Raptor Journal 2025, Vol. 19: 17–28. DOI: 10.2478/srj-2025-0003

Movement patterns, roosting sites and diet composition during the breeding season of three different forest-dwelling owl species in an area of sympatry: a case study of male home ranges

Pohybové vzorce, miesta odpočinku a zloženie potravy troch sympatricky žijúcich druhov lesných sov počas hniezdneho obdobia: prípadová štúdia domovských okrskov samcov

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Abstract: In areas of sympatry, animals face risks associated with predation pressure and competition for space and/or food from individuals within the same or different ecological guilds. In birds of prey, intraguild competitors and adversaries may adapt to coexistence through various mechanisms, such as spatial avoidance, dietary differentiation, or using distinct habitat types in the shared environment. However, studies examining multiple sympatric owl species and simultaneously investigating their home ranges, diet, and roosting sites remain exceptional. Therefore, we studied four sympatric owl species to obtain findings on spatial arrangements of their diurnal roosting home ranges, and prey and habitat selection during the breeding season. Individual males from three of the four studied species [Eurasian pygmy owl (*Glaucidium passerinum*), boreal owl (*Aegolius funereus*), and tawny owl (*Strix aluco*)] were radio-tracked in an area co-inhabited by an apex intraguild predator, the Eurasian eagle-owl (*Bubo bubo*). The diurnal roosting home range, calculated using a 95% kernel density estimation method, was 111, 117, and 7 ha for the pygmy, boreal, and tawny owl male, respectively. The diurnal roosting home ranges overlapped by 55% in the case of the boreal and pygmy owl males; in contrast, their ranges overlapped only by 2% and 4%, respectively, with that of the tawny owl male. The tawny owl male roosted at a respectful distance from the eagle-owl's nest site in all recorded cases, while it was included within the diurnal roosting home ranges of both smaller owl species, indicating the subordinate owl species may use the presence of an apex predator to protect themselves from medium-intraguild enemies. The study results suggest that intraguild competitors/enemies may mitigate direct conflict through spatial avoidance and dietary differentiation, and such partial niche separation may help reduce food competition within the guild, promoting coexistence among species.

Abstrakt: V oblastiach sympatrického výskytu čelia živočíchy rizikám spojeným s tlakom predátorov a konkurenciou o priestor a/alebo potravu zo strany jedincov v rámci rovnakých alebo odlišných ekologických gíld. U dravých vtákov sa vnútrodruhoví konkurenti a protivníci môžu adaptovať na koexistenciu prostredníctvom rôznych mechanizmov, ako je priestorové vyhýbanie sa, potravinová diferenciácia alebo využívanie odlišných typov biotopov v zdieľanom prostredí. Avšak štúdie skúmajúce viacero sympatrických druhov sov a súčasne analyzujúce ich domovské okrsky, potravu a miesta odpočinku zostávajú výnimočné. Preto sme študovali štyri sympatrické druhy sov s cieľom získať poznatky o priestorovom usporiadaní ich denných hniezdnych domovských okrskov a výbere koristi a biotopov počas hniezdneho obdobia. Jednotliví samce troch zo štyroch študovaných druhov [kuvičok vrabčí (*Glaucidium passerinum*), pôtik kapcavý (*Aegolius funereus*) a sova lesná (*Strix aluco*)] boli rádiovo sledované v oblasti spoluobývanej vrcholovým vnútrogildovým predátorom, výrom skalným (*Bubo bubo*). Denný odpočinkový domovský okrsok, vypočítaný pomocou metódy 95% odhadu jadrovej hustoty, bol 111, 117 a 7 ha pre samca kuvička, pôtika a sovy lesnej. Denné hniezdne domovské okrsky sa prekrývali na 55 % v prípade samcov pôtika a kuvička; naopak, ich okrsky sa prekrývali len na 2 % a 4 % s okrskom samca sovy lesnej. Vo všetkých zaznamenaných prípadoch samec sovy lesnej odpočíval v značnej vzdialenosti od hniezdiska výra skalného, ktoré však bolo zharnuté v dennom odpočinkovom okrsku oboch menších druhov sov, čo naznačuje, že nižšie postavené druhy sov môžu využívať prítomnosť vrcholového predátora na ochranu pred stredne veľkými vnútrogildovými nepriateľmi. Výsledky štúdie naznačujú, že vnútrogildoví konkurenti/nepriatelia môžu zmierňovať priamy konflikt prostredníctvom priestorového vyhýbania sa a potravinovej diferenciácie, a takéto čiastočné rozdelenie niky môže pomôcť znížiť potravnú konkurenciu v rámci zoskupenia, čím podporuje koexistenciu medzi druhmi.

Key words: diurnal roosting, Eurasian pygmy owl, intraguild relationships, radio-telemetry, tawny owl, boreal owl

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Acknowledgements: We thank Zita Hrůzová, Kristýna Procházková and Luděk Tenkrát for their help in collecting field data. Our thanks are also due to the Forest Administration of the city of Náměšť nad Oslavou of the Czech Forest Institute (Lesy ČR, s.p.) for limiting disturbing activities in the area of interest during the study period, and especially for their willingness to postpone the harvesting of dead young spruce stands. Further, we thank Erkki Korpimäki for his helpful comments and suggestions on an earlier manuscript draft.

Introduction

A diverse range of intra- and inter-species interactions, ranging from predation through food competition to obligatory cooperation (e.g., mutualism), have been examined across various organisms. Competition between territorial species is usually most intense among individuals of the same sex, and body size and/or mass commonly serve as the decisive factor in determining the outcomes of mutual competition or the trophic level of species within food chains (Begon et al. 2006). Exploitation competition represents the indirect interaction between competitors (intra- or inter-specifics) as they each deprive the other by utilising the same resources, i.e., they are sharing food, environmental and/or space niches (Nilsson 1984; Alatalo et al. 1987; Sarà et al. 2005). Interference competition refers to competitors directly preventing other individuals from obtaining access to resources (Dhondt 2012; Lang and Benbow 2013); this type of interaction involves various mechanisms, including the predation of adults or immature individuals (Case and Gilpin 1974; Schoener 1983). In extreme cases of interference competition, aggressive clashes can even result in death, and if an individual is consumed by his adversary in the course of this competition, the phenomenon is referred to as intraguild predation (Polis et al. 1989; Lourenço et al. 2014).

These ecological relationships significantly influence animals' areas of occurrence, distribution and home range sizes at both the conspecific and heterospecific levels (e.g., Don 1983; Ribble and Stanley 1998; Kajtoch et al. 2016). When selecting a habitat, animals evaluate various factors, e.g., the presence and abundance of competitors and predators. This behaviour becomes especially pronounced before the critical reproductive phase, such as the breeding season in birds (Fretwell and Lucas 1969; Grand and Dill 1999; Kajtoch et al. 2016; Morosinotto et al. 2017). Intraguild predation and competition are common among birds of prey, with species size playing a key role in shaping the predation patterns (Mikkola 1983; Sergio and Hiraldo 2008; Solonen 2011; Björklund et al. 2016; Kouba et al. 2023; 2024). Dominant species of birds of prey are known to prey upon and interfere with subordinate ones (Mikkola 1983; Hakkarainen and Korpimäki 1996; Sergio et al. 2003). Additionally, intraguild adversaries typically compete for food resources (Mikkola 1983), and their dietary composition varies in specialisation and diversity. For instance, the boreal owl (*Aegolius funereus*) specialises mainly in *Microtus* and *Myodes* voles (Korpimäki and Hakkarainen 2012), the Eurasian pygmy owl (*Glaucidium passerinum*) frequently supplements its diet with passerine birds (Mikusek et al. 2001; Šotnár et al. 2015), and the tawny owl's (*Strix aluco*) diet is highly diverse and includes even amphibians and reptiles (Obuch 2011). However, despite their differences in body size, all these owl species primarily prey upon small mammals (König and Weick 2008), leading to an overlap in their food niches.

The three above-mentioned owl species also inhabit similar habitat types, primarily mature and/or old coniferous and mixed forests (König and Weick 2008) and habitat sharing results inevitably in a higher likelihood of their food resource competition (Pepłowska-Marczak 2019). For example, boreal owls have been found to hunt in patches with high vole densities, leading to their loss and, in the end, decreased hunting success of pygmy owls (Korpimaki and Norrdahl 1989). The latter species also had to limit or avoid the best hunting patches when foraging under the boreal owl predation risk (Suhonen et al. 2007).

Despite the aspects mentioned above, the long-term coexistence of intraguild enemies is common; however, this cohabitation typically impacts the overall fitness of subordinate species (Hakkarainen and Korpimäki 1996;

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Solonen 2011; Kajtoch et al. 2016; Morosinotto et al. 2017). As a result, subordinate owl and raptor species are compelled to avoid dominant ones by adopting temporal or spatial segregation strategies (e.g., Jaksić 1982; Sergio et al. 2007; Kajtoch et al. 2016). Alternatively, smaller species may choose to avoid habitats associated with high predation risk, such as those preferred by predator species, a behaviour known as "habitat-mediated avoidance" (Sergio et al. 2007). This pattern can result in a concentration of smaller bird of prey species in refugia free of enemies (Sergio et al. 2003).

This study aimed to investigate simultaneously multiple Strigiformes species to obtain findings on sizes, overlaps and spatial arrangements of their diurnal roosting home ranges, as well as their prey and habitat selection during the breeding season. Individual pygmy, boreal, and tawny owl males were radio-tracked in an area of sympatry where an additional apex intraguild predator, the Eurasian eagle-owl (*Bubo bubo*), was also present. The current study complements the previously published one, focusing exclusively on hunting home range sizes and overlaps of the same individuals (Stehlíková Sovadinová et al. 2025).

Materials and Methods

Study Area

The study was conducted in Křižanovská vrchovina (the Krizanov Highlands) in the Vysočina region of Czechia (49° N, 16° E; ~500–660 m a. s. l.). The study area covers ~6 square km (depicted on the map with the recorded diurnal roosting home ranges; see Fig. 1). It is comprised of commercial forests (54%), agriculture areas (41%), bodies of water (3%) and human settlements (2%). The oldest local forest stands are over 50 years of age, but the majority (65%) are young to middle-aged (~30 years). Norway spruce (*Picea abies*) was

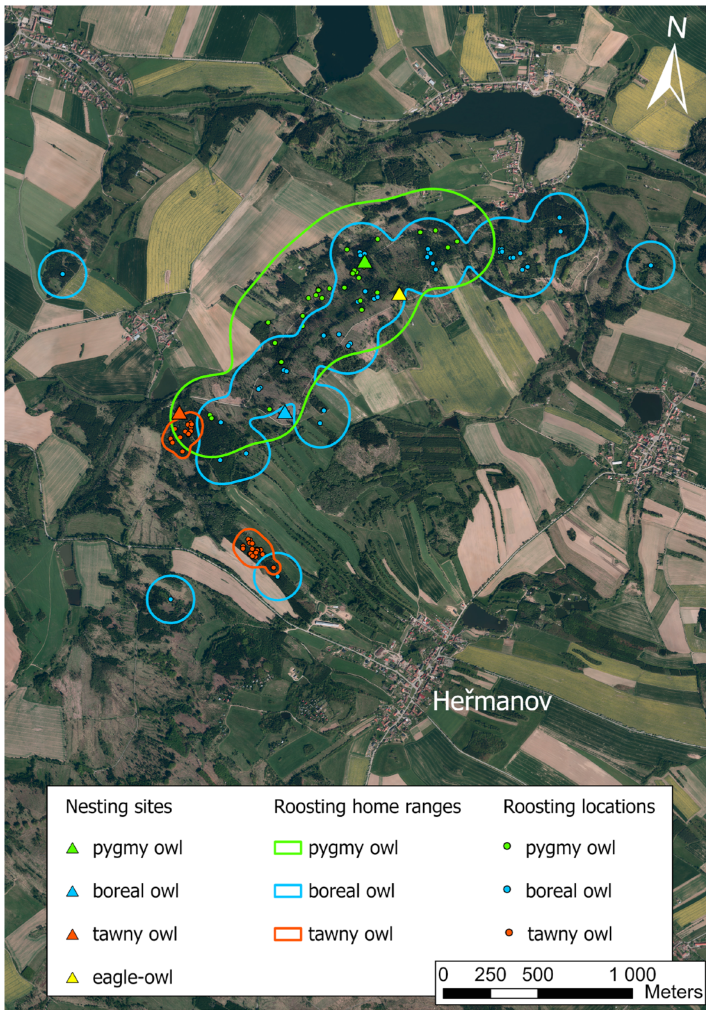

Fig. 1. Diurnal roosting home ranges of the monitored male owls. The nest sites, locations recorded during resting and diurnal roosting home ranges (calculated using the 95% Kernel Density Estimation method) recorded during breeding for the three radio-tracked male owls. The data for individual species are depicted as follows: Eurasian pygmy owl – green, boreal owl – blue, tawny owl – orange, and Eurasian eagle-owl nest site only – yellow.

Obr. 1. Denné odpočinkové okrsky sledovaných samcov sov. Hniezdiská, pozície zaznamenané počas odpočinku a denné odpočinkové okrsky (vypočítané metódou 95% Kernel Density Estimation) zaznamenané počas hniezdenia troch rádiovo sledovaných samcov sov. Údaje pre jednotlivé druhy sú znázornené nasledovne: kuvičok vrabčí - zelená, pôtik kapcavý - modrá, sova lesná - oranžová a výr skalný - žltá.

the predominant species in the forested areas (68%), complemented by stands of mixed deciduous trees (10%) and Scots pine (*Pinus sylvestris*; 7%). Sapling and clear-cut areas formed 15%. Due to the lack of natural nesting cavities within the study area, nest-boxes for boreal and tawny owls were installed around the site.

Field Procedures

From the end of February 2022, we monitored the vocal activity of owls and regularly visited local nest-boxes (installed in 2019) and known natural tree cavities in the study area. Nests of all four owl species (pygmy, boreal, tawny, and eagle-owl) were identified in the locality during March. The pygmy owl pair nested in a natural cavity, the boreal and tawny owl pairs laid clutches in nest-boxes, and the eagle-owl pair nested on a low rocky cliff. Their nests were visited regularly to determine hatching dates (± 2 days) and to count the number of eggs, hatchlings and fledglings (Table 1). However, the clutch of the eagle-owl pair disappeared soon after laying. This unfortunate incident prevented us from monitoring all four males with radio-tracking because our efforts to capture the eagle-owl male without an active nest were unsuccessful. The three other owl males were attracted to the vicinity of their nests using conspecific whistling or playbacks of prey species cries and were captured using mist nets and an appropriate decoy dummy on 29 March. The captured males were weighed and ringed, and their age was estimated based on the stage of the moulting cycle. Each individual was equipped with an Ag386 VHF radio-transmitter (Lotek Wireless Inc., UK), which was attached as a backpack and released at the capture site. The transmitter weights (Table 1) did not exceed 3% of the tagged individual's body mass (Withey et al. 2001). The three males were subsequently monitored using handheld receivers Yupiteru MVT-9000 (Yupiteru Industries Co. Ltd., Japan) and 3-element Yagi antennas.

The monitoring via radio-tracking was carried out from 30 March until 24 June. The locations of diurnal roosting

Tab. 1. Basic breeding data regarding the nests of the three radio-tracked male owls (Eurasian pygmy owl, boreal owl and tawny owl) and information regarding their home range sizes recorded during the breeding season 2022. The dates of nesting, hatching and fledging, clutch sizes, numbers of hatchlings and fledglings, parent male owl's age and body mass, numbers of diurnal roosting and nocturnal hunting locations recorded during the monitoring, home range sizes established using the 50%, 90% and 95% Kernel Density Estimation (KDE) and 100% Minimum Convex Polygon (MCP) methods, and the weight of the radio-transmitters used in the study are provided.
Tab. 1. Základné údaje o hniezdení troch rádiom sledovaných samcov sov (kuvička vrabčieho, pôtika kapcavého a sovy lesnej) a informácie o veľkosti ich domovského okrsku zaznamenané počas hniezdnej sezóny 2022. Uvádzame dátumy hniezdenia, vyliahnutia a vyletenia, veľkosti znášok, počty vyliahnutých a vyletených mláďat, vek a telesnú hmotnosť rodičovského samca, počty lokalizácií denného odpočinku a nočného lovu počas monitorovania, veľkosti domovského okrsku stanovené pomocou metód 50 %, 90 % a 95 % Kernel Density Estimation (KDE) a 100 % Minimum Convex Polygon (MCP) a hmotnosť rádiových vysielačov použitých v štúdii.

	pygmy owl	boreal owl	tawny owl
Date of nesting*	7 April	21 March	5 March
Date of hatching*	11 May	25 April	7 April
Date of fledging*	9 June	30 May	11 May
No. of eggs	5	5	2
No. of hatchlings	5	3	2
No. of fledglings	5	3	2
Male's age (years)	1+	3+	2
Male's weight (g)	58	101	413
No. of roosting locations	30**	44	38
Roosting KDE 50% (ha)	23.3	23.6	1.4
Roosting KDE 90% (ha)	88.6	92.1	5.5
Roosting KDE 95% (ha)	111.1	116.5	7.1
Roosting MCP 100% (ha)	43.5	343.8	9.1
No. of hunting locations	91	175	210
Hunting KDE 95% (ha)	106.6	155.3	260.3
Hunting MCP 100% (ha)	74.5	128.9	224.2
Radio transmitter weight (g)	1.7	2.9	3.6

*The stated dates of egg-laying, hatching and fledging starts are the best possible estimates (± 2 days).

**The Eurasian pygmy owl male's roosting location was identified 16 times by homing in and 14 times by triangulation.

were collected throughout the tracking period from 6 AM to 9 PM by the homing-in method (Kenward 2001), in which the signal was followed to a particular tree or until the individual was observed. Owl males' locations were recorded using handheld GPS receivers (Garmin GPSmap 60CSx or Astro 230, Garmin Ltd., USA). For the pygmy owl male, roosting locations were also considered to be the fixes recorded at the beginning and the end of the hunting period from which the individual had not moved or had already stopped moving. These roosting locations were recorded using triangulation as all the hunting fixes. The details of the nocturnal hunting data collection methodology are described in Stehlíková Sovadinová et al. (2025).

Although we were unable to capture, radio-tag and monitor the eagle-owl male due to the reasons given above, we decided to include the eagle-owl pair/male in the study due to the pivotal role of the species as an apex predator that exerts a significant influence on the behaviour of other subordinate owl species (e.g., Sergio et al. 2007; Solonen 2011). This decision was further supported and justified by the fact that the vocalisation of the eagle-owl pair/male continued to be recorded throughout the study, confirming their ongoing presence at the study site.

Recording owl vocal activities within the study area is done by voice recorders every spring. Based on the analysis of individual spectrograms (e.g., Galeotti and Pavan 1991; Grava et al. 2008), all the males studied by radio-telemetry almost certainly inhabited the study area at least from 2021. Thus, each male's space use within the study area most probably reflected and was adapted to the presence of all other intraguild species/individuals.

Diet Composition

The composition of the owls' diet was, in the case of boreal and tawny owls, determined by analysing pellets collected at the males' diurnal roosting places and by examining leftover nesting material taken from the nest-boxes after breeding; in the case of pygmy owl, material collected around and in the close vicinity of the breeding cavity was analysed. The pellets and nesting material were soaked in a 5% sodium hydroxide (NaOH) solution to dissolve all undigested prey remains, leaving only the bones intact. The osteological material was then used to identify the prey species by comparing the samples with reference collections (for more details, see Obuch 2001; 2011; 2021). Prey species with a significant deviation from the mean are indicated by additional numbers in front of the count of individuals on a scale of 2– to 1+. This significant deviation from the mean is calculated as the difference between real abundances (real number of prey species) and theoretical abundances, which is a value obtained from the real and relative representations of elements. Elements with significant deviations from the mean are considered diagnostic (Obuch 2001). Food niche overlap was measured using Pianka's index ($O_{jk} = \sum p_{ij}\, p_{ik} / \sqrt{\sum p_{ij}^2\, p_{ik}^2}$, where p_i is the proportion of prey item "i" in the diet of species "j" and "k") (Pianka 1973). Pianka's index ranges from 0 (total separation) to 1 (total overlap).

Spatial Data Evaluation

All the spatial data, i.e., the distances between the nests of the individual study species, the distances among diurnal roosting locations and nocturnal hunting fixes from their nests and those of other owls, and the diurnal and nocturnal home range shapes and sizes and their mutual overlaps, were evaluated and calculated using ArcGIS 10.5 software (Esri, Redlands, U.S.A.). Individual home ranges were established using Home Range Tools (Rodgers et al. 2007; Rodgers and Kie 2011), a freeware extension for ArcGIS. The home ranges of diurnal roosting and nocturnal hunting for each radio-tracked male were calculated based on all recorded locations/fixes using the 100% Minimum Convex Polygon method (MCP; Mohr 1947; Hayne 1949) and 50%, 90%, and 95% Kernel Density Estimation method (KDE; Silverman 1986; Worton 1989) with fixed smoothing parameter *h* established by the Least Squares Cross-Validation method (LSCV; Seaman and Powell 1996; Seaman et al. 1999; Börger et al. 2006). The diurnal roosting home range overlaps were calculated using the procedure described by Sonerud et al. (1986) only for those established by the 95% KDE method.

Results

During monitoring, 37 ± 6 (mean ± SD) locations of diurnal roosting were recorded for the three owl males. The smallest diurnal roosting home range, 7 ha, established by the 95% KDE method, was recorded for the tawny owl male, while range sizes of 117 and 111 ha were recorded for the boreal and pygmy owl males, respectively (Fig. 1). The home range sizes calculated using other methods, including further details, are given in Table 1.

The joint total overlap of the three monitored males' diurnal roosting home ranges (95% KDE) was 0.3%. The largest roosting home range overlap of 55.2% was recorded for the boreal and pygmy owl males; the overlaps of their roosting ranges with that of the tawny owl male were 1.7% and 3.7%, respectively.

Tab. 2. The owls' nest distances. The individual between-nest distances of the three radio-tracked males (Eurasian pygmy owl, boreal owl and tawny owl), including the nest of eagle-owl pair, and mean (± standard deviation) and minimum and maximum (range) distances of the three tracked males' nocturnal hunting fixes and diurnal roosting locations from their own and other owl's nests.
Tab. 2. Vzdialenosti hniezd sov. Individuálne vzdialenosti medzi hniezdami troch rádiovo sledovaných samcov (kuvička vrabčieho, pôtika kapcavého a sovy lesnej) vrátane hniezda páru výra skalného a priemerné (± smerodajná odchýlka) a minimálne a maximálne (rozsah) vzdialenosti nočných loveckých a denných odpočinkových lokalizácií troch sledovaných samcov od ich vlastných a ostatných hniezd.

Nest	Distance of pygmy owl nest		Distance of boreal owl nest		Distance of tawny owl nest	
boreal owl	900		-		-	
tawny owl	1266		558		-	
eagle-owl	250		872		1323	
Nest	Distance of pygmy owl roosting locations (n = 30)		Distance of boreal owl roosting locations (n = 44)		Distance of tawny owl roosting locations (n = 37)	
	range	mean ± SD	range	mean ± SD	range	mean ± SD
pygmy owl	35–1164	372 ± 296	34–2066	698 ± 458	1257–1695	1519 ± 161
boreal owl	80–1276	717 ± 285	178–2082	937 ± 507	498–832	676 ± 109
tawny owl	162–1721	1034 ± 382	226–2609	1303 ± 584	84–965	565 ± 348
eagle-owl	116–1195	452 ± 266	118–2024	649 ± 447	1300–1600	1486 ± 107
Nest	Distance of pygmy owl hunting locations (n = 91)		Distance of boreal owl hunting locations (n = 175)		Distance of tawny owl hunting locations (n = 210)	
	range	mean ± SD	range	mean ± SD	range	mean ± SD
pygmy owl	16–982	341 ± 236	56–1251	598 ± 322	658–2236	1474 ± 334
boreal owl	80–1472	749 ± 298	7–1589	569 ± 417	33–1489	700 ± 305
tawny owl	284–1943	1089 ± 341	95–2042	917 ± 459	17–1478	470 ± 302
eagle-owl	17–1039	433 ± 202	50–1253	619 ± 295	760–2295	1489 ± 328

The distances among individual nests, along with the mean distances among males' diurnal roosting and nocturnal hunting locations/fixes from other owls' nests, showed that the tawny owl male remained at a considerably greater distance from the eagle-owl's nest compared to the pygmy and boreal owl males. The specific distances are presented in Table 2.

The males of the two smaller owl species (pygmy and boreal owl) primarily hunted in forest interiors and at the forest edges next to the sapling and clear-cut areas, i.e., at inner forest stand edges (overall 85% and 75%, respectively). In contrast, the larger tawny owl male predominantly hunted at the forest edges adjacent to agricultural fields and meadows, i.e., at outer forest stand edges (in 56%). For resting during diurnal roosting, all three monitored males primarily used Norway spruce trees, more specifically 56%, 93%, and 79% for the pygmy, boreal and tawny owl male, respectively. Further details regarding the males' habitat choice for diurnal roosting and nocturnal hunting are provided in Table 3.

The analysis of pellets and leftovers from the nest-boxes showed that the pygmy owl male hunted during the breeding season mainly passerine birds. In contrast, the boreal owl male focused primarily on hunting small mammals, predominantly common shrews (*Sorex araneus*) and yellow-necked mice (*Apodemus flavicollis*). The diet of the tawny owl male was relatively diverse and included mammals, birds, amphibians, reptiles and even fish. The species hunted most frequently by the tawny owl male were the common vole (*Microtus arvalis*) and the Eurasian water shrew (*Neomys fodiens*) (Table 4). The overlap of food niches ranged from 0.1 (for the boreal and tawny owl males) through 0.35 (for the pygmy and boreal owl males) to the highest value of 0.4 (for the pygmy and tawny owl males).

Discussion

We found the tawny owl male roosted during the day at a respectful distance from the eagle-owl's nest site in all cases. In contrast, the eagle-owl nest site was included within the diurnal roosting home ranges of smaller owl species, the pygmy and boreal owl. These results on space arrangements of roosting home ranges of the three

Tab. 3. Owls' habitat choice. The roosting places (tree species or nest-box) used for diurnal resting and composition of habitats used during the nocturnal hunting (based on KDE 95% home ranges) by the three radio-tracked male owls (Eurasian pygmy owl, boreal owl, and tawny owl) during the breeding season. The proportion of used roosting sites (%) and their observed numbers in particular places, as well as the proportion of habitats (%) and their areas in hectares used during hunting, are given for each male.
Tab. 3. Výber biotopov sovami. Miesta odpočinku (druhy stromov alebo hniezdna búdka) využívané na denný odpočinok a zloženie biotopov využívaných počas nočného lovu (na základe KDE 95 % domovských okrskov) tromi rádiovo sledovanými samcami sov (kuvička vrabčieho, pôtika kapcavého a sovy lesnej) počas hniezdneho obdobia. Pre každého samca je uvedený podiel využívaných odpočinkových miest (%) a ich pozorovaný počet na jednotlivých miestach, ako aj podiel biotopov (%) a ich plochy v hektároch využívaných počas lovu.

	pygmy owl	boreal owl	tawny owl
Habitat choice during diurnal roosting (number of locations)			
Norway spruce (*Picea abies*)	56.1% (9)	93.1% (41)	78.9% (30)
Scots pine (*Pinus sylvestris*)	31.3% (5)	-	-
European beech (*Fagus sylvatica*)	-	-	15.8% (6)
common alder (*Alnus glutinosa*)	6.3% (1)	-	-
European larch (*Larix decidua*)	6.3% (1)	2.3% (1)	-
silver fir (*Abies alba*)	-	2.3% (1)	-
sycamore (*Acer pseudoplatanus*)	-	2.3% (1)	-
empty nest-box	-	-	5.3% (2)
Habitat choice during nocturnal hunting (area in hectares)			
Norway spruce dominated forest stands	50.5% (54)	45.8% (71)	24.6% (64)
deciduous trees dominated forest stands	6.5% (7)	6.5% (10)	7.3% (19)
sapling and clear-cut areas	28.0% (30)	22.6% (35)	11.9% (31)
agricultural fields and meadows (forest edges)	15.0% (16)	25.1% (39)	56.2% (146)

studied owl males concerning the eagle-owl's nest site fit the previous findings on their hunting home ranges (Stehlíková Sovadinová et al. 2025). The pygmy and boreal owl male hunting range overlapped by 78%; in contrast, their hunting ranges overlapped with that of the tawny owl male only by 15% and 25%, respectively. Similar to the currently described roosting ranges, the tawny owl's hunting range was situated at an apparent distance from the eagle-owl's nest site compared to the hunting ranges of the two smaller owl species that both contained it (Stehlíková Sovadinová et al. 2025). Thus, the roosting home range space arrangements align with and support our previous conclusions that medium-sized owl species may avoid areas occupied by apex intraguild predator/s (Stehlíková Sovadinová et al. 2025). In contrast, the small owl species may use the apex intraguild predator/s for their protection, likely because they do not represent suitable prey. Thus, apex intraguild predator/s may indirectly create a "protective umbrella" effect, providing refugia free from medium-intraguild enemies for the smaller species (Stehlíková Sovadinová et al. 2025).

The fact that the pygmy and boreal owl males had almost identical diurnal roosting home ranges (Fig. 1) and nocturnal hunting home ranges (Stehlíková Sovadinová et al. 2025), too, and shared their environment so closely, although they also are intraguild enemies, is fascinating. On the other hand, they pose only a minor threat to each other, and attacks by boreal owl on pygmy owl have been observed only very rarely (Mikkola 1983; Korpimäki and Hakkarainen 2012). The very close spatiotemporal sharing of the environment by boreal and pygmy owls is probably enabled by their different dietary preferences during the breeding season (Korpimäki and Hakkarainen 2012; Šotnár et al. 2015). This was also reflected in our analysis of the owls' diets, confirming that boreal owl is a food specialist focusing on voles (Korpimäki and Hakkarainen 2012), while the primary prey of the pygmy owl during breeding consists of passerine birds (Mikusek et al. 2001). Moreover, there is temporal segregation within the hunting activities of the two species because boreal owls hunt exclusively at night (Korpimäki 1981), while pygmy owls' are a crepuscular species (Mikkola 1983; Pačenovský and Šotnár 2010). Lastly, our findings regarding the closely shared home range areas of the two petite owl

Tab. 4. The diet composition of the Eurasian pygmy owls, boreal owls and tawny owls collected in Křižanovská vrchovina (the Krizanov Highlands), Vysočina region, Czechia, in the year 2022, and expressed by the count of individuals found in pellets or leftover nesting materials (see Materials and Methods for methodological details).

Tab. 4. Zloženie potravy kuvička vrabčieho, pôtika kapcavého a sovy lesnej zozbieranej na Křižanovskej vrchovine v kraji Vysočina v Česku v roku 2022 a vyjadrené počtom jedincov nájdených vo vývržkoch alebo zvyškoch hniezdneho materiálu (pre viac podrobnosti pozri Materials and Methods).

	pygmy owl		boreal owl		tawny owl		Total	%
Species	natural cavity	roosting place	natural cavity	roosting place	natural cavity	roosting place		
Talpa europaea					2	1	3	0.73
Sorex araneus	2- 0	1- 0	1+ 52	1	50	1- 25	128	31.7
Sorex minutus	1		1	1	2	1+ 11	16	3.88
Neomys milleri						1	1	0.24
Neomys fodiens	1				1+ 10	3	14	3.40
Crocidura leucodon						1	1	0.24
Lepus europaeus						1	1	0.24
Muscardinus avellanarius			4	1	4	5	14	3.40
Micromys minutus				1		2	3	0.73
Apodemus flavicollis	4	1	1+ 25	3	1- 8	18	59	14.32
Apodemus sylvaticus		1	1	1	12	8	23	5.58
Clethrionomys glareolus	1+ 8	2	9	5	17	1- 5	46	11.17
Arvicola amphibius					3		3	0.73
Microtus subterraneus						1	1	0.24
Microtus arvalis		3	2- 0	1	13	1+ 21	38	9.22
Microtus agrestis		4				1	5	1.21
Sylvia communis					1		1	0.24
Sylvia atricapilla	1						1	0.24
Phylloscopus trochilus						1	1	0.24
Regulus sp.	1			1			2	0.49
Erithacus rubecula	1	1			1		3	0.73
Turdus merula					3	3	6	1.46
Turdus pilaris					3		3	0.73
Turdus iliacus						1	1	0.24
Turdus philomelos					1	2	3	0.73
Turdus viscivorus					1	1	2	0.49
Aegithalos caudatus	1						1	0.24
Parus major	1						1	0.24
Periparus ater		1					1	0.24
Cyanistes caeruleus	1						1	0.24
Poecile palustris	3						3	0.73
Sitta europaea		1					1	0.24
Certhia sp.	1						1	0.24
Emberiza citrinella					1		1	0.24
Fringilla coelebs					1	2	3	0.73
Loxia curvirostra	1						1	0.24
Garrulus glandarius					1	1	2	0.49
Passeriformes sp.	1						1	0.24
Passeriformes sp. juv			1				1	0.24
Rana temporaria					7	2	9	2.18
Zootoca vivipara						1	1	0.24
Serpentes sp.					1		1	0.24
Cypriniformes sp.						2	2	0.49
Coleoptera sp.					2		2	0.49
Mammalia	**1- 14**	**11**	**92**	**14**	**121**	**104**	**356**	**86.41**
Aves	**1+ 12**	**3**	**1- 1**	**1**	**13**	**11**	**41**	**9.95**
Amphibia, Reptilia, Pisces	**0**	**0**	**0**	**0**	**8**	**5**	**13**	**3.16**
Evertebrata	**0**	**0**	**0**	**0**	**2**	**0**	**2**	**0.49**
Total	**26**	**14**	**93**	**15**	**144**	**120**	**412**	**100**
Diversity index H'	**2.28**	**1.91**	**1.19**	**1.95**	**2.33**	**2.55**	**2.53**	

species align with observations that pygmy owls did not spatially avoid boreal owls even though the presence of the latter species can exert a negative influence on the reproductive success of pygmy owls (Morosinotto et al. 2017).

The roosting ranges (95% KDE) of the two smaller owl species males were of comparable size, which was also the case for their hunting ranges. In contrast, the male tawny owl's roosting range was tiny, approximately 16 times smaller than the pygmy and boreal owl roosting ranges and around 40 times smaller than his hunting range. This difference is hard to explain, but we can speculate that it was due to habitat composition and the individual's preference for roosting in specific forest stands. The tawny owl male used roosts exclusively in two small patches near his nest-box, invariably in the very dense treetops of relatively young mixed spruces and beeches. The male likely returned regularly to familiar and safe locations where he could hide perfectly during the day, a presumption which aligns with findings that tawny owls avoid roost sites where they have been mobbed in the past (Flasskamp 1994), preferring instead sites which offer protection against avian predators and mobbers (Sunde et al. 2003).

The male owls' hunting home range sizes recorded during the breeding season (snap-trapping at the study site revealed prey abundance of 4.2 small mammals captured per 100 trap-nights) are comparable with those reported previously for all three study species. For example, different studies have recorded pygmy owls' mean hunting home range sizes of 67 ha (Barbaro et al. 2016), 95 ha (Baroni 2022) and 173 ha (Rothgänger 2023), while research from Norway has identified pygmy owls' ranges around three times larger than those in our study (median = 230 ha), but they monitored pygmy owls also during the non-breeding seasons and in the low phase of the vole cycle (Strøm and Sonerud 2001). The difference between these and our results can be explained by the fact that we tracked the male pygmy owl during the breeding season only, moreover with high prey abundance, and it is widely known that high abundances of prey species can negatively affect hunting home range sizes (Kouba et al. 2017). Regarding tawny owls, our findings match the mean hunting home ranges of 196 ha (Burgos and Zuberogoitia 2020) and 213 ha (Choi et al. 2020) recorded in other studies. The hunting home ranges of boreal owls have also been studied, including two studies from Czechia. The mean home range size recorded during the breeding season in the Ore Mts. was 191 ha (Kouba et al. 2017), while the ranges of two males from the Jizera Mts. covered an area of 310 ha (Kouba and Tomášek 2018). The findings of the first study are clearly closer to those of our research, while the ranges observed in the second study are two times larger.

The sizes of diurnal roosting home ranges were not correlated with the study species' weight (i.e., the body mass of the tracked individuals). This finding is not consistent with the 'body weight hypothesis', which posits that larger species inhabit more spacious home ranges because the overall higher energy needs for themselves and their offspring require them to hunt in larger areas (Harestad and Bunnel 1979; Saiful et al. 2001; Ottaviani et al. 2006). Unlike the diurnal home ranges, the sizes of nocturnal hunting ones correlated positively with the study species' weight. These findings demonstrate that very different factors determine the sizes of roosting compared to hunting home ranges. In this context, however, it is essential to note that the hunting home ranges of the nesting male owls are also influenced by other external factors, such as prey abundance and the number of fledglings (Campioni et al. 2013; Kouba et al. 2017). However, because the three owl males were tracked under the same circumstances and inhabited the same spatiotemporal environment, thereby exposing them to identical external influences, it is possible to suggest that the species' body mass is one of the decisive factors determining their hunting home range size.

This study provides new insights into the three jointly exanimated aspects: the sizes and spatial arrangements of diurnal roosting home ranges, diet composition, and roosting sites of males of three owl species, the pygmy, boreal and tawny owl, during the breeding season within the area of sympatry also inhabited by an apex intraguild predator, the eagle-owl. The results of this study indicate that intraguild competitors/enemies may mitigate direct conflict through spatial avoidance and dietary differentiation. This partial niche separation may help to reduce food competition within the guild, promoting coexistence among species.

In conclusion, however, we acknowledge the limitations of our case report study. Our sample size is undoubtedly limited, and the study results should be taken as preliminary and not generalised. Finally, we encourage researchers to employ similar study designs to investigate interactions among multiple sympatric intraguild species under identical spatiotemporal conditions, as this topic has been considerably understudied to date.

Ethics Approval

Owl males were trapped, handled and tagged under Permit No. ŽP/163/2020-chme /351/2020 issued by the Ministry of the Environment of the Czech Republic and ringed under the supervision of the Ringing Centre of the National Museum in Prague, Permit No. 1172.

Data Availability

The raw data supporting this article are available from the corresponding author upon reasonable request.

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Received 1.3.2025
Accepted: 24.4.2025