxed competition for avian prey when microtines are abundant has been supported by observations of high predation on eggs and nestlings or chicks of both small passerines and grouse in microtine crash years (Dunn 1977; Angelstam 1983; Angelstam et al. 1984; Järvinen 1985; Sørensen et al. 1990; Wegge and Storaas 1990). However, as pointed out by Widén et al. (1987), the alternative prey hypothesis (e.g. Hörnfeldt 1978; Angelstam et al. 1985; Hörnfeldt et al. 1986) does not exclude the plant cycle hypothesis. The latter states that cyclic fluctuations in food quality influence the reproduction of microtines, grouse and herbivorous insects, and thus also the reproduction of insectivorous birds and bird-hunting raptors.

According to the mast depression hypothesis (MDH), which is a further development of the plant cycle hypothesis, cyclic population fluctuations of herbivores are an effect of the cyclic seed cropping of plants (Selås 1997a). This is because high seed crops, termed masts, are produced at the expense of chemical defence against herbivores. The MDH was developed on the basis of reported relationships between microtine numbers and seed production (Laine and Henttonen 1983) or levels of proteinase inhibitors in plants (Seldal et al. 1994a). Proteinase inhibitors, which have an adverse effect on both microtines and insects (Seldal et al. 1994a, b), consist of proteins and may thus be profitable to resynthesise in mast years (Selås 1997a).

The relationship between mast seeding and herbivore numbers predicted by the MDH was tested by use of historical data from southern Norway (Selås 1997a). Here, all masts of bilberry *Vaccinium myrtillus* and cowberry *V. vitis-idaea* during 1952–1995 were followed by outbreaks of bank vole *Clethrionomys glareolus*, which to a large extent feeds on *Vaccinium*. Similarly, all masts of forest trees during 1930–1987 were followed by outbreaks of autumnal moth *Epirrita autumnata* on mountain birch *Betula pubescens*.

Recently, Thingstad (1997) found a positive correlation between the number of fledged young of the pied flycatcher *Ficedula hypoleuca* and the hunting bag of black grouse *Tetrao tetrix* and capercaillie *T. urogallus*. Since lepidoptera larvae feeding on bilberry are important as food for the pied flycatcher (Atlegrim 1991), as well as for grouse chicks (Kastdalen and Wegge 1991), the level of chemical defence compounds of bilberry may be a key factor in synchronising the breeding success of these species. The problem, however, is to distinguish between effects of fluctuating food quality and effects of fluctuating predation pressures caused by fluctuating microtine numbers.

The alternative prey hypothesis predicts that, in the absence of predation, there should be no correlation between the breeding success of pied flycatchers and microtine numbers. The MDH, on the other hand, predicts that there should be a positive correlation between the breeding success of pied flycatchers and microtine numbers even in the absence of predation. In the cavity-nesting pied flycatcher, only two microtine-hunting predators will act as nest robbers, namely the stoat *Mustela erminea* and the weasel *M. nivalis*. Both of these would usually destroy all eggs or nestlings when robbing a nest (see e.g. Sørensen et al. 1990). Thus, if one selects only successful nesting attempts, the effect of nest predation is eliminated. If then the breeding performance in successful nests is higher in peak microtine years than in other years, factors other than nest predation must be involved.

In this paper we test the MDH by examining the correlation between vole numbers and the brood sizes of successful nesting attempts of pied flycatchers. In addition, we present data on the breeding success of two bird-hunting raptors, the goshawk *A. gentilis* and the sparrowhawk *A. nisus*, and data on the occurrence of four *Vaccinium*-feeding moth species, taken from a previously published study.

Methods

In or near the forest area in southern Norway investigated by Selås (1997a), vole numbers have been estimated by snap trapping each autumn during 1971–1996 (Røstad 1981; Christiansen 1983; Spidsø and Selås 1988; Kålås et al. 1991, 1992, 1994, 1995; Kålås and Framstad 1993; Framstad 1996; E. Christiansen, E. Framstad and T.K. Spidsø, personal communication). The trapped animals mainly consisted of bank voles, but a few field voles *Microtus agrestis* were also caught. From 1969 and 1970, information on the vole population level in the study area is given by Grasaas (1971) and Wegge and Grasaas (1977).

The abundance and diversity in the fauna of nocturnal moths were investigated by Bakke (1974) in a thorough light-trap study in central parts of the study area (Åmli municipality) during 1969–1971. Among the large number of moth species caught, four live primarily on *Vaccinium* species: *Syngrapha interrogationis*, *Eugraphe subrosea*, *Polia hepatica* and *Cerastis rubricosa* (Skou 1991). The three former species winter as small larvae, develop in early summer, pupate, and hatch in late summer (Skou 1991). Assuming that the level of chemical defence compounds in *Vaccinium* plants is low in late summer in the mast year and early summer in the post-mast year, the imago of these moths should be expected to be most numerous in peak vole years. Larvae of the latter species develop in mid and late summer, and the imago hatches in the following spring (Skou 1991). Hence, the imago of this species might be expected to be numerous both in peak and post-peak years of the vole cycle.

Brood sizes of goshawks and sparrowhawks were recorded during 1988–1996 (Table 1). For the pied flycatcher, a common prey of the sparrowhawk in the study area (Selås 1993), data on both clutch and brood sizes have been collected by us and other ornithologists along an 80-km zone of the south-eastern coast of Norway and as far as 30 km inland from the coast, in Aust-Agder county, during 1969–1996 (Appendix 1). All brood sizes were recorded as the number of young present at the time of ringing. For the pied flycatcher, where the number of fledglings varies more than for the hawks, only years for which we had data on at least ten clutches or broods were used in the analyses.

For the hawk species, mean brood sizes in years with peak vole populations in autumn were tested against mean brood sizes in other years. For the pied flycatcher, we also tested for correlations between egg or fledgling production and the vole trapping index. For this species, however, the proportion of large clutches or broods (>6 eggs or fledglings) was used rather than the mean clutch or brood size. This was because with a limited sample of 10–15 nests for some years, the absence or presence of a clutch or brood of only one or two eggs or fledglings had large effect on the average clutch or brood size. Besides, the method chosen should reduce the risk of biases caused by annual variations in the frequency of bigamy, i.e. in the proportion of small broods raised by the female alone (e.g. Lundberg and Alatalo 1992).

The reproductive effort of insectivorous bird species also depends on the weather conditions during the breeding season (e.g. Lundberg and Alatalo 1992). In our coastal study area, heavy rainfall rather than low temperatures might have influenced the

Table 1 Total number of broods and prey of goshawks and sparrowhawks

	Number of broods		Number of prey items	
	Goshawk	Sparrowhawk	Goshawk	Sparrowhawk
1987			41	389
1988	8	8	194	1772
1989	9	9	255	834
1990	6	8	302	
1991	13	22	493	
1992	17	12	707	
1993	13	18	553	
1994	16	25	588	
1995	14	14	594	
1996	10	22	210	

brood sizes of pied flycatchers negatively. Low temperatures may however have influenced the clutch sizes. Hence, we tested for correlations between the proportion of large broods and the amount of precipitation in May and June, and for correlations between the proportion of large clutches and the mean temperature in May. Data on precipitation and temperatures from central parts of the study area were provided by the Norwegian Meteorological Institute.

To investigate the impact of voles as prey for the hawk species, we obtained data on the proportion of voles in diet, for the goshawk from the period 1987–1996 and for the sparrowhawk from 1987–1989, estimated from prey remains collected at nest sites (Table 1). The annual proportion of voles in the diet was compared with the annual offspring production and the autumn population of voles.

Results

In the light-traps of Bakke (1974), the proportions of the four moth species with larvae on *Vaccinium* plants differed significantly between the three years investigated (Kruskal-Wallis test, $H = 6$, $P < 0.05$). In contrast to the total number of moths caught, which decreased throughout the period, the *Vaccinium*-feeding species occurred in higher numbers in the peak vole year 1970 than in 1969 and 1971 (Fig. 1).

In the pied flycatcher, the proportion of large broods among successful nesting attempts was 33% (SD = 8.9, $n = 7$) in peak vole years and 25% (SD = 6.2, $n = 19$) in other years (Mann-Whitney *U*-test, $U = 26$, $P = 0.019$, $n = 26$; Fig. 1). The proportion of large broods was correlated both with the proportion of large clutches (Kendall's rank correlation, $T = 0.52$, $P < 0.001$, $n = 23$) and the vole index ($T = 0.36$, $P = 0.014$, $n = 24$; Fig. 1), and negatively correlated with the amount of precipitation in May-June ($T = -0.31$, $P = 0.029$, $n = 25$; Fig. 2). The proportion of large clutches was positively, though not significantly, correlated with the vole index ($T = 0.24$, $P = 0.14$, $n = 21$) and the mean temperature in May ($T = 0.25$, $P = 0.10$, $n = 23$). In years with especially high proportions of large clutches (> 50%; Fig. 1), there were either high vole populations (1973, 1978, 1994) or high mean temperatures in May (1984, 1989, 1993).

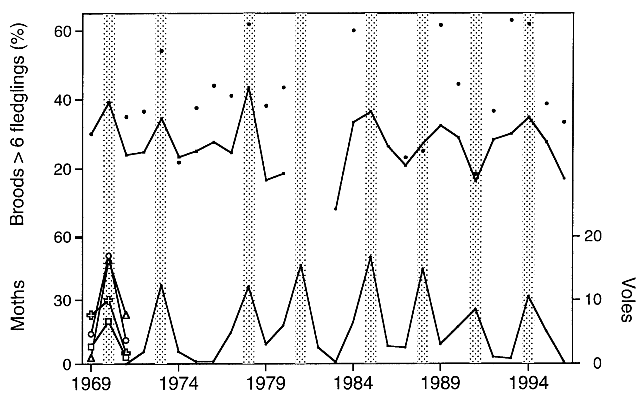

Fig. 1 Annual variation in the proportion of large broods (> 6 fledglings) among successful nesting attempts of pied flycatcher. For years with at least ten investigated clutches, the proportion of large clutches (> 6 eggs) is given by a *dot*. Autumn population sizes of voles are estimated from snap traps (Røstad 1981; Christiansen 1983; Spidsø and Selås 1988; Kålås et al. 1991, 1992, 1994, 1995; Kålås and Framstad 1993; Framstad 1996; E. Christiansen, E. Framstad and T. K. Spidsø, personal communication), while the number of four moth species (*triangle Cerastis rubricosa*, *square Syngrapha interrogationis*, *circle Eugraphe subrosea*, *cross Polia hepatica*) with larvae on *Vaccinium* plants are taken from a light-trap study (Bakke 1974). The total number of all moths trapped was 5698 in 1969, 4285 in 1970 and 3087 in 1971. Years with high vole populations in autumn are *shaded*; information from 1969 and 1970 from Grasaas (1971) and Wegge and Grasaas (1977)

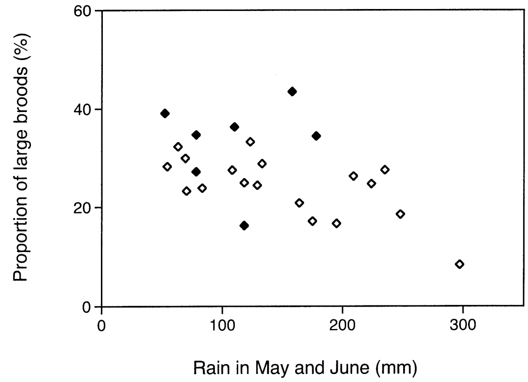

Fig. 2 Proportion of large broods (> 6 fledglings) among successful nesting attempts of pied flycatcher in relation to the amount of precipitation in May and June (data provided by the Norwegian Meteorological Institute) (*filled squares* peak vole years)

For some of the peak vole years, the proportion of large broods was constrained by the proportion of large clutches (Fig. 1). This was especially the case in 1991, when clutch sizes were lower than for any other year during the study period. According to S. Dale and T. Slagsvold (personal communication), this year had the most unfavourable weather conditions (continuous north wind) during spring migration observed during 1988–1996. Most flycatchers arrived late at the breeding areas, and therefore produced small clutches. As a result, 1991 was a poor year for the reproduction of the pied flycatcher in southern Norway in general (S. Dale and T. Slagsvold, personal communication).

During 1988–1996, the mean annual number of fledglings produced per successful goshawk nest was significantly higher in peak vole years than in non-peak years (Fig. 3; Mann-Whitney *U*-test, $U = 0$, $P = 0.020$, $n = 9$); results for sparrowhawk nests were suggestive ($U = 2$, $P = 0.068$, $n = 9$) though not significant. The mean brood size of the goshawk was 2.57 (SD = 0.09, $n = 3$) in peak vole years and 2.26 (SD = 0.11, $n = 7$) in other years, whereas the corresponding values for the sparrowhawk was 4.17 (SD = 0.08, $n = 3$) and 3.80 (SD = 0.23, $n = 7$), respectively.

For the goshawk, we found no correlation between the mean brood size and the proportion of voles in the diet during 1988–1996 (Kendall's rank correlation, $T = 0.14$, $P = 0.60$, $n = 9$), nor between the proportion of voles in the diet and the vole autumn index

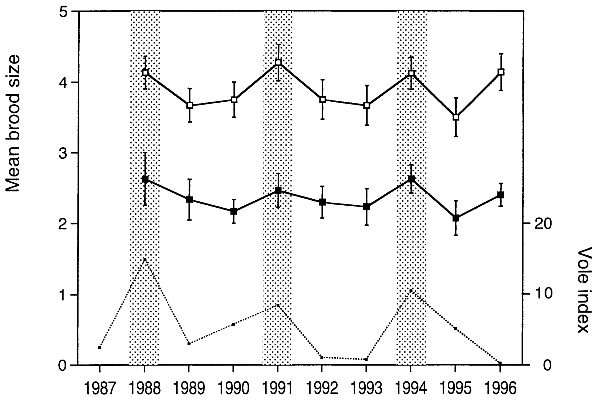

Fig. 3 Annual variation in brood sizes (±SE) of goshawk (*filled squares*) and sparrowhawk (*open squares*), given as mean number of young produced per successful nesting attempt, and autumn population size of voles (*dotted line*) estimated from snap traps (see Fig. 1). Years with high vole populations in autumn are *shaded*

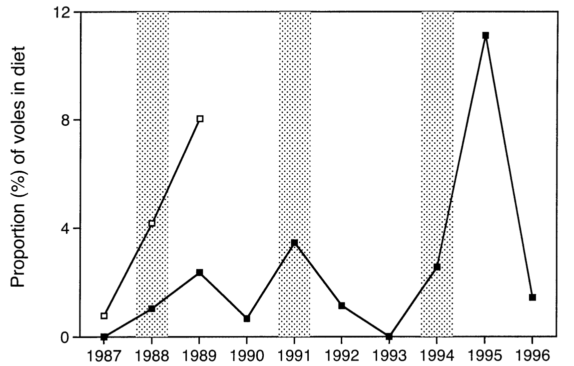

Fig. 4 Proportion of voles in the diet of goshawk (*filled squares*) and sparrowhawk (*open squares*). Years with high vole populations in autumn (see Fig. 1) are *shaded*

($T = 0.17$, $P = 0.53$, $n = 9$). For two of the three peak vole years (1988 and 1994), there was a high vole population also in spring in the year following that with the peak in autumn density (see Selås 1997a). This high spring population apparently influenced the occurrence of voles in the diet of both goshawks and sparrowhawks (Fig. 4), but did not cause an increased offspring production (Fig. 3).

Discussion

During his 3-year study of the abundance of nocturnal moths, Bakke (1974) found the highest number of species with larvae on *Vaccinium*-plants in a peak vole year. A similar result was obtained in eastern Norway by Kastdalen and Wegge (1991), who investigated the volume of insects in the field layer over 4 years. They found the highest insect population in the peak vole year 1987, mainly because of a peak in the number of lepidopteran larvae, which led to a pronounced defoliation of the *Vaccinium* host plants. The MDH is supported also by a 10-year light-trapping study of Lepidoptera in eastern Norway, where species feeding on the same plants showed similar population fluctuations, but differed from those of species feeding on other plants (Kobro 1991, 1994). It should be noted that the abundance of lepidopteran larvae feeding on bilberry leaves is usually highest in mid-June (Atlegrim 1991), i.e. when passerines such as the pied flycatcher, as well as predators like sparrowhawks and goshawks, rear their young.

As predicted by the MDH, the number of fledglings produced by pied flycatchers was higher in peak vole years than in other years. Because only successful nesting attempts were included in the sample, nest predation was eliminated as a synchronising factor. Other factors that might have influenced the results, for instance the time of egg laying (Lundberg and Alatalo 1992), the proportion of monogamous females (Lundberg and Alatalo 1992), weather conditions (e.g. Järvinen 1993; Siikamäki 1996), or biases due to differences between habitats (e.g. Lundberg and Alatalo 1992) or geographic areas where the data were collected, are unlikely to coincide with vole peaks, and may rather have masked the effect of a high food supply in years of high vole densities.

High insect production in post-mast years may influence not only the reproduction, but also the number of insectivorous birds. If surplus non-breeding individuals usually are present (e.g. Newton 1992), increased food supply may allow a higher number of pairs to breed. In the alpine heath, the breeding density of several bird species is positively correlated with the density of small rodents (Lien et al. 1975; Stenseth et al. 1979; Järvinen 1990). If, on the other hand, the number of breeding pairs depends on the offspring production in the previous year, a time lag between vole number and breeding density would be expected. In Finland, the number of breeding redstarts *Phoenicurus phoenicurus* has been highest in the same or in the next year relative to the microtine peak (Järvinen 1990, Veistola et al. 1996).

The offspring production of sparrowhawks and goshawks was also highest in peak vole years. Since voles seemed to be most commonly hunted in spring, and were apparently of minor importance to the brood sizes, the results indicate that there were also higher numbers of some other prey species in peak vole years. In general, the breeding success of bird-hunting raptors depends mainly on the availability of fledglings of their avian prey (Hagen 1952; Tornberg 1997). Hence, our results are consistent with the assumption of high fledgling production of avian prey in peak vole years.

In contrast to what Hagen (1969) found for the merlin in mountainous areas in central Norway, the breeding density of the forest-dwelling sparrowhawk and goshawk seems not to be correlated with microtine numbers (Selås 1997b, c). One reason for this may be that fluctuations in the level of chemical defences of herbs and dwarf shrubs are more important to bird communities in mountainous habitats than in forests, due to the lack of alternative feeding sites in trees. Besides, the greater amplitude of microtine cycles in mountainous areas indicates that fluctuations in plant quality increase with increasing altitude.

Based on the results from the study of the reproduction of pied flycatchers, we believe that the high breeding success of bird-hunting raptors in peak microtine years is not solely a result of reduced competition from other predators, as suggested by Hagen (1969), but also reflects generally higher production of herbivores in post-mast years. Variations in the predation pressure from generalist predators on different bird species may however strengthen the fluctuation in the breeding performance of bird-hunting raptors. Further research is needed to reveal the importance of such interspecific competition for avian prey.

Because of the correlation between the number of microtines and the production of other bird and mammalian species, several researchers have continuously investigated the population fluctuations of microtines in Fennoscandia. If, however, these correlations are not due to predation alone, as has usually been assumed, but merely to fluctuations in the quality of plants, ongoing investigations on microtine populations should also include estimations of the population level of other herbivorous animals, as well as of the seed production of different food plants. In addition to such correlative studies, critical tests of the MDH should be carried out by testing the impact of seed production on the level of chemical defence compounds in plants, and by studying the effect of any chemical defence compounds on different herbivorous species.

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Appendix 1 Number of successful broods of different sizes for pied flycatchers in Aust-Agder during 1969–1996

Year	Number of fledglings								Total number of broods
	1	2	3	4	5	6	7	8	
1969	0	0	0	1	1	12	6	0	20
1970	0	0	0	0	8	6	9	0	23
1971	2	3	8	21	36	54	39	0	163
1972	0	2	5	15	27	33	22	5	109
1973	0	0	2	5	4	8	10	0	29
1974	0	0	0	2	6	15	7	0	30
1975	0	2	3	1	5	4	5	0	20
1976	0	0	1	2	10	8	7	1	29
1977	0	2	6	5	12	12	11	1	49
1978	0	2	0	3	3	5	9	1	23
1979	0	0	1	4	12	8	5	0	30
1980	1	2	2	2	5	10	3	2	27
1981	0	0	0	0	0	1	0	0	1
1982	0	0	1	1	2	3	0	0	7
1983	0	0	1	2	2	6	0	1	12
1984	0	1	0	2	5	2	4	1	15
1985	0	0	0	0	2	5	3	1	11
1986	0	1	0	4	2	7	5	0	19
1987	1	0	3	1	3	11	5	0	24
1988	0	0	1	5	7	11	9	0	33
1989	0	0	2	5	5	11	9	2	34
1990	1	2	2	4	8	15	13	0	45
1991	0	1	1	8	9	17	6	1	43
1992	1	1	3	11	6	21	13	4	60
1993	0	1	1	5	3	11	9	0	30
1994	0	0	0	2	6	7	6	2	23
1995	0	3	1	5	6	6	8	0	29
1996	0	1	1	5	5	17	6	0	35
Total	6	24	45	121	200	326	229	22	973

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