

Population changes of different predators during a water vole cycle in a central European mountainous habitat

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Population changes in long-eared owls *Asio otus*, polecats *Mustela putorius*, red foxes *Vulpes vulpes*, stone martens *Martes foina* and badgers *Meles meles* were monitored during a water vole *Arvicola terrestris scherman* cycle in western Switzerland. Long-eared owls confirmed their status of highly mobile specialist predators in responding strongly and without time lag to water vole population changes. Even though polecats are considered generalists, they exhibited also a strong response to water vole fluctuations. Their numbers tracked water vole densities with a 1-yr time lag. Marked population changes were also recorded in red foxes and stone martens, but these changes were not related to water vole densities. Lastly, badgers did not show any significant population changes during the water vole cycle. We discuss the possible reasons for these differences and conclude that multi-factorial approach is clearly required to understand population processes in predator-prey systems.

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Interactions between predators and cyclic fluctuating prey have been extensively studied in the northern hemisphere (e.g. Erlinge et al. 1983, Henttonen et al. 1987, Hanski et al. 1991, Krebs et al. 1995, O'Donoghue et al. 1997, Angerbjörn et al. 1999). Predators have an undeniable influence on small mammal population dynamics (e.g. Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998, Boonstra et al. 1998). Small mammal cycles, in turn, have also significant effects on predator populations as predators often respond numerically to fluctuating prey densities (e.g. Andersson and Erlinge 1977, Korpimäki et al. 1991). The numerical response results from changes in predators' natality, mortality, immigration and emigration. It is also influenced by a predator's degree of specialization and local prey diversity (Andersson and Erlinge 1977). In the boreal forest of Fennoscandia, where microtine populations exhibit 3–5 yr cycles (Hansson and Henttonen 1988), the numerical response to fluctu-

ations of vole populations is generally less pronounced in generalist than in specialist predators (Andersson and Erlinge 1977). Mobility is also an important factor: poor mobility causes resident predator densities to lag behind the vole fluctuations, whereas nomadic avian predators respond immediately to fluctuating vole densities (e.g. Korpimäki and Norrdahl 1989, Korpimäki et al. 1991, Korpimäki 1994).

The fossorial form of the water vole *Arvicola terrestris scherman* is found at middle elevation in the central European mountains and undergoes population cycles. Vole densities at peak reach several hundreds of individuals ha⁻¹ (Morel 1981). Despite its wide distribution and periodical high numbers, there have been few investigations of the interactions between this rodent and its predators. To our knowledge, only one study described the numerical response of predators to water vole fluctuations. Debrot (1983) found that stoat *Mustela erminea* numbers responded to water vole

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population changes with a 1-yr time lag in the Swiss Jura Mountains. Furthermore, several studies carried out in the same area have emphasized the importance of water voles in the diet of local predators during vole highs. In addition to stoats (Debrot 1983), polecats *Mustela putorius*, stone martens *Martes foina*, red foxes *Vulpes vulpes*, and badgers *Meles meles* showed a functional response to water vole population changes (Mermod et al. 1983, Lachat Feller 1993a, Weber and Aubry 1993, 1994). Long-eared owls *Asio otus* also predominantly incorporated water voles in their diet when voles were abundant (Mermod 1991).

In this paper, we examine population changes of five predators in relation to fluctuating water vole densities over a 9-yr period. The study area is characterized by a very low availability of wild alternative prey when water voles are scarce. Only invertebrates and rubbish are available in reasonable quantities during vole lows (Ferrari and Weber 1995). In these circumstances, we predict that specialist predators, in this case the long-eared owl, should exhibit a strong numerical response to water vole population changes. Moreover, long-eared owl numbers should respond to water vole fluctuations without time lag. Conversely, the generalist predators – red fox, polecat, stone marten and badger – should respond less markedly than specialists providing they find suitable alternative food sources during the low phase of the water vole cycle.

Methods

Study area

The 30 km² study area was situated in the Swiss Jura Mountain (47°09'N, 6°56'E) of western Switzerland. The altitude ranges from 995 to 1288 m a.s.l., and the climate is wet (average annual rainfall: 1460 mm) and cold (average annual temperature: 6.5°C; Weber and Meia 1996). Grasslands cover 52% of the area, wooded pastures 25% and spruce *Picea abies* dominated forests 20%. The remaining 3% is covered by human settlements.

Water vole densities

Density estimates of water voles were measured from 1988 to 1997 by seasonal trapping in two grassland areas located 4 km apart. Trapping was performed three times per year, usually in May, August and October. No trapping occurred during the winter because of snow cover and frozen ground. In addition, summer 1990 trapping session was cancelled at one site because of cattle disturbance. Trapping was carried out on a 100 × 5 m strip divided into 20 adjoining squares with no more than two Sherman live traps per square

(Pascal and Meylan 1986). Traps were set for three days, and checked eight times. They were not prebaited. Details on how to transform trapping results into density estimates are given in Rodolphe and Pascal (1985) and Pascal and Meylan (1986).

Predator populations

Population changes of predators were monitored by nightlighting counts (Weber et al. 1991), from 1988 to 1997 for red fox and from 1989 to 1997 for other species. Spotlighting was made with a slow moving car (ca 15 km h⁻¹), on a 30-km standard circuit representative of the entire study area. The countryside was lighted with a portable spotlight and regularly swept, on both sides of the car, by the beam within a range of ca 400 m. The observations were made with 10 × 40 binoculars. The sampling occurred every month, three nights in a row, according to the following scheme: 1st night: from 9.00 pm to midnight; 2nd night: from midnight to 3.00 am; 3rd night: from 3.00 am to 6.00 am. Every animal seen was identified and recorded. The mean number of observations (sightings) recorded for a given species during the three monthly counts was considered a population index for the month. Results are averaged and divided by seasons: spring (March–May), summer (June–August), autumn (September–November) and winter (December–February).

To determine the influence of water vole population changes on predator numbers, Pearson correlations were performed between the number of sightings of a given predator during the spring and spring densities of water voles in the current and previous year.

Results

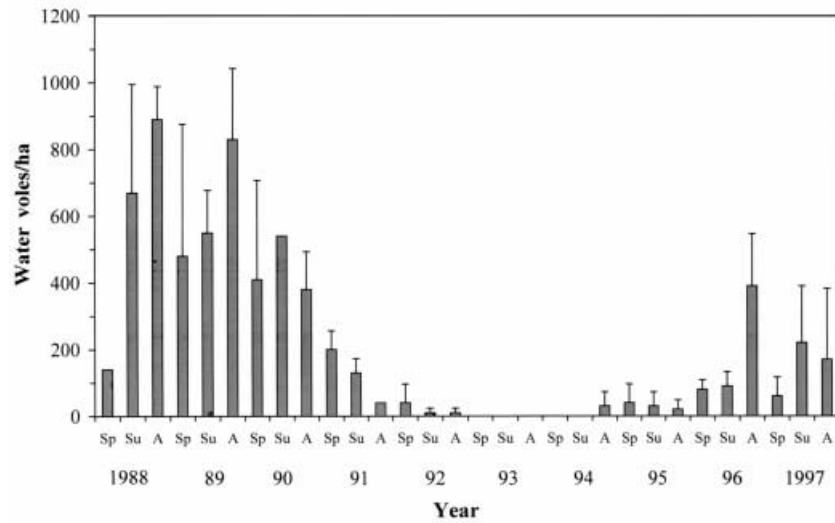
Water vole densities

Water voles peaked in 1988–89 (Fig. 1). Density estimates close to 1000 individuals ha⁻¹ were recorded in the study area at that time. A regular decrease in vole numbers was then observed, and in 1993–94, the species was close to extinction in the area. A population recovery occurred in autumn 1994, and water voles started to increase again. In autumn 1996, water vole populations reached a new peak, and densities of 280 and 500 individuals ha⁻¹ were recorded in both trapping sites respectively.

Predator populations

Long-eared owls exhibited a strong numerical response to water vole population changes (Fig. 2). As predicted, long-eared owl numbers tracked water vole densities

Fig. 1. Mean seasonal (Sp = spring; Su = summer; A = autumn) densities of water voles in the study area during 1988–1997.



without time lag ($r_s = 0.76$, $p = 0.00001$). Sightings of long-eared owls peaked in 1989. Coinciding with water vole decline, the number of owl observations dropped in 1990 with an amplitude of change of 10.7-fold to remain low but relatively stable in 1991. Eventually, no more long-eared owls were seen while vole populations were at their lowest levels. A few owl sightings were recorded again from winter 1996 onwards.

The red fox was by far the most common wild carnivore in the area. At their lowest levels in 1988, numbers increased by 2.4-fold one year later. Despite some marked seasonal decreases, fox sightings kept on increasing during water vole decline and low densities (Fig. 3). Fox numbers showed no correlation with water vole densities in the current year ($r_s = 0.48$, $p = 0.17$) or previous year ($r_s = -0.28$, $p = 0.15$).

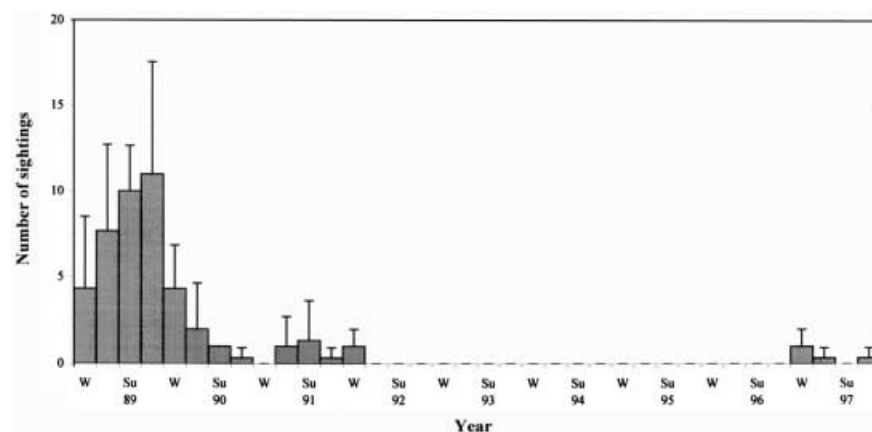
The first stone marten sightings were recorded in 1990, one year after the vole peak. Their numbers increased steadily by approximately 6-fold until 1994 and then declined (Fig. 4). A negative relationship was

found between stone marten sightings and water vole densities in the current year ($r_s = -0.72$, $p = 0.03$) and previous year ($r_s = -0.58$, $p = 0.001$).

The badger was an uncommon mustelid in the area and did not show any marked population changes during the vole cycle (Fig. 5). A negative relationship was found between badger sightings and water vole densities in the current year ($r_s = -0.73$, $p = 0.03$). No correlation was found between badger numbers and water vole densities in the previous year ($r_s = -0.19$, $p = 0.32$).

The polecat was also an uncommon predator in the study area as suggested by the low number of observations (Fig. 6). However, most sightings were recorded during water vole highs and early population decline. From 1993 onwards, no more polecats were seen in the study area. Polecat numbers did not correlate with water vole densities in the current year ($r_s = 0.67$, $p = 0.06$). On the other hand, polecats responded to water vole fluctuations with a 1-yr time lag ($r_s = 0.60$, $p = 0.0008$).

Fig. 2. Mean seasonal (Su = summer; W = winter) number of long-eared owl sightings in the study area during 1988–1997.



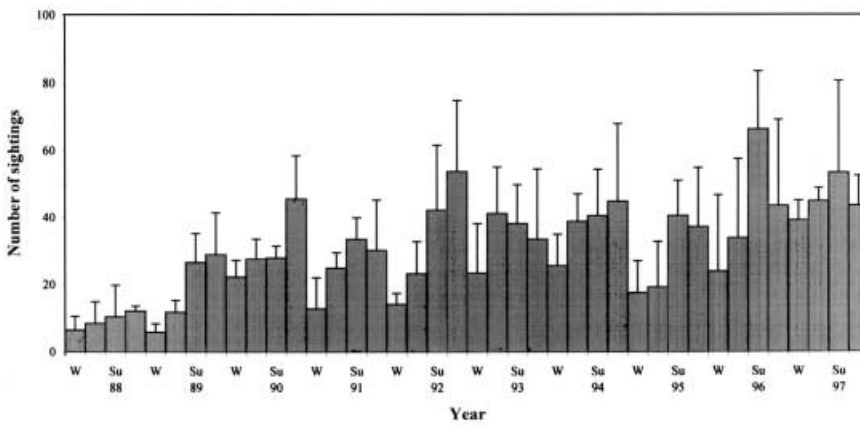


Fig. 3. Mean seasonal (Su = summer; W = winter) number of red fox sightings in the study area during 1988–1997.

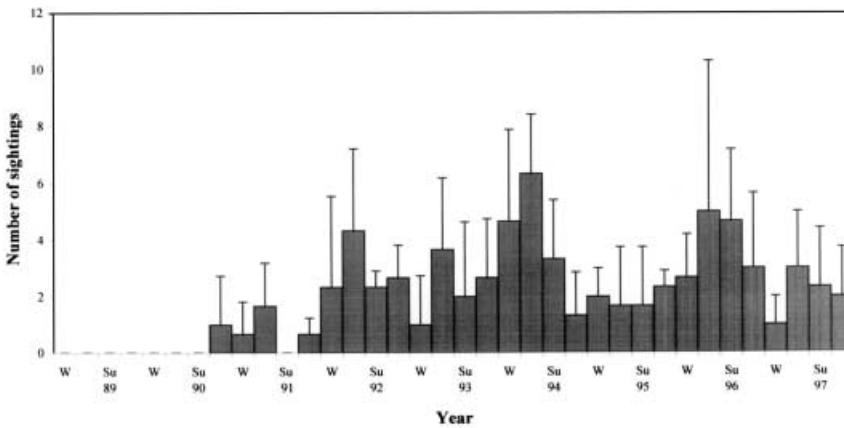


Fig. 4. Mean seasonal (Su = summer; W = winter) number of stone marten sightings in the study area during 1988–1997.

Discussion

Water vole cycles

A 7-yr cycle was recorded during our study. Water vole cycles are generally longer than the 3–5 yr period recorded in fluctuating small microtines (Hansson and Henttonen 1988). Large-scale demographic studies showed that the cycle length in fossorial water voles

averaged 6 yr (range: 4–8 yr) in the Swiss Jura Mountains and the Alps (Saucy 1988). A similar periodicity was also recorded in water vole populations from eastern France and southern Germany (Pascal and Boujard 1987, Fröschle 1991). Considering the allometric relationship between body size and cycle length in cyclic mammals (Calder 1983, Peterson et al. 1984), Saucy (1994) suggested that the larger body size of the fosso-

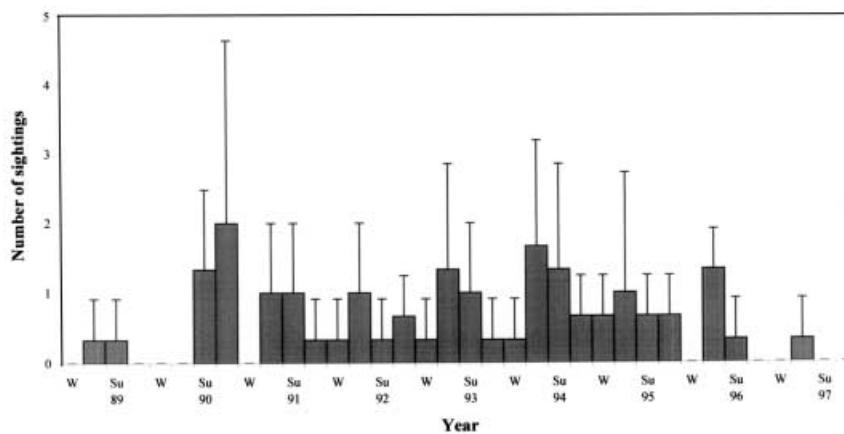


Fig. 5. Mean seasonal (Su = summer; W = winter) number of badger sightings in the study area during 1988–1997.

rial *A. terrestris* compared with other cyclic small rodents could possibly account for the longer population cycles observed in this species. To explain local variations in cycle length, Saucy (1994) hypothesized that the length of water vole cycle could increase following elevation in mountainous areas of central Europe in a similar pattern that latitude influences cyclicality in Fennoscandia (e.g. Hansson and Henttonen 1985, Hanski et al. 1991, Turchin and Hanski 1997). Saucy (1994) analysed long-term population fluctuations of the water vole from nine different sites of which six were located > 1000 m, and three between 630 and 770 m. The longest water vole cycles (7 yr) were reported at the highest sites. With a 7-yr interval between the two peaks and trapping sites situated at 1050 m a.s.l., our results do not contradict Saucy's hypothesis, but evidence remains weak to support it without reservation.

Interactions between herbivores and predators may generate cyclicality and shape population cycles at northern latitudes (Norrdahl 1995). In Fennoscandia, resident specialist predators, e.g. small mustelids, owing to their time-delayed numerical responses to changes in vole density, are believed to be responsible for population oscillations in microtine rodents (e.g. Hanski et al. 1991, Korpimäki 1993). Although this hypothesis has not been properly tested in water voles so far, Debrot (1981, 1983) documented circumstantial evidence that small mustelids could also drive water vole cycles. In addition to the feeding habits of the stoat which showed a high dependence on water voles, Debrot examined the population changes of stoats and water voles over a 25-yr period, and found that stoat numbers were tracking water vole fluctuations with a 1-yr time lag. Stoats and weasels *M. nivalis* were present in our study area, and hence could have potentially played a role in driving the water vole cycle. However, unlike in the study area of Debrot, live trapping revealed that both species were uncommon in our area even when water voles were abundant (Weber unpubl.). Thus, their influence on the cycle is likely to have been minor.

On the other hand, another water vole specialist was abundant in the region. With a density of 18 individuals km⁻² the domestic or farm cat *Felis catus* was indeed the most common carnivore in the study area, and despite a variable degree of dependence on man it preyed to a large extent on water voles: up to 86% of the total items according to the year (Sen-Gupta 1993). Furthermore, farm cats reduced significantly their hunting activities when water voles were rare to rely almost exclusively on anthropogenic food (Weber and Dailly 1998). Therefore, at first glance, a possible role of this species in driving the water vole cycle should not be dismissed.

According to the predation hypothesis, generalist predators are expected to modify the shape of the vole cycle (Hanski et al. 1991, Norrdahl 1995). Whether or not this is the case in our predator-prey system still remains an open question.

Predator populations

Two predators responded numerically to water vole fluctuations. Long-eared owls responded strongly and without time lag to water vole populations changes, probably influenced by the scarcity of suitable alternative prey, e.g. small microtines, in the study area (Ferrari and Weber 1995). These marked and rapid changes in owl numbers confirm their status of highly mobile specialist predators (Korpimäki 1994). In contrast, polecats are considered generalist predators (Andersson and Erlinge 1977). Therefore, one could have expected a less marked numerical response of this species to water vole fluctuations. However, generalists living in areas with little alternative food, e.g. red foxes in Fennoscandia, are known to respond in a specialist pattern (Andersson and Erlinge 1977, Lindström 1989). Although the number of polecat sightings was globally small, the absence of observation during water vole lows and the 1-yr delayed numerical response of

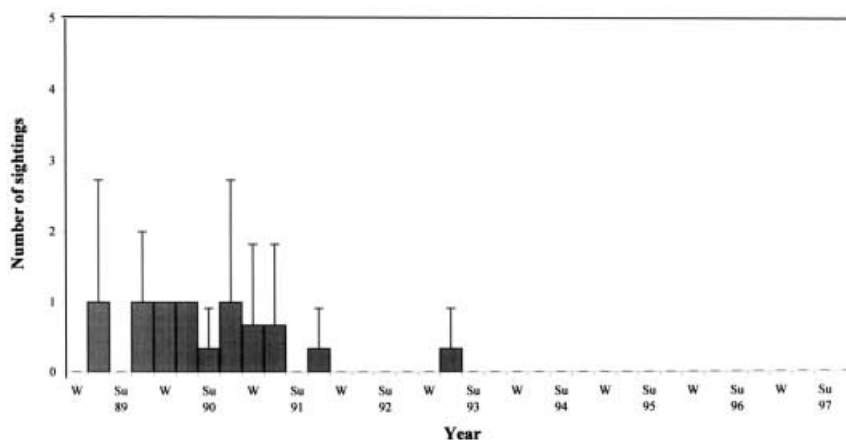


Fig. 6. Mean seasonal (Su = summer; W = winter) number of polecat sightings in the study area during 1988–1997.

polecats tend to confirm the dependence of polecats on water voles. Amphibians and small microtines which are essential components of polecat's diet elsewhere in Switzerland are scarce in our study area (Weber 1989, Ferrari and Weber 1995).

Significant changes were also recorded in red fox and stone marten populations, but these changes were not related to water vole densities. Fox numbers did not show any decline when water vole declined but rather increased from year to year. Deeply affected by a local rabies epidemic in the early 1980s, fox populations started to recover only in the late 1980s owing to annual vaccination campaigns (Zanoni et al. 2000). This regular increase in fox numbers and the low fox density observed in the area at the beginning of the study – from 2.3 to 3.2 individuals km^{-2} depending on the season (Meia and Weber 1996) – suggest that fox populations had not reached the carrying capacity so far. Besides, density estimates were close to 10 individuals km^{-2} a decade later in similar regions (U. Müller pers. comm.). Intensively preyed upon by foxes during vole highs, water voles certainly contributed positively to fox recovery while rubbish consumption, an abundant and quickly renewable food item, prevented the decrease in fox breeding success, respectively fox numbers during the low phase of the water vole cycle (Weber 1996, Weber et al. 1999).

The figure given by stone marten population changes was unexpected. Heavily hunted in the study area during the 1980s and possibly affected by rabies (Zanoni et al. 2000), stone martens were rarely observed until 1991. Then, the number of sightings – and captures (Lachat Feller 1993b) – increased presumably as a consequence of the progressive disappearance of rabies in the area and of a loss of interest amongst hunters for stone marten hunting. Preying to a great extent on water voles when the rodents were abundant, stone martens switched to alternative prey during vole lows and fed more frequently on anthropogenic food (Lachat Feller 1993a, Fleury 1996). A change in stone marten feeding habits does not explain per se the decrease in stone marten numbers recorded from 1994 onwards. Rubbish was abundant in the study area, but its availability was limited to the farm middens (Ferrari and Weber 1995). As these food patches were also intensively exploited by foxes, interactions between both predators were probably more frequent during vole lows than before. The significant increase in predation on stone martens by red foxes during that period supports this hypothesis (Meyer unpubl.) and could explain the decreasing population trend observed in stone martens. In this respect, Lindström et al. (1995) also suggest that red fox might limit pine marten *Martes martes* population size through intra-guild predation.

Water voles made up to 40% of relative volume of food ingested by badgers when water voles were in high

densities (Weber and Aubry 1994). However, unlike other predators, badger numbers remained stable during the study, with their densities never exceeding 1 individual km^{-2} (Ferrari 1997). Prey switching to earthworms *Lumbricus* sp., a permanently available and abundant alternative prey for badgers, likely prevented the decline of these predators with changes in water vole numbers. On the other hand, extrinsic factors such as altitude and climate could have limited a potential population growth of badgers in response to increasing water vole densities (Ferrari 1997).

In this paper, we have documented the population changes of several predators in relation to water vole fluctuations. All predators but one exhibited marked variations in their numbers, and in two of them the population changes were not related to water vole fluctuations. Multi-factorial approach is clearly required to understand population processes in predator-prey systems. In this regard, our long-term monitoring suggests that factors such as disease, alternative prey availability or intra-guild predation could be of first importance in the dynamics of these systems, and consequently they should be taken into account in forthcoming predator-prey models.

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