Ann. Zool. Fennici 41: 599–607 ISSN 0003-455X
Helsinki 31 August 2004

Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions

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Received 4 Mar. 2004, revised version received 23 Mar. 2004, accepted 23 Mar. 2004

Reif, V., Jungell, S., Korpimäki, E., Tornberg, R. & Mykrä, S. 2004: Numerical response of common buzzards and predation rate of main and alternative prey under fluctuating food conditions. — *Ann. Zool. Fennici* 41: 599–607.

We studied the numerical response of a population of the common buzzard *Buteo buteo* to the fluctuations of its main prey (voles) and alternative prey (forest grouse) in western Finland between 1979 and 1996. Populations of main prey fluctuated in a cyclic manner with three years between peak densities. The nesting success of buzzards averaged 1.7 fledglings per nesting attempt and the brood size averaged 2.2 fledglings per brood. The nesting rate (no. of active nests per number of occupied territories) and the productivity rate (no. of chicks for all territories) positively correlated with the abundance of *Microtus* voles in the current spring but not with the abundance of grouse. The Alternative Prey Hypothesis (APH) predicts that, in the years when the main prey species decline, generalist predators can shift their diet to alternative prey and thus cause its decline. The Shared Predation Hypothesis (SPH) states that all important prey species, including alternative prey, are under high hunting pressure when the density of predators is high. The predation rate (the combination of numerical response and previously studied functional response) of *Microtus* voles by buzzards was positively correlated with the densities of these voles in the current spring, whereas the predation rate of grouse tended to peak one year after peak densities of *Microtus* voles. Therefore, our results appear to support APH rather than SPH and indicate that predation by buzzards may dampen population cycles of main prey (voles) but amplify population fluctuations of grouse.

Introduction

Predators respond both functionally and numerically to density changes in their prey (Solomon 1949, Holling 1959). Generalists are considered to respond mainly functionally through diet shifts, while specialists respond mainly numerically (Crawley 1992). However, such dichotomy of response types is likely to be rare in nature, and in reality predators make a combined response, which actually defines the impact of predators on their prey populations (Korpimäki & Krebs 1996). Of these, the functional response is thought to be fundamental because it determines the numerical response (Keith *et al*. 1977). Reproductive success, which is an important component of the numerical response (Korpimäki & Norrdahl 1991a), may or may not supplement the functional response and hence affect the predation impact on the alternative prey. Thus, a nomadic generalist predator that always has some amount of alternative prey in the diet but concentrates on hunting the main prey in its peak years, might increase pressure on the alternative prey (1) in the same (peak) years (if numerical response is immediate), or (2) in the years when the main prey crashes (in case of a lagged response). In birds of prey, there are numerical responses with and without obvious time-lag (e.g. Galushin 1974, Keith *et al*. 1977, Korpimäki 1984, 1985, 1994, Rohner 1996, Nielsen 1999, Tornberg 2001, Newton 2002).

The Alternative Prey Hypothesis (APH) predicts that, in the years when the main prey species declines, generalist predators can shift their diet to alternative prey and thus cause its decline (Angelstam *et al*. 1984). Moreover, in spite of low proportion of alternative prey in the diet in peak years of main prey, the effect of predators on alternative prey may also be high in such years due to their numerical response, given by increased breeding density and production of young. This is suggested by the Shared Predation Hypothesis (SPH) which states that predators are less selective in killing their prey and all important prey species, including the alternative prey, are affected detrimentally when the densities of predators are high (Norrdahl & Korpimäki 2000).

The common buzzard *Buteo buteo* (hereafter "buzzard") belongs to a guild of predators that feed mainly on small mammals. In our previous study on buzzards in western Finland (Reif *et al*. 2001) we found that cyclic vole populations of the genus *Microtus* (the field vole *M. agrestis* and the sibling vole *M. rossiaemeridionalis*) were the main prey of buzzards. Buzzards shifted their diets to small game (the mountain hare *Lepus timidus* and forest grouse species (the willow grouse *Lagopus lagopus*, the black grouse *Tetrao tetrix*, the capercaillie *Tetrao urogallus* and the hazel grouse *Bonasa bonasia*) in poor vole years. Since mainly young individuals of these species were hunted, we concluded that buzzards may reduce the breeding success of small game populations.

Breeding performance of buzzards has been studied widely in Europe (Mebs 1964, Tubbs 1967, 1972, Picozzi & Weir 1974, Rockenbauch 1975, Spidsø & Selås 1988, Kostrzewa & Kostrzewa 1990, Jędrzejewski *et al*. 1994, Graham *et al*. 1995, Swann & Etheridge 1995, Goszczyński 1997, Kenward *et al*. 2000), but mostly in areas where they are year-round residents and without marked multiannual population oscillations of the main prey, or without any proper density estimates of the main and alternative prey types. Therefore, most studies report that the breeding density and success of buzzards is fairly stable between years, indicating that it is a typical generalist.

In this study we aim to examine the numerical response of the common buzzard from the viewpoint of its possible impact on main and alternative prey that have wide inter-annual density variations. This raptor is a suitable study object because it is the most abundant avian predator, which eats both voles and small game in northern Europe (Korpimäki & Norrdahl 1997, Forsman 1999).

First, we investigate the between-year variation in the breeding density and reproductive success of buzzards in an area where they are migrants and where their main prey (voles) fluctuate cyclically in 3-year periods. Then, we study potential effects of buzzard predation on populations of main prey (voles). Finally, we try to find out whether buzzard predation on the alternative prey (grouse) is consistent with the patterns predicted by APH or SPH. According to APH, the predation pressure on the alternative prey (grouse) should be less severe when the main prey (voles) is abundant than when the main prey is scarce. To be consistent with SPH, the predation pressure on the alternative prey should in turn be positively related to the densities of the main prey.

Material and methods

Study area

The study was carried out in the South Ostrobothnia region, western Finland (ca. 63°–64°N, 23°–24°E). The study area covers ca. 3000 km^2, and is characterised by flat terrain with small rivers, creeks and ditches. About two thirds of the area is covered by mixed coniferous-dominated forest and one third by agricultural fields (*see* Reif *et al*. 2001).

Breeding performance

The large stick-nests of buzzards and other raptors (mainly goshawks *Accipiter gentilis* and honey buzzards *Pernis apivorus*) and ravens *Corvus corax* were sought and also artificial nests were built in this area by Sven Jungell from 1977 onwards. Once found, the nests and the whole nesting territories were monitored in subsequent years. The following information concerning the nests were recorded: species, state of the nest/territory (unoccupied, decorated but not used, nesting started — defined by observations of incubating birds, nests were not climbed at this time), and breeding success (number of fledglings; nests were climbed and young were ringed). The data set contains 2921 records for nests in the years 1977–1996, among which 852 records are for buzzards. Altogether 146 buzzard nesting territories were found. Because other large raptors (goshawks and honey buzzards) often used the same nesting sites as buzzards, we defined each territory as buzzard's from the first observed buzzard nesting onwards regardless whether it was later used by other species. In many cases there were several nests (up to four) within a territory, all of which could be decorated in any given years, even thought no more than one was used for nesting.

Given the small number of nests checked during the first years of the study, only the data beginning from 1979 were included in the analysis. Based on the breeding data, for each year we calculated: territory occupancy rate (proportion of territories occupied by buzzards in relation to all territories of any raptor species known for a given year and ever occupied by buzzards during the whole period of study), nesting rate (proportion of occupied territories where nesting was started), success rate (proportion of active nests that were successful, i.e. produced at least one fledgling), population productivity rate (number of fledglings per occupied territory) and average brood size (number of fledglings per successful nest).

Availability of prey

The abundance of small mammals (i.e. voles, mice and shrews) was estimated each spring (in May) and autumn (in September) by snap-trap captures in the Kauhava region (*see* Korpimäki & Norrdahl 1991b, Korpimäki 1994, Norrdahl & Korpimäki 1995, 2002a, 2002b). Habitats of the main types (a cultivated field, an abandoned field, a spruce forest and a pine forest) were sampled in two sites 14 km apart by using four-day trapping sessions with Finnish metal mouse snap-traps. Water vole (*Arvicola terrestris*) density was estimated by using Finnish metal rat snap-traps also in May and September beginning from 1982 (*see* Korpimäki *et al*. 1991). The density index derived from both the mouse and rat snap-trapping results was the mean number of small mammals trapped per 100 trap nights for two parts of the study area (for more details *see* Korpimäki & Wiehn 1998, Reif *et al*. 2001, Norrdahl & Korpimäki 2002b). The distance between the southern limit of the buzzard study area and the snap-trap sampling plots of small mammals was 15–20 km, but the spatial synchrony of population fluctuations of voles in this area is over 80 km (Huitu *et al*. 2003).

Small mammals (voles and shrews) showed cyclic fluctuations in western Finland as previously described (e.g. Korpimäki & Norrdahl 1991b, Korpimäki 1994, Norrdahl & Korpimäki

1995, 2002a, 2002b). *Microtus* voles and bank voles *Clethrionomys glareolus* fluctuated in close temporal synchrony with a prevailing cycle period of three years. Common shrews *Sorex araneus* fluctuated in weak but significant temporal synchrony with *Microtus* voles, but water voles did not show any significant synchrony with other vole species (Korpimäki *et al.* 2002 and unpubl. data). There were four 3-year cycles of *Microtus* vole numbers during this study period with the peaks in 1982, 1985, 1988 and 1991. The strong cyclicity disappeared after 1993 (*see* Laaksonen *et al.* 2002), and because of that we analysed the data also separately for the period 1979–1993 (till the end of the last distinct cycle).

Density estimates of grouse were taken from the publications of the Finnish Game Research Institute (Rajala & Lindén 1982, 1983, 1984, 1985, 1986a, 1986b, Lindén & Wikman 1987, 1988, Lindén *et al.* 1988, Wikman & Lindén 1989, Helle *et al.* 1991, Lindén *et al.* 1992, Helle *et al.* 1993, 1994, 1995, 1996). Grouse censuses (*see* Lindén *et al.* 1989 for the method) are made only once per year, in August (in a few cases in July).

Table 1. Breeding density and reproductive success of the population of common buzzards in South Ostrobothnia during 1979–1996.

Years	No. of occupied territories	No. of active nests	No. of successful nests	Total no. of chicks
1979	12	9	4	10
1980	12	7	6	8
1981	15	11	9	18
1982	20	17	7	17
1983	30	18	11	25
1984	38	27	23	49
1985	46	36	27	68
1986	58	44	33	74
1987	58	23	16	23
1988	49	38	29	70
1989	67	43	29	82
1990	45	27	23	41
1991	63	44	39	82
1992	59	45	37	83
1993	47	25	20	40
1994	49	41	36	83
1995	39	32	30	76
1996	38	32	29	59

Predation rate

For evaluation of total response (pooled functional and numerical responses) we calculated the index of buzzard predation on the four grouse species during the years 1985–1992. For each of these years we selected nests within a permanent core area which included 50% of all active buzzard nests known by the year 1992 (485 km^2). The area was selected by the Ranges V programme (Kenward & Hodder 1996) with harmonic mean analysis (Dixon & Chapman 1980). We believe that by the year 1985 all buzzard territories in this area were already known and therefore annually checked. For each year during 1985–1992 we counted numbers of nests located within this area and pooled numbers of fledglings in these nests. However, the diet data were not solely associated with these nests and were pooled for the whole study area (Reif *et al.* 2001). We assumed that the diet of buzzard pairs in the core area did not differ from the average of the population.

For calculation of the predation rate we simplified the formula for estimation of consumption of different food items (Lindén & Wikman 1983, Korpimäki & Norrdahl 1991a) by excluding variables which would be constant (consumption by adults and young and weight of grouse chicks in the diet):

$$R = (N + F)D,$$

where R = predation rate, N = number of active buzzard nests, F = pooled number of fledglings, D = average numbers of a food item found per nest. All values for these calculations were standardized by range and incremented by one to avoid zero values.

Since some of the prey abundance indices were not normally distributed, we used nonparametric tests (Spearman rank correlation, two-tailed).

Results

The number of breeding pairs and breeding success of the buzzard population varied markedly among the years (Table 1). Occupancy rate of

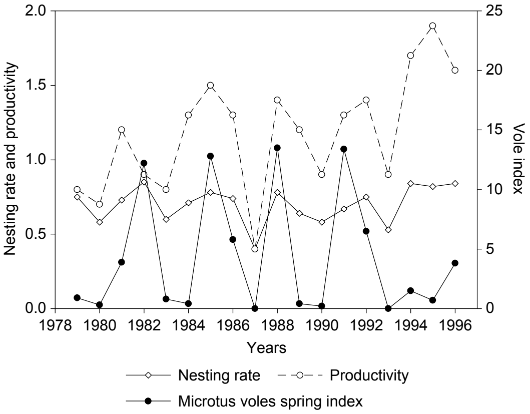

Fig. 1. Nesting rate (no. of active nests per total no. of territories) and productivity (no. of chicks per total no. of territories) of buzzards in relation to density fluctuations of *Microtus* voles in South Ostrobothnia in 1979–1996.

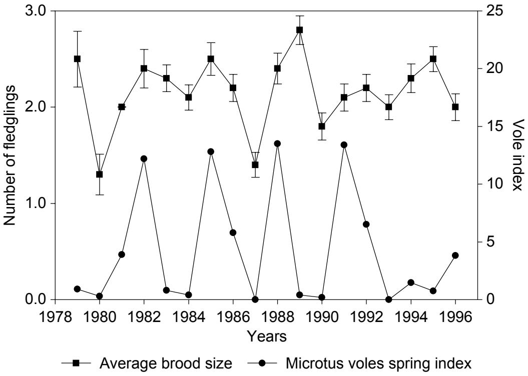

Fig. 2. Average brood size (with standard errors) of the common buzzard and spring density indices of *Microtus* voles during 1979–1996.

territories varied from 26% to 57%, being on average 44%. Nesting was started in 40% to 85% (on average 70%) of the buzzard territories; 44% to 95% (on average 85%) of the active nests were successful. The occupancy rate of territories did not correlate with the density indices of small mammals in the spring with or without a time-lag or with the grouse index in the current summer. Nesting rate and productivity rate of buzzards correlated positively with the abundance of the *Microtus* voles in the current spring during the cyclic period of voles (Table 2 and Fig. 1). We also found a significant positive correlation between the productivity of the buzzards and the density index of the shrews (Table 2).

The average brood size amounted to 2.2 fledglings per successful nest and varied two fold, from 1.3 to 2.8 (Table 1 and Fig. 2). It did not show a significant relationship with the density indices of small mammals in the current spring (Table 2), but indicated a tendency to lag behind the fluctuations of the *Microtus* voles (Fig. 2), though the correlations with lags were not significant ($r_s = 0.19$, $P = 0.49$). There were no obvious correlations between the breeding parameters of buzzards and the grouse density during the vole cyclic period (Table 2).

The combination of numerical and functional responses (the latter described in Reif *et al.* 2001) enables us to estimate the predation rate of buzzards on prey (or total response) during 1985–1992 for the nests within the permanent core area of 485 km^2. During 1985–1992 the area contained on average 14 active buzzard nests (Fig. 3). The predation rate of four grouse species by buzzards tended to peak one year after the peak densities of the *Microtus* voles (Fig. 3), although did not show a significant correlation with the density index of these voles with and without a 1-year lag ($r_s = 0.42$, $P = 0.3$ and $r_s = -0.14$, $P = 0.74$, respectively). The predation rate of the *Microtus* voles by the buzzards correlated

Table 2. Spearman rank correlations between the yearly density indices of small mammals (trap index of the current spring) and grouse and breeding density and reproductive success of the common buzzard during 1979–1993. Significance levels after sequential Bonferroni correction (Rice 1989). * = significance level for two-tailed *P* value 0.05, ns = not significant.

	Microtus voles	Bank vole	Common shrew	Water vole	Grouse total
Nesting rate (no. of active/all occupied territories)	0.85*	0.08 ns	0.55 ns	0.28 ns	0.25 ns
Success rate (no. of successful/active nests)	0.22 ns	–0.35 ns	0.11 ns	0.56 ns	–0.58 ns
Average brood size	0.56 ns	0.14 ns	0.21 ns	0.34 ns	0.23 ns
Productivity (no. of chicks/all territories)	0.70*	0.21 ns	0.65*	0.36 ns	–0.11 ns

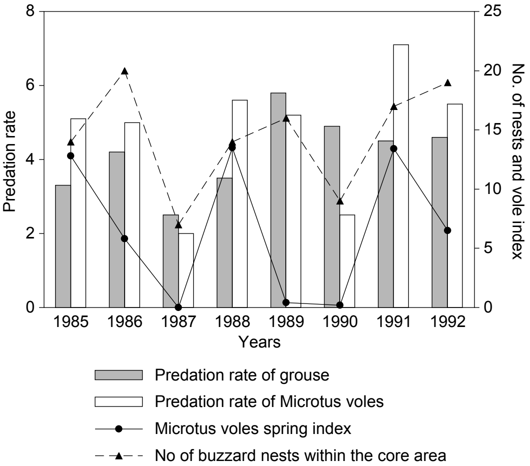

Fig. 3. Predation rates of *Microtus* voles and forest grouse by the buzzard pairs within the core area (485 km^2), density index of *Microtus* voles and number of buzzard nests within the core area during 1985–1992.

with the density indices of these voles in the current spring ($r_s = 0.86$, $P < 0.01$).

Discussion

The population of common buzzards showed large fluctuations in the breeding density and reproductive success. The nesting success of the whole population varied markedly between the years, but the average success of nesting pairs was quite stable. That is, if a pair was able to initiate a nesting attempt, it was likely to rear at least one fledgling, but in years of food scarcity (low vole density) few pairs attempted to breed.

The nesting success, on average 1.7 fledglings per nesting pair and 2.2 per successful pair, was higher than observed in central Europe, Great Britain and Norway (Mebs 1964, Tubbs 1967, Picozzi & Weir 1974, Rockenbauch 1975, Spidsø & Selås 1988, Jędrzejewski *et al.* 1994, Swann & Etheridge 1995, Goszczyński 1997), but the average brood size and its variance in Poland (Goszczyński 1997) did not differ from that in our study ($t = –1.209$, $P = 0.24$).

The nesting success of the buzzards in our study area was higher in the years when *Microtus* voles were abundant than in the years when they were scarce. *Microtus* voles were the main prey of the buzzards in our study area (Reif *et al.* 2001) and, as a consequence, buzzard reproduction (nesting rate and productivity) correlated with the vole abundance. The goshawks inhabiting our study area were found to have a negative effect on nesting success of buzzards in some territories (H. Hakkarainen *et al.* unpubl. data, *see* also Krüger 2002). Nevertheless, we suggest that, for the buzzard population as a whole, marked among-year density fluctuations of the main food were the major factor determining breeding performance. In Germany and Norway buzzards also produced more young during good vole years (Mebs 1964, Spidsø & Selås 1988). In Poland breeding success of the buzzards nesting close to open grasslands was positively related to the abundance of *Microtus* voles, probably because forest rodents did not show marked multiannual cycles in densities (Jędrzejewski *et al.* 1994). In Scotland breeding density of buzzards was positively related to the abundance of rabbits that were the main prey (Graham *et al.* 1995).

Although the average proportion of water voles in the diet of buzzards was almost as high as that of *Microtus* voles by prey number and even higher by prey weight (Reif *et al.* 2001), we did not find statistically significant relationships between the water vole density and reproductive parameters of the buzzards. Our diet data are from the nestling period and we do not know whether water voles are eaten in early spring. Although they are known to live mostly under ground in early spring when buzzards start to breed (*see* e.g. Myllymäki 1972, Jeppson 1990), yet adult and particularly young water voles may be an important prey species later in the breeding season.

It was unexpected to find a positive relationship between the density index of the shrews and the productivity of the buzzards, because shrews constitute a minor proportion in the diet (0.5% by weight, Reif *et al.* 2001). It is possible that this correlation is due to temporal synchrony of population oscillations of *Microtus* voles and shrews in our study area (Korpimäki *et al.* 2002 and unpubl. data). Alternatively, the proportion of small shrews in the diet may be underestimated in assessing the diet composition on the basis of food remains collected in the nest, as it has been earlier found with respect to other small prey species in the diets of raptors (e.g. Suomus 1952, Sulkava 1964, Sonerud 1992, but *see* Korpimäki *et al*. 1994). Although small prey for buzzards, shrews are fairly stable food source as compared with *Microtus* and bank voles because their population densities fluctuate much less than those of voles.

We found that the numerical response of the buzzards expressed as the nesting and productivity rates closely followed the fluctuations in the densities of the *Microtus* voles. However, decline years of the vole abundance (one year after the peaks) appeared to deviate from this relationship so that the nesting and productivity rates tended to remain relatively high (Fig. 1). Therefore, the predation rate of grouse by buzzards (Fig. 3) in decline vole years appeared to be increased due to both the dietary and the numerical responses. However, we did not find an obvious correlation between the predation rate of grouse and the *Microtus* voles density with one-year lag. Given the diet data limitations our tests for predation rates cover only two full vole cycles. Nevertheless, our results seem to support the reasoning of conventional thinking suggested by APH rather than by SPH, because the predation rate of grouse by buzzards in decline vole years appeared to be amplified by the numerical response. Most of the grouse killed by buzzards were juveniles (Reif *et al*. 2001). Consequently, increase of the predation rate also concerned mainly grouse chicks, which is in accord with APH (Angelstam *et al*. 1984).

The predation rate of the *Microtus* voles by the buzzards correlated with the density indices of these voles in the field (Fig. 3). This suggests that buzzards can have a stabilising effect on vole populations, like a nomadic specialist. The common buzzard is a more versatile predator than most of the vole specialists, but, being a migratory species, may show faster numerical responses to changes in vole numbers than the resident owls (Korpimäki 1994). However, the pattern of its predation rate suggests that in some years it probably can dampen the peak densities of vole populations (e.g. in 1985, 1988, 1991) but deepen cyclic lows (e.g. in 1989) (Fig. 3), i.e. its effect is not always stabilizing.

A large proportion of non-territorial ‘floaters’, like ones observed in Germany by Rockenbauch (1975) and in England by Kenward *et al*. (2000) could change the expression of the numerical response of the whole buzzard population. However, although we do not have any estimation of the amount of floaters in our buzzard population, neither do we have a good reason to suspect a high number of them, because there was always a surplus of empty nests in the study area (new nests were constantly built artificially). This can be taken as an evidence that the density of nesting pairs in the best years was close to the maximum possible in this area. Since buzzards usually defend their nesting territories, floaters could be driven out.

To summarize, our results indicate a marked numerical response of the common buzzard to the density fluctuation of *Microtus* voles. Combination of both the functional and the numerical responses (the total response, or predation rate) by buzzards for *Microtus* voles still followed the fluctuations of *Microtus* voles, suggesting that this raptor may dampen population cycles of the main prey (voles), like generalists or nomadic specialists. However, the pattern of predation rate suggests that, because of the slight time lag in the numerical response, in certain years buzzards may also deepen them at low phases, like resident specialists. Thus, the common buzzard in our study area in western Finland holds an intermediate position between generalists and resident specialist predators. The total response relating to the alternative prey (grouse chicks) peaked one year after the *Microtus* vole peaks, supporting traditional reasoning of the Alternative Prey Hypothesis over the recent substitute, the Shared Prey Hypothesis. Our example also demonstrates that the numerical response of a predator should be considered in further tests of APH and SPH.

Acknowledgements

We are grateful to Folmer Bokma for advice in the data analysis and to Harri Hakkarainen, Ian Newton, John Spence, Hannu Pietiäinen and an anonymous referee for valuable comments to the early versions of the manuscript. The study at various stages was financially supported by the Jenny and Antti Wihuri Foundation, the Environmental Graduate School of EnviroNet of the University of Oulu and Ella and Georg Ehrnrooth Foundation (to VR).

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