

Competitors and predators alter settlement patterns and reproductive success of an intraguild prey

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Abstract. The spatial distribution of predators is affected by intra- and interspecific interactions within the predator guild. Studying these interactions under fluctuating food availability, while taking habitat characteristics into account, offers a quasi-experimental setup to determine the relative impact of con- and heterospecifics on reproductive success of predators. We analyzed the settlement decisions and reproductive success of Eurasian Pygmy Owls (*Glaucidium passerinum*) in the presence of both breeding conspecifics and their competitor and intraguild predator, Tengmalm's Owls (*Aegolius funereus*), under fluctuating abundance of their primary prey (voles). We used detailed data, collected across 11 years in a large study area (1300 km²), on the spatial and temporal variation of habitat characteristics in all available nesting sites, local densities of both species, and vole abundance. We found that Pygmy Owls strongly avoided breeding close to conspecifics but did not avoid Tengmalm's Owl nests. Nest box occupation of Pygmy Owls was positively correlated to the proportion of old spruce, mature and old pine forests, and farmlands, and occupation probability was higher at high vole abundance and in areas occupied in previous years. Pygmy Owl avoidance of conspecifics decreased when voles were abundant. At high conspecific density, Pygmy Owls showed lower hatching success and delayed hatching date, in agreement with the observed spatial avoidance. Finally, even though breeding Pygmy Owls did not spatially avoid Tengmalm's Owls, the density of heterospecifics correlated with low hatching and fledging success in Pygmy Owls. This suggests short term fitness costs when living close to competitors, even when lethal effects of intraguild interactions are subtle. Our results suggest that joint costs of exploitative and interference competition by Tengmalm's Owls, as well as intraguild predation, were lower than those induced by intraspecific competition only. This result might be due to the similar body size between the species considered, Tengmalm's Owls being only twice as large as Pygmy Owls. Interactions among con- and heterospecifics can therefore modify the spatial settlement and reproductive success of individuals on a landscape scale, also within the predator guild.

Key words: boreal forest; Boreal Owl; density dependence; habitat selection; interspecific competition; intraguild predation; intraspecific competition; predation risk; Pygmy Owl.

INTRODUCTION

Competition and predation are fundamental biotic interactions that largely determine the densities of animals (Sih et al. 1985, Gurevitch et al. 2000). Individuals of the same or different species may compete for resources through exploitation, depriving others from using the same resources effectively (exploitative competition; Miller 1967, Charnov et al. 1976, Schoener 1983, review in Dhondt 2012). Alternatively, individuals may interfere with the foraging or use of other resources by their competitors (interference competition; Miller 1967, Schoener 1983, review in Dhondt 2012). In extreme cases of interference competition, competitors may have aggressive

encounters and even kill each other, and when these competitors are not only killed but also consumed, intraguild predation occurs (i.e., predation among competitors, IGP; Polis et al. 1989, Polis and Holt 1992; review in Lourenço et al. 2014). At this level, competition and predation interactions are not mutually exclusive, but their relative importance remains unclear.

When settling to breed, animals take into account the resources available, and also the number of competitors and predators present in the area. Density-dependent habitat selection, based on ideal free distribution (Fretwell and Lucas 1969), assumes that individuals with equal competing abilities will select sites to maximize their fitness. This will result in an increment in the use of low-quality habitat when the population density increases, because of a reduction in resources available at high population density. However, when individuals differ in their competitive abilities, animals will follow an ideal despotic

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distribution (Fretwell 1972). Highly territorial dominant individuals will settle in high-quality territories, occupying the best unoccupied sites still available (ideal pre-emptive distribution; Pulliam and Danielson 1991), while less effective competitors will shift to unfavorable habitats (e.g., Ziv et al. 1993, Calsbeek and Sinervo 2002). However, the spatial distribution of animals will also depend on predator distribution and on whether the risk of mortality varies among competitors and habitat type (e.g., Grand and Dill 1999). When competitors are also potential predators, the predictions for the spatial outcome are less clear, and more empirical research is needed.

High densities of competitors and predators may both lead to demographic or individual density dependent effects, i.e., causing a decrease in fitness components such as survival (Armstrong et al. 2002) or fecundity (Ferrer and Donazar 1996, Both 1998). Small or less competitive predator species may suffer the accumulated costs of intraspecific competition together with the costs of interspecific competition and predation risk imposed by a dominant predator (Sih et al. 1985, Gurevitch et al. 2000, Cresswell 2008). These costs combined may lead to reduced parental investment and reproductive success (Hakkarainen and Korpimäki 1996, Sergio et al. 2007, Watts and Holekamp 2008, Mueller et al. 2016). The interactive effects of competition and predation on the spatial settlement and reproductive success of small predator species, however, have rarely been investigated on a large spatial scale in natural environments (but see Mueller et al. 2016). Distinguishing their relative impacts is important, as it has clear implications to lower trophic levels, since the spatial distribution of prey will strongly depend on the distribution of their predators, as well as resources.

In addition to interactions with other individuals (e.g., competitors and/or predators), also landscape characteristics can constrain the distribution and reproductive success of species. Accounting for landscape effects is needed when investigating spatial dispersion and habitat choice, since spatial aggregation or avoidance between animals could result from habitat characteristics and/or social interactions. For example, nests of little Owls (*Athene noctua*) are spatially clustered but this aggregation is solely due to habitat preferences, through the selection of nesting sites (buildings) that are spatially clustered. Conversely, the semi colonial Montagu's Harrier (*Circus pygargus*) displays spatial clustering due to conspecific attraction (Cornulier and Bretagnolle 2006), even when habitat preferences have been accounted for. Accounting for habitat characteristics, while distinguishing between the forces of both con- and heterospecific interactions in habitat choice, and subsequent reproductive investment, is challenging, but absolutely necessary to properly understand the relative contribution of the different mechanisms involved.

High amplitude fluctuations of food availability provide, in a natural setting, a quasi-experimental design to study the interactions among conspecific and heterospecific predators. Indeed, sizable temporal change in food

abundance is expected to alter the level of competition and this may allow separating the impact of intraspecific and interspecific interactions on a focal predator species, and will provide rare insight into the spatial structure of predator guilds. Previous studies extensively investigated the impact of competition and intraguild predation on predator populations according to natural multiannual fluctuations in populations of shared prey (Korpimäki and Norrdahl 1989, reviews in Krebs et al. 2001, Korpimäki and Hakkarainen 2012). However, a comprehensive investigation of the impact of habitat characteristics and natural prey fluctuations, together with competition and predation, on the habitat choice and reproductive success of wild predators is still lacking (but see Krebs et al. 2001).

We studied the spatial settlement and reproductive success of Eurasian Pygmy Owls (*Glaucidium passerinum*; hereafter Pygmy Owl) depending on intraspecific competition and interspecific interactions (competition and intraguild predation) occurring between Pygmy Owls and Tengmalm's Owls (*Aegolius funereus*; also known as boreal Owl). We used extensive data on the settlement and breeding success of the two Owl species at a large spatial scale and under fluctuating food conditions. In Finland, where this study was conducted, voles of the genera *Microtus* and *Myodes* follow 3-year high-amplitude (100 to 200-fold) population cycles (Korpimäki et al. 2005). Vole abundance is an essential factor in this study system because highly fluctuating food conditions may alter interactions between predators: intraguild predation is supposedly more intense when the abundance of the shared prey is declining or low (i.e., during the decline and low phases of the prey population cycle; Korpimäki and Norrdahl 1989, Krebs et al. 2001). Intra- and interspecific competition in this system are thus expected to be greater in years with declining and low vole abundance. Tengmalm's Owls (the intraguild predator) are also known to occasionally prey upon (kill and consume) smaller Pygmy Owls (the intraguild prey; Korpimäki and Hakkarainen 2012).

We investigated whether the selection of breeding sites by Pygmy Owls (breeding habitat selection) was affected by (1) the presence and density of a larger competitor and intraguild predator, the Tengmalm's Owl, which settles first for breeding sites, and (2) the presence of conspecific neighbors. We determined the influence and controlled for the effect of habitat characteristics and annual vole abundance. In addition, we assessed (3) whether breeding phenology, reproductive investment, and success of Pygmy Owls were detrimentally affected by the densities of Tengmalm's Owls and conspecifics. We expected that Pygmy Owls would avoid breeding in areas with high densities of their intraguild predator, the Tengmalm's Owl, and would also avoid conspecifics to reduce the costs of exploitative competition. Second, we predicted that the presence of Tengmalm's Owls and conspecifics would negatively impact the reproductive investment and success of Pygmy Owls, especially in poor food conditions. Finally, we expected a greater impact of

Tengmalm's Owl presence on Pygmy Owl settlement and breeding success compared to conspecifics, because of joint costs represented by exploitative and interference competition as well as risk of intraguild predation.

METHODS

Study area and vole population cycles

Data were collected in a 1300 km² study area of the Kauhava region, western Finland (63° N, 23° E) from 2002 to 2012. The landscape consists of commercially managed forests, mainly pine and spruce with some birch-dominated patches, interspersed with agricultural land and clear-cut areas (Hakkarainen et al. 2003, Korpimäki and Hakkarainen 2012). As a consequence of forestry practices, the proportion of old-growth forest in our study area was low (Hakkarainen et al. 2003), and thus suitable natural cavities for Pygmy and Tengmalm's Owls are scarce. In the study area, 230 forest patches (at least 1–2 km apart) were provided with two nest boxes for Pygmy Owls (see Appendix S1: Table S1, Fig. S1). Two boxes were placed 80–100 m apart in each patch because Siberian flying squirrels (*Pteromys volans*) may also use nest boxes for roosting and reproduction throughout the year and this ensured availability of the nest site to Pygmy Owls. Approximately 80 natural cavities, excavated by Great-spotted Woodpeckers (*Dendrocopos major*), are also available for breeding Pygmy Owls in the study area. In addition, 470 nest boxes and 30 natural cavities were available for Tengmalm's Owls (Korpimäki and Hakkarainen 2012). The diameter of the entrance hole of Tengmalm's Owl boxes was 80–100 mm, and that of Pygmy Owl boxes 45 mm. The two species do not compete for available cavities; Pygmy Owls do not breed in cavities with large entrance holes and Tengmalm's Owls cannot enter the cavities used by Pygmy Owls.

The density of Tengmalm's Owl nest boxes in our study area (approximately 1 nest box/2 km²) does not substantially differ from natural conditions: the density of suitable natural cavities in pristine coniferous forests of southern Finland is 0.5–1.5 cavities/km² (Virkkala et al. 1994). In addition, in coniferous forests managed for forestry in Central Sweden, the density of natural cavities made by black woodpeckers (*Dryocopus martius*), which are suitable in size also for Tengmalm's Owls, is 0.3–0.4 per km² (Johnsson et al. 1993). We are confident that the interactions found between the two Owl species are not the product of breeding in nest boxes, because we provided nest boxes in densities that are comparable to natural cavities in pristine coniferous forests in the area (e.g., Mikkola 1983). Moreover, owl populations in our study area were not constrained by the availability of nesting sites. Even in good vole years, characterized by the highest owl numbers, only 27% of Tengmalm's Owl and 10% of Pygmy Owl boxes were occupied. Nest boxes were also homogeneously distributed across the landscape (distance between available Pygmy Owl

nest-boxes [mean ± SD], 1429.04 ± 721.35 m, and between available Tengmalm's Owls boxes, 760 ± 406 m; see Appendix S1: Table S1, Fig. S1). Admittedly, nest boxes are not comparable to natural cavities in all characteristics (e.g., microclimate), and might partly affect breeding performance. In Tengmalm's Owls, for example, clutch size and breeding success is higher in nest boxes than in natural cavities (Korpimäki 1984). This is likely also true for Pygmy Owls, because nest boxes for Pygmy Owls have larger bottom area than natural cavities made by Great-spotted Woodpeckers.

All owl boxes, and known natural cavities, were inspected twice every spring (in April and again in late May to early June) to detect breeding attempts. In all nests of both owl species, clutch size, hatching date, number of chicks hatched, and number of fledglings were recorded, but, in this study, we analyzed reproductive measures of Pygmy Owls only. Despite efforts to find and inspect new natural cavities every year, we cannot completely exclude the possibility that a few Pygmy Owls or Tengmalm's Owls bred in natural cavities thus marginally increasing their density in the landscape.

Nest-boxes of Pygmy Owls were occupied for 123 breeding events. We studied settlement and reproductive investment of these Pygmy Owl nests with respect to the location of 521 Tengmalm's Owl nests (see Appendix S1: Table S1 for the sample size per year per species). Of the 123 Pygmy Owl breeding events considered, 39 nests were in increasing, 65 in decreasing, and 19 in low phases of the vole cycle. The main prey of both owl species are voles of the genera *Microtus* and *Myodes* that, in northern Europe, follow high-amplitude (50–200 fold) 3-year cycles with sequential low, increasing, and decreasing densities (Korpimäki et al. 2005). During increasing phases of the cycle (2002, 2005, 2008, and 2011), the density index of voles rapidly increased from early spring and reached high densities during late summer and autumn (from 8.6 to 25.1 voles per 100 trap nights). In decreasing phases (2003, 2006, 2009, and 2012), vole densities were relatively high in early spring but decreased during the breeding season of owls and reached low densities in late summer, when owl chicks fledged and became independent of provisioning by parents (from 5.0 to 1.2 voles per 100 trap nights). During low phases (2004, 2007, and 2010), vole densities remained low throughout the owl breeding season (0.7 voles per 100 trap nights; Korpimäki et al. 2005; see Figure 1 in Korpimäki and Hakkarainen 2012).

Biology of the species

Pygmy and Tengmalm's Owls breed in similar habitats, preferring mature spruce forests (Schönn 1980, Mikkola 1983, Korpimäki and Hakkarainen 2012), but differ in time of settlement for breeding. Tengmalm's Owl males start hooting in early February followed by nest site choice from early March to early April, after which most hooting males are mainly bachelors (Korpimäki 1991). Settlement of Pygmy Owls occurs on average two

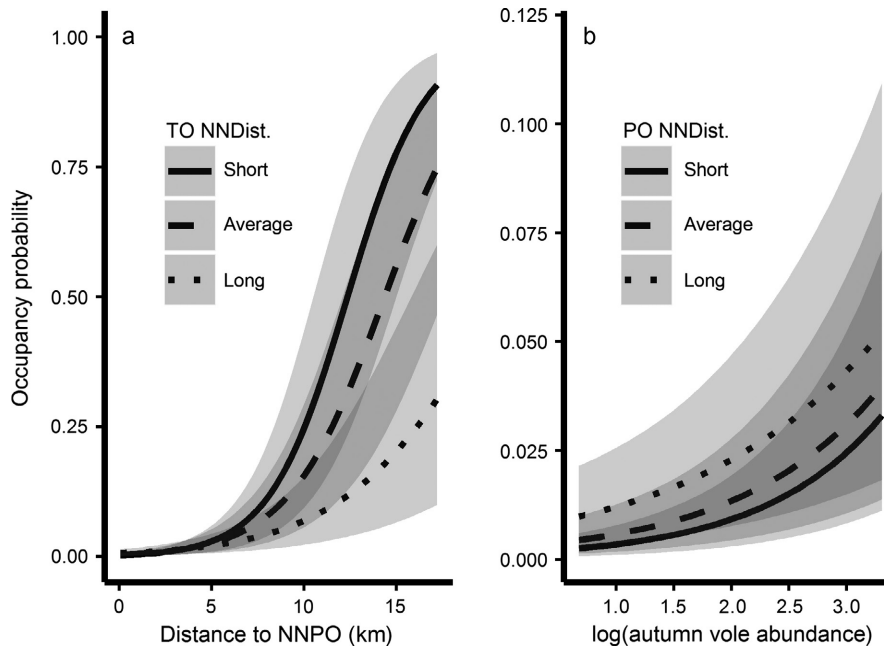


FIG. 1. (a) Probability of occupation of nest sites of Pygmy Owls in relation to the interaction between the distance to the nearest nest of Pygmy Owl (NNPO) and the nearest nest of Tengmalm's Owl (TO NNDist). (b) Probability of occupation of nest sites of Pygmy Owls in relation to the interaction between the abundance of vole species in the previous autumn and the distance to the nearest nest of Pygmy Owl (NNPO). Nearest neighbor distance to Tengmalm's Owl in panel a and to Pygmy Owls in b were divided in three classes (short, average, and long distance) representative of the observed range of values (presented with continuous, dashed, and dotted lines, respectively). The 95% credible intervals for each curve is presented in gray in the surrounding of the curves. Statistics of the interactions are in Table 1.

to three weeks later, from late March to early May, and, as a consequence, broods of Pygmy Owls generally hatch two to three weeks later than those of Tengmalm's Owls (E. Korpimäki, *unpublished data*; see also Lehtinen et al. 2011).

Characteristics of the two owl species' life history are important to consider. First, Pygmy Owls are more opportunistic: their diet consists roughly of 40–60% small passerine birds (Kellomäki 1977, Jędrzejewska and Jędrzejewski 1993). Tengmalm's Owls are more selective: 77% of diet consists of voles (Korpimäki 1988). When vole density is low, both owl species need to hunt alternative prey (Kellomäki 1977, Korpimäki 1988, Hakkarainen et al. 1997a). Second, Pygmy Owls are diurnal with activity peaks at dusk and dawn (Mikkola 1970, Kullberg 1995), whereas Tengmalm's Owls are strictly nocturnal (Hakkarainen et al. 1997a). This difference is less evident in northern Europe with long summer days and short nights (3–4 h of night during mid-summer at the study site). Therefore, both species overlap in daily activity to a large extent, increasing the potential for food competition and predation risk. Third, the home range of Pygmy Owls was found to average 0.67 km² during the breeding season in the French Alps (Barbaro et al. 2016) and 1.5 km² (range 0.2–6 km²) during both the breeding and non-breeding seasons in Norway (Strøm and Sonerud 2001). The mean home range of Tengmalm's Owls during breeding was 1.5 km² in the increase and 2.3 km² in the decrease phase

of the vole cycle in our study area (Korpimäki and Hakkarainen 2012, Santangeli et al. 2012).

Previous studies have documented intraguild predation between these owl species. Pygmy Owls have been recorded, although rarely, in the diet of Tengmalm's Owls, both during the breeding season (Mikkola 1983) and winter (Korpimäki and Hakkarainen 2012), and Tengmalm's Owls are known to attack playbacks of Pygmy Owls (Schönn 1980). The killing of Pygmy Owls by Tengmalm's Owls probably occur mostly during late winter, i.e., during the courtship period of both owl species, and in years with low vole abundance when both the food competition and the risk of starvation for both species are high (Suhonen et al. 2007, Korpimäki and Hakkarainen 2012). Even if lethal events may be rare, intraguild predation risk between these species could still affect behavior and reproductive success of Pygmy Owls. Perceived predation risk alone may still trigger carried-over stress responses and antipredator behaviors in the prey, that may lead to reduced reproductive success (Preisser et al. 2005, Cresswell 2008, Zanette et al. 2011) and even cause behaviorally mediated trophic cascades (Suraci et al. 2016).

Methodological approach

When faced with understanding the effect a certain variable can have on an ecological process, such as habitat

selection or reproductive parameters, two options can be considered regarding the selection of the spatial scale at which this variable will be investigated. The first one consists in using available data on the species of interest (e.g., home range size) in order to select an a priori distance, whereas the second estimates the scale at which the variable has the greatest explanatory power, by investigating several increasing sizes of buffer (the so-called focal site multiscale approach; Jackson and Fahrig 2015). We used a combined approach: we accounted for available information on home range size of Pygmy and Tengmalm's Owls in order to set up the lower and upper limits of the scales we investigated, and then we used the second approach, i.e., measuring each variable at different scales within this range, as information was relatively scarce on what variables and scales would be the most relevant in boreal forests.

In order to assess the effects that the density of competitors and predators could have on habitat selection, we selected landscape variables that were relevant for the species (biologically speaking) and we computed their proportions in the surroundings of each Pygmy Owl nest, at different radii (see *Environmental covariates and Intra- and interspecific covariates* subsections and Appendix S2 for environmental covariates and for densities of competitors and predators).

We also included an index of vole abundance (main prey of both owl species) in order to account for between-year variation in food resources. Vole abundance was estimated in spring (early May) and fall (mid-September) by snap-trapping and an index was calculated as 100 trap nights. This index only informed about year to year variations and not about density variations in space. We considered either spring or fall estimates of vole abundance, depending on the response variable considered (see the *Statistical analyses* subsection).

Here we used Bayesian approximations for latent Gaussian models (Rue et al. 2009) and Gauss Markov Random Fields (Lindgren and Rue 2011, Cameletti et al. 2012). These techniques allowed us to estimate simultaneously both the contribution of landscape characteristics and intra-, as well as interspecific, interactions within the habitat selection process. These new methods are able to model, in a tractable, fast, and efficient way, spatial and temporal autocorrelations that both violate the assumption of observation independency, leading to biased parameter estimates when not properly accounted for (Dormann et al. 2007). The best model for each variable was chosen by comparing the DIC value (deviance information criterion, which is a model selection parameter similar to the Akaike information criterion [AIC]; see the *Statistical analyses* subsection and Appendix S2: Table S2, S3). All the analyses were conducted in R 3.0.2 (R Development Core Team 2014).

Environmental covariates

Environmental variables considered were: proportions of tree cover (pine, spruce, or birch) at three different age

classes: young (52–101 m³/ha wood volume), mature (i.e., ready to be harvested, 102–151 m³/ha wood volume), and old forest (>152 m³/ha wood volume), clear-cut areas, farmlands, peatland bogs, and inhabited areas (see Appendix S1: Fig. S1 and Appendix S2: Table S1). We considered each environmental category at 14 different radii (from 100 m to 1000 m every 100 m, then every 500 m up to 3000 m) from each Pygmy Owl focal nest. We then identified the impact of environmental variables on habitat selection and nest cavity occupation of Pygmy Owls (see the *Statistical analyses* subsection). The number of available nesting sites and the proportion of forest type cover varied between years but the model took this into account, making results among years comparable.

Environmental covariates consisted of landscape features that were considered fixed over the study period—namely farmlands, peatland bogs, and built-up areas extracted from the SLICE data set (Mikkola et al. 1999)—and of changing elements, woodlands that varied principally through the clear cutting of mature and old-growth forests (given that it takes much longer for forest patch to become mature than for an old forest patch to be clear cut). Two forest classifications were available for 1997 (National Land Survey, Vuerola 1997) and 2009 (METLA 2009)⁵ and the main task was thus to find out, for mature or old forest patches that had been clear cut between 1997 and 2009, the exact year forestry activities took place, and to control for whether a mature/old forest had been subject to clear cutting after 2009. This was achieved thanks to the analysis of Landsat Images from which an index of vegetation cover (the Normal Difference Moisture Index; hereafter NDMI) was estimated. This index allows identifying areas with and without vegetation by measuring the variation in the moisture level due to the degree of vegetation cover (Jin and Sader 2005), which can thus be used to reveal the moment vegetation has been removed from a plot (see Appendix S2 for details on this method). We were thus able to produce accurate landscapes (on a 25 × 25 m pixels grid) on a yearly basis.

Intra- and interspecific covariates

We calculated the distance from each Pygmy Owl nest to the nearest active breeding site of either Pygmy Owl or Tengmalm's Owl (i.e., nearest neighbor distance) nests. We also calculated the density of nests of both conspecifics and Tengmalm's Owls for six radii (ranging 500 to 3000 m every 500 m) surrounding each focal Pygmy Owl nest, in order to explore the spatial scale at which interactions had the strongest effects (same as analyses of habitat variables). Densities within these radii were measured using a kernel smoothing function, where the intensity λ at point u is given by the following:

$$\lambda(u) = \sum_i^n k(x_i - u) \times w_i e^{x_i}$$

⁵ <http://www.maanmittauslaitos.fi/en/opendata>

where w_i are the associated weights at i and, in our case, are equal to 1. In this formula, we applied the edge correction method by Diggle (1985) where e^{x_i} is an edge correction factor and k is the Gaussian smoothing kernel.

$$k(x,y) = \frac{1}{2\pi\sigma^2} e^{-\frac{x^2+y^2}{2\sigma^2}}$$

Vole abundance

The abundance of voles was estimated by snap-trapping sessions in early May and mid-September each year (2002–2012) at two fixed locations (14 km apart) within the study area (Korpimäki et al. 2005). In both locations, snap-trapping plots were set up in the main habitat types: cultivated agricultural fields, un-cultivated fields, spruce-dominated forest, and pine-dominated forest. The area of these snap-trapping plots varied from 0.5 to 1.0 ha and consisted of 50–100 snap traps set up at 10-m intervals. Trapping lasted for three nights per period and results were expressed per 100 trap nights (a total of 1100 trap night per season). Because the amplitude of the 3-year vole cycle in our study area is approximately 100-fold and the spatial synchrony extends the whole study area (Huitu et al. 2003, Korpimäki et al. 2005), this variable accounts for the annual variation in vole abundances. Vole abundance (either in spring or fall) was then included in the model to determine the importance of annual food abundance on the habitat selection and breeding success of Pygmy Owls.

Statistical analyses

Occupation of nest sites.—We used a Generalized Linear Mixed Model (GLMM) with a binomial likelihood and logit link function to investigate how the habitat selection of Pygmy Owls, estimated through nest box occupancy, was affected by environmental variables and the presence of con- and heterospecifics. The modelling took into account the spatiotemporal variation of these species, which is essential as breeding habitat selection can be strongly affected by variables that cannot necessarily be accounted for, and which may have strong effects on habitat selection between successive years. We used a Stochastic Partial Differential Equation (SPDE; Lindgren 2012) within the framework of Integrated Nested Laplace Approximation (INLA), which allows easily fitting accurate models accounting for spatiotemporal structure (see below and Appendix S2). The spatiotemporal analyses were conducted using the R package INLA (Rue et al. 2014).

As a first step, we focused on environmental covariates (proportions of different habitat types) around all nest boxes and cavities, either occupied or not. Starting from a null model with a random effect for the year variable, we sequentially added a randomly selected environmental covariate, e.g., proportion of old spruce, at each of the 14 different available scales. The fit of the model for each spatial scale of a certain covariate was investigated

according to the deviance information criterion (hereafter DIC, a Bayesian equivalent to Akaike information criterion) and models with $\Delta\text{DIC} < 2$ were considered as competing models (see Spiegelhalter et al. 2002). We retained in the final model the scale (radius) at which the DIC value was the lowest; if none of the scales improved the fit of the model, the environmental covariate was discarded. Model selection at different scales was conducted for all the environmental covariates considered (see *Environmental covariates* and Appendix S2). For forest covers (young, mature, and old age classes of spruce, pine, and birch forests), we either tested the covariates one by one or in combination, i.e., by merging all conifers of the same age category. The original categories had more explanatory power than the combined ones, and we only present the results for these land cover types.

At this point, the final model included all the environmental variables, at the spatial range that best explained occupation of Pygmy Owls. We then tested whether the index of vole abundance in spring or in fall best explained territory occupancy of Pygmy Owls. The model including abundance of vole species in the previous fall had a better fit than the model including vole abundance in the current spring, and we thus included vole abundance in the previous autumn to the final model.

We also tested the effects of presence of both con- and heterospecifics on Pygmy Owl occupation. We compared the impact of local densities at different spatial scales and the nearest neighbor distance among conspecifics and heterospecifics and their interactions. We then performed a backward model selection to remove non-informative interactions, and compared the models including either the nearest distance or local density covariates. The variables with the best DIC value were included in the final model (see Appendix S2: Table S2).

Not accounting for spatiotemporal dependencies can lead to an underestimation of confidence intervals of the parameters of interest (Dormann et al. 2007). Therefore, we tested the final model with two spatiotemporal structures. This was possible using the SPDE approach developed in R-INLA package (see Lindgren and Rue 2011 for details). The first spatiotemporal structure considered “years” as independent replicates, as in Lindgren (2012), whereas the second one included an Autoregressive term (AR1), where the spatial effect estimated in a given year depended upon the previous year, as in Cameletti et al. 2012 (see Appendix S2 for the description of the hierarchical model used to test these structures). We then compared the DIC score of these two spatiotemporal models and we kept the best, which was the one including the autoregressive term (see Appendix S2: Table S2, Fig. S1).

Breeding parameters.—We assessed the effects of intra- and interspecific interactions on breeding parameters of Pygmy Owls: hatching date (a proxy of laying date), clutch size, hatching success (i.e., the number of chicks hatched per total number of eggs in each clutch), and fledging success (i.e., the number of chicks fledged per

total number of eggs in each clutch). We used GLMMs with Gaussian, Poisson, and Binomial likelihoods with identity, log, and logit link functions and controlled for environmental factors and food variability. We included in the initial model all the environmental covariates that were retained in the best model of habitat selection (see *Occupation of nest sites*), given these variables were a priori relevant for the species at the time of choosing the breeding sites.

From the initial model containing the whole set of landscape covariates, we removed uninformative terms based on DIC scores (compared to a null model). We then added the index of vole abundance in current spring (which gave a better fit than vole abundance index in the previous fall). Finally, we included both the local density at different ranges and the nearest neighboring distance of both intra- and interspecific competitors, as well as their interactions, but we kept only the variables with the best DIC value (see Appendix S2: Table S3).

In contrast to the habitat selection models (that had large sample size because of the high number of available nesting cavities), we were not able to account for spatiotemporal structures when testing the breeding parameters models. Low numbers of breeding Pygmy Owl pairs in low vole years did not provide enough statistical power to estimate complex terms in space and time, and thus for breeding parameters models we could only include years as random effect.

RESULTS

Habitat selection

Spatiotemporal effects and con- and heterospecific presence.—The probability of nest-site occupancy of Pygmy Owls varied between years, from 1% in 2010 to 18% in 2003 with an average of 7%. Including a

spatiotemporal structure with an autoregressive term (AR1) substantially improved the explanatory power of the models (see Appendix S2: Table S2, Fig. S1). In particular, the statistically significant AR1 rho term (mean \pm SD = 0.84 ± 0.11 , 95%CI 0.54–0.98) suggested a positive relationship between occupancy at times t and $t - 1$. This indicates that the probability of nest box occupancy was higher if nesting occurred in the surroundings in the previous year, and similarly, that an empty site in a given year was likely to remain so in the following year.

Habitat selection of Pygmy Owls was explained by the distance to both breeding con- and heterospecifics. Overall, the probability of nest site occupancy of Pygmy Owls was higher as distance to the conspecific nest increased (Table 1, Fig. 1a). This relationship was partly modulated by distance to the nearest Tengmalm's Owl nest. Nest box occupancy of Pygmy Owls rapidly increased closer to a nest of Tengmalm's Owl, but only as the distance to the nearest Pygmy Owl nest increased too; near to a conspecific the probability of occupancy was close to zero irrespective of distance to Tengmalm's Owls (see Table 1, Fig. 1a).

Avoidance among conspecific Pygmy Owls decreased when vole abundance was high (see Table 1, Fig. 1b). Closer spatial proximity is indicated by the negative interaction between distance to the nearest Pygmy Owl nest and vole abundance in the previous autumn. At high vole abundance, the nest box occupancy was higher at shorter distances to other Pygmy Owl nests whereas occupancy decreased when vole abundance was low.

Environmental characteristics.—The proportion of farmlands, old spruce, mature and old pine forests (at 1000, 700, 900, and 2500 m radius, respectively) increased the probability of nest box occupancy of Pygmy Owls (see Table 1, Fig. 2a for old spruce and Fig. 2b for old pine impact). Conversely, the amount of inhabited area within a

TABLE 1. Estimates of the best model for occupancy of nest boxes of Pygmy Owls.

Cavity occupancy effects	Mean	SD	2.5%	97.5%	Mode
Intercept	-4.15	0.88	-6.31	-2.61	-3.86
Buildings_200 m	-0.84	0.38	-1.70	-0.21	-0.71
Farmlands_1000 m	0.45	0.17	0.12	0.78	0.45
Mature spruce_300 m	-0.18	0.13	-0.45	0.07	-0.16
Old spruce_700 m	0.33	0.09	0.14	0.51	0.33
Mature pine_900 m	0.57	0.15	0.28	0.87	0.57
Old pine_2500 m	0.27	0.10	0.07	0.46	0.27
Neighbor distance PO	0.69	0.11	0.47	0.92	0.69
Neighbor distance TO	-0.02	0.15	-0.32	0.27	-0.01
Vole abundance (fall)	0.76	0.18	0.43	1.14	0.74
Neighbor distance PO×Neighbor distance TO	-0.38	0.14	-0.66	-0.11	-0.38
Neighbor distance PO×vole abundance (fall)	-0.24	0.11	-0.47	-0.02	-0.24

Notes: Values presented in boldface type are statistically different from random. Confidence intervals (0.025 and 0.975 quantiles [2.5% and 97.5%]) are presented. Variables are presented at the radius most explicative in model selection for the 14 different ranges tested (from 100 to 3000 m; underscore stands for “at a radius of”). Covariates were excluded from the final model if none of the ranges tested improved the fit of the model according to DIC value (See Appendix S2: Table S2). Both environmental covariates and nearest neighbor distance (to Pygmy Owl nest, PO or to Tengmalm's Owl nest, TO) are estimated for each focal Pygmy Owl nest. Vole abundance used in the model is the estimate of abundance in previous fall. The model has an autoregressive spatiotemporal structure.

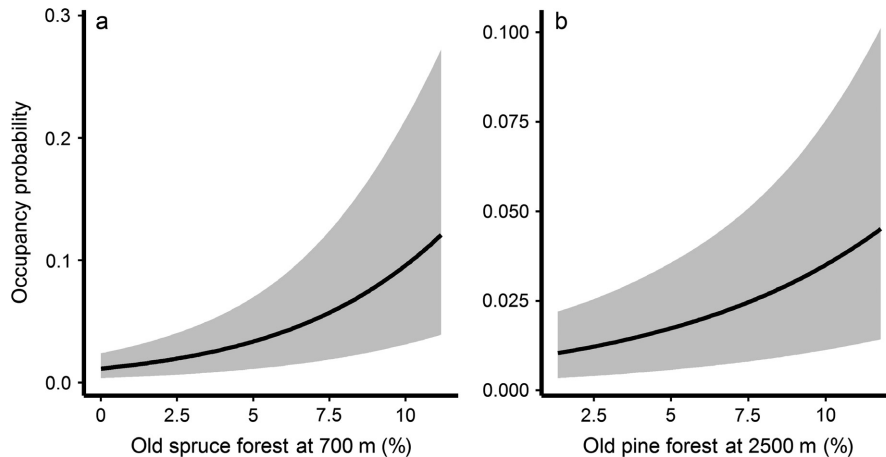


FIG. 2. Probability of occupation of nest sites of Pygmy Owls in relation to (a) percentage of old spruce forest at 700 m radius and to (b) the percentage of old pine forest at 2500 m radius. The 95% credible intervals for each curve is presented in gray in the surrounding of the curves. Statistics are in Table 1.

small spatial scale (200 m) decreased occupancy (Table 1). Vole abundance in the previous fall was positively correlated with the probability of nest box occupancy (Table 1).

Breeding parameters

Presence of con- and heterospecifics.—Hatching success of Pygmy Owls was lower at both high conspecific density and high Tengmalm's Owl densities (both at 3000 m radius; Table 2, Fig. 3a). The maximum observed conspecific kernel density was 0.05 individual/km² within the 3000 m radius. Conspecific and heterospecific densities also positively interacted (Table 2), with hatching success of Pygmy Owls decreasing when both species were present, although the decrement was less pronounced when breeding at high density of Tengmalm's Owls (Fig. 3a). Pygmy Owl broods hatched later when the density of conspecific nests was high (Table 2) and as expected, hatching success was reduced when hatching date was delayed (Table 2). Furthermore, hatching success was low at medium and high densities of Tengmalm's Owls when abundance of main food was low, whereas hatching success rapidly increased with higher abundance of voles in current spring (Table 2, Fig. 3b).

Fledging success of Pygmy Owls decreased with increasing local Tengmalm's Owl density at small scales (within 500 m, Table 2). In addition to the main effect of Tengmalm's Owl density, fledging success of Pygmy Owls decreased at low and intermediate densities of Tengmalm's Owls when the density of conspecifics within 3000 m of the nests increased. There was, however, a slight increment in Pygmy Owl fledging success when densities of both owl species were high (Table 2, Fig. 4a). Similarly to what was observed for the hatching success, fledging success of Pygmy Owls rapidly increased when spring vole abundance increased, especially when breeding at intermediate and high densities of Tengmalm's Owls (Table 2, Fig. 4b). Therefore, because the interaction between vole

abundance and Tengmalm's Owl density showed a similar pattern as the one observed for the hatching success, the interactive effects of heterospecifics and food availability appear to be similar across the nestling phase. Clutch size was not affected by any of the variables considered (see Appendix S2: Table S3), with none of the models tested performing better than the null model.

Habitat characteristics.—Pygmy Owls bred earlier in sites with a large proportion of farmlands within 1000 m radius (Table 1). Despite the positive effect of farmland during the habitat choice and early settlement phase (Tables 1 and 2; Fig. 5a, b), an increasing proportion of farmlands within 1000 m from the nests decreased both hatching and fledging success of Pygmy Owls (Table 2; Fig. 5c, d). Reduced fledging success was also associated with an increasing proportion of mature pine forests within 900 m (Table 2), whereas the proportion of mature spruce forest at a local scale (300 m) was positively associated with hatching success. Overall, late breeders had lower hatching success and reduced fledging success (Table 2).

DISCUSSION

Our results highlight how the presence of conspecifics and intraguild predators can modify the spatial settlement and reproductive success of predators on a landscape scale. We found that the density of both con- and heterospecifics affected breeding investment and success of a small predator, the Pygmy Owl. Spatial settlement and investment decisions of this intraguild prey were, however, strongly dependent on the availability of food. Our long-term data set provides some of the most convincing evidence of how fluctuations in food abundance can impact interactions between species and individuals within the predatory guild.

Prey availability affects interactions within the predator guild. High-amplitude fluctuations in prey populations

TABLE 2. Best fit model for hatching date, hatching success, and fledging success of Pygmy Owls.

Parameters	Mean	SD	2.5%	97.5%	Mode
Hatching date ($n = 111$)					
Intercept	22.56	1.44	19.70	25.45	22.54
Farmlands_1000 m	-1.48	0.54	-2.54	-0.42	-1.49
Vole abundance (spring)	-2.65	1.49	-5.64	0.32	-2.64
PO density_500 m	1.63	0.78	0.09	3.16	1.63
Vole abundance (spring)×PO density_500 m	-2.23	1.22	-4.64	0.17	-2.23
Hatching success ($n = 122$)					
Intercept	2.01	0.20	1.64	2.41	2.00
Hatching date	-0.36	0.14	-0.63	-0.09	-0.37
Farmlands_1000 m	-0.29	0.14	-0.57	-0.02	-0.29
Mature spruce_300 m	0.57	0.26	0.10	1.12	0.52
Old pine_2500 m	0.24	0.15	-0.04	0.54	0.23
Vole abundance (spring)	1.16	0.36	0.48	1.90	1.13
TO density_3000 m	-0.34	0.16	-0.65	-0.02	-0.34
PO density_3000 m	-0.36	0.13	-0.60	-0.11	-0.36
Vole abundance (spring)×TO density_3000 m	1.61	0.48	0.71	2.58	1.56
Vole abundance (spring)×PO density_3000 m	0.21	0.15	-0.09	0.51	0.21
TO density_3000 m×PO density_3000 m	0.32	0.16	0.03	0.64	0.31
Fledging success ($n = 121$)					
Intercept	1.39	0.23	0.94	1.86	1.39
Hatching date	-0.21	0.10	-0.41	-0.01	-0.21
Farmlands_1000 m	-0.75	0.15	-1.06	-0.46	-0.75
Mature pine_900 m	-0.46	0.14	-0.74	-0.18	-0.46
Vole abundance (spring)	0.45	0.22	0.03	0.89	0.44
PO density_3000 m	0.03	0.11	-0.18	0.24	0.03
TO density_500 m	-0.28	0.13	-0.55	-0.02	-0.28
PO density_3000 m×TO density_500 m	0.35	0.10	0.15	0.56	0.34
Vole abundance (spring)×PO density_3000 m	0.07	0.11	-0.15	0.30	0.07
Vole abundance (spring)×TO density_500 m	0.55	0.24	0.10	1.03	0.54

Notes: Values presented in bold are statistically different from random. Confidence intervals (0.025 and 0.975 quantiles [2.5% and 97.5%]) and the number of Pygmy Owl nests considered for each variable are presented. Each variable is presented at the radius that was most explicative in model selection (underscore stands for “at a radius of”). Environmental variables included are at the radius at which they were most representative in the best model for occupation, since that is representative of the habitat choice of the owls. Pygmy Owl (PO) density represents the density of Pygmy Owl nests (nests/km²) around the focal nest at that certain radius (either 500 m or 3000 m). Tengmalm’s Owl (TO) density represents the density of Tengmalm’s Owl nests (nests/km²) around the focal Pygmy Owl nest at a certain radius (either 500 m or 3000 m). Covariates were excluded from the final model if none of the ranges tested improved the fit of the model according to deviance information criterion (DIC) value (See Appendix S2: Table S3 for model selection). Vole abundance used in the model is the estimate of spring abundance.

(vole population cycle) influenced the spatial settlement and reproductive success of Pygmy Owls by determining the strength of exploitative competition, and appeared to determine also the strength of interference competition and intraguild predation. When food resources are scarce, competing predator species may shift to alternative prey, and even the killing and consumption of competitors, i.e., intraguild predation, may be more common. Previous studies have indeed shown an increment in intraguild predation events during the decline phase, rather than in the increase and peak phases of multiannual population cycles of both voles and snowshoe hares, *Lepus americanus* (Korpimäki and Norrdahl 1989, O’Donoghue et al. 1995, Krebs et al. 2001).

Intraspecific competition had stronger impacts on the spatial structure of the predator than the impact of intraguild predation. This result was unexpected given that costs associated with predation far exceed those of competition. We expected that the predation risk associated with an intraguild predator would structure Pygmy Owl settlement (third prediction in introduction) as has been found in other systems (Sergio et al. 2003, 2007, Brambilla

et al. 2010). Our system deviates from those used in previous intraguild predation studies, where generally the intraguild predator was considerably larger (more than three times) than the intraguild prey (reviews in Palomares and Caro 1999, Sergio and Hiraldo 2008). The small difference in size between the two owl species involved in our system (Tengmalm’s Owl being only twice as large as Pygmy Owls) probably led to less frequent lethal predation events than in other intraguild predation interactions, although the non-lethal costs of predator presence may still persist. As a consequence, in our study system, the joint costs of competition, as well as intraguild predation, were lower than those induced by competition by conspecifics only. Strong intraspecific competition among Pygmy Owls matches well with theory that increasing ecological niche overlap between individuals increases the costs of interactions (Schoener 1974). This finding is significant to our understanding of community structure, and requires further research at large spatial scale in other systems.

Nevertheless, the intraguild predator did impact the reproductive output of the intraguild prey. Our results therefore provide further evidence that competition and

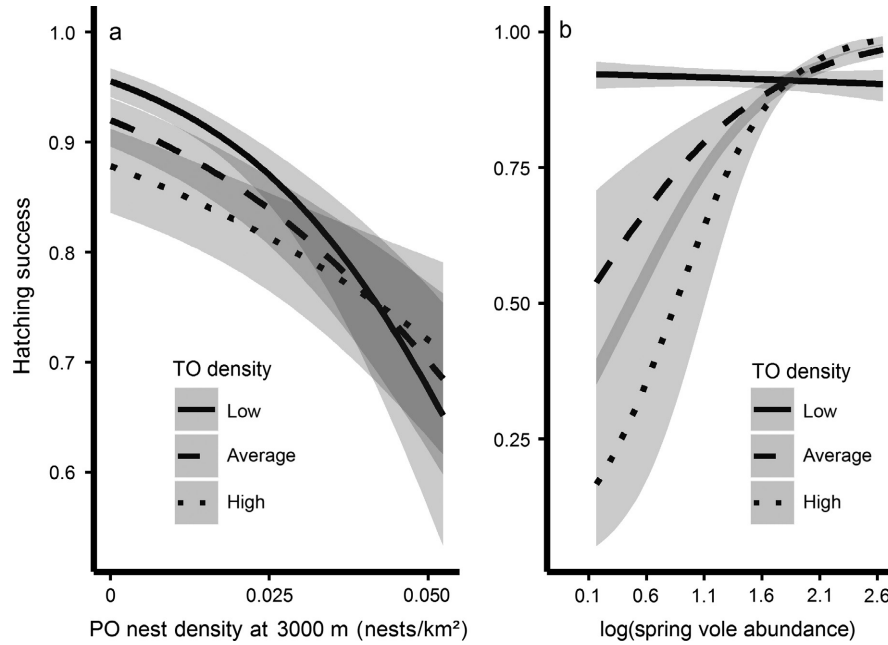


FIG. 3. (a) Hatching success (number of hatchlings per no. of eggs) of Pygmy Owls in relation to the interaction of nest density of Pygmy Owls (PO density, calculated at 3000 m radius from each focal Pygmy Owl nest) and to the nest density of Tengmalm's Owls (TO). (b) Hatching success of Pygmy Owls in relation to the interaction of spring vole abundance and nest density of Tengmalm's Owls. In both panels, the local density of Tengmalm's Owl nests (nests/km²) at a radius of 3 km from a focal nest of Pygmy Owls is presented. Density was classified as low, average, and high density (marked by continuous, dashed, and dotted lines, respectively). The 95% credible intervals for each curve is presented in gray surrounding the curves. See Table 2 for statistics of the interactions.

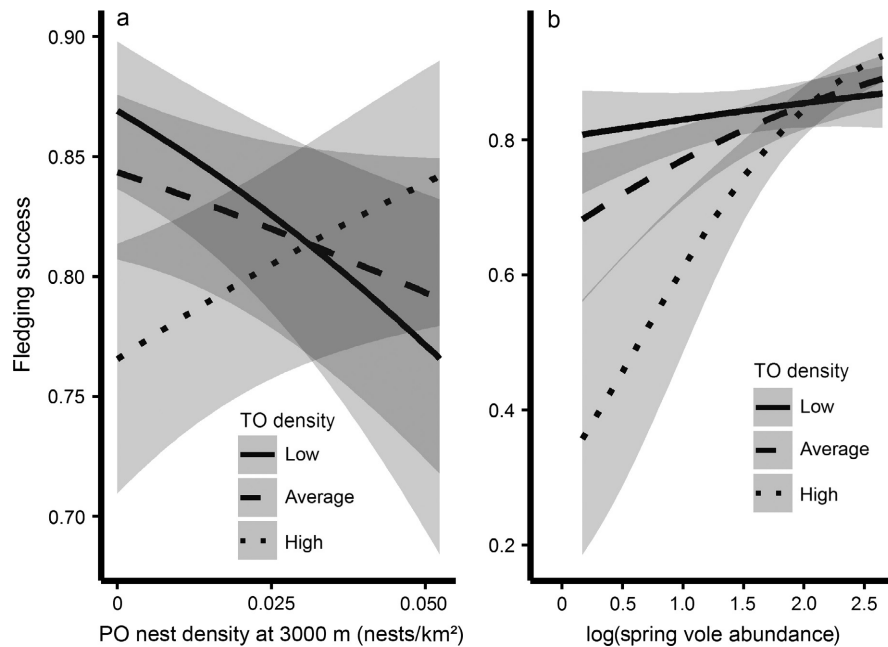


FIG. 4. (a) Fledging success (i.e., the number of fledglings per number of eggs) of Pygmy Owls in relation to the interaction between Pygmy Owl nests density (PO density, calculated as the density of nests at 3000 m radius from each focal nest) and Tengmalm's Owl (TO) nest density. (b) Fledging success of Pygmy Owl nests in relation to the interaction of spring vole abundance and Tengmalm's Owl nest density. In both panels, the density of Tengmalm's Owl nests (nests/km²) at a radius of 500 m from a focal nest of Pygmy Owls is presented. The density is classified as low, average, and high (marked by continuous, dashed, and dotted line, respectively). The 95% credible intervals for each curve is presented in gray in the surrounding of the curves. Statistics for the interactions in Table 2.

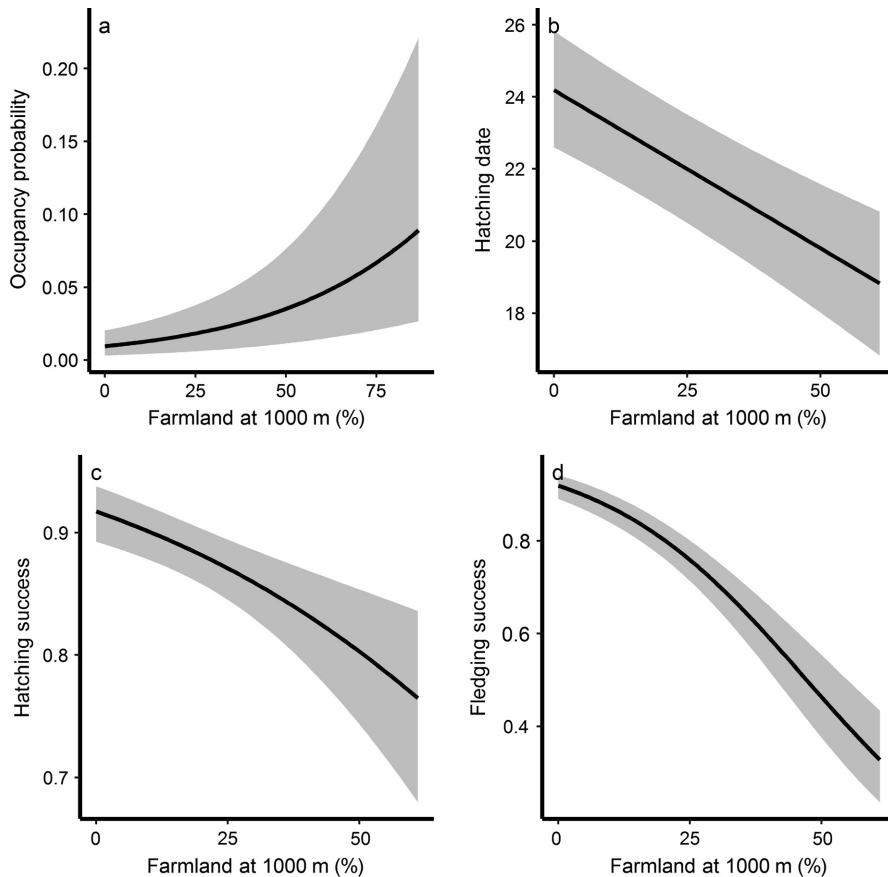


FIG. 5. (a) Probability of occupation of nest sites, (b) hatching date, (c) hatching success, and (d) fledging success of Pygmy Owls in relation to the proportion of farmland at 1000 m radius of focal Pygmy Owl nest. The 95% credible intervals for each curve is presented in gray in the surrounding of the curves. Statistics are in Tables 1 and 2.

intraguild predation can modify animal behavior and often cause reduced reproductive success. This was previously observed both in birds of prey (e.g., Korpimäki 1987a, Ferrer and Donazar 1996, Hakkarainen and Korpimäki 1996, Krüger 2002, Sergio et al. 2003, 2007, Mueller et al. 2016; review in Sergio and Hiraldo 2008) and in mammals (e.g., Ziv et al. 1993, Palomares and Caro 1999, St-Pierre et al. 2006, Watts and Holekamp 2008, Suraci et al. 2016).

Conspecific and heterospecific density dependence

Our results showed that the spatial distribution of breeding Pygmy Owls was mainly explained by strong and consistent conspecific avoidance (intraspecific negative density dependence; in agreement with our first expectation). However, the strength of conspecific avoidance decreased when the main food resource (voles) was abundant. In terms of resource overlap, for any given individual, a conspecific will present the strongest competition. In many animal populations there is a negative relationship between population growth rate and size (e.g., review in Sibly and Hone 2003). This negative

density dependence can also affect individuals' breeding frequency (Fasce et al. 2011) and body condition (Bårdsen and Tveraa 2012). Our results demonstrated that Pygmy Owls displayed strong avoidance for their conspecifics when choosing a breeding site, probably as a consequence of exploitative and interference competition, similarly to what has been found in other birds of prey (e.g., Newton et al. 1986, Korpimäki 1987a, Martinez et al. 2008). Conspecific interactions were also mediated by food resources with avoidance in settlement decreasing when food was abundant, suggesting that high food availability led to weaker intraspecific density dependence, probably through a decrease of territory size (see, e.g., Finstad et al. 2009).

The habitat selection decisions of Pygmy Owls, showing repulsion in a conspecific context, were adaptive in term of reproductive success. Pygmy Owls showed delayed breeding and lower hatching success when breeding at high conspecific density, probably due to exploitative (consumptive) and interference (territorial) competition. Unexpectedly for a small (~60–80 g) predator species, however, these detrimental effects of conspecific neighbors on reproductive output measures

were manifest at large distances (500 m for hatching date but 3000 m for hatching and fledging success). Ottaviani and collaborators (2006) estimated that the ideal home range for a 100 g avian predator ranges from 0.31 km² up to 1 km², whereas Pygmy Owls in boreal regions have a home range of up to six times this predicted average (see Strøm and Sønnerud 2001). This discrepancy between body size and territory size may be caused by the overall scarcity of food resources in boreal forest ecosystems: the densities of small rodents are relatively low compared to more southern temperate environments. Moreover, given Pygmy Owl also prey upon small birds that exhibit high rates of mobbing and other antipredator behaviors, it might be necessary for hunting Pygmy Owls to ensure a sufficient large hunting territory in order to limit interference competition with other neighbors.

The heterospecific competitors and intraguild predators did not affect spatial settlement of Pygmy Owls. Quite surprisingly, cavity occupancy increased closer to Tengmalm's Owl nests, but only when conspecific nests were farther away (see Appendix S3 for a detailed discussion on this interaction). The spatial pattern observed suggests that in this system, costs imposed by intraguild predation are lower than expected. This settlement pattern is probably due to a convergence in habitat choice for the two owl species, e.g., as a response to spatial clustering in prey distribution (main prey, voles, and alternative prey, small birds). Similar spatial aggregation has been observed also between Peregrine Falcons *Falco peregrinus* and Eagle Owls *Bubo bubo*. Since Eagle Owls are known to prey upon chicks and adults of Peregrine Falcons, the co-occurrence of the two species should be regarded as the consequence of attraction to high-quality nest sites (Brambilla et al. 2010).

In agreement with our second prediction, proximity to Tengmalm's Owls was associated with low hatching and fledging success of Pygmy Owls. This is similar to the results documented in other interspecific interactions (Both 1998, Watts and Holekamp 2008, Dhondt 2010, 2012). The negative impact of heterospecific density on reproductive success of Pygmy Owls probably arises from both exploitative and interference interspecific competition, since these species have overlapping diet (mostly small rodents and small passerines birds). Owls and other predators have been shown to reduce high density patches of cyclic voles (Korpimäki et al. 2002, 2005). Vole patches in the vicinity of these breeding owl species are probably rapidly depleted, which in turn would lead to lower hatching and reproductive success of the inferior competitor, the Pygmy Owl (see Appendix S3 for further discussion).

Intraguild predation risk related costs also likely negatively affect the Pygmy Owl, as has been shown in other predator guilds. The negative impact of Tengmalm's Owls on Pygmy Owl reproductive success is therefore a result of not only competition, but also both lethal and non-lethal effects of intraguild predation. Intraguild predation events in this system have been observed, albeit

only rarely, in winter (Schönn 1980, Korpimäki and Hakkarainen 2012), when Pygmy Owls are probably more vulnerable to predation by Tengmalm's Owls (see *Methods* and Appendix S3). Carry-over effects of predation risk from winter and early spring could nevertheless persist during the breeding season given predation risk alone can negatively affect the reproductive success, behavior, and physiology of the smaller predator when breeding near to, or at high densities of, intraguild predators (Korpimäki 1987a, Hakkarainen and Korpimäki 1996, Krüger 2002, Sergio et al. 2003, 2007, Preisser et al. 2005, Lyly et al. 2015, Mueller et al. 2016). As a consequence, even the sole presence of Tengmalm's Owl in the area may lead to non-lethal costs in breeding Pygmy Owls (see further discussion in Appendix S3).

Overall, our results show that conspecific density induced larger detrimental effects on settlement patterns and reproductive success of intraguild prey than interspecific competitors and intraguild predators. This is in contrast with our third prediction and suggests that intraspecific competition can under specific circumstances have more weight than predation risk in shaping biological interactions. Such comparisons of the relative effects of the density of conspecifics and other competitors and/or predators are, to our knowledge, relatively scarce in animals (but see Carrete et al. 2006), though it has already been extensively assessed in plants (Comita et al. 2010). In plants the strength of density dependence generated by conspecifics has been reported to be higher than heterospecific density dependence (Johnson et al. 2012), as suggested also by this study. In birds of prey, previous studies instead suggest that the strength of intra- vs. interspecific density dependence is related to the species involved in the interaction. Young Golden Eagles *Aquila chrysaetos* were affected by the proximity of conspecific nests, whereas young Bonelli's Eagles *Aquila fasciata* were mostly affected by the presence of the larger competitor, i.e., Golden Eagles (Carrete et al. 2006). Competitive and predatory interactions (with both lethal and non-lethal effects) thus clearly affect animal habitat choice and the distribution of different species in the landscape (e.g., Sergio and Hiraldo 2008, Dhondt 2012, Thaker et al. 2011, Lyly et al. 2015; this paper). The outcome of interactions among predators will also indirectly impact prey populations (Ritchie and Johnson 2009), because prey will modify their habitat choice according to the spatial distribution of predators (Korpimäki et al. 1996, Morosinotto et al. 2010, Byholm et al. 2012). The fear induced by intraguild predators to their intraguild prey will thus indirectly affect also the behavior and reproductive success of their shared prey, leading to behaviorally mediated trophic cascades. Indeed, a recent experimental study showed that fear of intraguild predators alone can affect the foraging of raccoons (*Procyon lotor*). This change in foraging will impact not only raccoon prey but will also have cascading impacts on other species not directly interacting with raccoons (Suraci et al. 2016).

The role of landscape variables in habitat selection

Animals actively select breeding or foraging grounds according to different habitat features (Cornulier and Bretagnolle 2006, Morellet et al. 2011, Schwemmer et al. 2016) that can subsequently impact demographic parameters such as reproductive success (Pärt 2001, Hakkarainen et al. 2003), nest survival (Marchand and Litvaitis 2004, Newmark and Stanley 2011) or individual survival (Hakkarainen et al. 2008, Low et al. 2010, Ekroos et al. 2012). We found that Pygmy Owls, a specialist of coniferous forests, selected variables linked to mature and old coniferous forests (old spruce forests within 700 m and old and mature pine forests, respectively, within 2500 m and 900 m radii). Access to food resources and protection from potential predators are two common explanations for the habitat parameters selected by animals (Dussault et al. 2005, Fontaine and Martin 2006). In boreal forests, old and mature spruce and pine forests harbor larger populations of Pygmy Owl main prey, the bank vole *Myodes glareolus*, and passerine birds with body mass < 60 g (Jędrzejewska and Jędrzejewski 1993, Hakkarainen et al. 1997a, b, Santangeli et al. 2012). In addition, dense tree cover in mature forests offers refuges for Pygmy Owls against larger avian predators including, e.g., Sparrowhawks *Accipiter nisus*, Goshawks *A. gentilis*, and Ural Owls *Strix uralensis*.

We also found evidence of spatial predictability across years impacting the spatial outcomes of Pygmy Owls, independently of con- or heterospecific influences. The probability of Pygmy Owl nest site occupancy was partially explained by occupancy in the previous year. Higher probability of occupancy of a focal nest cavity in consecutive years was probably induced by the high quality of the habitat in the surrounding of these cavities. This could be either because the same individuals tend to occupy the same sites year after year or because newcomers are attracted to these high-quality sites (Newton and Marquiss 1986, Korpimäki 1987b, Lecomte et al. 2008, Ekroos et al. 2012). Nest-site fidelity of adult Pygmy Owls, however, appeared to be an unlikely explanation, since 81% of the females (99 out of 122) and 75% of the males (77 out of 103), trapped in the study area during 2002–2012, were observed only once (recorded breeding dispersal distances of males 1433 ± 2574 m [mean \pm SD] in 44 dispersal events; recorded breeding dispersal distances of females 1576 ± 2060 m in 34 dispersal events; E. Korpimäki et al., unpublished data). This suggests that the occupancy pattern observed is mainly due to the preference for these forest patches from immigrant birds.

The proportions of farmlands at 1 km was also positively correlated with nest sites occupancy but led to reduced reproductive success of Pygmy Owls, i.e., delayed hatching date as well as lower hatching and fledging success, similar to what has been demonstrated for Tengmalm's Owls (Hakkarainen et al. 2003). This counterintuitive result could indicate the existence of an

ecological trap (Battin 2004, Robertson and Hutto 2006), i.e., individuals preferentially selecting a habitat irrespectively of achieved fitness return (in this case, fitness returns could be considered as lower). Individuals could be attracted by higher availability of food resources in farmlands, either because rodents and birds are more abundant close to farmlands due heterogeneous landscape composition (Hakkarainen et al. 2003, Heikkinen et al. 2004) or because of earlier access to voles in spring, since the snow cover tends to melt earlier than in dense forests. However, farmlands also attract other vole-eating predators, and their high densities likely induce keener competition between predators, which could subsequently decrease breeding success.

Conclusions

We investigated spatiotemporal variations in prey abundance and habitat characteristics, which are essential to disentangle the tricky effects of temporal fluctuations in food resources and habitat composition in shaping intra- and interspecific interactions (Korpimäki and Norrdahl 1991, Boutin et al. 1995, Krüger 2002, Sergio et al. 2003, 2007). Habitat variables proved to be a necessary element to account for, affecting both habitat selection process and reproductive parameters of intraguild prey. In point pattern analyses, habitat variables drive first-order processes that primarily determine the spatial distribution of animals' density. Not including these variables in a modelling framework investigating second order processes, i.e., interactions between individuals, may lead to doomed conclusions.

Our results further suggest that joint costs of exploitative and interference competition by Tengmalm's Owls, as well as intraguild predation, were lower than those induced by exploitative (consumptive) and interference (territorial) competition by conspecifics only. This result might be due to the small size difference between Tengmalm's and Pygmy Owls, with intraguild predators being only twice as large as intraguild prey. Interactions among con- and heterospecifics can therefore modify the spatial settlement and reproductive success of individuals on a landscape scale, also within the predator guild. The present work highlights the fact that to comprehensively understand the interactions within a guild, it is necessary to account for both spatial overlap and year-to-year fluctuations in resources that potentially modulate the strength of the relationships between species. In this sense, the system constituted by vole-eating predators and their high-amplitude cyclic main prey offers a unique opportunity to study intraguild predation in nature, in pseudo-experimental settings.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecm.1238/full>

DATA AVAILABILITY

Data associated with this paper are available in Dryad: <https://doi.org/10.5061/dryad.r2rc8>