Habitat alteration impacts predation risk in an aposematic amphibian

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Abstract

Predator-prey interactions can be viewed as an evolutionary arms race influenced by environmental factors. Forest management, for example, can influence such interactions and alter community structure. A common anti-predator strategy, known as aposematism, lies on the coupling of warning signals with secondary (e.g., chemical) defences to deter predators. The European fire salamander (*Salamandra salamandra*), an emblematic, aposematic amphibian of the Vienna woods, has distinct yellow and black warning colouration and skin toxins that protect it from most predators. Previous research has shown that the amount of yellow in their dorsum is negatively correlated with predation attempts. Here, we compare predation rates on clay models of fire salamanders with the same amount of dorsal yellow colouration distributed across either many small or few large markings, and placed in either protected or managed zones of the Biosphere Reserve Wienerwald. We observed no differences in predation rates based on marking size: all models were attacked with similar frequency. However, we found that bird attacks were more frequent in managed forest zones than in protected ones. The main differences between these forest zones were in tree diversity and evenness. We suggest that forest structure and complexity may lead to differences in either abundance or composition of predator communities which, in turn, might influence attack rates. Finally, we highlight the importance of protected zones as potential havens for fire salamanders, and propose further research to test specifically the effect of differences in predator community composition on predation risk across forest zones.

Keywords: predator-prey interactions; warning signals; forest management; Biosphere Reserve Wienerwald; clay models

Introduction

In the last decades the impacts of disturbances, discrete events that disrupt ecosystems, communities or populations and alter their resources or physical environment (White and Pickett 1985), have increased remarkably, leading to higher ecosystem heterogeneity and changes in wildlife communities and their dynamics (Turner 2010). Land use, for example, can change the dynamics between predators and their prey by altering habitat structure (Kuntze et al. 2023; Labadie et al. 2023), leading, for instance, to differences in species abundance as a function of the intensity of human impact (Thompson and Donelly 2018). Likewise, changes in forest structure, which range from sustainable management to extensive clear-cutting, can alter the habitats of bird (Czeszczewik et al. 2015; Reif et al. 2022), mammal (Krojerová-Prokešová et al. 2016; Zárybnická et al. 2017), amphibian (Asad et al. 2022; Kpan et al. 2021) and arthropod (Grevé et al. 2018; Lange et al. 2011; Leidinger et al. 2019) communities.

Management practices in European temperate forests have been in place for centuries (McGrath et al. 2015) with known effects on biodiversity at different levels (Zavala and Oria 1995; Spiecker 2003). Bird species richness and stability are higher in protected zones than in managed ones (Floigl et al. 2022), whereas generalist species of small mammals tend to increase with clear-cutting (Bogdziewicz and Zwolak 2014). However, all managed zones are not equal, as they can have fine-scale differences in habitat complexity (Liira et al. 2007). Such differences can, in turn, affect interactions such as those between predators and prey (Vélová et al. 2021). For example, habitat heterogeneity within managed zones has been identified as a reliable predictor of decreased predation pressure for adders. However, for mammalian predators, this is only the case in non-linear habitats (Duchesne et al.

2022). The risk of predation by avian predators, in contrast, is not affected by habitat linearity (Duchesne et al. 2022). Taken together, this suggests that comparing predation risk between managed and protected forest zones, or among differently managed zones, requires having finer measures of habitat characterisation (Liira et al. 2007).

Changes in predator community composition can alter the magnitude and direction of selection pressure on prey animals (Rönkä et al. 2020), and thus shape their anti-predator adaptations. Colouration is often a crucial component of such adaptations, enabling animals to either blend in with their surroundings (Nokelainen and Stevens 2016), or to stand out with conspicuous colour patterns that warn predators about their unprofitability as prey (Rojas et al. 2015). Species exhibiting the latter, known as aposematic (Poulton 1890), are expected to have limited phenotypic variation within populations (Kapan 2001; Joron and Mallet 1998; Mallet and Barton 1989), as deviations from the most common signal may prevent predators from learning the association between colouration and unprofitability. However, differences in predator community composition have been proposed as a possible mechanism contributing to the maintenance of within-population phenotypic variation in aposematic species (Nokelainen et al. 2014; Rönkä et al. 2020).

The fire salamander (*Salamandra salamandra*) is widely distributed throughout Europe, where it inhabits mixed deciduous forests (Thiesmeier 2004). Its characteristic warning colouration, which consists of conspicuous yellow markings on a contrasting black background (Thiesmeier 2004), is considered a qualitatively reliable signal of their possession of chemical defences (Barzaghi et al. 2022; Lüddecke et al. 2018). In Central Europe, fire salamanders show an irregular pattern consisting of a mix of dorsal yellow spots and stripes (Thiesmeier 2004), which varies within and between populations in e.g. size, number and colour intensity (Brejcha et al. 2021; Preißler et al. 2019). Using fire salamander clay models, Caspers et al. (2020) showed that models with a higher proportion of yellow are attacked at a lower rate, despite the apparent lack of correlation between higher amounts of yellow colouration and increased toxicity in this species (Preißler et al. 2019; Sanchez et al. 2019). While adult fire salamanders appear to be well protected from predators, with only a few known bird and mammal predators (e.g., birds of prey: Bustamante 1985, Łaciak 2022, rats: Velo-Antón 2024, wild-boars: Thiesmeier and Grossenbacher 2004), juveniles seem to be more vulnerable to predation. Indeed, species such as rats, chickens, and ducks, have been reported to feed on them (Horter and Greven 1981), likely because metamorphs are as conspicuous as adults but less chemically defended (Sanchez et al. 2019).

Here, we focused on one of the fire salamander hotspots in Austria, the Biosphere Reserve Wienerwald (BRWW), and used clay models of juvenile fire salamanders to test whether predation risk on this species varies in function of (1) whether they are in a protected or managed forest zone; and (2) marking size, given the same amount of yellow (e.g. colouration distributed across many small or a few big yellow markings). We hypothesised that (1) attack rates will differ between protected and managed forest zones, with higher predation rates in protected zones due to more diverse and specialist predator species (Carrara et al. 2015; Mönkkönen et al. 2014), higher efficiency in prey capture (Andruskiw et al. 2008), and predator preferences for foraging in mature forest zones (Beier and Drennan, 1997); and (2) that models with larger markings will face a lower attack rate, as increasing pattern element size enhances warning signals (Preißler and Pröhl 2017), independently of body size (Remmel and Tammaru 2011). Alternatively, models with larger markings could be more frequently attacked due to greater detectability while those with smaller markings may blend in better with the surrounding environment, benefiting, for example, from distance-dependent aposematism (Barnett et al. 2017).

Methods

Study area

The BRWW, where fire salamanders (*Salamandra salamandra*) are highly abundant (Sztatecsny et al. 2014), was founded in 2005 and stretches over parts of Lower Austria and the city of Vienna in eastern Austria (Fig. 1). One of the principal criteria for conferring this status is the establishment of distinct zones for the management and protection of biodiversity in accordance with human development and well-being (UNESCO 2022). Therefore, 37 zones became protected (core) areas in 2005. In these areas no forestry occurs and the concept of process-oriented nature conservation is pursued: dead trees are left in place as coarse woody debris, providing microhabitats and refugia for insects and other species (Pabijan et al. 2023), and in turn contributing to a more complex habitat structure. The managed areas, in contrast, are subject to ongoing management activities, including timber harvesting. For the present study, a total of six distinct locations were selected, comprising three protected (e.g., Fig. 2a) and three managed zones (e.g., Fig. 2b). The distance between each managed zone and its corresponding protected zone was approximately 2 km (Fig. 1). All zones were composed of either pure beech (*Fagus sylvatica*) forests or mixed forests where beech trees were dominant. Data on the forest structure was provided by the Österreichische Bundesforste AG (Öbf AG) for forest patches within the specific zone; forest patches are designated, smaller compartments within the forest based on their structure and composition. Specifically, we used data on number of strata (designated as 1, 2 or 3, based on the extent of stratification: stratum 1 represented the most abundant layer in the absence of rejuvenation, while strata 2 and 3 represented the next and final stages of rejuvenation, respectively) and their relative abundance, the mean age of every stratum (years), and the number of tree species and relative abundance of each species in each stratum. We use this data to compute a Simpson index of diversity ($D = -\boldsymbol{\Sigma}(p_i^2)$), where p is the proportion of a species in relation to the total number of species (Simpson 1949). If a forest patch had more than one strata we used a weighted index based on the proportion of strata within the patch. Additionally, we calculated the Shannon index ($H' = -\boldsymbol{\Sigma} p_i * \ln p_i$) (Shannon 1948).

In each zone, clay models were deployed along one to three transects of approximately 500–750 m in length, primarily along pre-existing trails. The number of transects per zone was contingent on forest conditions, specifically changes in visibility, light conditions, and forest structure. Transects were positioned at a minimum distance of 500 m from one another. All landscape analyses and visualisations were made using QGIS (version 3.30.1) (QGIS Development Team 2023).

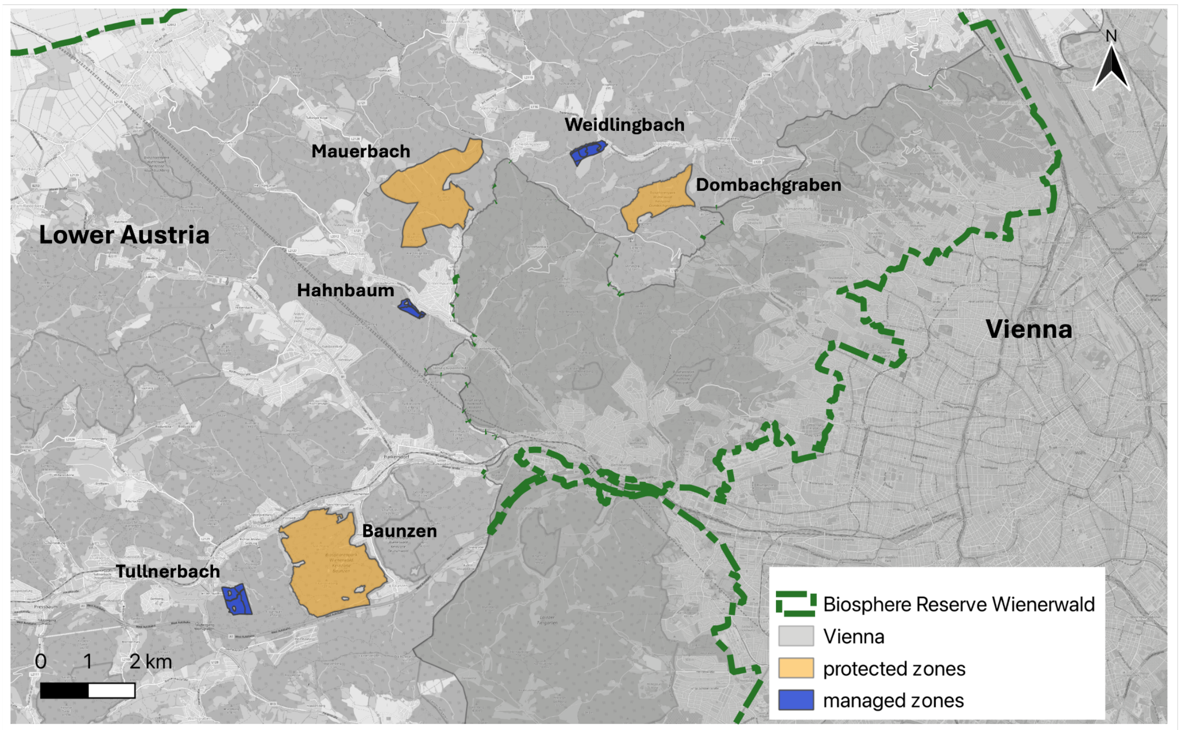


Fig. 1 Map of our study sites in Lower Austria, within the Biosphere Reserve Wienerwald. Protected zones (N = 3) are shown in yellow and managed zones (N = 3) in blue, Source Basemap: OpenstreetMap.org

Clay model elaboration and deployment

We crafted 800 clay models out of Noris® plasticine clay (8421-9, black) using a silicon-rubber template made from a 3D-printed resistant model of a juvenile fire salamander (snout-vent length 3.5 cm) and disposable gloves to minimise the transfer of human odour. We painted the plasticine models with non-toxic and odourless yellow paint (Akademie ® acrylic colour, series: 23 224, pigment: PW6 PY74 PY3). We wanted to test whether the distribution of yellow markings on the dorsum (i.e., a few large markings (Fig. 2c) vs. many small (Fig. 2d)) has an influence on predation risk. Therefore, we created two morphs with the same amount of yellow colouration but with either three large (Fig. 2e, top) or 12 small markings (Fig. 2e, bottom). We used plastic Pasteur pipettes whose tips were cut to get circles of 4 mm (large marking treatment; LM) or 2 mm (small marking treatment; SM). We placed the models along the transects, starting randomly with either a SM or LM model, then alternating the morphs. We placed models approximately 5 m apart from each other on a leaf found in the leaf litter to ensure a similar background for all, and used environmental structures like tree trunks, logs, or rocks to maximise retrieval. In total, we deployed 800 models (LM = 399; SM = 401), which were left in the forest for either five (one site in the “Dombachgraben” protected zone) or four (the remaining five sites) days and subsequently checked for any signs of predation attempts (see details below) and collected. In the protected zones “Dombachgraben” and “Baunzen”, we placed 130 and 150 models along one transect, respectively. In the managed zones “Weidlingbach” (N = 150) and “Hahnbaum” (N = 100) we placed models along two transects and in the last two, protected zone “Mauerbach” (N = 150) and managed zone “Tullnerbach” (N = 120) we placed them along three transects. All models were deployed between mid-April and early May 2023, which coincides with one of the peak activity periods for adult fire salamanders and post-metamorphic individuals from the previous year. Therefore, the latter should be encountered in high frequencies.

Assessment of predation attempts

Upon collection, models were thoroughly inspected for any marks that indicated a predation attempt. Attack marks were assigned directly in the field to different predator types, i.e., bird, mammal (with the distinction of rodent bites marks*),* or unknown, using photographs from previous studies (e.g., Rößler et al. 2020) as guidelines. Each attacked model was photographed on graph paper, examined for bite marks by three people independently, and further compared to additional reference material (see supplementary material for details, Fig. S1). Bird attacks (Fig. 2f) were identified by the U- or V-shaped and stab-like marks that the beak leaves on the model (Brodie 1993; Lawrence and Rojas et al. 2019; Low et al. 2014). Mammal bite marks (Fig. 2g) showed either distinct ‘clean’ holes probably inflicted by canines, or marks from pairs of incisors (rodents; Fig. 2h, 2i).

Fig. 2 Examples of protected (a) and managed (b) forest zones, and of fire salamanders with large (c) and small (d) markings; (e) Plasticine models representing juvenile fire salamanders with small (SM; top) and large (LM; bottom) markings; (f) bird attack on the head of a fire salamander model; (g) non-rodent mammal attack on the model’s head; rodent bite marks on a clay model (h) and on a plasticine ball (i)

Rodents do not seem to be a relevant predator of fire salamanders, except for black rats (*Rattus rattus*) (Velo-Antón and Cordero-Rivera 2011; Velo-Antón 2024), which are considered commensals of human settlements and should be less abundant in forest habitats (Aplin et al. 2003). Nevertheless, rodent marks were regularly found on clay models (Fig. 2h). Therefore, we placed 27 clay balls (yellow and black) in close proximity to the models to check whether rodents were solely attracted by the plasticine, independent of the shape and colour of our models. From 27 balls deployed, 11 showed rodent bite marks (Fig. 2i). In total, 187 bite marks on models were identified as rodent marks and these models were treated as non-attacked.

Statistical analysis

We assessed differences in tree diversity between forest zones (protected/managed) by comparing the number of tree species and age of the first tree strata, and calculated the Simpson and Shannon indices per forest patch. The number of patches (number of forest inventory zones for the specific location) differed among locations. In total, for the protected zones, we obtained data from three patches for Dombachgraben, seven for Mauerbach and four for Baunzen (protected N = 14). For managed zones, we obtained data from four patches for Weidlingbach, four for Hahnbaum and two for Tullnerbach (managed N = 10). Protected and managed forest zones are used as a grouping factor and analysis on the habitat is conducted with the data per patch. Data are analysed with Welch two sample t-tests, to account for unequal sample size and variance (Ruxton 2006) and we calculated the effect size Hedges g (Hedges 1981).

We tested for differences in predation rates between forest zones and between large- and small-marking models with binomial generalised mixed models (GLMM), one with bird attacks as response variable and a second one with mammal attacks, with the probability of attack (1, 0) corrected for deployment time, and forest zone (protected, managed), treatment (SM, LM) and their interaction as predictors. We also included a random factor (location) in each of the two models to account for the non-independency of attacks within a particular location. We checked the model fit with the AIC values. Any missing clay models were excluded from analyses. To assess whether the observed differences in proportions between two conditions (the difference between the number of attacks in protected vs. managed zones or between LM vs. SM) were indeed statistically significant, we used permutations to increase statistical power (see supplementary material).

Additionally, we investigated the influence of forest zone (managed vs. protected) and diversity indices (Shannon and Simpson) on predation probability using the number of attacks per forest patch (counted based on the model and track ID) as a response variable. We separated the analysis for bird and mammal attacks to increase statistical power. We fitted negative binomial generalised linear models because the response variables are overdispersed count data.

All data was analysed with the software R (R Core team 2024, version 4.4.1) in the RStudio interface (R Studio Team 2024, version 2024.04.2+764), using the packages AICcmodeavg (Mazerolle 2023, version 2.3.3), gridExtra (Auguie 2017, version 2.3), lme4 (Bates et al. 2015, version 1.1-35.5), MASS (Venables and Ripley 2002, version 7.3-61), DHARMa (Hartig 2022, version 0.4.6), reshape2 (Wickham 2007, version 1.4.4), vegan (Oksanen et al. 2024, version 2.6-6.1), effsize (Torchiano 2020, version 0.8.1) and tidyverse (Wickham et al. 2019, version 2.0.0).

Results

Habitat variability in managed vs. protected zones

Overall, managed zones had a higher tree species richness and showed a large effect size (number of tree species, t-test; mean: protected = 2.4, managed = 3.9, t = -2.49, df = 15.53, p = 0.03; Hedges g = -1.05, CI -1.93 to -0.17). Managed zones showed trends towards larger Shannon (t-test; mean: protected = 0.43, managed = 0.73, t = -1.82, df = 18.77, p = 0.08; Hedges g = -0.74, CI -1.59 to 0.12) and Simpson (t-test; mean: protected = 0.25, managed = 0.40, t = -1.66, df = 20.52, p = 0.11; Hedges g = -0.65, CI -1.5 to 0.20) indices with medium effect sizes. Further, managed zones were slightly younger in age, although not significantly and with a small effect size (t-test; mean: protected = 94.9 years, managed = 78 years, t = 1.08, df = 19.35, p = 0.32; Hedges g = 0.36, CI -0.47 to 1.2; Fig. 3).

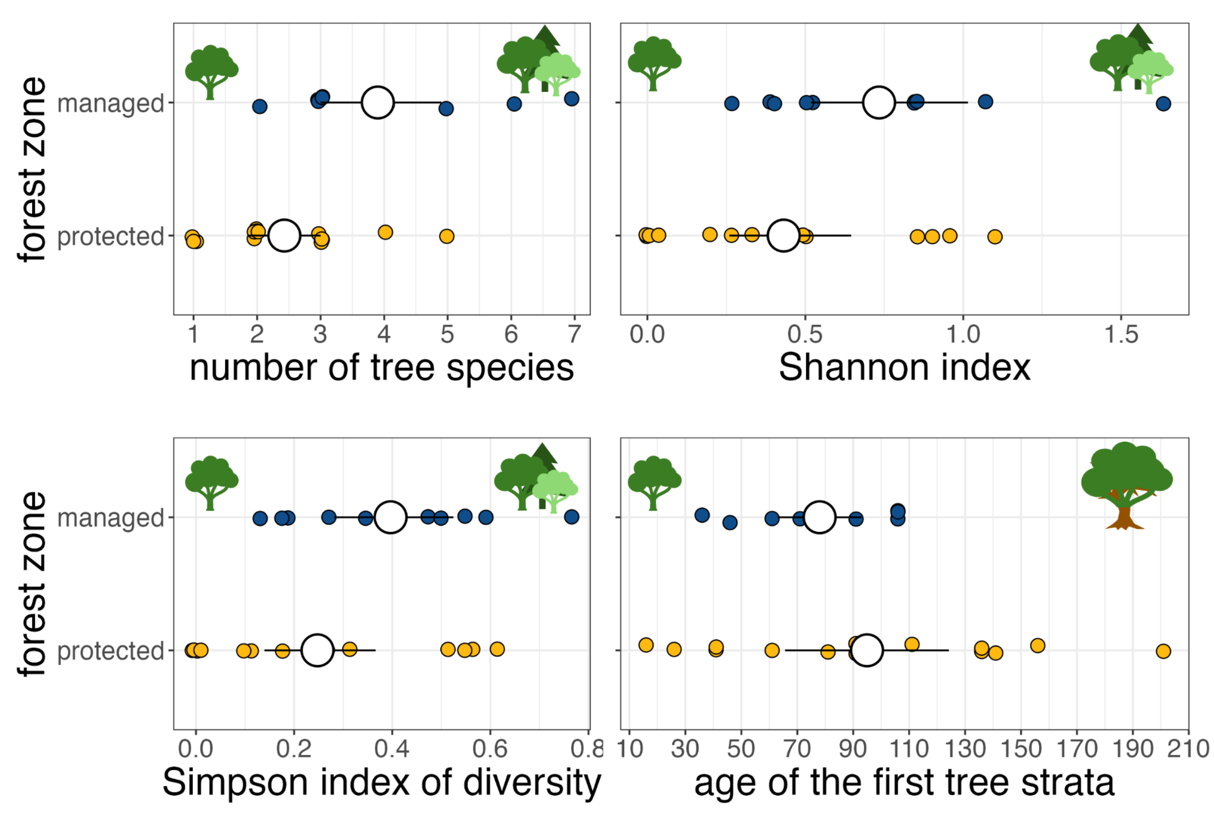
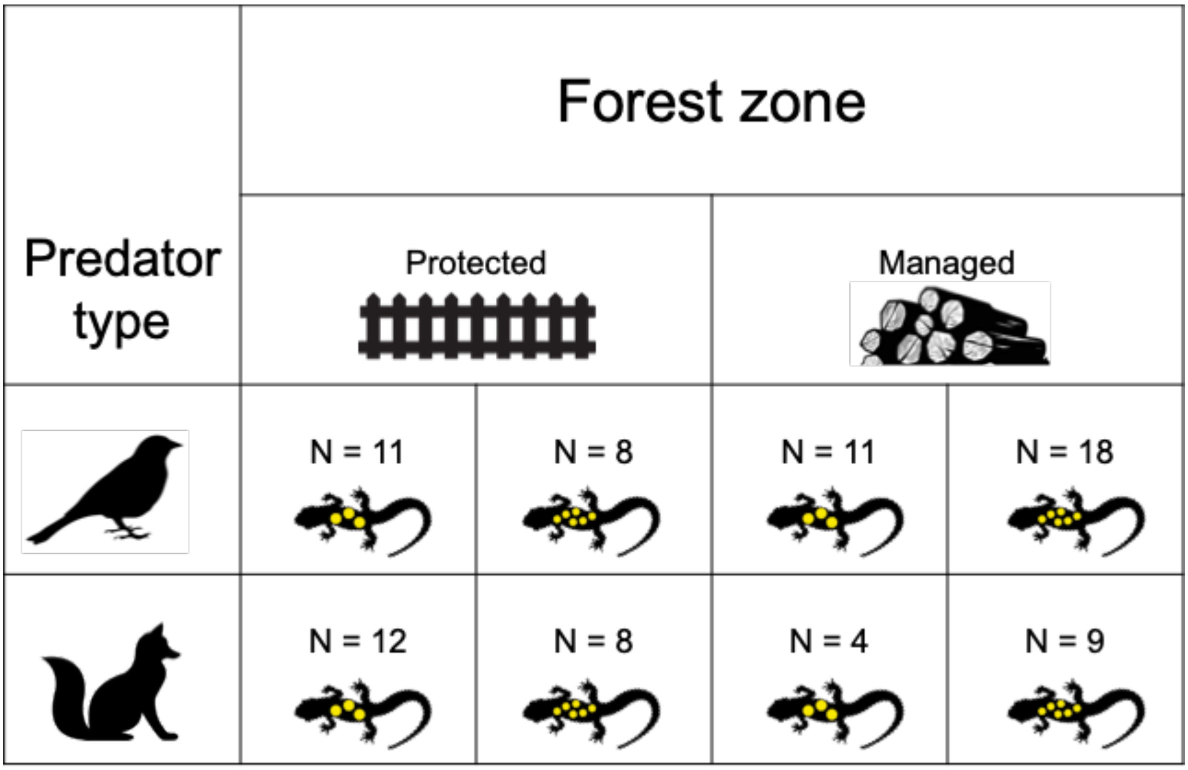


Fig. 3 Comparison of diversity measures taken in forest patches between managed (N = 10) and protected zones (N = 14). Large circles represent mean values for a specific zone and whiskers denote the 95% confidence interval. Small filled circles are raw values and are slightly jittered to increase visibility

Predation experiment with clay models

Out of the 800 models deployed, 38 were missing (4.75%, LM = 18, SM = 20). These were discarded from the analysis because their disappearance could not be attributed to predation attempts. Out of the remaining 762 models 54.1% of models were deployed in protected zones (N = 412, LM = 204, SM = 208) and 45.9 % in managed zones (N = 350, LM = 177, SM = 173). In total, 80 models (10.5%) had marks attributed to predation attempts by either birds or non-rodent mammals. Of those 80 models, one (SM) was attacked by an unknown predator, and two were attacked by both mammals and birds (both SM). We detected bird bite marks on 48 models (60%) and mammal bite marks on 33 models (40%) (Table 3).

Table 3 Summary of predation events depending on predator type (bird and mammal), forest zone (protected and managed zone) and morph (LM, SM). N models = 762, N attacks = 80. Note that two models were attacked by both types of predators and are counted twice in the summary table (not for the statistical analyses, as attacks from both predator types were analysed separately)



Predator type	Forest zone			
	Protected		Managed	
	N = 11	N = 8	N = 11	N = 18
	N = 12	N = 8	N = 4	N = 9

We found differences in attack rate based on forest zone and predator type (Fig. 4). For bird attacks, the best model showed a significant effect of forest zone, with managed forest zones having a higher probability of bird attacks (GLMM, AIC = 344.6, N = 760, estimate protected = -0.66, z = -2.2, p = 0.03). The distribution of yellow colouration had no effect on bird predation rate (estimate small marking = 0.17, z = 0.59, p = 0.56). Because the statistical models were highly singular, likely due to the use of only categorical/binary variables, we decided to check the robustness of this result by running a permutation with 10,000 iterations. We ran a permutation keeping the bird attack fixed and permuting the forest zone in which they were attacked and found that the bird attack rate was lower in protected zones (39.58%, N = 19) than in managed zones (60.42%, N = 29), (p = 0.05), confirming our model results (Fig. S2). The same approach also confirmed our finding that both morphs were equally attacked by birds (LM = 45.8%, SM = 54.2%, p = 0.65, Fig. S3).

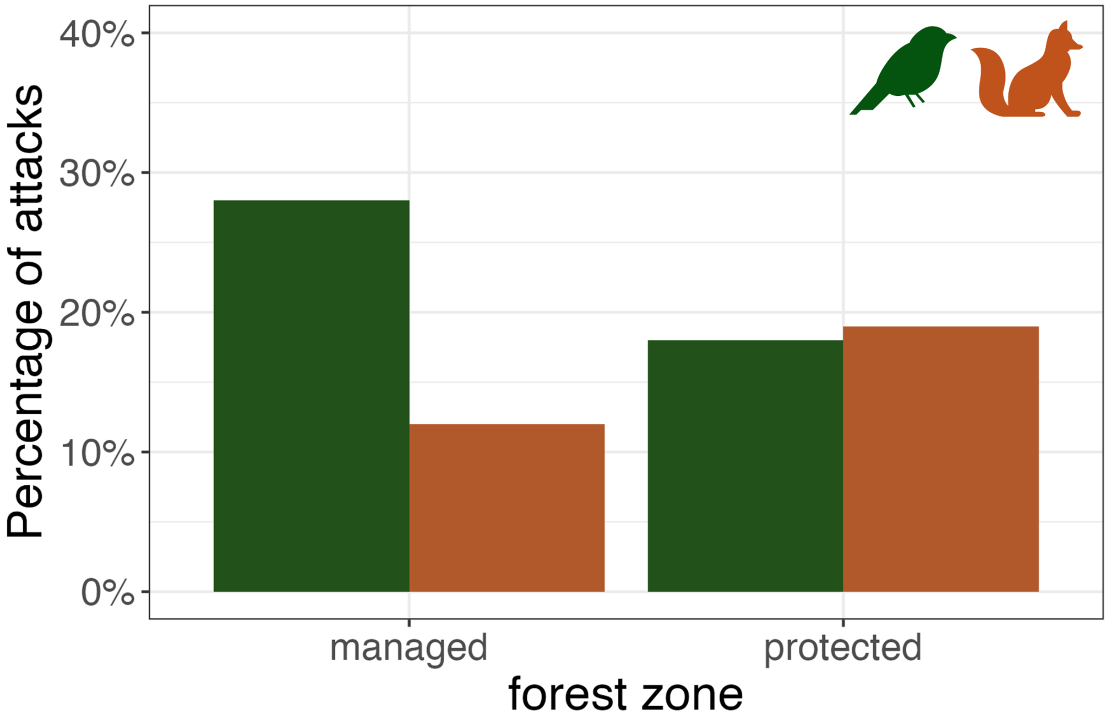


Fig. 4 Percentage of attacks by different predators (birds = green, mammals = brown) in function of forest zone (managed vs protected)

When considering mammal attacks, the model with the lowest AIC also included only the forest zone (protected/managed) as an explanatory variable. However, the difference in AIC between the two models did not exceed two, so we decided to use the model including forest zone and morph type as it was more informative. We found no effect of forest zone or morph on mammal predation rates (GLMM, AIC = 266.2, N = 760, forest zone: estimate protected = -0.20, z = 0.55, p = 0.58, morph: estimate small marking = 0.06, z = 0.16, p = 0.86). We ran a permutation with 10,000 iterations on the forest zone and morph while holding the mammal attack rate fixed. Similar to the GLMM, the forest zone was not found to influence attack rates with 60.6% (N = 20) of attacks occurring in protected zones and 39.4% in managed zones (N = 13) (p = 0.45, Fig. S4). Additionally, the distribution of yellow (large vs. small markings) did not affect the predation rate by mammals, as they were all equally attacked (LM = 48.5%, SM = 51.5%, N = 33, p = 0.87, Fig. S5).

Following previous studies where clay models were used (Rößler et al., 2018; Hernández-Palma et al. 2023), attacks on the head were considered as lethal. When we analysed patterns for such attacks, GLMM models did not follow the assumptions of normality and homoscedasticity. Thus, we ran permutations (N = 10,000) in which we first permuted the forest zone (protected/managed), and then the morph (LM/SM), while keeping the head attack rate as fixed values. Out of the 80 bite marks, 50 were located on the head. However, head attacks did not differ between zones (48% in protected zones, 52% in managed zones, p = 0.77), morphs (LM = 50%, SM = 50%) or predators (birds = 58%, mammals = 60%, p = 0.5).

We counted the number of bird and mammal attacks per forest patch to investigate whether forest diversity influenced attack numbers. Generalised linear models with a negative binomial distribution fitted best with number of bird or mammal attacks as response variable and forest zone and diversity index as predictors. The models indicate disparate trends between predator types. While the number of bird attacks exhibits a slight increase with higher biodiversity indices, the number of mammal attacks decrease with higher biodiversity indices. Additionally, we observe an interaction between forest zone and diversity index in the mammal dataset. (Fig. 5). The models for bird attack numbers explained 16.9% and 18.89% of deviance respectively, although they show only a trend and are not statistically significant (Shannon index, estimate = 0.65, SE = 0.49, p = 0.19 forest zone, estimate = 0.57, SE = 0.42, p = 0.17; Simpson index, estimate = 1.40, SE = 0.90, p = 0.12, model details supplementary material). The models for mammal attack numbers explained 24.4% and 25.7% of deviance respectively, they show a statistically significant effect of lower biodiversity indices on attack numbers (Shannon index, estimate = -3.38, SE = 1.39, p = 0.02; forest zone, estimate = 0.57, SE = 0.42, p = 0.17; Simpson index, estimate = -5.89, SE = 2.42, p = 0.02 (model details supplementary material).

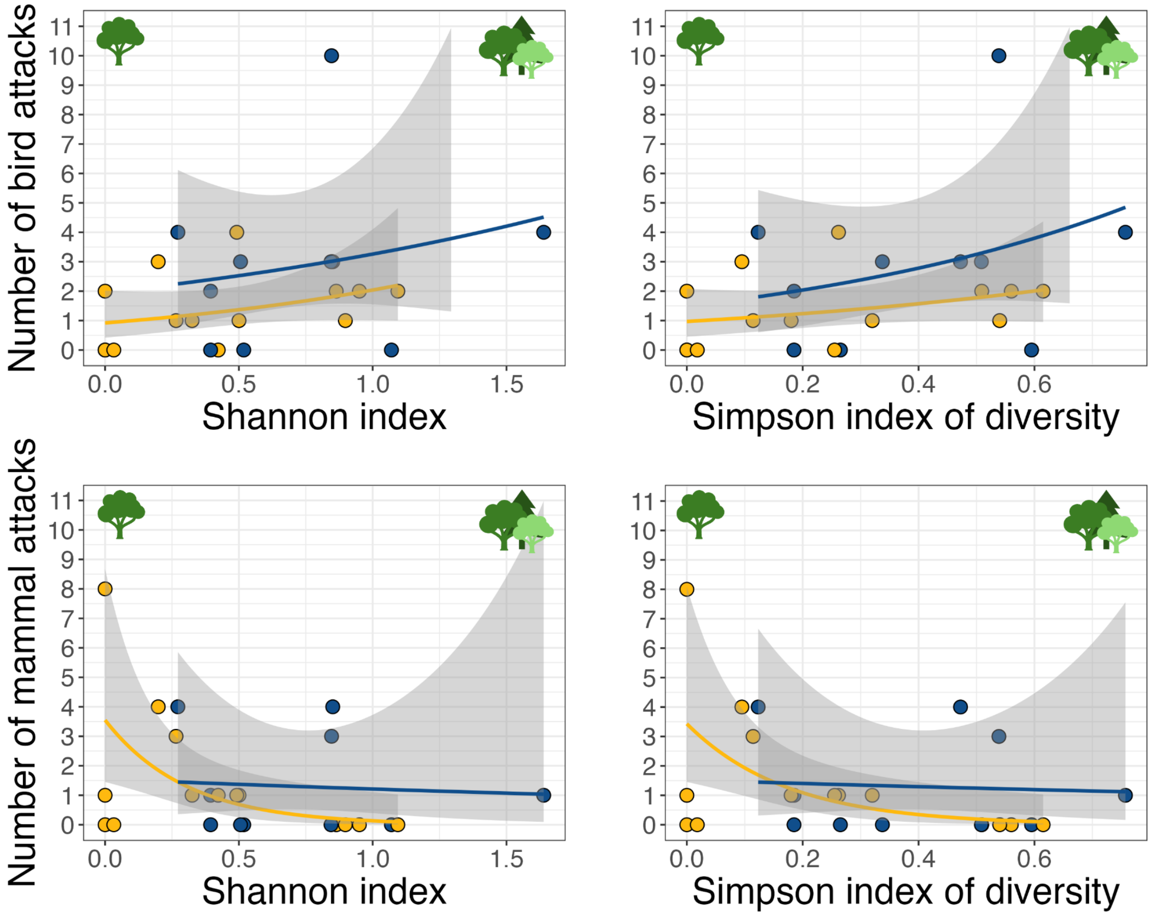


Fig. 5 Relationship between bird (upper two panels) and mammal (lower panels) attacks and diversity indices of forest patches in the two forest zones (protected = yellow, N = 14; managed = blue, N = 10). Details on statistical models in supplementary material

Discussion

Forest management practices are a form of habitat alteration known to impact animal communities and interactions such as those between predators and their prey (Floigl et al. 2022; Rönkä et al. 2020; Vélová et al. 2021). In this study, we used clay models of juvenile fire salamanders (*Salamandra salamandra*) to assess whether predation risk was higher in managed vs. protected forest zones and influenced by the salamanders' colour patterns (large vs. small markings). We found that while attacks by mammals did not differ between forest zones (despite a trend for increased predation pressure in zones with low diversity), bird attacks were more frequent in managed and diverse forest zones than in protected zones. Salamander models with small markings were as frequently attacked as those with large markings by both birds and mammals. In 62.5% of the cases, attacks were targeted at the head of the deployed models, suggesting that predators did recognise them as potential prey (attacks on vital body parts are considered lethal; Rößler et al. 2018; Hernández-Palma et al. 2023; Van Tran and Nishikawa 2023) and thus providing internal validity to our study. Below we discuss possible explanations for our findings.

Predation pressure can vary among habitats (Van Tran and Nishikawa, 2023) mainly due to changes in land use and habitat structure (Turner 2010; Labadie et al. 2023). Complex habitats may provide more refuges for prey (Pabijan et al. 2023), likely decreasing the probability of predator-prey encounters, but they can also harbour a higher diversity or abundance of predators (Ghadiri Khanaposhtani et al. 2012; Kuntze et al. 2023). The observed patterns of predation risk in our study may thus be due to differences in composition between the two forest zones, as managed zones were found to be more diverse regarding tree species and to have a higher evenness than protected zones. Further, the understorey of the managed forest zones might be more complex because it takes longer for beech forests to recover (it can take 200 years for old growth forests to reach their full biodiversity potential, Moning and Müller 2009). This may have led to higher bird density and/or species richness, as found in previous studies (Ghadiri Khanaposhtani et al. 2012; Sam et al. 2019). Indeed, bird diversity has been shown to vary based on forest type and management practices (Czeszczewik et al. 2015; Reif et al. 2022), and non-migratory birds have been shown to be more abundant in managed forests as management increases tree diversity (Schulze et al. 2019). Whether the higher frequency of bird attacks observed in managed zones is due to differences in bird community abundance or composition, warrants further research. Additionally, the distribution of generalistic mesopredators is influenced by higher landscape heterogeneity and edge effects (Günthlin et al. 2013). The observation that the largest number of mammal attacks occurred in a homogeneous protected forest zone may be attributed to variations in hunting pressure and human disturbance across the forest zones. This could potentially lead to an increase in mammal abundance within protected zones.

Clay models have proven useful for testing warning signal efficacy against predator attacks (e.g. Brodie 1993; Duchesne et al. 2022; Kuchta 2005; Saporito et al. 2007; Rojas et al. 2014, 2019; Rößler et al. 2020), with wild predators usually inflicting more attacks on models with non-aposematic colour patterns. However, in some cases, pattern geometry or distribution has proven more important than the mere presence of the warning signal (Preißler and Pröhl 2017). We predicted differences in predation rates between large and small markings, with larger markings

(LM) showing a lower predation risk due to presumed increased conspicuousness. Our alternative hypothesis stated that models with small-markings (SM) may receive fewer attacks, likely due to them benefitting from camouflage or from the so-called distance-dependent defensive colouration (Barnett and Cuthill 2014). Indeed, warning signal conspicuousness is not always necessary as long as the pattern is distinct and memorable (Valkonen et al. 2011; Wüster et al. 2004), and increased conspicuousness can sometimes lead to a higher attack rate (Dreher et al. 2015). Larger contrasting spots for the same overall amount of colouration in the strawberry poison frog, *Oophaga pumilio*, have been shown to result in fewer attacks compared to smaller ones (Preißler and Pröhl 2017). Our results, in contrast, suggest that marking size does not have an impact on the predation rate on juvenile fire salamanders, regardless of predator type. Using clay models, too, previous research has shown that the amount of yellow colouration on the dorsum is negatively related to the frequency of predator attacks in fire salamanders (Caspers et al. 2020). Further, animal vision models for birds, snakes and polecats showed that both adult and juvenile fire salamanders are conspicuous, even under dim- and night-light conditions (Aguilar et al. 2024; Sanchez et al. 2019). We therefore think that the high contrast of yellow markings, whatever the size, on a black background might be enough to provide the fire salamanders with protection from predators.

We encountered a high prevalence of rodent “attacks” on models. Although rats (*Rattus rattus)* are known to prey/scavenge on fire salamanders at particular locations (Velo-Antón and Cordero-Rivera, 2011, 2017; Velo-Antón 2024), we chose not to classify rodent bites as “attacks” for two reasons: first, because rats are not considered to be common in forests (Aplin et al. 2003); and, second, because the plasticine balls we placed to check whether rodents were “simply” attracted to the plasticine itself were “attacked” mostly by rodents and slugs. The common shrew (*Sorex araneus*) was the most likely expected rodent predator of juvenile salamanders in our study area, but the characteristic bite marks with a distinct "zigzag" pattern that shrews would leave on plasticine (see supplementary information) were not observed on any of the clay models. Other mammals such as polecats, badgers, wild boars and red foxes have been suggested to prey on fire salamanders (Thiesmeier and Grossenbacher 2004). However, while we were able to identify some of the non-rodent mammal attacks based on imprints obtained from museum specimens on plasticine (see supplementary material), in most cases it was not possible to assign such “attacks” to a specific mammal. In any case, they support previous studies indicating that mammals are likely relevant predators of fire salamanders. Like most mammals mentioned above, fire salamanders have also been reported to be nocturnal or crepuscular (Thiesmeier and Grossenbacher 2004). However, the populations observed in the BRWW and in the Vienna woods are also active during the day, particularly when it is (or has recently been) rainy (pers. obs.). Therefore, birds, which are primarily diurnal, can represent a significant pressure on fire salamanders, too. This is in line with our findings, particularly in managed areas, and with previous studies suggesting that increased diurnal activity may reflect a high predation pressure by mammals at night (Van Tran and Nishikawa 2023; Velo-Antón and Cordero-Rivera 2017; Velo-Antón 2024).

Despite the widespread use of clay models to study different aspects of predator-prey interactions, they have several limitations, such as the lack of movement, which can be crucial in the detection of prey by predators (Bateman et al.

2017). Previous research has demonstrated that moving models experience higher attack rates (Paluh et al. 2014). In addition, controlling for model detectability is challenging, leading to some extent of uncertainty about whether certain prey types are not attacked because of their phenotype or because they were not detected by a potential predator, which is particularly important when examining the role of colouration in aposematic species (Rößler et al. 2018). Finally, plasticine has a characteristic odour which can influence attacks, particularly by small mammals (Bateman et al. 2017). One more limitation is that clay models are usually placed on exposed locations. This may lead to an overestimation of attack rates, as it cannot account for the possibility that animals look for shelters to hide. Given these limitations, clay model experiments do not fully capture all aspects of predator-prey interactions, and thus these and other results need to be interpreted with caution.

While further research is needed for a comprehensive understanding of predator community composition between the managed and protected forest ones, and how these might affect selective pressures on prey animals, we highlight the importance of protected forest zones to act as potential refuges for juvenile fire salamanders. Our study highlights the intricate relationships between evolutionary strategies, ecological interactions and human land use, and emphasises the need for an integrated approach to forest management that considers the complex balance of natural ecosystems.

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Statements & Declarations

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Data availability

Data is provided within the manuscript or supplementary information files, and will be uploaded to the data repository of the University of Veterinary Medicine Vienna upon acceptance.

Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Compliance with Ethical Standards

The study was reviewed and approved by the Ethics and Animal Welfare Committee (ETK-032/03/2023) of the University of Veterinary Medicine, Vienna in accordance with the University's guidelines for Good Scientific Practice. The permit to lay out fire salamander models and to enter protected zones was given by the local state authority of nature protection in Lower Austria (RU5-BE-1936-001-2023).

CRediT authorship contribution statement

The study was conceptualised by DH, CD, MB and BR, who also defined the methodology and took part in the investigation. DH and CD were responsible for data curation and formal analysis and CD prepared the figures. The original draft was written by DH, CD and BR. BR supervised the project, obtained funding and provided resources. All authors reviewed the manuscript.