

Research article

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## The role of skin colour in camouflage: experiment with green plasticine models of the European tree frog *Hyla arborea*

Jenő J. Purger<sup>1,2,\*</sup>, Bianka Pál-Dittrich<sup>1</sup>, Dávid Szép<sup>1</sup> & Krisztián Samu<sup>3</sup>

<sup>1</sup> Department of Ecology, Faculty of Sciences, University of Pécs, 7624 Pécs, Ifjúság útja 6, Hungary.

<sup>2</sup> BioRes Limited Partnership, 7624 Pécs, Barackvirág utca 27, Hungary.

<sup>3</sup> Department of Mechatronics, Optics and Engineering Informatics, Faculty of Mechanical Engineering, Budapest University of Technology and Economics, H-1111 Budapest, Műegyetem rkp. 3, Hungary.

\* Corresponding author: [purger@gamma.ttk.pte.hu](mailto:purger@gamma.ttk.pte.hu)

**Abstract.** The role of skin colour variations in the survival of European tree frogs is unknown. We presumed that green frogs become more noticeable to predators in the autumn when the colour of the leaves changes. For the study of their survival chance, we made plasticine models of European tree frogs with the same shape and the same dominant colour spectrum of 550 nm. The experiment was conducted in autumn 2018 in three vegetation types with varied backgrounds (vineyard, bulrush belts and reed bed) and in the habitat with a permanent background (concrete wall). In our experiment lasting more than a month we used 50 green coloured tree frog plasticine models in every habitat. Only 10% of the models were damaged by predators. Daily survival rates were high in all habitats (above 99%), and predation pressure on the concrete wall was significantly higher than in the different vegetation types. This was caused by the fact that the colour contrast of frog models on concrete walls (13.3) was twice as high as on grape (6.8), bulrush (4.2), or reed (5.0) leaves. Predators in the vineyard, bulrush belts and reed bed were mostly birds which left traces primarily on the heads of the models, while on the models displayed on the wall most of the traces (on the trunk and limbs) were left by mammals (small mammals, red foxes, and domestic cats). The colour spectrum of the vegetation background of the European tree frog models changed to brownish in autumn, but predation pressure did not increase. The constant green colour of the European tree frog models in natural habitats did not affect predation, from which we conclude that the colour variants may have other functions besides camouflage.

**Keywords.** Crypsis, daily survival rate, different background, predation, spectral reflection.

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## Introduction

Many animal species can change their skin colour, the primary function of which is camouflage (Duarte *et al.* 2017). Amphibians are also able to adapt their skin colour to the substrate of their environment to

make them less conspicuous to predators, thus increasing their fitness and chances of survival (Caro *et al.* 2016). The cryptic coloration of amphibians is an important form of defence against predators (Wells 2007). The defence strategy of tree frogs is background matching (Choi & Jang 2014; Kang *et al.* 2016; Park *et al.* 2023), but the level of predation pressure to which they are exposed in nature is less known. The European tree frog *Hyla arborea* is a small bodied species which is active from March to November (Dely 1967; Grosse 2009). Unlike any other European frogs, it possesses toe pads that allow it to climb into bushes and trees (Vos & Stumpel 1995). Its voice can also be heard from spring to the end of autumn (Dely 1967); however, it is rarely observed due to its hidden lifestyle and ability to change its green colour and blend in with the environment (Toledo & Haddad 2009; Pinto *et al.* 2013). Colour changes of European tree frog can occur quickly, in less than a minute, or slowly, over weeks or months (Đorđević *et al.* 2016). There are various triggers for colour change (e.g., Nielsen 1978; Stegen *et al.* 2004; Mirč *et al.* 2023; Radovanović *et al.* 2023). Among environmental cues the most important are intensity of sunlight (stronger sunlight - lighter colour), colour of the environment, and water temperature (warmer water - lighter skin colour). The skin colour is affected by different internal processes such as osmosis and thermoregulation, nitrogen metabolism, sexual excretion, protection against stress. The important ecological driver for colour changes is the protection against predators. The European tree frog is a generalist species and opportunistic predator with nocturnal activity; it moves little during the day and is mostly resting or basking on plants (Kovács & Török 1997). The primary predators of European tree frogs are birds with good eyesight (e.g., Martín & López 1990; Kazantzidis & Goutner 2005), which is why skin colour can play a key role in their survival. Birds are largely tetrachromatic (Bennett & Théry 2007) with the ability to see in the ultraviolet light spectrum, in addition to the spectrum visible to humans (Ödeen & Håstad 2013; Pinto *et al.* 2013). Because direct observation of predatory events on small-bodied animals is difficult, plasticine-models of prey animals have been widely used in predation experiments instead (Bateman *et al.* 2017). The advantage of this method is that living animals are not harmed during the experiments (Yeager *et al.* 2011), and the soft texture of the plasticine preserves the beak, tooth, and claw marks of predators (Bateman *et al.* 2017). The method was often used in studies of predation pressure on strikingly coloured poison frog species (e.g., Saporito *et al.* 2007; Noonan & Comeault 2009; Hegna *et al.* 2011; Stuart *et al.* 2012; Paluh *et al.* 2014; Dreher *et al.* 2015). The models were made of coloured plasticine (e.g., Hegna *et al.* 2011; Paluh *et al.* 2014) or subsequently painted (e.g., Lawrence *et al.* 2018; Umbers *et al.* 2020). In studies on the role of camouflage, it is important that the colour of plasticine models resembles the colour of live animals as closely as possible; otherwise, the results of the experiments may be distorted, as diurnal predator species mostly respond to visual stimuli (Bateman *et al.* 2017). For the design of the models, it is also important how different predators perceive the colour of potential preys and their background (Macedonia *et al.* 2009; Michalis *et al.* 2017). For our investigation, it was important to make plasticine models that resemble European tree frogs resting on green leaves in shape, size, and colour. The frogs' most common colour variation is green. However, since the colour of the vegetation gradually changes in autumn, animals become more noticeable and presumably their survival chances decrease if animals can not follow the colour changes in the background.

With the help of plasticine models, we tried to answer the question whether the chances of survival of green coloured European tree frogs change in different habitats as the autumn progresses. We wanted to know how the contrast between the colour of frog models and their background affects predation. Furthermore, we were curious about the proportion of bird and mammalian predators preying on tree frogs and their preference for certain body parts of the prey.

## Material and methods

The study was carried out in the southern part of Hungary, in the surroundings of the city of Pécs, at two sites: at the Institute of Viticulture and Oenology (vineyard and concrete walls) and at the Pellérd

fishpond (with two vegetation types: bulrush belts and reed beds) (Fig. 1). The first study site was a vineyard located in the western part of the city, on the southern slope of the Mecsek Mountains, at an altitude of 180–240 m above sea level, where terraces with concrete retaining walls have been created (Purger *et al.* 2017). The 16-hectare area has been used for viticulture since the 1750s, and it is bordered in the north by a mixed forest consisting of the flowering ash *Fraxinus ornus* and the downy oak *Quercus pubescens* (Fig. 1). The second study site was the area of the Pellérd fishponds, south-west of the city (Purger & Gyetvai 2001). There are bulrush belts and reed beds on the edge of the fishponds, while the whole area is surrounded by wet meadows and agricultural fields (Horváth 1945).

We made 200 plasticine models for the experiment and another 100 in case that plasticine frog models needed to be replaced during our study. A non-toxic natural colour plasticine (produced by KOH-I-NOOR Hardtmuth, Czech Republic) was used. First, the frog trunks were made by hand (35–45 mm in length), to which the legs and eyes were fitted. Spectrophotometric measurements were performed on the backs of four individuals of European tree frogs at the Pellérd fishpond to make the green colour of the plasticine models as similar as possible. Two different types of spectrophotometers were used: DataCOLOR - Microflash 45 (limit: 380–780 nm), which was calibrated with a TECHKON white standard and Konica-Minolta CM-2600D (limit: 360–740 nm), which was calibrated with a Konica-Minolta CM-A145 white standard. Live European tree frogs were measured several times by both instruments with these three methods: 1) Microflash – to measure the spectral reflection corresponding to visual perception, 2) Minolta SCI (Specular Component Included) – to measure the nature of the substance with its surface reflection components, 3) Minolta SCE (Specular Component Excluded) – to measure the nature of the substance without a reflection component.



Figure 1 – Study area: the first study site, the vineyard (black arrow), is situated on the southern slope of the Mecsek, and the second study site, the Pellérd fishpond, is shown with its bulrush belts and reed beds at the bottom of the picture (photo by J.J. Purger).



Based on the spectrophotometric measurements, we determined that they have a skin surface with spectral reflection corresponding to quasi-monochromatic green colour stimuli. Examining the spectral reflectance intensity of plasticine frogs (smeared with different paints and then sprayed with a colourless matt rubber to make a protection layer on the surface), we found that the spectral reflection curves of Royal Talens: Amsterdam Standard (Apeldoorn, The Netherlands) olive green acrylic paint was closest to the average spectrum of living tree frogs. However, the reflection proved to be too high, which was reduced by the addition of black dye. Knowing the appropriate colour combination, all 300 plasticine frogs were painted. We used a water-based (black, yellow, red), environment- friendly tempera (produced by ASTRA: Farby Plakatowe, Poland) to paint the black stripe running along their sides. The plasticine models were allowed to dry for a few weeks and then coated with a colourless, odourless rubber layer (produced by Plasti Dip, Blaine, USA) to prevent the plasticine from spreading any odour and to protect the models from precipitation (Purger *et al.* 2012).

On October 2, 2018, in the vineyard, 50 plasticine frog models were attached to the stems of grapevines *Vitis vinifera*, and 50 models were placed on the concrete walls separating the terraces. On the same day in the fishponds of Pellérd 50 tree frog models were attached with thin aluminium wire to leaves and stems of the plants in the bulrush *Typha latifolia* belt, and 50 models were placed in the reed *Phragmites australis* beds in the same way. Frog models were placed at least 10 m apart. In the vegetation the posture of the frog models was mostly vertical (always with the head upwards), while on the concrete walls they were in a horizontal posture. The models were checked on the first day after placement and weekly thereafter. The experiment lasted while the call of tree frogs in the area could be heard. As the vegetation began to lose its green colour and more yellow, red, brown and dried leaves appeared, we measured the spectral reflections of the frog models and background colours (October 16<sup>th</sup>). Around halfway through the study, most of the bulrush plants died within a few days; therefore, we replaced the lost or damaged frog models on the closest plants of the same species. During the study, photos documented models which were damaged by predators. At the end of the experiment, all models were collected.

The estimation of the daily survival rates for plasticine models was performed as described by Mayfield (1975) and the results were compared as recommended by Johnson (1979). The minimum probability level of  $P < 0.05$  was accepted and all P-values were estimated in two-tailed tests.

The vision of most known potential bird predators of European tree frogs belongs to the violet sensitive (VS) category (Ödeen & Håstad 2013). Therefore, we determined the (V, S, M, L) colour channel

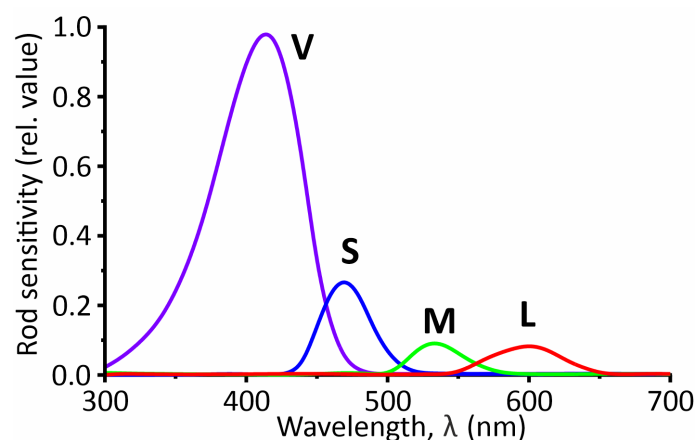


Figure 2 – Spectral visual sensitivity of eye types of violet sensitive (VS) birds. The curves are labelled according to the wave lengths of sensory receptors of these birds: V = violet wavelength; S = short (blue) wavelength; M = medium (green) wavelength; L = long (red) wavelength.

signals perceived by bird predators with their typical cone spectral sensitivities (Kelber 2019) (Fig. 2) at daylight (Ohta & Robertson 2005) (Fig. 3):

$$V = \int_{300 \text{ nm}}^{700 \text{ nm}} V_{\lambda} \cdot D65 \cdot \rho \, d\lambda$$

$$S = \int_{300 \text{ nm}}^{700 \text{ nm}} S_{\lambda} \cdot D65 \cdot \rho \, d\lambda$$

$$M = \int_{300 \text{ nm}}^{700 \text{ nm}} M_{\lambda} \cdot D65 \cdot \rho \, d\lambda$$

$$L = \int_{300 \text{ nm}}^{700 \text{ nm}} L_{\lambda} \cdot D65 \cdot \rho \, d\lambda$$

where

$V_{\lambda}, S_{\lambda}, M_{\lambda}, L_{\lambda}$  = cone spectral sensitivities

D65 = spectral power distribution of D65 daylight illumination

$\rho$  = spectral reflectance distribution of surface

We calculated the colour contrast values (the colour difference between the frogs and the backgrounds) from the (V, S, M, L) colour channel signals induced by the coloured surfaces. The colour difference (CD) was determined based on the red, green and blue (RGB) colour model (Akiyama *et al.* 2019) where the colour difference (CD) between COLOR1 and COLOR2 is equal to the Euclidean distance between the detected colour channel signals. For VS type birds, this is a four-dimensional formula:

$$CD = \sqrt{(V_1 - V_2)^2 + (S_1 - S_2)^2 + (M_1 - M_2)^2 + (L_1 - L_2)^2}$$

$$CD = \sqrt{(V_1 - V_2)^2 + (S_1 - S_2)^2 + (M_1 - M_2)^2 + (L_1 - L_2)^2}$$

where

CD = colour difference

$V_1, S_1, M_1, L_1$  = COLOR<sub>1</sub> channel signal (tree frog model colour)

$V_2, S_2, M_2, L_2$  = COLOR<sub>2</sub> channel signal (background colours)

The correlation between the colour contrast values established between the frog models and the backgrounds and the predation events was investigated using linear regression analysis (Zar 2010).

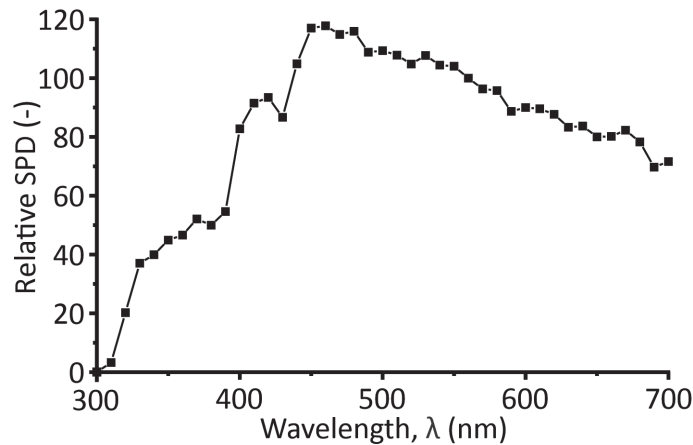


Figure 3 – Relative spectral power distribution (SPD) of D65 daylight illumination, used as the average reference solar irradiance for the calculations of colour contrast values.

## Results

### Model making

Upon measurements of representative spectral reflection of living individuals of European tree frogs, we managed to make frog plasticine models lifelike not only in shape but also in colour (Fig. 4). During our study the wavelength peak of frog models remained unchanged at around 550 nm as in the curve of the previously measured live tree frogs, however halfway through the study, the reflectance of the plasticine frog models decreased by 10% from the optimal colour reflection (Fig. 4).

### Colour camouflage of frog models at the study sites

Results of measurements of spectral reflectance of a plasticine tree frog models and their background indicated that the highest contrast was between frog models and concrete wall (Fig. 5A). At the time of measurement in the vineyard, most of the grape leaves were still green with a peak at 550 nm. The green reflection of the yellowish-reddish leaves was also detectable, as the leaves absorb light in their green state, so the green reflection of the yellow leaves is higher. The dry leaves reflected a greyish-brown colour (Fig. 5B). The values measured in the bulrush belt (Fig. 5C) and in the reed bed (Fig. 5D) were similar and in both cases the green leaves had a peak of 550 nm, so the frog models blended perfectly into the background.

### Predation on frog models

The colour of the vegetation gradually changed, therefore the colour of the plasticine models stood out even more from the background. At the same time, however, the rate of predation did not increase, the daily survival rate of the tree frog models remained remarkably high (Table 1). Based on the colour contrast of the tree frog models and their backgrounds perceived by violet sensitive birds (Table 2), the colour contrast of frog models on concrete walls (13.3) was twice as high as on grape (6.8), bulrush (4.2),

TABLE 1

Differences between the daily survival rates (DSR) of European tree frog plasticine models in the four habitats.

Habitat		Reed bed	Bulrush belt	Vineyard	Wall
Wall	DSR	0.9994	0.9989	0.9980	0.9909
	Z-value	3.453	3.150	2.850	
	P	<b>0.0005</b>	<b>0.0016</b>	<b>0.0043</b>	
Vineyard	Z-value	1.026	0.643		
	P	0.304	0.462		
Bulrush belt	Z-value	0.593			
	P	0.552			

TABLE 2

The determined values of the colour channel signals (V, S, M, L) perceived by violet sensitive (VS) bird predators for models of the European tree frog and their backgrounds.

Channel	V	S	M	L
Frog model	36.38	11.06	11.18	9.09
Concrete wall	26.74	8.29	3.76	4.53
Grape leaves	32.45	13.86	10.64	13.79
Bulrush leaves	35.49	12.01	7.35	7.89
Reed leaves	38.85	13.08	7.41	8.10

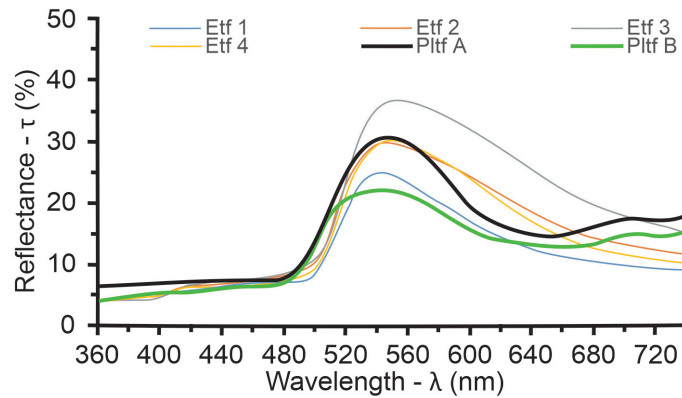


Figure 4 – Representative spectral reflection curves of four European tree frogs (Etf 1–4) and a plasticine tree frog model at the beginning of experiment (Pltf A - black line) and halfway through the study (Pltf B - green line).

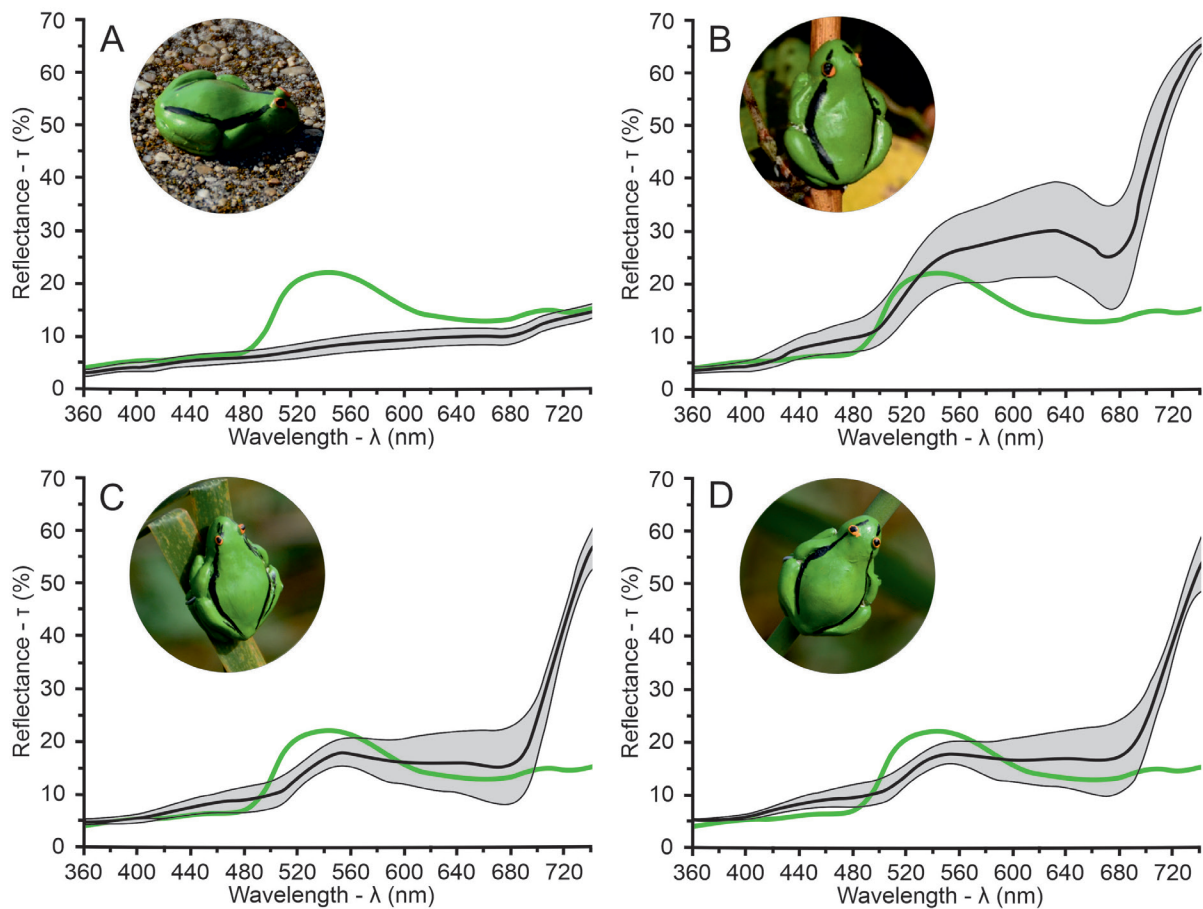


Figure 5 – Spectral reflectance curve of a plasticine tree frog model (green line) and average reflectance (black line) of the 16 measuring points of the concrete wall (A), grape leaves (B), bulrush leaves (C), reed leaves (D). The grey area around the average reflectance curve represents the 95% confidence interval.



or reed (5.0) leaves. With the increase of contrast between the tree frog models and the background, the probability of predation events also increased significantly (Fig. 6). During our experiment, there was an unexpected observation when we found more than 20 living tree frogs of different colours in one pit (Fig. 7). The presence of tree frogs of different colours in an area with a homogeneous background suggests that the colour may not only serve to hide (Fig. 7).

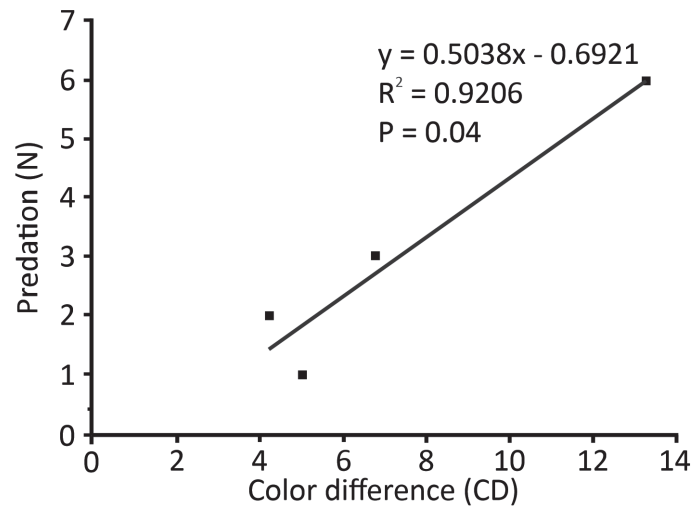


Figure 6 – The relationship between the number of predation events and increasing colour contrast between the frog models and their backgrounds.



Figure 7 – European tree frogs with different colour variations found on October 29, 2018, in a pit close to the study area (photo by Zsófia Lanszki).



Only 10% ( $n = 20$ ) of the plasticine models were damaged by predators, mostly in the first half of the study ( $n = 13$ ). Most of the predation events were on the concrete walls ( $n = 14$ ), so the daily survival rates of the plasticine frogs placed there were significantly lower than those of the models placed in the reed beds ( $n = 1$ ), in the bulrush belt ( $n=2$ ) and in the vineyards ( $n = 3$ ) (Table 1). On the plasticine models, 11 smaller birds and 1 larger bird left a beak imprint. The mammalian imprints suggested that the predators were rodents in two cases, a red fox *Vulpes vulpes* in two cases, and a domestic cat *Felis silvestris catus* in four cases.

Bird predators mainly targeted the head of the models ( $n = 10$ ) (Fig. 8), but there were examples of beak marks on the trunk ( $n = 4$ ) and limbs ( $n = 3$ ), respectively, whereas a tooth imprint of mammals was left on the trunk ( $n = 7$ ) and limbs ( $n = 8$ ) of the models.



Figure 8 – Traces of bird predation on the head of a frog model (photo by J.J. Purger).

## Discussion

### Model making

At the beginning of our study, we managed to create a dye combination with a spectral reflection peak around 550 nm, which was like the values that we measured on living green coloured tree frogs and that is also known from other studies (e.g., King *et al.* 1994). Halfway through our study, we noticed that the reflectance of the plasticine frog models decreased from the optimal colour reflection, probably due to homogenous fading. It was not significant but observable. We suggest that future studies should estimate more quantitatively how strong colour fading is and if it could possibly affect the obtained results when using a model approach.

### Colour camouflage of frog models at the study sites

There was a good contrast between the colour of the concrete wall at the vineyard and the green plasticine frogs, so they stood out from the background, making them more visible to potential predators. The intensity of light yellow and yellow on the greyish surface of the concrete walls depended on the number of lichens. Due to their colour, plasticine frogs were still camouflaged well in the green environment (between grape, bulrush and reed leaves), but as its colour gradually changed during the season, their ability to be hidden decreased. As the experiment progressed, the leaves began to turn yellow and dry out. Yellow leaves with very low chlorophyll concentrations show significantly higher reflectance of green light than green leaves (Virtanen *et al.* 2022). The green colour of the plasticine frogs was thus clearly different from this background type. Despite this, predation pressure remained low.

When the vision of violet sensitive birds was taken into account, the colour contrast of the frog models on the greyish-yellow concrete walls was twice as high as on the mostly green leaves of grapes, bulrush and reed. We confirmed the results of Stuart-Fox *et al.* (2002), who suggested that models with different background colours were exposed to twice as much predation pressure as those that merge into their environment. Several colour variants of tree frogs are known (Koren & Jelić 2011), which may help them to hide better. Experiments on tadpoles also showed that they actively choose the background that suits them to achieve maximum crypsis (Mirč *et al.* 2023). Adult tree frogs hide successfully (which increases their survival and thus also their fitness) by colour adaptation to the background or by actively choosing the right background (Degani & Biton 2013; Degani 2022). It is known that physiologically changing colours may also be used to hydro- and (or) thermo-regulation (Stegen *et al.* 2004). Our finding that European tree frogs occurred in several different colour variations at the same time and in the same place may indicate that colour may have additional purposes besides avoiding predation.

### Predation on frog models

The plasticine frogs placed on the plants were easily accessible to birds, while the models on the concrete wall were furthermore accessible to mammals. According to the literature, the predators of adult European tree frogs are mainly birds such as red-backed shrikes *Lanius collurio*, European starlings *Sturnus vulgaris*, owls (Strigidae), herons (Ardeidae), storks (Ciconiidae) and diurnal birds of prey (Accipitriformes) (Martín & López 1990; Kazantzidis & Goutner 2005). The bird fauna of the fishpond was relatively rich (Horváth 1945; Papp 1974) and during our study coincided with the migration period. Despite this, participation of birds in the predation on tree frog models was low. Plasticine frog models on concrete walls could easily be found by small mammals, red foxes and domestic cats that regularly occurred in the vineyards, but that are not typical predators of tree frogs. Mice and voles eat mainly plant-based food and invertebrates (Butet & Delettre 2011). The diet of red foxes and stone martens *Martes foina* studied in the same area did not include tree frogs (Lanszki *et al.* 2019). In the diet of domestic cats, very few cases of consumption of tree frogs are documented (Széles *et al.* 2018).

Bird predators capture prey primarily at the head and neck region when killing prey (e.g., Vervust *et al.* 2011; Vazquez & Hilje 2015). Most predatory mammals are active at night, and because of that they respond primarily to odours of prey (Bennie *et al.* 2014). Plasticine frog models do not have a natural odour or strategies to avoid predation, such as chemical defence or movement. Paluh *et al.* (2014) showed in their experiment that mobile models were seven times more damaged than immobile ones. The lack of movement of models in our study can be one of the explanations for the small number of predation events. This could be followed up by future studies.

The predation events on the green non-moving tree frog plasticine models did not increase with the change of the background colours during the season. This leads us to conclude that the constant green colour of the frogs in their natural environment is not a disadvantage. This study did not address the role

of different colour variants of tree frogs for their survival, so the research question remains why they are present in multiple colour variants at the same location and at the same time.

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