

ORIGINAL RESEARCH

Habitat alteration impacts predation risk in an aposematic amphibianD. Hagnier^{1,2,*}, C. Dittrich^{1,3,*} , M. van den Bos^{1,4} & B. Rojas¹ ¹Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine, Vienna, Austria²Department of Biology, Aarhus University, Aarhus, Denmark³Department of Biology and Environmental Sciences, University of Jyväskylä, Jyväskylä, Finland⁴Department of Biology, Graduate School of Life Sciences, Utrecht University, Utrecht, The Netherlands**Keywords***Salamandra salamandra*; predator–prey interactions; warning signals; aposematic prey; forest management; Biosphere Reserve Wienerwald; clay models; predation risk.**Correspondence**

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Abstract

Predator–prey interactions can be viewed as an evolutionary arms race influenced by environmental factors. A common anti-predator strategy, known as aposematism, relies on the coupling of warning signals with secondary (e.g., chemical) defences to deter predators. The European fire salamander (*Salamandra salamandra*) is an emblematic, aposematic amphibian of the Biosphere Reserve Wienerwald (BRWW), a forest region where both protected areas and areas with forest management can be found. Differences between these areas are likely to affect the structure of predator communities and, in turn, their interactions with prey. Fire salamanders have a distinct yellow and black warning colouration and skin toxins that provide protection from predators, and 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 BRWW. We observed no differences in predation rates based on marking size, as 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.

Introduction

In the last decades, the impacts of disturbances, discrete events that disrupt ecosystems, communities, or populations altering their resources or physical environment (White & 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). This, in turn, may trigger, for instance, differences in species abundance as a function of the intensity of human impact (Thompson & Donnelly, 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; Zárbynická 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 (Spiecker, 2003; Zavala & Oria, 1995). 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 & Zwo-lak, 2014). However, 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 (Duchesne *et al.*, 2022). 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 zone characterisation (Liira *et al.*, 2007), e.g. tree species composition and biodiversity indices.

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 & 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 (Joron & Mallet, 1998; Kapan, 2001; Mallet & 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 & 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 & 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 & Drennan, 1997); and (2) models with larger markings will face a lower attack rate, as increasing pattern element size enhances warning signals (Preißler & Pröhl, 2017), independently of body size (Remmel & Tamaru, 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).

Materials and 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 the status of Biosphere Reserve 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 forest management (no timber harvest, no reforestation) takes place, 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 were 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 the 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 used these data to compute a Simpson index of diversity ($D = -(p_i^2)$), 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 stratum, we used a weighted index based on the proportion of strata within the patch. Additionally, we calculated the Shannon index ($H' = -\sum p_i \ln p_i$) (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, we paid attention to changes in the light environment and forest structure to make sure that a single transect had similar conditions throughout. This ensured, for example, that a given transect did not have a segment under a closed canopy and another segment in an open area. 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).

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 chose to use juvenile-sized clay models because juveniles appear to be more vulnerable to predation than adults (Thiesmeier, 2004). 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 an SM or LM model and 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 5 (one site in the

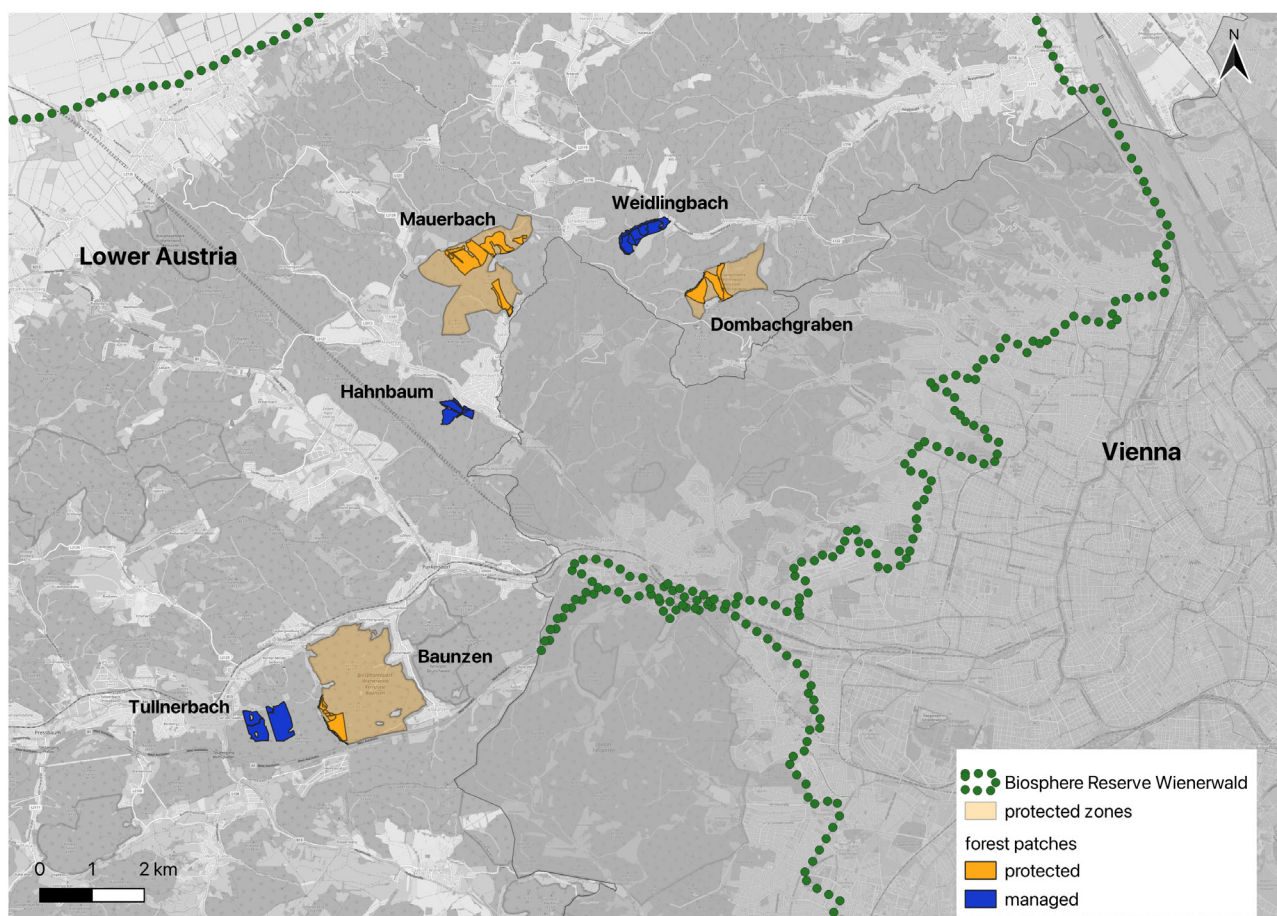


Figure 1 Map of our study sites in Lower Austria, within the Biosphere Reserve Wienerwald. Protected zones ($N = 3$) are shown in orange shading and single forest patches used for the analysis of forest parameters in orange. The managed zones ($N = 3$) and respective forest patches used for analysis are shown in blue. Source Basemap: [OpenstreetMap.org](https://openstreetmap.org).



Figure 2 Examples of (a) protected and (b) managed forest zones and of fire salamanders with (c) large and (d) small 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 body; rodent bite marks on (h) a clay model and on (i) a plasticine ball.

“Dombachgraben” protected zone) or 4 (the remaining five sites) days. Differences in time of exposure in our analysis were accounted for in the statistical analyses. The models were 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., birds, mammals (with the distinction of rodent bite 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 the 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 *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,i).

Rodents do not seem to be a relevant predator of fire salamanders, except for black rats (*Rattus rattus*) (Velo-Antón, 2024; Velo-Antón & Cordero-Rivera, 2011), 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 the 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, depending on where our transects were

placed. 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 of the habitat was conducted with the data per patch. Data were analysed with Welch's 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 the 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 the 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 Data S1).

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 (Posit team, 2024; version 2024.04.2 + 764), using the packages AICcmodavg (Mazerolle, 2023; version 2.3.3), gridExtra (Auguie, 2017; version 2.3), lme4 (Bates et al., 2015; version 1.1-35.5), MASS (Venables & 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 versus protected zones

Overall, the forest patch area did not differ between protected and managed forest zones (forest patch size in ha, t -test, mean: protected = 6.66, managed = 8.47, $t = -0.64$, d.f. = 15.26, $P = 0.53$; Hedges $g = 0.27$, CI -1.10 to 0.56). The 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, $t = -2.49$, d.f. = 15.53,

$P = 0.03$; Hedges $g = -1.05$, CI -1.93 to -0.17 , Fig. 3). Managed zones showed a trend towards a higher Shannon index (t -test; mean: protected = 0.43, managed = 0.73, $t = -1.82$, d.f. = 18.77, $P = 0.08$; Hedges $g = -0.74$, CI -1.59 to 0.12 , Fig. 3) but we found no significant differences in Simpson index (t -test; mean: protected = 0.25, managed = 0.40, $t = -1.66$, d.f. = 20.52, $P = 0.11$; Hedges $g = -0.65$, CI -1.5 to 0.20 , Fig. S2) despite the medium effect size. 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, $t = 1.08$, d.f. = 19.35, $P = 0.32$; Hedges $g = 0.36$, CI -0.47 to 1.2 ; Fig. S2).

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% 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). These models were counted once for mammals and once for bird attacks. We detected bird bite marks on 48 models (60%) and mammal bite marks on 33 models (40%) (Table 1).

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 birds' attack fixed and permuting the forest zone in which they were attacked and found that the birds' attack rate was lower ($P = 0.05$) in protected zones (39.58%, $N = 19$) than in managed zones (60.42%, $N = 29$), confirming our model results (Fig. S3). 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. S4).

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 , $z = 0.55$, $P = 0.58$,

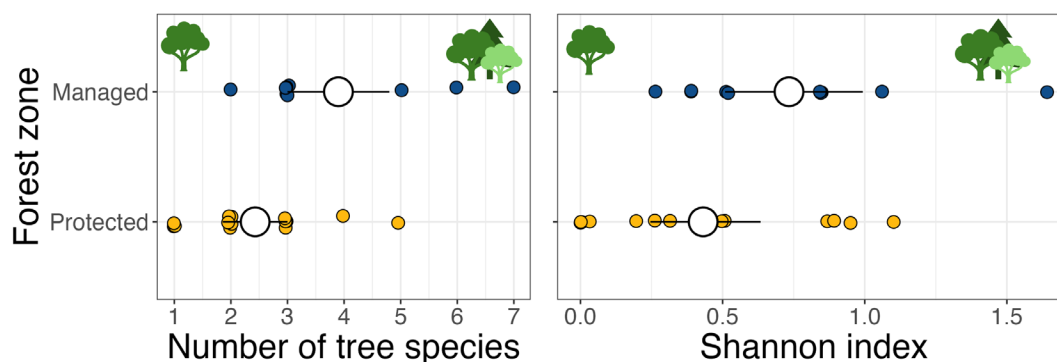


Figure 3 Comparison of diversity measurements taken in forest patches between managed ($N = 10$) and protected zones ($N = 14$). Large circles represent mean values for a specific zone and whiskers denote the 95% confidence interval. Small-filled circles represent raw values and are slightly jittered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

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. S5). 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. S6).

Following previous studies where clay models were used (Hernández-Palma *et al.*, 2023; Röbner *et al.*, 2018), 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 the number of bird or mammal attacks as the 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 but non-significant increase with higher biodiversity indices, the number of mammal attacks decreases significantly with higher biodiversity indices. Additionally, we observed 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, 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 in Data S1). 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 in Data S1).

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; Vélková *et al.*, 2021). We found that attacks by mammals did not differ between the broad categories of forest zones, managed versus protected, but we observed an increased number of attacks in forest patches with low tree diversity. Bird attacks, in contrast, were more frequent in managed forest zones than in protected zones. However, we did not find a significant increase in the number of attacks with increasing forest patch diversity. 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; Hernández-Palma *et al.*, 2023; Röbner *et al.*, 2018; Van Tran & Nishikawa, 2023) and thus providing internal validity to our study.

Predation pressure can vary among habitats (Van Tran & Nishikawa, 2023) due to changes in land use and habitat structure (Labadie *et al.*, 2023; Turner, 2010). 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

Table 1 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 

200 years for old-growth forests to reach their full biodiversity potential, Moning & 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 (Güthlin *et al.*, 2013). The observation that the largest number of mammal attacks occurred in protected forest patches with low tree diversity 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.

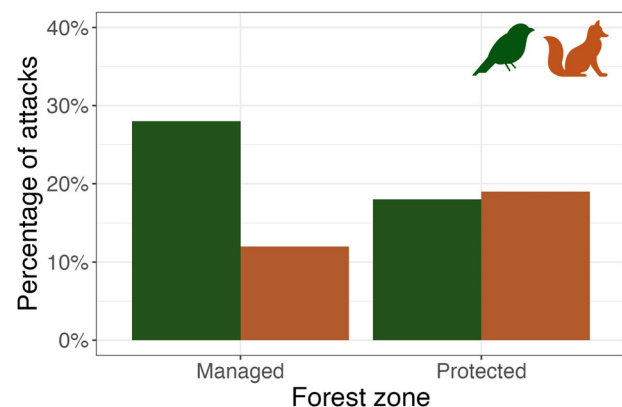


Figure 4 Percentage of attacks by different predators (birds = green, mammals = brown) in function of forest zone (managed vs. protected).

Clay models have proven useful for testing warning signal efficacy against predator attacks (e.g. Brodie, 1993; Duchesne *et al.*, 2022; Kuchta, 2005; Rojas *et al.*, 2014; Röbber *et al.*, 2020; Saporito *et al.*, 2007), 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 & Pröhl, 2017). We predicted differences in predation rates between large and small markings, with larger markings (LM) being expected to show 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 benefiting from camouflage or from the so-called distance-dependent defensive colouration (Barnett & 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

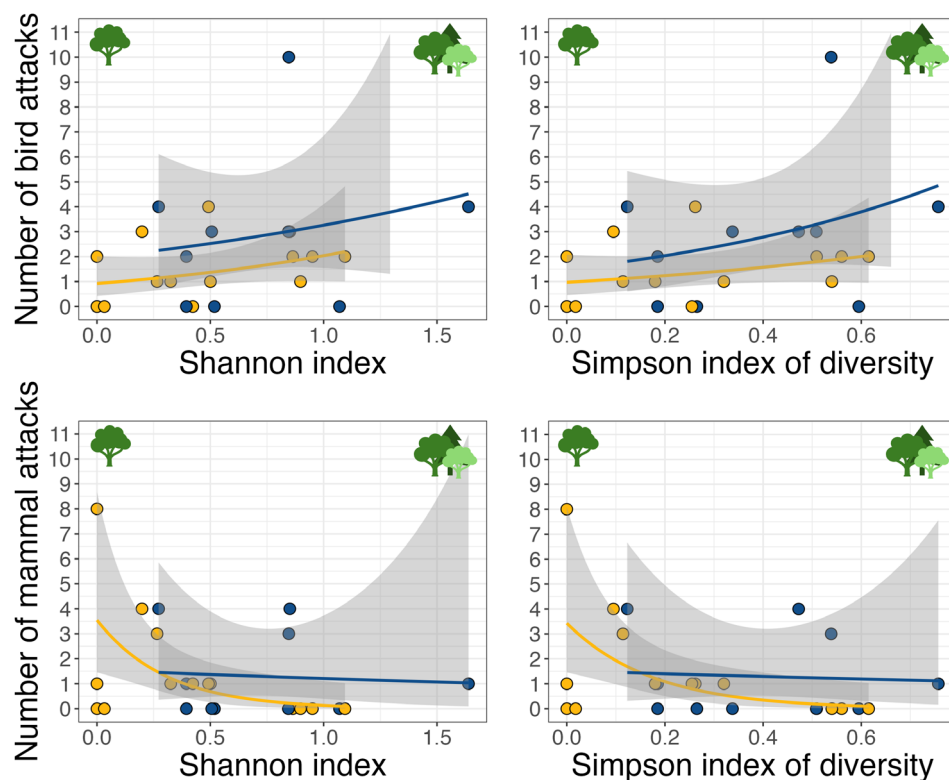


Figure 5 Relationship between bird (upper two panels) and mammal (lower panels) attacks and diversity indices of forest patches in the two forest zones (protected = yellow, $N = 14$; managed = blue, $N = 10$). Details of the statistical models can be found in Data S1.

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 & Pröhl, 2017). Our results, in contrast, suggest that marking size does not have an impact on the predation rate of 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, namely islands (Velo-Antón, 2024; Velo-Antón & Cordero-Rivera, 2011, 2017), we chose not to classify rodent bites as “attacks” for two reasons: first, because the plasticine balls we placed to check whether rodents were “simply” attracted to the plasticine itself were “attacked” mostly by rodents and slugs, and second, because rats are considered to be true commensals of humans and are thus more common in urban areas than in forests

(Aplin et al., 2003). 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 Data S1) 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 & 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 Data S1), 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 & 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 & Nishikawa, 2023; Velo-Antón, 2024; Velo-Antón & Cordero-Rivera, 2017).

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 in 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 managed and protected forest zones, 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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Conflict of interests

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

Author contributions

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.

Ethics statement

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).

Data availability statement

Data and R script of our analysis are available at the data repository of the University of Veterinary Medicine Vienna. Persistent identifiers: <https://phaidra.vetmeduni.ac.at/o:4168>, <https://phaidra.vetmeduni.ac.at/o:4169>, <https://phaidra.vetmeduni.ac.at/o:4173>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Electronic supplement (supporting Methods and Results, permutations, models).