

Intraguild predator drives forest edge avoidance of a mesopredator

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Abstract. Interactions between top predators and mesopredators of the same guild often result in habitat segregation restricting interactions to shared habitat edges. Although negative edge effects are recognized as important spatial patterns in the ecology of fragmented landscapes, the underlying mechanisms of predator–prey interactions resulting in negative edge effects remain unknown. To disentangle top-down effects of intraguild predators and bottom-up effects of shared resources on mesopredator spatial distribution, we recorded the occurrence of tawny owls *Strix aluco* in forests and their prey, the little owl *Athene noctua* in adjacent open areas over 2 yr across 687 km² in Southern Germany. We developed a new, asymmetrical dynamic two-species occupancy model investigating spatial interactions while accounting for imperfect detection. Little owl occupancy was strongly reduced within 150 m of forests, but only in the presence of tawny owls. Analysis of over 30 000 telemetry locations of 275 little owls showed that little owls strongly avoided areas closer than 150 m from the forest during range use. These results suggest that the negative edge effect is due to forest edge avoidance rather than direct predation. Potential confounding mechanisms such as food depletion or habitat avoidance at forest edges can be ruled out. Thus, top-down effects caused by avoidance of intraguild top predators shape the spatial distribution of mesopredators such as the little owl. While habitat complexity mitigates multitrophic interactions within habitats, it is expected to reinforce multitrophic interactions between habitats, potentially leading to the suppression of mesopredators from suitable habitats.

Key words: *Athene noctua*; edge effect; food availability; intraguild predation; little owl; risk effects; Southern Germany; *Strix aluco*; tawny owl.

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INTRODUCTION

The spatial structure of species communities is affected by food webs whose predator–prey interactions may act by direct lethal predation or by nonlethal risk effects based on anti-predator behavior (Creel and Christianson 2008, Cresswell et al. 2010). Nonlethal effects include chang-

es in the spatial behavior of prey such as avoidance of areas of high predation risk (Lima and Dill 1990, Heithaus and Dill 2006, Cresswell et al. 2010). Since predation risk varies according to landscape topology, habitat composition, and the abundance of specific predators, prey species constantly adapt their behavior to a “landscape of fear” (Brown et al. 1999, Laundré et al. 2001).

Perceived predation risk can shape the spatial behavior of prey at different levels: home-range selection (Fontaine and Martin 2006), habitat use (Willems and Hill 2009), dispersal movements (Otsuki and Yano 2014) and thus, distribution and dynamics of prey animals throughout their lives (Cresswell 2008).

Intraguild predator-prey interactions, i.e., interactions between a top predator and a mesopredator sharing the same food resources (Polis et al. 1989) are intensified by mutual competition for food. In the absence of avoidance behavior, encounter rates of mesopredators and their intraguild predator at shared foraging sites of high food availability are expected to exceed those of predator and prey with completely distinct diets, resulting in elevated predation risk in intraguild systems (Morris 2005). Compared to simple predator-prey interactions, intraguild predators additionally profit from exclusion of their intraguild prey from shared food patches by reduced depletion (Polis and Holt 1992). Life-history theory predicts that in prey strategies to minimize predation should evolve, for example exploitation of alternative food sources or use of distinct habitats (Korpimäki 1987), depending on the densities of both predator and prey (Heithaus 2001). As a result of increased encounter rates and predation pressure, this should particularly apply to intraguild systems. However, hitherto investigations of the consequences of predator-prey interactions on range use were rarely based on intraguild systems.

Negative effects of interspecific competition and predation may be reduced by temporal segregation (Fedriani et al. 2000), by small scale behavioral avoidance (Swanson et al. 2014), or by complete habitat segregation (Schoener 1974, Thiollay 1993), all of which reduce the encounter rates between the two species. Structured habitats can further reduce encounter rates and create refuges for prey, thereby mitigating the effect of intraguild predators on prey populations (Janssen et al. 2007, Thompson and Gese 2007). Interactions between habitat segregated intraguild predators and their prey are limited to shared habitat edges. Nonetheless, in fragmented landscapes, the amount of edge habitat is considerable and interactions at habitat edges may be important determinants of mesopredator spatial behavior. Although intraguild predation is recognized as an important factor shaping range use of me-

sopredators (Ritchie and Johnson 2009, Swanson et al. 2014), spatial patterns of mesopredators at shared habitat edges remain unknown. Furthermore, it remains unclear if reduced occupancy or prey density near habitat edges is due to direct predation, due to edge avoidance in response to perceived predation risk, or both (Suhonen et al. 1994, Lima 2009, Fonderflick et al. 2013). Behavioral studies are needed to differentiate between the two mechanisms (Lima and Valone 1991).

Our study aims to close this gap by investigating the interaction between the little owl *Athene noctua* living in open habitat and its intraguild predator, the tawny owl *Strix aluco* inhabiting adjacent forests (Redpath 1995, Van Nieuwenhuyse et al. 2008). While tawny owls often forage at the forest edge, little owls avoid forests (e.g., Lack 1946, Zabala et al. 2006). We examine three alternative hypotheses explaining this observed forest avoidance: (1) the “avoidance hypothesis” suggests active avoidance of forest edges in response to perceived predation threat (Fontaine and Martin 2006); (2) the “predation hypothesis” assumes predation close to the forest resulting in apparent forest avoidance (Suhonen et al. 1994); and (3) the “resource hypothesis” attributes the avoidance to the lack of important resources such as food or suitable hunting grounds near the edge (Ries and Sisk 2004). The “resource hypothesis” predicts that both occupancy and individual range use of little owls correspond to the distribution of resources. Thus, inconsistency between range use or occupancy patterns and resource distribution would provide evidence against it. While both the “avoidance hypothesis” and the “predation hypothesis” predict that little owls occupy territories further away from forests inhabited by tawny owls than from forests without tawny owls, only the “avoidance hypothesis” predicts behavioral avoidance during night-to-night range use. In contrast, under the “predation hypothesis” little owls should use their range according to resource availability, whereby individuals foraging close to the forest are preyed. Accordingly, increased predation rates at sites close to forests are predicted. To test these predictions, we first developed a novel, asymmetrical dynamic two-species occupancy model based on presence-absence data (an extension of the models of Waddle et al. 2010 and MacKenzie et al. 2003). Second, we analyzed

data of individual spatial behavior and survival of little owls from a 4-yr telemetry study. Third, we investigated the availability of the main little owl food and of the preferred foraging habitats in relation to the distance to the forest edge. Our results give insights into predator avoidance strategies at shared habitat edges and their consequences for range use and distribution of intraguild prey.

MATERIALS AND METHODS

Study species and study area

The little owl is a small nocturnal owl species of open habitats (Van Nieuwenhuyse et al. 2008). It is a mesopredator feeding on small rodents (mainly *Microtus* spp.), insects, earthworms, and birds (Juillard 1984). Particularly in open areas, where tawny owls frequently prey upon *Microtus* spp. (Petty 1999), the diets of little owls and tawny owls overlap considerably. Due to its small size, the little owl is susceptible to predation from several larger species, and there is a lot of evidence for little owl predation by tawny owls (Mikkola 1976, Schönn et al. 1991). Besides the eagle owl (*Bubo bubo*), which is rare in our study area, the tawny owl is considered as the second most important predator of the little owl (Van Nieuwenhuyse et al. 2008).

Our study was carried out in Southern Germany (District of Ludwigsburg, Baden-Württemberg, 48°53'43" N, 9°11'45" E). The study area with a surface of 687 km² is composed of a mosaic of forests (25%), human settlements (17%) and farmland (58%). The agricultural landscape is dominated by fields of intensive agriculture, interspersed with pastures, meadows, orchards, and vineyards (Bock et al. 2013). The little owl subpopulation within our study area currently consists of roughly 220 breeding pairs (H. Keil, unpublished data), mostly breeding in artificial nest boxes, which include a protection against martens. While the little owls breeding in nest boxes are being closely monitored, an unknown number of pairs breeds in natural nests within tree cavities every year.

Field methods

Playback procedure

A survey of little owls and tawny owls was conducted in February–March 2012 and 2013

using call playbacks. An overview and details about the selection of the 156 playback sites are given in Fig. A1 (see Appendix A). Each playback site was visited three times using one of three different call sequences of each species (see Appendix A for detailed methods). Since the weather conditions can affect the detection probability, the occurrence of precipitation, wind, cloudiness, and the amount of background noise were recorded (variables are defined in Table A1, Appendix A). This approach resulted in a data set consisting of encounter histories of both species over three visits per year.

Radio tracking

To investigate the range use and direct avian predation of little owls in relation to the distance to the forest edge, point location data of little owls collected in a telemetry study from summer 2009 until summer 2013 were analyzed (Bock et al. 2013). Little owls were equipped with very high frequency (VHF) transmitters of own construction (Naef-Daenzer et al. 2005) weighing 6.9–7.2 g (corresponding to 4–5% of a bird's body mass), with an operational range of up to 40 km in the field and an expected life span of 400 d. For details about tagging procedures, see Bock et al. (2013). During 2–4 visits per week, each bird was located twice at an interval of 5 min by homing in using a 3-element Yagi antenna and a handheld receiver (Kenward 2001). Only night-time locations were considered, amounting to a total of 30 721 locations of 275 little owls (65 females, 58 males, and 152 juveniles).

Remains of depredated individuals were usually found shortly after death, allowing us to distinguish between mammalian and avian predation (Bock et al. 2013). In many cases, it was impossible to ascertain, which avian predator was responsible for the predation. Data of 167 little owls with known fate from 1 yr to the next were available for the investigation of mortality rates due to avian predation. Since several birds were followed over multiple years, these data originate from 120 individual adults (63 females, 57 males).

Food abundance

The range use of little owls is expected to vary according to the abundance of food

resources. Although little owls have a broad prey spectrum, small mammals generally comprise the largest part of their biomass intake (e.g., Šálek et al. 2010). Therefore, we quantitated the number of field signs (i.e., runways and holes) of common voles (*Microtus* spp.) along transects with a width of 0.5 m and a length of 5 m as a proxy for food abundance (Giraudoux et al. 1995, Apolloni 2013). This proxy correlates well with live-trappings (Lambin et al. 2000).

Spatial variables

The distance of each playback site to the closest forest patch (area $\geq 2\,500\text{ m}^2$) was measured in Google Earth (Version 7.1.2.2041, © Google 2013) with an accuracy of 10 m. Points within the forest were assigned negative values corresponding to the distance to the forest edge. Since Central European little owls are often associated with orchards (Gottschalk et al. 2011) and their breeding success correlates with distance to human habitations (Tomé et al. 2004), distances of each playback site to the closest orchard (≥ 6 fruit trees), and to the closest village (≥ 6 houses) were extracted.

To compare the habitat compositions at different distances from the forest and to test whether little owls preferentially use areas at larger distances from the forest, the study area was split into areas of similar distance from the forest. Distance buffers (0–50 m, 50–100 m, ..., 450–500 m, >500 m) were created around forest areas extracted from a land use raster of Baden-Württemberg (adapted from Gottschalk et al. 2011) using ArcGIS 10.0 (ESRI, Redlands, California, USA). Within each distance buffer, the relative proportion of three habitat types important for little owls (arable fields, orchards, and meadows) was calculated. Since range use of breeding little owls depends on the distance to the nest or roost site (Sunde et al. 2014), the availability of areas at different forest distances and their use were assessed separately for ten distance classes from the little owl nest (see Appendix A, Fig. A2 for details).

Statistical analyses

Occupancy model

We developed a dynamic two-species occupancy model to analyze the presence-absence data of both owl species. Three visits at each

playback site allowed quantitation of the detection probability. Our model (developed with the help of M. Kéry) accounts for the asymmetrical relationship between predator and prey, extending the parameterization developed by Waddle et al. (2010) to a multiseason model (MacKenzie et al. 2003), thereby creating an asymmetrical dynamic two-species occupancy model. We used colonization (γ ; i.e., the rate at which previously unoccupied sites were occupied in the following year) and persistence (ϕ ; i.e., the rate of sites occupied in both years) to model the differences in occupancy (ψ) between year t and year $t + 1$:

$$\psi_{t+1} = \psi_t * \phi + (1 - \psi_t) * \gamma \quad (1)$$

Initial occupancy of tawny owls was given by

$$\text{logit}(\psi_1^{\text{tawny}}) = \alpha_{\psi}^{\text{tawny}} + \beta_{\psi}^{\text{tawny}} * \text{cov}_i \quad (2)$$

where cov_i are the different site-specific spatial distance variables described above (i.e., distance to forest, orchard and village). To avoid numerical overflow (Kéry and Schaub 2012), distance variables were standardized (see Appendix A). Detection probability (p) of tawny owls as well as ϕ and γ were modelled in an analogous way. Weather and noise variables entered the detection probability model as visit-specific covariates (cov_{ij} in Eqs 2 and 3). In addition, the little owl detection model included tawny owl occupancy:

$$\text{logit}(p^{\text{little}}) = \psi_t^{\text{tawny}} * \alpha_{p,+} + (1 - \psi_t^{\text{tawny}}) * \alpha_{p,-} + \beta_p * \text{cov}_{ij} \quad (3)$$

The initial occupancy by little owls was modelled as a function of tawny owl presence, site-specific habitat covariates and an interaction between the two:

$$\begin{aligned} \text{logit}(\psi_1^{\text{little}}) = & \psi_1^{\text{tawny}} * \alpha_{\psi,+} + (1 - \psi_1^{\text{tawny}}) * \alpha_{\psi,-} \\ & + \psi_1^{\text{tawny}} * \beta_{i,\psi,+} * \text{cov}_i \\ & + (1 - \psi_1^{\text{tawny}}) * \beta_{i,\psi,-} * \text{cov}_i \end{aligned} \quad (4)$$

Finally, little owl dynamics were modelled depending on tawny owl occupancy:

$$\begin{aligned} \psi_{t+1}^{\text{little}} = & \psi_t^{\text{little}} * \psi_t^{\text{tawny}} * \varphi_+^{\text{little}} + \psi_t^{\text{little}} * (1 - \psi_t^{\text{tawny}}) \\ & * \varphi_-^{\text{little}} + (1 - \psi_t^{\text{little}}) * \psi_t^{\text{tawny}} * \gamma_+^{\text{little}} \\ & + (1 - \psi_t^{\text{little}}) * (1 - \psi_t^{\text{tawny}}) * \gamma_-^{\text{little}} \end{aligned} \quad (5)$$

The symbols + or – represent the presence or absence of tawny owls, respectively.

All models were written in the BUGS language and run in the software JAGS (Plummer 2003) controlled by the package R2jags (Su and Yajima 2012) in R Version 3.0.2. (R Core Team 2012). To reach convergence, the models were run for 1 000 000 iterations with a burn in of 100 000, a thinning parameter of 10, and 3 chains. As priors for intercepts and parameters, we used a uniform distribution from –10 to 10, for the dynamic parameters of the little owls a uniform distribution from 0 to 1. Covariates were sequentially removed from the model if the 95% credible interval of the posterior distribution included 0. Goodness of fit of the final model was assessed using predictive model checking (for the predictive model check see Appendix B, the data and code to run the final model are given as Data S1).

Range use

Small scale behavior of little owls near forest edges might provide insight into the mechanism of edge avoidance. Within each distance class from the nest (see Appendix A, Fig. A2), Manly's resource selection ratio W_i , the ratio of used and available habitat was calculated using the package adehabitatHS in R (Manly et al. 2002, Calenge 2006). This analysis relates the proportion of locations within each distance buffer from the forest (proportion used) to the proportion of area belonging to the according distance buffer (proportion available).

Avian predation and vole density

Reduced occupancy or range use near forest edges might be caused by direct predation of little owls or low food abundance. Therefore, we investigated if little owls nesting close to the forest were at a higher risk of being killed by avian predators. In four cases, tawny owls were calling repeatedly near the site of recovery of the remains or transmitter, strongly suggesting predation by tawny owls. Since this low

sample size did not allow complex modelling, we compared the distance of the nests of these little owls to the rest using a two-sided *t*-test. Including the data of little owls killed by an unknown avian predator, a generalized linear mixed model (GLMM) with binomial error structure and logit link function was used to relate the occurrence of avian predation to the distance to the forest. Forest distance was log-transformed to improve convergence. Since many individuals were observed over several years, the individual identity was included as a random factor. The distance to the forest edge, sex, and the estimated occurrence of tawny owls nearby (extracted from the occupancy model) were included as fixed factors. To test whether a potential edge effect was due to reduced food abundance in the vicinity of the forest, we added a binary factor (distance <150 m = 1, *n* = 159; >150 m from the forest = 0, *n* = 3656) to a well-established model investigating which factors affect the frequency of vole signs (Apolloni 2013). This binomial GLMM includes the habitat type (arable field, grassland, orchard, and buffer zone) as a fixed factor and the sampling surface as a random factor. Both GLMMs were fit in R using function glmer in package lme4 (Bates et al. 2014).

RESULTS

Detection probability

Precipitation and cloudiness did not affect the detection probability of either owl species. Thus, these factors were removed from the final model. The presence of wind reduced the detection probability of tawny owls in 2012, but not in 2013 (Table 1, Appendix C, Fig. C1). Detection of little owls was not affected by wind. High background noise reduced tawny owl detection in 2013 and little owl detection in both years (Table 1, Appendix C, Fig. C1). In 81% of the MCMC-simulations, little owl detection was lower in the presence than in the absence of tawny owls (Table 1, Appendix C, Fig. C1).

Occupancy pattern

Both the occupancy probability and the year-to-year persistence of tawny owls declined with increasing distance of a playback site to the

Table 1. Model estimates and 95% credible intervals (CrI) of the dynamic two-species occupancy model.

Parameter	Predictor†	Posterior mean	Posterior SD	CrI
Tawny owl sub-model				
Detection 2012 (p)	Intercept	0.73	0.16	0.42 to 1.05
	Wind	-1.22	0.44	-2.10 to -0.37
	Noise	-0.09	0.36	-0.78 to 0.63
Detection 2013 (p)	Intercept	0.53	0.18	0.18 to 0.89
	Wind	0.58	0.76	-0.82 to 2.19
	Noise	-0.98	0.31	-1.59 to -0.37
Occupancy (ψ)	Intercept	0.42	0.22	-0.01 to 0.87
	Forest	-0.39	0.07	-0.54 to -0.26
Persistence (ϕ)	Intercept	1.36	0.91	0.28 to 3.79
	City	0.48	0.25	0.13 to 1.11
	Forest	-0.62	0.32	-1.47 to -0.24
Colonization (γ)	Intercept	-0.77	0.47	-1.69 to 0.12
	Forest	-0.42	0.18	-0.80 to -0.13
Little owl sub-model				
Detection 2012 (p)	Intercept +	0.59	0.23	0.15 to 1.04
	Intercept -	0.91	0.28	0.38 to 1.47
	Noise	-1.06	0.35	-1.73 to -0.38
Detection 2013 (p)	Intercept +	0.41	0.27	-0.11 to 0.94
	Intercept -	0.74	0.26	0.24 to 1.27
	Noise	-0.82	0.36	-1.53 to -0.11
Occupancy (ψ)	Intercept +	1.83	0.59	0.84 to 3.07
	Forest +	0.30	0.17	0.06 to 0.59
	Forest ² +	-0.15	0.05	-0.26 to -0.06
	Intercept -	0.44	0.37	-0.26 to 1.20
Persistence (ϕ)	Forest -	-0.05	0.08	-0.21 to 0.10
	+	0.71	0.08	0.54 to 0.87
	-	0.84	0.08	0.68 to 0.98
	Difference	-0.13	0.11	-0.35 to 0.09
Colonization (γ)	+	0.10	0.05	0.02 to 0.21
	-	0.18	0.09	0.03 to 0.38
	Difference	-0.08	0.10	-0.30 to 0.11

† Predictors in presence and absence of tawny owls are indicated with + and -, respectively.

closest forest patch (Table 1). Tawny owl persistence increased with distance from the closest village, whereas their occupancy and colonization rates were not affected (Table 1). The colonization rate of previously unoccupied sites by tawny owls was higher inside the forest or near its edge than at greater distances (Table 1). In summary, these results confirm the close association of tawny owls with forest habitats.

Little owl occupancy was neither related to the distance to the closest orchard nor to the distance to the closest village. Thus, both covariates were removed from the final model. There was a positive correlation between the presence of little owls and the distance to the forest. However, this relationship only occurred in the presence of tawny owls (Fig. 1, Table 1). Persistence and

colonization rate of little owls were higher in the absence of tawny owls in 88% and 78% of the MCMC-simulations, respectively (Table 1).

Potential underlying mechanisms

Range use: behavioral avoidance

Areas close to the nest were strongly preferred: 33.3% of all locations ($n = 12\,408$) were situated within 50 m of an individual's nest. Due to the high abundance of locations in this small area, the forest avoidance pattern was not as clear as at larger distances (Appendix C, Table C1). The preference index revealed that beyond 50 m from the nest, areas within 150 m of the forest were avoided, while areas farther than 150 m from the forest were used according to availability or were even preferred (Fig. 2). The distance from the nest affected

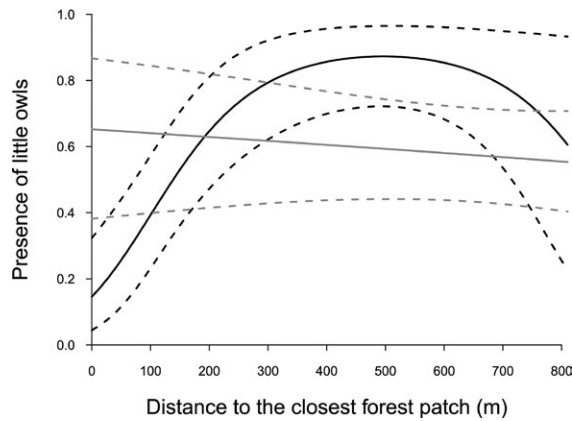


Figure 1. Relationship between the distance to the closest forest and the occurrence of little owls in the presence (black lines) and absence (gray lines) of tawny owls. Dashed lines represent the 95% credible interval. $N = 156$ playback sites.

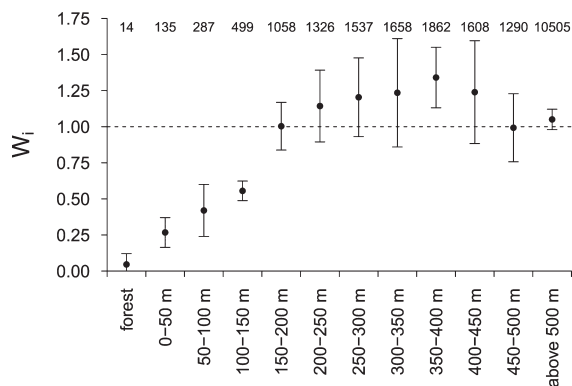


Figure 2. Manly's resource selection ratio W_i (use relative to availability) of distances from the forest averaged across nine distance classes from the nest (50–100 m, 100–150 m, ..., 450–500 m). Points below the dashed line ($W_i = 1$) indicate avoidance, points above the line preference. Error bars represent the 95% confidence interval. Numbers indicate the sum of telemetry locations within each forest buffer.

the strength of the avoidance: areas within 50 m of the forest edge were more strongly avoided when located far from (>100 m) than close to the nest (<100 m; Appendix C, Table C1). Thus, the distance between nest and forest was an important factor modulating forest avoidance.

Direct predation

Low little owl occupancy in areas close to forests might be due to increased predation rates of little owls settling there. Of the 167 birds observed over the course of a year, 21 birds were killed by an avian predator. Nests of the four little owls most likely killed by tawny owls were located significantly closer to the forest than those of the other 163 little owls (mean distance $\pm$ SE: 255 ± 54 m vs. 522 ± 41 m; two-sided t -test: $t = -3.944$, $df = 4.046$, $P = 0.017$). When including the data of little owls killed by an unknown avian predator, the occurrence of avian predation was not significantly related to the distance of the nest to the forest (Table 2). Thus, little owls living close to the forest were not more susceptible to avian predation than those living at larger distances. The occurrence of tawny owls did not affect the probability of little owl mortality due to avian predation, either (Table 2).

Vole density and habitat composition: food availability

Irrespective of the intraguild predator, differential vole abundance as well as the habitat composition near the forest might affect the range use of little owls. When controlling for habitat type, the occurrence of voles did not differ significantly between areas within 150 m of the forest and areas farther away (estimate = 0.882, CI = -1.755 – 3.485 , $\chi^2 = 0.565$, $P = 0.453$). However, vole abundance was shown to be higher in grassland and orchards than

Table 2. Generalized linear mixed effects model (GLMM) investigating the factors affecting the occurrence of avian predation.

Predictor	Estimate	SE	CI	χ^2	P
Intercept	-4.667	2.467	-9.376 to -0.058	–	–
Sex	-0.149	0.471	-1.067 to 0.750	0.100	0.752
Distance to the forest	0.415	0.387	-0.321 to 1.167	1.191	0.275
Presence of tawny owls	0.657	0.504	-0.286 to 1.668	1.687	0.194

in arable fields (Apolloni 2013). Across our study area, the relative proportion of meadows close to the forest was twice as high as the proportion at greater distances (<150 m: 36.5%, >150 m: 17.8%). In contrast, the relative proportion of arable fields far from the forest exceeded the proportion near the forest by half (<150 m: 44.9%, >150 m: 67.1%). The abundance of orchards was similar (<150 m: 18.6%, >150 m: 15.1%, see Appendix C, Fig. C2). These results indicate an environment of higher food abundance near the forest.

DISCUSSION

By applying different methods, we found distinct spatial patterns in a habitat-segregated intraguild predator-prey system. First, territory occupancy of the mesopredator showed a strong negative edge effect: the presence of the mesopredator rapidly decreased near forest edges in the presence but not in the absence of the top predator. Second, movement behavior of the mesopredator showed a strong negative edge effect as well: mesopredator individuals avoided movements into areas near forest edges. Third, the availability of preferred food resources was not reduced near forest edges. In combination, our results support the “avoidance hypothesis”: the intraguild mesopredator actively avoids the use of suitable habitats shared with a habitat segregated top predator, although these habitats would comprise preferred prey.

Edge avoidance might arise due to confounding factors such as differences in habitat composition or resource availability at habitat edges, possibly due to food depletion around habitat edges as a consequence of exploitative competition (Schoener 1983). However, there was no evidence for this “resource hypothesis”: preferred habitat types with high vole abundance (Šálek et al. 2010, Apolloni 2013) were more frequent within the avoided area than further from the forest, supporting the two remaining hypotheses. Since accessibility is not expected to differ between the same habitats at different distances from the forest it is unlikely that food availability is confounded by its accessibility.

The large-scale distribution of the mesopredator and its individual movement behavior showed the same edge effect. Assuming the same

underlying mechanism in range use and settlement decisions, the predator-induced edge effect likely results from predator avoidance behavior by the mesopredator (“avoidance hypothesis”) and not from direct predation (“predation hypothesis”). The “avoidance hypothesis” is also supported by the finding that direct predation of the mesopredator was not increased at forest edges. However, we have to keep in mind that mesopredators are part of a complex multitrophic system including more than one predator. In our study system, additional intraguild top predators prey on little owls far from forest edges (e.g., common buzzard *Buteo buteo*, barn owl *Tyto alba*: Penteriani and Faivre 1997, Zuberogitia et al. 2008), potentially blurring the effect of direct predation by the tawny owl. Mesopredators need to adapt their avoidance strategies to the type, distribution, and density of different intraguild predators: habitat segregation and large scale avoidance is only possible if there are gaps in the distribution of the top predator, or if the mesopredator can resort to a habitat which is not used by the predator (Treinys et al. 2011, Swanson et al. 2014). In the absence of such predator-free areas, the mesopredator needs to apply avoidance strategies on a small temporal or spatial scale to avoid suppression (Swanson et al. 2014). Little owls reduce their activity or move to shelter to avoid predation by barn owls co-occurring within the same habitat (Zuberogitia et al. 2008). Here, we show that little owls reduce predation risk from tawny owls through forest edge avoidance. Thus, vertebrate mesopredators not only vary in their response to the same top predator, our results suggest that a single mesopredator applies different strategies to avoid different top predators, depending on the extent of habitat segregation.

Avoidance of favored, food-rich habitats near the forest edge attests to the trade-off between costs and benefits of using edge habitat (Cresswell 2008). Our results suggest that the costs of using these areas exceed the benefits in our study area. As a result, home-ranges containing many forest edges are low in quality. The cost-benefit function of occupying habitats of different quality is expected to be density dependent (Bollinger and Switzer 2002, van Beest et al. 2014). As intraspecific competition increases, edge-sensitive animals are forced to use suboptimal habitats

near edges (Huhta et al. 1999). Thus, whether occupancy patterns result from direct or indirect predation effects will depend on the density of both mesopredators and top predators. Within our study area, mesopredator density is low (~ 0.55 breeding pairs per km^2 : H. Keil, unpublished data, compared to a mean density ± 1 SD of 1.84 ± 5.25 breeding pairs per km^2 across 69 western European studies: Génot and Van Nieuwenhuyse 2002) indicating that density-dependent effects are not strong enough to interfere with habitat selection. We suggest that predator-induced edge effects change from non-lethal avoidance to lethal predation with increasing mesopredator density, and that interactions and avoidance behavior act in larger areas with increasing top predator density (St-Pierre et al. 2006).

Recent research on carnivores suggests that bottom-up effects (i.e., the density of the shared prey) determine the range use of top predators, whereas the range use of mesopredators depends on the trade-off between predation risk and food availability (Fedriani et al. 2000, Heithaus 2001, Thompson and Gese 2007, Wilson et al. 2010, Kozłowski et al. 2012). Therefore, edge avoidance by habitat-segregated mesopredators likely depends on the relationship between predation risk and the distance to habitats used by top predators (Cresswell et al. 2010). The little owl, which shows a woodpecker-like flight of little maneuverability, is expected to depend on minimizing the encounter rate rather than escaping an attack. In contrast, species with more notable escape abilities are expected to use high quality habitat patches shared with the top predator despite the linked predation risk. Instead of minimizing potential encounters with a predator, they are expected to adapt their flight initiation distance to the perceived predation risk and the distance to shelter.

Habitat complexity moderates the strength of top-down effects by reducing encounter rates, by providing refuges and by improving the escape ability of prey (Janssen et al. 2007, Wirsing et al. 2010). Thus, habitat complexity promotes coexistence of intraguild predators and their prey living in the same habitat (Finke and Denno 2002, Janssen et al. 2007). In contrast to other studies, the top predator and mesopredator in our study system use distinct habitats and mainly interact

at the edges in-between. Since landscape complexity affects the distribution and length of habitat edges, intraguild predator-prey interactions at habitat edges become a key issue at the landscape scale, particularly in the light of ongoing habitat fragmentation (Haddad et al. 2015). We show that the mesopredator avoids suitable habitat along forest edges. Thus, landscape features such as size, edge-area ratio and habitat fragmentation of mesopredator habitat patches determine the impact of the intraguild predator on mesopredator populations. In contrast to the mitigating effect of habitat complexity on multitrophic interactions within habitats (Hartman et al. 2014), increasing landscape complexity is expected to reinforce multitrophic interactions between habitats by creating edge habitat, potentially completely excluding mesopredators from suitable habitats.

Top predator induced suppression of mesopredators at habitat edges may relax the predation pressure on lower trophic levels. However, this release effect is expected to be stronger in traditional predator-prey interactions than in intraguild systems, because predation pressure by intraguild predators persists. Similar to the well-investigated “mesopredator release” (Soulé et al. 1988, Crooks and Soulé 1999), where the top predator is suppressed, the trophic cascades to lower trophic levels in areas of suppressed intraguild mesopredators might be complex. Further studies are necessary to elucidate whether reduced predation pressure as a result of local mesopredator suppression leads to prey release or whether the intraguild predator compensates for the reduced predation pressure.

For our study, we developed an asymmetrical, dynamic two-species occupancy model. Occupancy modeling has several advantages over analyses of home-range use based on tracking data. First, repeated assessment of occurrence at regular temporal and spatial intervals is a cost-efficient method to gather data across a large area and multiple species. The models can be extended to include additional species at different levels of food webs, integrating simultaneous information on predator and prey species. Second, it is possible to investigate change rates from 1 yr to the next and their dependence on interspecific interactions or habitat features. Third, telemetry is often limited to individuals breeding in accessible nest boxes,

whereas occupancy models based on responses to playbacks do not have this constraint. However, occupancy modeling provides no information about the mechanisms responsible for the observed patterns (Waddle et al. 2010). Therefore, we suggest that future studies should combine large scale occupancy modeling with the analysis of individual behavioral data to gain deeper insights into the mechanisms shaping the spatial patterns at different trophic levels of food webs.

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