

Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis

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Abstract The alternative prey hypothesis (APH) states that when the density of the main prey declines, generalist predators switch to alternative prey and vice versa, meaning that predation pressure on the alternative prey should be negatively correlated with the density of the main prey. We tested the APH in a system comprising one generalist predator (pine marten, *Martes martes*), cyclic main prey (microtine voles, *Microtus agrestis* and *Myodes glareolus*) and alternative prey (cavity nests of common goldeneye, *Bucephala clangula*); pine marten is an important predator of both voles and common goldeneye nests. Specifically, we studied whether annual predation rate of real common goldeneye nests and experimental nests is negatively associated with fluctuation in the density of voles in four study areas in southern Finland in 2000–2011. Both vole density and nest predation rate varied considerably between years in all study areas. However, we did not find support for the hypothesis that vole dynamics indirectly affects predation rate of cavity nests in the way predicted by the APH. On

the contrary, the probability of predation increased with vole spring abundance for both real and experimental nests. Furthermore, a crash in vole abundance from previous autumn to spring did not increase the probability of predation of real nests, although it increased that of experimental nests. We suggest that learned predation by pine marten individuals, coupled with efficient search image for cavities, overrides possible indirect positive effects of high vole density on the alternative prey in our study system.

Keywords *Bucephala clangula* · *Martes martes* · Nest predation · Search image · Vole cycles

Introduction

When predators are faced with changes in the density of their prey, they may respond either numerically or functionally, both of which have fundamental consequences to the dynamics of coexisting prey populations (e.g., Holt and Lawton 1994). Generalist predators, by definition, use many prey and therefore are usually expected to respond functionally to changes in prey density (e.g., Turchin and Hanski 1997). If the density of their main prey declines, generalist predators can switch to alternative prey. This type of functional response is the core of the alternative prey hypothesis (APH, sensu Angelstam et al. 1984; see also Lack 1954), whereby a switch in diet when the preferred prey population declines results in the increase in predation pressure on alternative prey. While the APH was originally formulated to explain cyclic population dynamics of alternative prey and synchronism of population dynamics between main and alternative prey (Angelstam et al. 1985), it has linkages to predator responses to prey dynamics and predator–prey interactions in resource

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pulse-driven systems in general (see Schmidt and Ostfeld 2008). In both cyclic and non-cyclic systems, the principal mechanism linking prey population dynamics to resource pulses is through the effects of prey-switching predators on reproduction and survival of alternative prey.

Studying changes in avian nest (alternative prey) predation rate in relation to changes in the abundance of the primary prey provides one of the most direct tests to assess the mechanisms underlying the APH. This has been done in a number of studies, and a general conclusion is that peaks of primary prey decrease nest predation rate (reviews in Schmidt and Ostfeld 2008; Ježková et al. 2014). However, the universal applicability of the APH to explain patterns in nest predation rate has been challenged due to nonrandom geographical distribution of studies testing the APH (Ježková et al. 2014); most of the studies come from northern latitudes where food webs are simple and prey population cyclicity is strong. Interestingly, two recent studies testing the APH with data from temperate Europe reached contradicting conclusions. While Ježková et al. (2014) did not find support for the APH in a study based on artificial ground nests of birds, Zárbybnická et al. (2015) did find support for the APH in a cavity-nesting owl. This comparison actually reveals another bias in the testing of the APH. While the APH has been extensively tested in ground-nesting birds, studies testing the APH in hole-nesting birds are very few (see reviews in Schmidt and Ostfeld 2008; Ježková et al. 2014). This is surprising, considering that one of the first studies demonstrating the association between nest predation rate and vole abundance was done with hole-nesting tits (Dunn 1977). Because the idea of prey switching by predators is central in explaining indirect food web interactions and consequent population dynamics (Holt and Lawton 1994; Van Leeuwen et al. 2007; Barraquand et al. 2015), it is essential that the APH is scrutinized in a wide range of vole cyclicity regimes and predator and prey community compositions. Moreover, considering recent findings that population cycles of voles have dampened over large areas in Fennoscandia and Europe (Hörnfeldt et al. 2005; Ims et al. 2008; Cornulier et al. 2013), probably bringing about deleterious effects on predators and cascading impacts on trophic webs across ecosystems (Ims et al. 2008; Cornulier et al. 2013), addressing the basic prey-switching prediction is valuable for conservation.

Voies are important prey of several generalist predators in temperate and boreal regions of the eastern hemisphere. Their population dynamics are characterized by strong cyclicity (e.g., Stenseth 1999; Zub et al. 2012; Korpela et al. 2013), providing a drastically varying food source for predators. The pine marten (*Martes martes*) is a long-lived forest-dwelling generalist predator, voies being its important prey (Helldin 1999, 2000; Lanszki et al. 2007; Zhou et al. 2011; Caryl et al. 2012). The consumption of voies by

pine martens is correlated with vole density, switching to alternative prey taking place in the absence of voies (Pulliainen and Ollinmäki 1996; Helldin 1999; Lanszki et al. 2007). For example, Helldin (1999) found that the proportion of bank voies (*Myodes glareolus*) in scats of pine marten varied from 0 to 30 % and that of field voies (*Microtus agrestis*) from 1 to 15 %, the variation following inter-annual changes in the density of these species (i.e., vole cycles), more clearly so for bank voies than for field voies. Pulliainen and Ollinmäki (1996) in turn reported that the occurrence of *Myodes* voies in the scats of pine marten in December–March varied from 12 to 61 % and correlated with inter-annual variation in the density of this prey. There is also evidence that pine martens increase the consumption of alternative prey such as bird eggs, red squirrels (*Sciurus vulgaris*), cervid carcasses and hares (*Lepus* spp.) at low vole density (Pulliainen and Ollinmäki 1996; Helldin 1999). The pine marten is also the main predator of common goldeneye (*Bucephala clangula*) clutches in boreal areas (Dow and Fredga 1983; Pöysä et al. 1997), and predation rate of common goldeneye nests varies much between years (Fredga and Dow 1984; Pöysä 1999). The pine marten and common goldeneye use cavities excavated by black woodpeckers and nest boxes provided by man, the former species mainly for resting and denning but sometimes also for breeding (Brainerd et al. 1995), the latter species solely for breeding. This simple predator-two prey system (one generalist predator-cyclic main prey-cavity nests) provides an excellent opportunity to test the APH.

Here we use long-term observational and experimental data from four study areas in southern Finland to test the APH. To that end, we monitored inter-annual variation in the abundance of voies (bank vole and field vole) and predation of real common goldeneye nests and experimental nests by pine martens in 2000–2011. We test the fundamental prey-switching prediction of the APH (Angelstam et al. 1984); assuming that vole population dynamics modify nest success of common goldeneye through pine marten predation, we predicted that nest predation rate should follow changes in the abundance of voies, being lowest in vole peak years and highest in vole trough years.

Materials and methods

Study areas

This study was carried out in four areas in southern Finland: Lammi (61°10'N, 25°05'E), Padasjoki (61°19'N, 25°06'E), Mäntyharju (61°22'N, 26°58'E) and Parikkala (61°35'N, 29°40'E). The study areas are dominated by Scots pine *Pinus sylvestris* or mixed (pine, birch *Betula* spp. and spruce *Picea abies*) forests interspersed with lakes

of varying size. In Lammi, Padasjoki and Parikkala nest boxes have been available for common goldeneyes and nest success and various other aspects of the breeding ecology of the species in the boxes have been studied since early 1990s (e.g., Pöysä et al. 1997; Pöysä and Pöysä 2002; Paasivaara and Pöysä 2008). In Mäntyharju 30 new nest boxes (2 boxes per each of 15 small lakes) were provided for common goldeneyes in autumn 1999 and nest success in the boxes has been followed since the breeding season 2000. The nest boxes were within an area of 8.4 (south–north) \times 11.3 (west–east) km in Lammi, 6.6 \times 5.6 km in Padasjoki, 3.4 \times 2.4 km in Mäntyharju and 11.8 \times 6.8 km in Parikkala.

Data

Data for this study were gathered in 2000–2011. All nesting attempts by the common goldeneye in the nest boxes in each study area and year were followed and their fate (depredated or not depredated) recorded. A nest was defined depredated if one or more eggs were missing or eaten in the nest and the nest was abandoned (usually all eggs were missing). The pine marten was the main predator of the nests in all study areas (Pöysä et al. 1997; H. Pöysä unpubl. data), occasional nest predators being the great spotted woodpecker (*Dendrocopos major*), jay (*Garulus glandarius*) and American mink (*Neovision vision*). Pöysä et al. (1997) reported that the proportion of nests preyed upon by pine marten was 70–86 % in a study done with dummy nests in three of the four study areas of the current study. Identification of the predator species was based on markings in the egg and nest box: hairs at the entrance hole and markings of claws meant pine marten; if the broken egg was in the nest (not common), it usually had markings of bill, meaning predation by bird. The proportion of nests preyed upon by pine marten is even higher for real common goldeneye nests (H. Pöysä, unpubl. data). Identification of nest predation events by the pine marten is relatively easy. Pine martens usually remove all the eggs, hoarding most of them for later use, and there are no broken eggs near the nest box. If the nest is depredated during incubation, there is always some down at the entrance hole, outside the nest box, at tree trunk and on the ground. Similarly, Nilsson et al. (1991) reported a high nest predation rate (82 %) of black woodpecker (*Dryocopus martius*) nests and mention that hair of pine martens were found at the entrance hole in nearly all cases of predation. The number of nesting attempts per year varied both within and between the study areas (Lammi 20–37; Padasjoki 2–17; Mäntyharju 1–6; Parikkala 23–40). For the analyses of nest predation rate of real common goldeneye nests, we included only areas and years with at least ten nesting attempts per year.

Later in the breeding season, after most of the ducklings had hatched and left the nest boxes in late June–early July, a nest predation experiment was established in the nest boxes each year in 2000–2011. Same nest boxes were used in the experiment each year (Lammi 52 nest boxes; Padasjoki 48 nest boxes; Mäntyharju 30 nest boxes; Parikkala 34 nest boxes). The experimental protocol followed that in Pöysä et al. (1997) and Elmberg and Pöysä (2011). In brief, each experimental nest was initiated by placing one unfertilized chicken egg in the nest box. To mimic the smell and appearance of natural nests, a small tuft of fresh common goldeneye down gathered from natural nests was attached to the lower edge of the entrance hole (occupied nest boxes and natural cavities usually have some down at the entrance hole). Twenty-one days after initiation, the experimental nests were checked for their fate (depredated or not depredated; a nest was classified depredated if the egg was missing or eaten in the nest).

The abundance of small mammals was measured by trapping in late spring (late May/early June) and early autumn (late August/early September) each year in 2000–2011 (no trapping in spring 2000 in Padasjoki and in autumns 2000 and 2001 in Mäntyharju). Ten 10 \times 10 m² with three snap traps in each corner were scattered within the study area; trapping was done over three consecutive nights (i.e., 360 trap nights in all) in both periods in all study areas. This is a standard trapping method used in Finland for monitoring vole populations (e.g., Huitu et al. 2009). Vole abundance indices were calculated from pooled numbers of field vole and bank vole and are given as the number of voles per 100 trap nights. These two species made up the vast majority of the total catch in all study areas (range 91–95 %), and are the most important vole species characterizing the cyclic vole dynamics in Finland (e.g., Hanski et al. 2001; Korpela et al. 2013; Sundell et al. 2013). Other prey species captured in the snap traps more or less frequently include common shrew (*Sorex araneus*) (1–6 % of total catch), yellow-necked field mouse (*Apodemus flavicollis*) (0–2 %) and striped field mouse (*Apodemus agrarius*) (0–2 %). The percentage of field voles and bank voles of all captured small mammals was high in all years irrespective of the phase of vole cycle. For example, in trapping periods (spring or autumn) when vole density was >15 voles/100 trap nights (see Fig. 1), the proportion of all captures for these species was 88–100 % (mean 95 %, $n = 13$ trapping periods), while in trapping periods when vole density was <5 voles/100 trap nights the corresponding proportion was 71–100 % (mean 94 %, $n = 47$ trapping periods).

As part of a long-term predator removal experiment, intensive removal of pine martens was started in Lammi in autumn 1998 (see Elmberg and Pöysä 2011). At the same time only limited hunting of pine marten has taken place in the other study areas. Results from this experiment will be

reported elsewhere but we briefly discuss possible effects of the pine marten removal on the hypothesized association between vole abundance and nest predation rate (see “Discussion”).

Statistical analyses

Real common goldeneye nests and experimental nests were analysed separately. ‘Nest fate’ (0 = nest not depredated; 1 = nest depredated) was used as response variable in the analyses (see Lewis 2004). We used two input variables describing different aspects of vole abundance dynamics. Spring vole index (‘Vole spring’) describes the overall abundance of voles during the nest phase of common goldeneyes. However, this index may not be sensitive enough to describe crashes in vole abundance that usually occur during the winter, just before the nesting season (see Fig. 1). To take an example, in Lammi, Padasjoki and Mäntyharju the spring vole index was at bottom in both 2006 and 2007; however, spring 2006 was preceded by a vole peak (i.e., a strong vole crash during the winter) while spring 2007 was preceded by a vole trough (i.e., no vole crash during the winter). Food conditions in the previous autumn and winter may affect pine marten survival, particularly that of juveniles (high in winter after a

vole peak, low in winter after a vole trough; see “Discussion”). Hence, irrespective of vole density in the spring, nest predation pressure may be relatively high after a peak in the previous autumn. Therefore, to capture the crash aspect, we calculated the difference in vole abundance index between autumn $t - 1$ and spring t (‘Vole crash’). It should be noted that ‘Vole crash’ was strongly correlated with vole abundance in the previous autumn (‘Vole crash’ vs. vole abundance index in autumn $t - 1$, $r = 0.907$, $p < 0.001$, $n = 42$ -year study area cases; correlation based on data standardized within study areas) but not with ‘Vole spring’ (‘Vole spring’ vs. ‘Vole crash’, $r = -0.028$, $p = 0.858$, $n = 42$); the correlation between ‘Vole spring’ and vole abundance index in the previous autumn was also weak ($r = 0.265$, $p = 0.090$, $n = 42$). In addition, because the nest predation experiments were run just after the nest phase in summer (see above), and vole abundance usually starts to increase in early summer, we ran for the experimental nests also a model in which ‘Vole spring’ was replaced with the mean of the spring t and autumn t vole indices (‘Vole spring–autumn mean’). We used standardized values of the input variables in the analyses to facilitate the comparison and interpretation of input variables between models and areas (Schielzeth 2010). Final data comprised 732 real nests for which information on all the

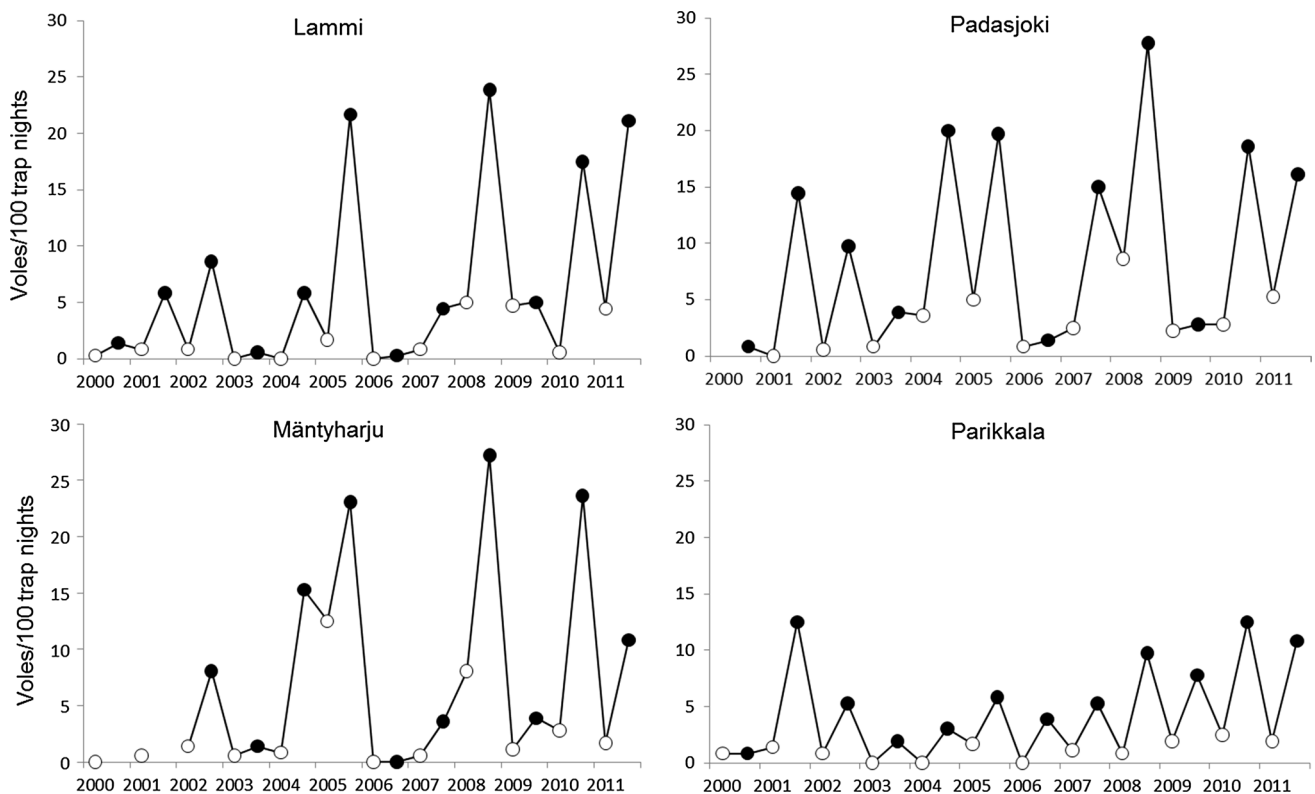


Fig. 1 Vole population density time series in four study areas in 2000–2011. *Open circles* depict spring densities and *black circles* autumn densities. Vole trapping was not done in spring 2000 in Padasjoki and in autumns 2000 and 2001 in Mäntyharju

input variables was available, the corresponding sample size for the experimental data being 1741 nests.

We used program R 2.12.2. (R Development Core Team 2011) and generalized linear mixed models (GLMM, lmer function) with logit link function to study the effect of vole abundance on nest predation. ‘Nest fate’ (real common goldeneye nests or experimental nests) was included as the response variable and standardized ‘Vole spring’ (or ‘Vole spring–autumn mean’, see above for experimental nests) and ‘Vole crash’ as predictors. Because the input variables were not strongly correlated (for ‘Vole spring’ vs. ‘Vole crash’ see above; ‘Vole spring–autumn mean’ vs. ‘Vole crash’, $r = -0.316$, $p = 0.042$, $n = 42$), the two input variables, as appropriate, were included in the same model. ‘Year’ was included as a random factor and ‘Area’/‘Lake’/‘Nest’ as a hierarchical nested random factor, i.e., ‘Nest’ nested within ‘Lake’ and ‘Lake’ within ‘Area’ in all the models testing the APH. In addition, we ran GLMMs to produce effects separately for each study area. In these models ‘Year’ was again included as a random factor and ‘Lake’/‘Nest’ as a nested random factor. Hierarchical nested random factor structure was used to take into account that nest predation in common goldeneyes often is spatially clumped (i.e., neighboring nests have same fate; Dow and Fredga 1983; Pöysä 1999) and lakes may differ considerably in terms of nest predation risk (Pöysä 2003).

Results

Several peak and crash years occurred in the vole abundance time series from Lammi, Padasjoki and Mäntyharju, while in Parikkala the variability was less pronounced (Fig. 1). The amplitude of vole population oscillations (measured by the standard deviation of log-transformed autumn vole abundance; also called ‘cyclic index’, e.g., Hansson and Henttonen 1985) in Lammi (0.634), Padasjoki (0.507) and Mäntyharju (0.492) was similar to that of cyclic field vole and bank vole populations in Fennoscandia, while the corresponding index for Parikkala (0.355) was closer to the ‘non-cyclic’ end of the cyclic gradient characterized by these species (see Hansson and Henttonen 1985; see also Hanski et al. 2001).

Population-level predation rate of both real common goldeneye nests and experimental nests varied considerably in all study areas (Fig. 2). The probability that a nest was depredated increased with vole spring abundance (‘Vole spring’) for both nest types (Table 1; Fig. 3). Replacing ‘Vole spring’ with ‘Vole spring–autumn mean’ for the experimental nests (see “Materials and methods”) did not change the result (Table 1; Fig. 3). The probability that a nest was depredated did not increase with the magnitude of the crash in vole abundance from autumn $t - 1$ to spring t

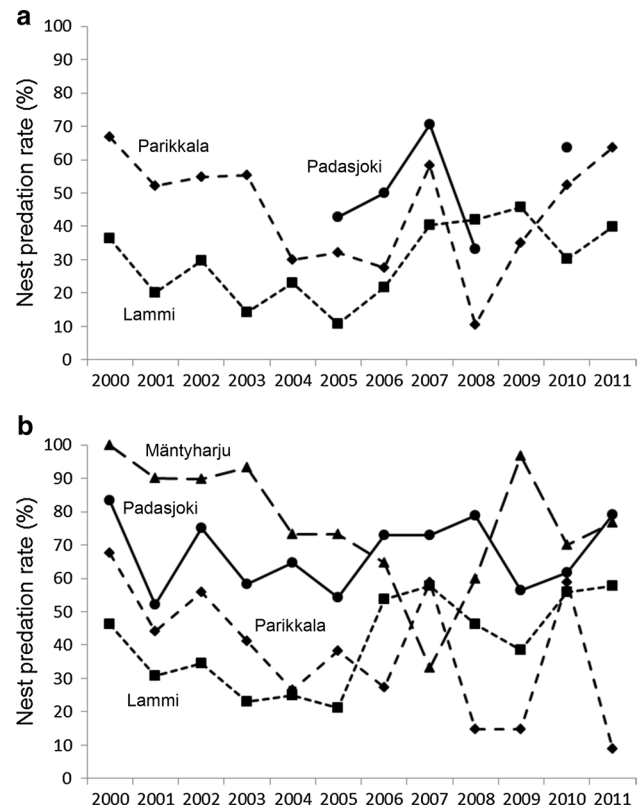


Fig. 2 Nest predation rate (%) of **a** common goldeneye nests and **b** experimental nests in four study areas in 2000–2011. Nest predation rate of common goldeneye nests are given only for study areas and years with at least ten nesting attempts per year

(‘Vole crash’) for the real nests but increased for the experimental nests (Table 1; Fig. 3).

Discussion

We tested the fundamental prediction of the APH in a simple one predator-cyclic voles-alternative prey system, viz. predation rate of common goldeneye nests (alternative prey) should be negatively associated with vole abundance. Our data failed to provide support for the prediction; on the contrary, the probability that a nest was depredated increased, not decreased, with vole abundance in the spring for both real and experimental nests. Moreover, the probability of predation of real nests did not increase with a crash in vole abundance, also a result contradicting the APH. On the other hand, a crash in vole abundance increased the probability of predation of the experimental nests, a finding seemingly contradicting that from real nests and supporting the APH (but see below). To our best knowledge, we had the longest time series from both real and experimental nests used so far to test the prediction. Furthermore, considering that our long-term data are from four study areas

Table 1 Generalized linear mixed models for testing the effect of vole abundance on the occurrence of predation (in year t) in real common goldeneye nests and in experimental nests

| | Effect | Estimate | SE | z | p |
|-----------------------|-------------------------|----------|-------|--------|--------|
| Real nests | Intercept | -0.375 | 0.265 | -1.347 | 0.178 |
| | Vole spring | 0.453 | 0.132 | 3.482 | <0.001 |
| | Vole crash | 0.043 | 0.129 | 0.332 | 0.740 |
| Experimental nests I | Intercept | 0.211 | 0.386 | 0.547 | 0.584 |
| | Vole spring | 0.391 | 0.088 | 4.436 | <0.001 |
| | Vole crash | 0.501 | 0.107 | 4.682 | <0.001 |
| Experimental nests II | Intercept | 0.216 | 0.373 | 0.580 | 0.562 |
| | Vole spring–autumn mean | 0.563 | 0.118 | 4.780 | <0.001 |
| | Vole crash | 0.664 | 0.119 | 5.588 | <0.001 |

‘Vole spring’ = vole abundance index in spring t ; ‘Vole crash’ = difference in vole abundance indices between autumn $t - 1$ and spring t ; ‘Vole spring–autumn mean’ = average of the vole abundance indices in spring t and autumn t . Two different models including either ‘Vole spring’ (Experimental nests I) or ‘Vole spring–autumn mean’ (Experimental nests II) were run for experimental nests. ‘Year’ was included as a random factor and ‘Area’/‘Lake’/‘Nest’ as a hierarchical nested random factor in all models. Total sample sizes are $n = 732$ for real nests and $n = 1741$ for experimental nests. For further details, see “[Materials and methods](#)”

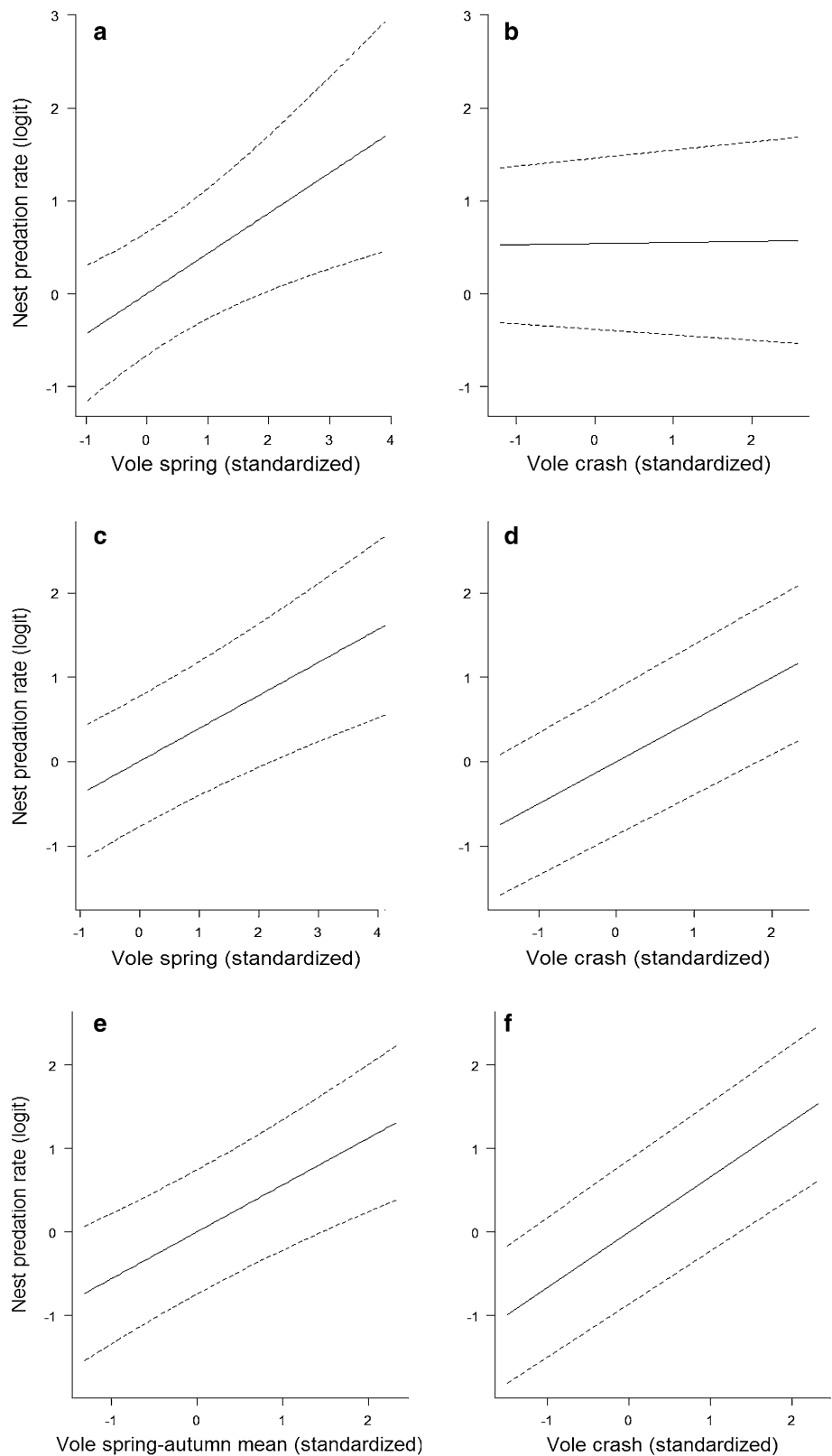
differing in relative vole abundance and cyclicity, and comprise several vole peak and crash years in the areas where cyclicity prevailed, we should have been able to find support for the APH had there been any.

The strong and consistent positive association between the probability of nest predation and vole spring abundance suggests that, rather than having a positive effect, an increase of vole abundance has a negative impact on alternative prey in our study system. This finding is consistent with the idea that one species (voles) negatively affects another species (cavity-nesting common goldeneye) through the action of a shared predator (pine marten), also called apparent competition (Holt 1977; Holt and Lawton 1994; Barraquand et al. 2015). This type of negative interaction between species has been documented in the context of nest predation in shrub-nesting song birds in North America (Schmidt and Whelan 1998). Interestingly, Brook et al. (2008) found in the Prairie Pothole Region of Canada that, at low vole densities, duck nests were buffered from predation by voles but, as vole densities increased further, nest predation rate increased. The authors suggested that this latter response was due to multipredator response, as numerous predators may have responded simultaneously to the higher rodent densities.

We do not know the variation of pine marten abundance in our study areas and whether the variation is associated with vole abundance. Zalewski and Jędrzejewski (2006) found in Białowieża Primeval Forest in eastern Europe that pine marten density in winter was positively correlated with the abundance of small rodents (bank vole and yellow-necked mouse combined) in the previous autumn. Korpela et al. (2014) found in southern Finland that the pooled winter density of generalist predators red fox (*Vulpes vulpes*) and pine marten responded

positively to the density of voles (*Myodes* and *Microtus* species combined) in the previous autumn. Helldin (1999) in turn found in south-central Sweden that juvenile pine martens are affected negatively by vole scarcity in terms of lower body condition, growth and possibly survival as suggested by the author. Hence, high vole density in the autumn may enhance winter survival of juvenile pine martens, meaning more successful recruitment and higher pine marten density in the spring. In the light of these observations, and taking into account the fact that the magnitude of ‘Vole crash’ was strongly correlated with the abundance of voles in the previous autumn (i.e., a drastic decrease in vole numbers from autumn $t - 1$ to spring t indicated high vole autumn abundance, see “[Materials and methods](#)”), it is possible that pine marten density in ‘Vole crash’ springs was high, increasing overall nest predation risk. This type of numerical response, rather than a switch in diet, may explain the positive association between vole crash and the probability of predation of the experimental nests. This interpretation is supported by the following analysis. When we compared, using an information theoretic approach and Akaike’s information criterion (AIC, see Burnham and Anderson 2002), the performance of ‘Vole crash’ and vole abundance in the previous autumn in explaining the probability of predation of the experimental nests, the latter variable clearly outperformed the former: a model including only vole abundance in the previous autumn had $AIC = 2070.9$ (effect size for vole abundance in the previous autumn, $\beta = 0.539$, $SE = 0.138$), while a model including only ‘Vole crash’ had $AIC = 2081.3$ (effect size for ‘Vole crash’, $\beta = 0.312$, $SE = 0.136$); i.e., the difference in the AIC values was 10.4 in favor of the model including only vole abundance in the previous autumn, indicating a clearly more competitive model (see

Fig. 3 The probability of nest predation in relation to vole abundance in the spring or spring–autumn mean (*left column*) and in relation to vole crash (*right column*) for **a, b** real nests and **c–f** experimental nests. Test statistics for the associations are given in Table 1; associations in **a** and **b** correspond to ‘Real nests’ in Table 1, associations in **c** and **d** to ‘Experimental nests I’ and associations in **e** and **f** to ‘Experimental nests II’ (for further details, see “Materials and methods”). *Lines* indicate model predictions for the association as derived from the GLMMs used in data analysis, and *dashed lines* indicate 95 % confidence error bands. Note logit scale of y-axes; vole variables (x-axes) are standardized



Burnham and Anderson 2002). Furthermore, we consider it unlikely that the suggested numerical response could be due to the predator’s aggregative behavior, because pine

martens have fixed home ranges and seem not to respond to changes in resource availability by adjusting their foraging area (Zalewski and Jędrzejewski 2006).

The seeming discrepancy between real nests and experimental nests in the response to ‘Vole crash’ (found for the latter but not for the former) could be explained by the development of foraging skills and search image in juvenile pine martens, and differences between real and experimental nests in timing, density and distribution. As we discuss in more detail below, learning and search image probably play important roles in pine marten foraging. In juveniles, learning the search tactic for cavity nests most probably takes place gradually in the first spring, i.e., when nests of common goldeneye and other cavity-nesting species are available. At the time of the nest predation experiments (in late June–early July, after the nesting phase of common goldeneyes; see “Materials and methods”; Pöysä et al. 1997), recruited juvenile pine martens probably were more experienced in finding common goldeneye nest boxes; probably they also had learned the location of the nest boxes. In addition, the density of experimental nests was higher than that of real nests in all study areas and years, possibly enhancing nest encounter rate and learning. We suggest that this type learning process of juvenile recruits could explain why the association between ‘Vole crash’ and nest depredation was significant for experimental nests but not for real nests.

Our results provide an interesting comparison with the recent findings by Zárbynická et al. (2015) from temperate Europe. These authors similarly hypothesized that the probability of Tengmalm’s owl (*Aegolius funereus*) nest predation by pine marten should decrease with increasing abundance of the primary prey of pine martens, *Microtus* and *Myodes* voles and *Apodemus* mice in their study area. The Tengmalm’s owl uses similar nest cavities and nest boxes than the common goldeneye. Zárbynická et al. (2015) found that the probability of nest predation was affected by the abundance of *Apodemus* mice, estimated by snap-trapping at the beginning of June, but not by the abundance of *Microtus* and *Myodes* voles. The authors suggested that the difference between the prey species was because *Apodemus* mice are more numerous and more important in the diet of pine marten than are *Microtus* and *Myodes* voles. Their study system differs from our in several ways. First, *Microtus* and *Myodes* voles are the most numerous small mammals in our study areas (see “Materials and methods”) and also elsewhere in Fennoscandia and, as already mentioned, exhibit strong cyclicality (e.g., Hansson and Henttonen 1985; Sundell et al. 2013; Korpela et al. 2014), while *Apodemus* mice occur only in very low numbers. Nevertheless, we were not able to find support for the APH, neither with data on vole spring abundance nor with data on vole spring–autumn mean. In line with our results, neither did Sonerud (1985) find that predation rate of Tengmalm’s owl nests would be lower in vole peak years; in fact the opposite seemed to be true. Sonerud (1985) did not specifically

address the APH but studied the role of nest predation risk in nest hole shift in Tengmalm’s owl. Second, like pine martens, Tengmalm’s owls feed on voles and mice, so the pine marten–rodents–Tengmalm’s owl interaction probably is more complex than the predator–prey interactions in our study system. For example, Sonerud (1985) pointed out that a positive correlation between vole abundance and Tengmalm’s owl breeding density may have affected temporal and spatial patterns of Tengmalm’s owl nest predation by pine martens. Finally, Zárbynická et al. (2015) suggested that pine martens foraged for Tengmalm’s owl nests at random, whereas our comparison of predation rates between experimental ground nests and cavity nests has suggested that cavity-nest predation by pine martens is learned rather than incidental (Elmberg and Pöysä 2011). Similarly, our results from studies addressing the role of nest predation risk in the occurrence of conspecific nest parasitism in the common goldeneye indicate that predation of cavity nests by pine martens is not random, i.e., a given nest site has same fate (depredated or not) in successive years and also neighboring nest sites have same fate (Pöysä 1999, 2003, 2006). In line with our findings, Sonerud (1985) concluded that pine martens did not encounter Tengmalm’s owl nest boxes randomly, but revisited those that they had found previously. Furthermore, in a nest box relocation experiment, Sorace et al. (2004) found support for the idea that learning plays an important role in pine marten predation upon nest boxes. Given these findings and the facts that pine martens are long-lived, have high fidelity to fixed home ranges and frequently reuse cavities as resting sites within their home ranges (Zalewski 1997; Zalewski and Jędrzejewski 2006), it is probable that memory and search image for cavities play an important role in nest predation behavior of the species. Learned predation, coupled with efficient search image for cavities, probably overrides possible indirect effects of cyclic main prey on the alternative prey; in other words, cavities learned by individual pine martens may be preyed upon anyway whatever the abundance of the main prey.

Interestingly, in accordance with our results, Ježková et al. (2014) did not find support for the APH in a study done with artificial bird ground nests. That study, like Zárbynická et al. (2015), was done in temperate Europe (Czech Republic) and *Apodemus* mice were the most numerous main prey. However, there was a difference in the predator communities between the studies: while the pine marten was the sole predator of the Tengmalm’s owl nests in Zárbynická et al. (2015), several predator species were identified for the artificial ground nests in Ježková et al. (2014), including wild boar (*Sus scrofa*), small mustelids (*Mustela* spp.), red fox (*Vulpes vulpes*) and birds. Indeed, Ježková et al. (2014) suggested that the high diversity of the predator and alternative prey communities probably

was one reason why the APH did not work in their system. On the other hand, Ackerman (2002) found in California, USA, that nest success of ground-nesting mallards (*Anas platyrhynchos*) was positively correlated with rodent abundance in a system comprising several potential predator species. Still another recent study from Europe, done with dummy ground nests in low-Arctic tundra of northeast Norway, found that nest predation rate increased in the crash phase of lemmings (*Lemmus lemmus*) but was not affected by changes in the abundance of voles (*Myodes rufocanus* and *Microtus oeconomus*) (Ims et al. 2013). Corvids were the most important egg predators of the ground nests, and the authors speculated that corvids also are efficient predators of lemmings. Similarly, McKinnon et al. (2014) found in the eastern Canadian High Arctic that predation rate of shorebird nests (both real and artificial nests studied) was associated with lemming abundance, the arctic fox (*Alopex lagopus*) being the main egg predator. These authors also speculated about the incidental vs. search image-based nest predation in their study system. Indeed, predator learning, rather than incidental predation, may be a common feature also in predators of ground nests (e.g., Pelech et al. 2010), and a recent modeling work suggests that predator foraging behavior is an important driver of nest success and dispersal in ground-nesting birds (Ringelman 2014). Taken together, our results from a cavity-nest predator and those by McKinnon et al. (2014) from ground-nest predators suggest that the mechanism how predators find nests is a critical component also in the context of APH and needs more attention in future studies.

Pine marten removal experiment was simultaneously run in one of the study areas (Lammi; see “Materials and methods”). One might, thus, expect that, assuming the role of voles in modifying predation on alternative prey diminishes under reduced predation pressure (a corollary of the APH; see Marcström et al. 1989), the association between nest predation rate and vole abundance should be weaker in the area where pine martens were removed. This expectation is analogous to that by Marcström et al. (1989; see also Marcström et al. 1988) who studied demographic responses of arctic hares (*Lepus timidus*) to experimental removal of foxes (*Vulpes vulpes*) and pine martens from one island in the Gulf of Bothnia. These authors predicted that annual survival of hares should decrease during vole population lows (i.e., the basic prediction of the APH), but the decrease should be less on the island where foxes and pine martens were reduced (see Marcström et al. 1989). In our study, the inclusion of ‘Area’ as a random factor in the models took into account possible differences between the areas. Nevertheless, standardized effect sizes of the vole parameters from Lammi did not differ in a consistent way from the other areas (see Online Resource 1). Moreover, despite pine marten removal, nest predation rate varied

considerably also in Lammi (see Fig. 2). We thus conclude that the removal of pine martens in Lammi did not affect the results. Nor did this additional comparison provide support for the corollary prediction of the APH sensu Marcström et al. (1989).

Testing the APH with observational data may result in spurious findings if, for example, inter-annual variation in nest density and vole density are driven by same factors. Hypotheses about drivers of the multiannual population cycles of voles and other small mammals are debated, especially the role of specialist predators such as the least weasel (*Mustela nivalis*) and the stoat (*Mustela ermine*) in generating the cycles (e.g., Graham and Lambin 2002; Oli 2003; Korpimäki et al. 2003, 2005). Current knowledge suggests that small mustelid predation may be the key cycle generating mechanism (Korpela et al. 2014) but that various population-intrinsic factors may also affect cycles, probably in interaction with external factors such as predation and winter food (Andreassen et al. 2013). Anyhow, we do not think that the drivers that have been recognized important for vole population cycles will directly affect annual nest density of the common goldeneyes, a migratory duck.

Our vole time series provide additional information concerning the recent concerns about the disappearance of vole cycles in Fennoscandia and Europe (e.g., Ims et al. 2008; Brommer et al. 2010; Cornulier et al. 2013). A visual inspection revealed that the variation in vole abundance was rather similar in Lammi, Padaşjoki and Mäntyharju, also resembling the current cyclicity pattern documented by Brommer et al. (2010) for bank voles and field voles in two study areas in southern Finland. For example, 2005 and 2008 were clear peak years in our study areas and in the two study areas of Brommer et al. (2010) and relatively high vole numbers prevailed also in 2001 and 2002 in all the five areas. Hence, our results and those of Brommer et al. (2010) and Korpela et al. (2013) together demonstrate that cyclicity again characterizes vole population dynamics in large parts of Finland. Parikkala (SE Finland) seems to be an exception to this general pattern but it fits in the irregular low-amplitude vole dynamics found to be prevailing in eastern Finland (see Korpela et al. 2013).

In conclusion, we did not find support for the hypothesis that vole dynamics indirectly and positively affects the success of cavity nests in the common goldeneye. In fact, the interaction appeared to be negative, as nest predation rate increased with vole abundance. Evidence in support of the APH in the context of nest predation is accumulating for the Arctic, while the evidence is less strong for more southern areas (this study and Jeřková et al. 2014). In addition to this geographical discrepancy, testing the APH has focused on ground-nesting species and their predators while almost nothing is known about the prevalence of the

APH in cavity-nesting species and their predators. Clearly, more work from southern boreal and temperate areas and from different predator-nesting guild systems are needed before the applicability of the APH is generally approved. Also the role of nest searching behavior of predators needs more attention in future studies addressing the APH.

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