High predation risk decimates survival during the reproduction season

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Abstract

Predators attack conspicuous prey phenotypes that are abundant in the environment. Male display behaviour of conspicuous nuptial colouration becomes risky in the presence of a predator, and adult males face higher predation risk. High predation risk in one sex will lead to low survival and sex ratio bias in adult cohorts, unless the increased predation risk is compensated by higher escape rate. Here, we tested the hypothesis that sand lizards (*Lacerta agilis*) have sex-specific predation risk and escape rate. We found statistically stable sex ratio in age groups, equal frequency of tail regenerates between sexes, and similar survival rate. Predation risk is similar between sexes, and escape rate increases survival by about 5%. We found low survival rate and a low number of tail autotomy events during the months when sand lizard females mate and lay eggs, indicating high predator pressure throughout reproduction, when females fail to escape predation. The risky reproduction season in an ectotherm is a convolution of morphological changes (conspicuous colouration in males, body allometry changes in gravid females), behaviour (nuptial displays), and environmental conditions which challenge lizard thermal performance, favouring performance of endotherm predators in cold spring months.

Keywords: reptile, predator pressure, caudal autotomy, CJS model

Running title: High predation risk during reproduction

Introduction

Wild organisms need to solve problems arising from abiotic and biotic interactions in the environment they inhabit. One crucial trade-off is navigating the predation risk. Ectotherms, animals strongly dependent on abiotic factors of the environment to modulate their performance, avoid detection by using camouflage (Stevens and Merilaita 2011), or by shifting their activity from thermal or time niche of the predator (Webb and Whiting 2005). The concept of finding the optimal survival strategy leads to a behavioral cascade where predators and prey interact (Angilletta Jr. 2009; Brown and Vincent 1992), creating a density- and frequency-dependent predator pressure on different prey phenotypes.

The prey influences the arms race in the predator-prey dynamic through mechanisms facilitating escape from the predator attack. One such mechanism is autotomy, and many species of ectothermal vertebrates are able to shed and regrow a body part (Maginnis 2006; Bateman and Fleming 2009). In lizards, tail autotomy is one of several anti-predation adaptations (Cooper Jr. et al. 2004). The animal under attack can break off its own tail in an attempt to escape. The tail thrashes after autotomy, potentially distracting the predator, and allowing the prey to escape the immediate attack (Naidenov and Allen 2021). From a short-term perspective, the animal with a broken tail can run faster compared to an animal with an intact tail, but locomotion of animals with tail autotomy is negatively impacted when jump-

ing (Fernández-Rodríguez and Braña 2020; Gillis et al. 2009) or climbing vertical surfaces (Fleming and Bateman 2012). On a long-term scale, tail autotomy imposes high energy and resource costs that negatively influence survival through the cost of injury, infection risk, lower ability to survive future predator attacks, and energy relocation to the regenerate (Wilson 1992; Bateman and Fleming 2009). Following appendage regrowth, survival of the post-autotomy animal improves (Lin et al. 2017).

The rationale explaining why lizard sexes might face different predation risk and perform with different escape rate follows sex differences in morphology and behaviour. Bright nuptial colouration and display behaviour in males lead to higher predation risk compared to females. The paradigm of conspicuous, and thus more vulnerable, males is widely accepted in behavioural ecology (Danchin et al. 2008), but conspicuous colouration itself might contribute to alleviating lethality of predation. A predator attacks brightly coloured males sooner, giving the prey more time to escape (Fowler-Finn and Hebets 2011). In females, body allometry and weight increase associated with gravidity decrease speed and agility compared to males (Bauwens and Thoen 1981; Shine 2003; Husak 2006), suggesting that females escape predator attacks less often.

Sex differences in predation risk and escape rate will manifest in differences in survival. Survival rate ϕ, the probability that an individual will survive a specific time period, is the residual of mortality rate m, $\phi = 1 - m$. The mortality rate can be attributed to predation (m_P) and other causes

(m_0), giving $\phi = 1 - (m_0 + m_P)$. To reduce dimensionality of the problem, we set $m_0 = 0$, and consider $\phi = 1 - m_P$. Mortality rate attributable to predation is predation risk (P) reduced by the escape rate (E). Escape rate can be thought of as a probability increasing survival, where the action of prey results in its immediate survival following the predator attack. While, the prey can escape an attack unharmed, here we consider the escape to represent a situation in which the prey lost its tail. A predator attack that did not result in prey mortality or tail autotomy will not manifest in the parameters measured in this study. Substituting m_P, the survival rate becomes

$$\phi = 1 + E - P. \tag{1}$$

Sex-specific survival rate will influence how the proportion of each sex changes in time. The ratio of male (ϕ_M) and female (ϕ_F) survival rate will be equal to the odds ratio of sex ratio between age classes

$$O_{sex} = \frac{\phi_M}{\phi_F}. \tag{2}$$

Substituting ϕ with (1), we get

$$O_{sex} = \frac{1 + E_M - P_M}{1 + E_F - P_F}, \tag{3}$$

where the indices M and F indicate males and females, respectively.

The ratio of male-to-female escape rate should reflect the odds of fre-

quency of tail autotomy in each sex. The relationship between sex-specific escape rate and odds ratio of tail autotomy in adults will be

$$O_{tail} = \frac{E_M}{E_F}. \tag{4}$$

Here, we study the influence of predation risk and escape rate on population dynamics and survival of sand lizards (*Lacerta agilis*, Lacertidae, Reptilia). The sand lizard is a small (< 19 cm), sexually dimorphic lizard, distributed in the temperate Palearctic. We hypothesize that sexual differences in predation risk influenced by the escape rate will affect sex ratio, frequency of tail autotomy and survival rate of sand lizards (Table 1).

Table 1: Hypotheses of predation risk and benefit of tail autotomy to escape from predation based on sex. Green – change of sex ratio between young and adult animals, blue – frequency of tail regenerates, red – sex-specific survival rate; ↑ – increase in males, ↓ – decrease in males, ∼ – no difference.

in males	Higher predation risk			Equal predation risk		
	sex ratio	autotomy	survival	sex ratio	autotomy	survival
Higher escape rate	∼	↑	∼	↑	↑	↑
Equal escape rate	↓	∼	↓	∼	∼	∼

If males face higher predation risk, but also benefit from higher escape rate, we expect to observe stable sex ratio in different age cohorts and similar survival rate between sexes, but males will have higher frequency of tail autotomy. If the escape rate does not differ between sexes, but males suffer from higher predation risk, the sex ratio will be skewed in favour of females in older cohorts and males will have lower survival rate (Table 1).

If predation risk does not differ between sexes, the putative higher escape rate in males will result in males dominating sex ratio in older cohorts, having suffered from tail autotomy more frequently, but also having higher survival rate (Table 1). We expect no difference in the observed parameters in the case where the predation risk and escape rate do not differ between sexes.

Materials and methods

Data

We sampled the sand lizard population during the months when the animals were active. Sand lizards from an orchard in Hustopeče (48.93 N, 16.72 E) in Czechia were apparent between May and August 2018, May and September 2020 and 2021. We caught the animals by hand or by noosing (García-Muñoz and Sillero 2010) at weekly intervals and marked each individual by toe clipping or heat branding (Ekner et al. 2011). Prior to release, we photographed the animals from dorsal, ventral and lateral sides, sexed them, and collected data and material for other studies (Dračková et al. 2020; Smolinský et al. 2021).

We used the obtained data either by filtering the last known capture of each animal or by evaluating all captures of all individuals. Unless specified, the analyses use the non-redundant database of last captures of each animal.

Age

We calculated the approximate age of sand lizards on the day of capture (a_d in days) according to

$$a_d = D_d - D_{a_{\min}} + 365(Y_d - C), \tag{5}$$

where D_d is the calendar day on the day of capture, $D_{a_{\min}}$ is the calendar day of the first time a hatchling was encountered, Y_d is the year of capture, and the cohort C is the latest possible year, when the animal could have hatched. For example, let's take a young and an adult animal captured for the first time on 1 June 2021. To estimate their ages, we need to know that the first hatchling was found on 1 August 2020 the previous year. The approximate age of the young sand lizard on the day of capture would be $a_d = 152 - 214 + 365(2021 - 2020) = 303$ days, because the young animal captured in spring had to have overwintered once and its year of hatching was 2020. The adult animal overwintered at least twice, bringing its year of hatching to, at most, 2019 and the corresponding approximate age to 668 days.

Sex

We sexed adult animals based on their nuptial colouration and presence of a swollen base of the tail. In young animals, we counted scales in the second rows from the ventral medial line (ventralia count) (Eplanova and Roitberg

2015) using digital images and an ensemble of three centroid-based object detectors (Dolezel et al. 2022) (Fig. S1). The detectors utilize localization maps generated using U-Net models (Ronneberger et al. 2015). Inputs and outputs of the models are 512×512 pixel (px) colour images and one class localization maps, respectively. The target scales in the maps are represented as circles with centroids placed at coordinates corresponding to the centres of the scales. The circle circumferences represent the borders of nonzero values in the maps, where values at the centroid coordinates are at one, and the values within a circle decrease to zero with increasing distance from the circle centroid (Dolezel et al. 2022). We trained and validated the U-Net models on a set of 227 expert-annotated photos. The annotator marked a center of each target scale in each photo. For each model, we generated a different set of localization maps using the centres (i.e. each model was trained on a different set of annotated photos). Specifically, we used maps with circles of 10 px diameters and linear decrease of gradients, maps with linear decrease of gradients and diameters respective to the size of scales (diameters 6–14 px), and maps with diameters respective to the size of scales but with nonlinear decrease of gradients. Before processing the photos, a uniform orientation of the photos and maps with the head facing left must be ensured. For this purpose, we utilize the YOLO detector (Bochkovskiy et al. 2020), which localises the head, body and tail on a photograph of the ventral side of a sand lizard. We trained the YOLO model on a set of 150 expert-annotated photos. To increase the accuracy of the detectors (preserving as much detail

as possible), we use square crops of the photos and maps centered at the centres of lizard bodies as the inputs and outputs of the U-Net models, respectively. The size of each square is 1.42 times the length of the lizard body. To keep the aspect ratio of the crops, if necessary, the photos and the maps are padded with zeros before their resizing to 512×512 px. The detectors return the coordinates of scale centroids. To count the scales at the left and the right side of the rows, we take into account subsequent positions of the centroids. We implemented all the processes into a custom algorithm ScalesCounter and used the algorithm to perform automated processing of unannotated photos (Fig. S1). The algorithm is available upon request.

Following the automatic detection and counting, we checked all outputs and corrected the number of detected scales in low quality images (saturated image, appendage partially obscuring the scales, scarred scales). To establish a threshold for sexing juveniles, we counted the ventralia scales in adults and estimated the threshold value using the receiver operating characteristic curve (ROC), maximizing the specificity and sensitivity of detecting the correct sex. We validated the threshold values with logistic regression.

Seasonality

We considered two seasonal phases with different biological realities determining assumed activity and predation risk of sand lizards. Phase I started from the arousal from hibernation, and lasted until the first adult male started to lose nuptial colouration. Adult animals participate in reproduction

in phase I, with males searching for mates and defending their territories, and females investing in gravidity. Phase II constituted the season after males started to lose nuptial colouration, and lasted until the beginning of hibernation. In phase II, the animals feed to accumulate sufficient resources for the winter.

Tail autotomy

To estimate individual body and tail lengths, we used tpsDig v.2.02 (Rohlf 2005) software to obtain measurements from digital images of sand lizard ventral side. We measured body length from rostrum to anus (L_{ra}), tail length from anus to tail tip (L_{cd}), and length of the tail regenerate from break point to tail tip (L_{reg}). We recorded a tail autotomy event, when the animal was first captured with a tail regenerate. Upon recapture, we compared the body measurements of the animals, and checked the photographic evidence for an additional tail autotomy event. If L_{cd} was shorter than on the day of the previous capture (with tolerance of 3 mm to account for muscle contraction), an additional tail autotomy event was recorded.

To calculate the date of the tail autotomy event, we first established individual recapture series starting with the record of the tail autotomy event and ending with the last capture in the same year as the first capture of the animal or before the additional tail autotomy event. We fitted linear models to the individual recapture series as $L_{reg} = \beta_0 + \beta_1 a$, where a is approximate age in days, β_1 is the daily growth rate of the tail regenerate, and β_0 is

an intercept. We used median of individual tail regenerate growth rates at 10 mm intervals of L_{reg} to project the tail regenerate growth backward to estimate the approximate date of a tail autotomy event.

Statistical analysis

We tested the proposed hypotheses in two ways. First, we calculated the odds ratios for sex ratio in age classes and frequency of tail autotomy in sex and age groups, estimating the respective confidence intervals from likelihood profiles. For this, we used the last captures of each individual. Second, we calculated the survival rate and recapture probability in a likelihood framework based on the open population Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965). For the survival rate analyses, we used the complete dataset that included the recaptures.

We calculated the odds ratio for the sex ratio change with age as

$$O_{sex} = \frac{n_M \left(n_m + n_f\right)}{n_m \left(n_M + n_F\right)}, \tag{6}$$

where n is the number of individuals, M and F represent males and females, respectively, with capital letters indicating adults and lower case letters indicating young animals.

We used data from adult and young animals separately to calculate the odds ratio for presence of tail regenerates. The change in odds of the presence

of a tail regenerate in males compared to females is given as

$$O_{tail} = \frac{n_F n_{M_{tail}}}{n_M n_{F_{tail}}}, \tag{7}$$

where $n_{M_{tail}}$ and $n_{F_{tail}}$ are the numbers of males and females with tail autotomy, respectively. Note, that we calculate the O_{tail} as ratio of male-to-female frequency of tail autotomy in sand lizards (7). To evaluate the escape rate, the animals with lower escape rate will have fewer observed tail regenerates, because they were removed from the population (4).

We calculated the survival rate (ϕ) and recapture probability (p) from the capture-mark-recapture data, using the CJS model implemented in MARK (Cooch and White 2021). We used sex, age class (young, adult) at first capture and season (phase I, phase II) as categorical variables and tail length corrected for body length L_{cd}/L_{ra} (mm mm^{-1}) at first capture as an individual covariate. We compared the models with AICc and corrected the parameter standard errors for overdispersion. We performed a goodness-of-fit test for the CJS model and tested for overdispersion with the median $\hat{c}$ approach. The global model for the overdispersion test was ϕ(sex*age*phase)p(sex*age*phase), where phase indicates the two seasonal phases.

Evaluating the change in the probability of a tail autotomy event with time, we modeled the relationship with logistic regression for males and females separately. We used the approximate age of the sand lizards as the predictor variable.

Estimating sex-specific predation risks and escape rates requires a four-dimensional optimisation. To solve the problem, we co-estimated the P_M, E_M, P_F, and E_F using equations (1), (3) and (4) with a Bayesian approach. We sampled the posterior with Metropolis-coupled Markov chain Monte Carlo (MCMC) using uninformative, uniform priors for sex-specific predation risks ($U(0.001, 0.999)$) and escape rates ($U(0.001, 1.000)$), and informative priors for sex-specific survival rates with normal distribution with parameters estimated from the CJS model. We ran the MCMC for 5 mil. steps, sampling every 1000th to avoid autocorrelation, and discarding 20% of initial steps as burnin. We evaluated MCMC convergence from two independent runs with random starting values and combined the results.

We performed the statistical analyses in R (R Core Team 2020) using packages imager (Barthelme 2020), pROC (Robin et al. 2011), RMark (Laake 2013), plot3D (Soetaert 2019), coda (Plummer et al. 2006), and RColorBrewer (Neuwirth 2014).

Ethics statement

Sampling was based on permits JMK 38000/2018 and JMK 42819/2021 issued by the Regional Authority of the South Moravian Region, Brno. Animal handling complied with Czech Act No. 114/1992 on Nature and Landscape Protection. The authors were authorised to handle wild lizards according to the Certificate of Professional Competence (Nos. CZ01287 and CZ03799; §15d, Act No. 246/1992 Coll.).

Results

To estimate the approximate age of the sand lizards, we used dates when the first hatchlings of the season were seen. These were on 28 July 2018, 16 August 2020, and 29 July 2021. To estimate the seasonal phases, we found the seasonal phases breakpoints on 23 June 2018, 25 July 2020, and 2 July 2021, when the first male started to lose the green, nuptial colouration.

For sex and presence of tail autotomy to evaluate escape rate and predation risk in sand lizards, we investigated 365 individuals in total. To estimate the sex differences in ventralia count, we first scored the adults. The ventralia scales could be counted from photographs of 126 adult females and 105 adult males. In adult sand lizards, the ventralia count differed between sexes (Welch two-sample t-test: $t = 19.7, df = 322.0, p < 0.001$) with females having on average 61.01 ventralia scales, and males having 56.39 ventralia scales (Fig. S2A). The area under the ROC was equal to 0.92 (Fig. S2B). At the threshold value of 58.5, established from the Youden's index, the specificity of determining sex based on the ventralia count was equal to 0.85, the respective sensitivity being 0.86. The threshold value was supported by the logistic regression ($p = 0.501$; Fig. S2C). Based on these results, we consider the ventralia count a sufficiently reliable sex-determination marker of sand lizard population from Hustopeče, and we used the threshold value of 58.5 to sex the juveniles.

In 22 individuals, we could not determine sex or the body measurements

due to the poor quality of pictures, caused by auto-focus malfunction. The study includes 343 animals with complete data that were captured 506 times (Table 2, Fig. 1A).

Table 2: Number of individual sand lizards *Lacerta agilis*. Animals with tail autotomy in parentheses.

Sex	Young	Adults
Males	48 (8)	112 (68)
Females	48 (16)	135 (79)

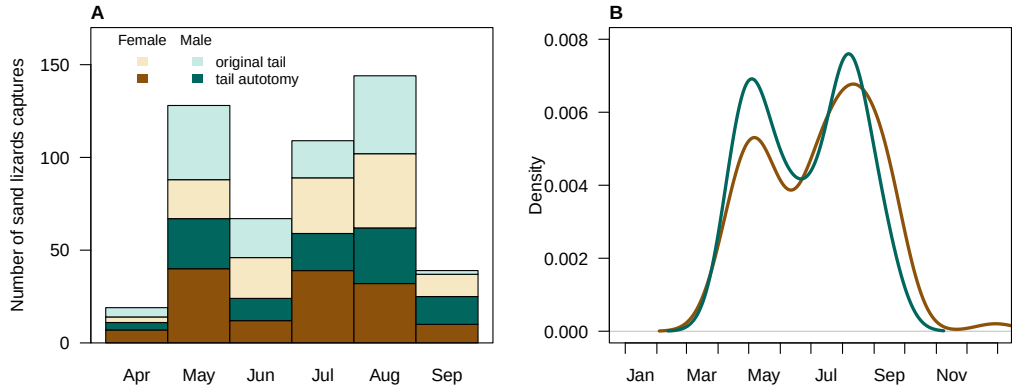

Figure 1: Seasonality of tail autotomy in sand lizards, *Lacerta agilis*. A. Observed number of captures of animals with their original tail and with a tail regenerate. B. Density of extrapolated dates when sand lizards experienced tail autotomy. The date of the tail autotomy was projected backward from the length of the tail regenerate on the day of capture, respecting the active season and hibernation periods.

The census sex ratio in young sand lizards was 0.500 (maximum likelihood confidence interval (CI) is $[0.41, 0.59]$; Fig. 2) and in adults, 0.453 (CI is $[0.39, 0.51]$), resulting in $O_{sex} = 0.907$ (Fisher's exact test: $p = 0.471$). The frequency of tail autotomy in adult males was 0.627 (CI is $[0.544, 0.71]$) and

in adult females 0.594 (CI is $[0.52, 0.67]$), giving $O_{tail} = 1.055$ (Fisher's exact test: $p = 0.609$). In young animals, the frequency of tail autotomy in males was 0.167 (CI is $[0.09, 0.28]$) and in young females 0.333 (CI is $[0.21, 0.48]$), giving the odds of tail autotomy in young sand lizards as equal to 0.500 (Fisher's exact test: $p = 0.098$).

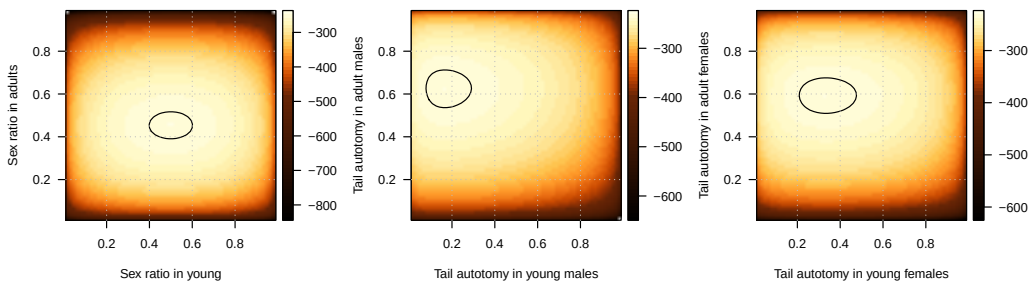

Figure 2: Log-likelihood profiles of sex ratio and probability of tail autotomy in sand lizards. Contours mark values up to 2 units lower than the maximum log-likelihood in the given test, indicating a confidence interval for the parameter value. Colour scale – log-likelihood.

The logistic regression models evaluating the increase in probability of tail autotomy with progressing approximate age were significant for both sexes (Table 3, Fig. 3). The probability of tail autotomy increases faster in aging males, but the difference between sexes is not significant and the 95% prediction intervals overlap (Fig. 3).

The goodness-of-fit statistic for the CJS capture-recapture model was not significant (Test2: $\chi^2 = 9.801, df = 78, p > 0.99$; Test3: $\chi^2 = 19.142, df = 61, p > 0.99$, indicating that there is no apparent lack of fit in the data. The median $\hat{c}$ was less then 1 ($\hat{c} = 0.461, \text{sampling SE} = 0.506$), and the survival

Table 3: Logistic regression models evaluating change in the probability of tail autotomy with progressing age in sand lizards (*Lacerta agilis*).

Sex	Parameter	Estimate	St. error	z statistic	p
Males	Intercept	-2.108	0.489	-4.309	< 0.001
	Age	0.004	0.001	4.577	< 0.001
Females	Intercept	-1.024	0.398	-2.570	0.010
	Age	0.002	0.001	2.988	0.003

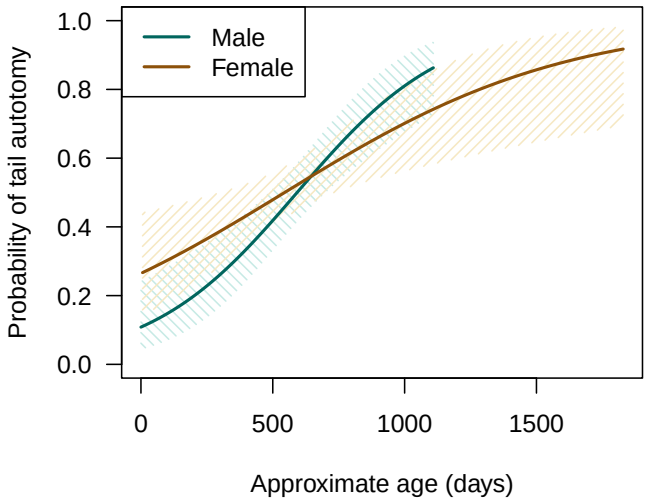

Figure 3: Logistic regression model evaluating the probability of tail autotomy with progressing approximate age in sand lizards (*Lacerta agilis*). Solid lines – model prediction, shaded area – 95% prediction intervals.

rate and recapture probability parameters did not need to be corrected for overdispersion.

The CJS model that best fitted the observed capture-recapture data used survival rate dependent on animal sex and seasonal phases and a uniform recapture probability (Table S1). During the season phase I, female survival rate was significantly lower than in the season phase II (estimate ± SE:

$\phi_{\text{phaseI}} = 0.009 \pm 0.009, \phi_{\text{phaseII}} = 0.286 \pm 0.083$; Fig. 4). In males, we observed a different pattern, where the survival rate was higher in season phase I than in phase II, but the difference was not significant in males ($\phi_{\text{phaseI}} = 0.086 \pm 0.039, \phi_{\text{phaseII}} = 0.006 \pm 0.012$; Fig. 4). The recapture probability remained statistically stable ($p = 0.075 \pm 0.007$). The best model that considered sex as an explanatory variable without the seasonal element was significantly worse ($\Delta\text{AIC}_\text{c} = 19.206$, $\phi_F = 0.103 \pm 0.036$, $\phi_M = 0.069 \pm 0.030$, $p = 0.069 \pm 0.007$; Table S1).

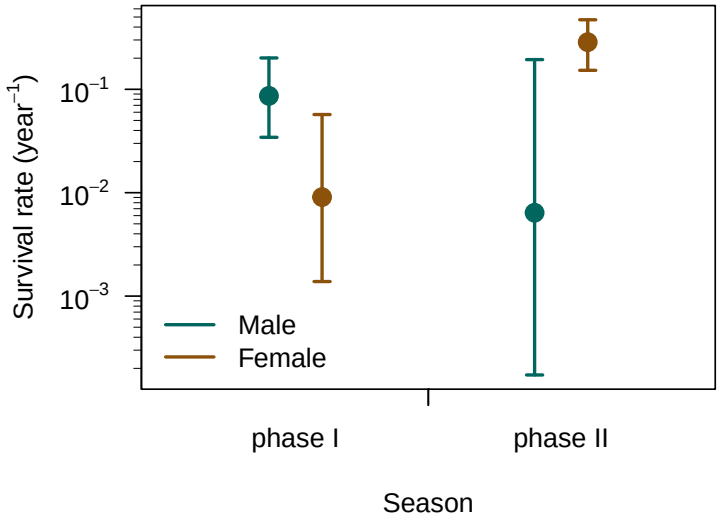

Figure 4: Survival rate of sand lizards (*Lacerta agilis*) based on the CJS capture-recapture model. The recapture probability was stable in the model and equal to 0.077 ± 0.008. Seasonal phase I represents the time characterised by mating behaviour and gestation, and phase II is the time with predominant resource accumulation prior to hibernation. Animals were categorized to seasonal phases based on the seasonal phase at the time of their first capture.

We recorded 180 tail autotomy events, where nine animals lost tails twice.

To calculate the date of the tail autotomy event, we first estimated the seasonal growth rate of the tail regenerate from retraps of an individual with tail autotomy. The individual tail regenerate growth rate ranged from 0.016 to 1.417 mm day^{-1} during active season, and from 0.001 to 0.012 mm day^{-1} during hibernation ($n = 27$ and 2, respectively; Fig. S3). Projecting the tail regenerate length backwards, we calculated that most tail autotomy events occurred in August in males, and in May in females (Fig. 1B). Out of 179 tail autotomy events that were dated to the sand lizard active season, 86 occurred in season phase I (42 in males, 44 in females) and 93 in season phase II (40 in males, 53 in females). The odds ratio of a tail autotomy event during the season phase I was equal to 1.050 for males (Fisher's exact test: $p = 0.893$), and 0.830 for females (Fisher's exact test: $p = 0.534$), indicating statistically identical odds of a tail autotomy event in the seasonal phases.

The set of equations estimating predation risk and escape rate (1), (3), and (4) did not have an analytical solution for the observed values of the odds ratios and the survival rates. Using MCMC, we estimated that in sand lizards, predation risk is equal to 0.975 (highest posterior density interval (HPD) is $[0.947, 0.999]$) in males and 0.0.942 (HPD is $[0.912, 0.971]$) in females. The respective escape is 0.045 (HPD is $[0.017, 0.070]$) in males and 0.044 ($[0.014, 0.073]$) in females (Fig. 5). The MCMC runs converged according to the $\ln L$ trace and the potential scale reduction factors (PSRF) for all parameters (Gelman and Rubin 1992). The upper confidence limit of PSRF indicating covergence should be close to 1, and we observed values from 1.01

for P_M to 1.02 for E_F.

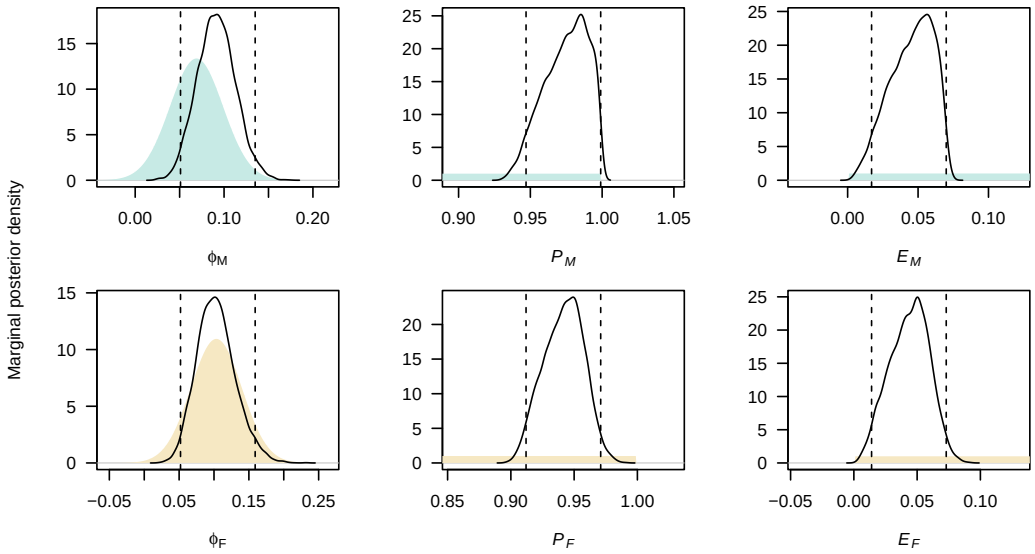

Figure 5: Marginal posterior density of survival rate (ϕ), predation risk (P) and escape rate (E) in sexes of sand lizards (*Lacerta agilis*). Coloured area – prior (green are males, brown females), dashed bars – highest posterior density interval at 95%.

Discussion

Theory suggests that visually-oriented predators will prey on conspicuous prey (Stevens and Merilaita 2011). In lizards, males in nuptial colouration signal their presence to attract mates and deter competitors (Olsson 1994; Bajer et al. 2011), and should thus face higher predation risk. We hypothesized that higher predation risk in males will manifest in changes in sex ratio, frequency of tail regenerates and survival depending on how successful males are at escaping the attack (Table 1). We observed adult sex ratio shifting in

favour of females (Fig. 2), faster increase in probability of tail autotomy in males (Fig. 3), and sex-specific differences in seasonal survival (Fig. 4). Co-estimating sex-specific predation risk and escape rate showed that males tend to face a higher predation risk, but also have a higher escape rate (Fig. 5). However, none of our results were significant, and we conclude that predation risk and escape rate are statistically equal in sand lizard sexes.

The obvious reason for insignificant results is the lack of power in the test for the given effect size; the solution for this being an increase in sample size. For example, for Fisher's exact test comparing young and adult sex ratio to be significant, we would have had to increase our sample size six times. This was not feasible in Hustopeče.

The result, where our data provided sufficient power, showed seasonal differences in the female survival rate (Fig. 4). Accounting for recapture probability, we found a significantly lower survival rate in females first captured at the beginning of the active season (phase I), when sand lizards mate and lay eggs. Projection of the dates of tail autotomy events showed females experienced more attacks in season phase II rather than earlier in the active season (Fig. 1B). Drivers of the low survival rate and low number of tail autotomy events in the first months after emergence from hibernation could be related to the following reproduction or environmental conditions during this time period.

Sand lizards alter their behaviour depending on their age, season and sex (Böhme and Bischoff 1984; Amat et al. 2003; Gvoždík and Boukal 1998).

Female locomotion is in some ways influenced by body allometry, where the females are less agile, particularly during gravidity (Shine 2003). Meanwhile, after successful mating, female locomotor activity increases due to higher physiological demand to provide nutrients for egg development (Shlyakhtin et al. 2019), exposing them to predators. Our results indeed show that females suffer from lower survival rate in seasonal phase I, when females tend to be gravid.

Adult males are more mobile in spring due to establishing and defending territory in competition with other males, and they seek exposed places to display their nuptial colouration (Olsson 1992, 1994). The display behavior makes males conspicuous to visually oriented predators, and increased mobility facilitates frequent encounters with parasites, increasing ectoparasite load during reproduction (Smolinský et al. 2021). High ectoparasite load can negatively influence the speed required to escape from predators (Ekner-Grzyb et al. 2013), make coloration less effective (Olsson et al. 2005) and cause the host to be more vulnerable to predation (Oppliger and Clobert 1997), exacerbating predation risk during reproduction season.

While behaviour and morphological changes associated with reproduction decrease seasonal survival, environmental conditions at the time when reproduction occurs further contribute to low survival and high predation risk. Spring and early summer months have lower mean diurnal temperatures, and ectotherm lizards need more time to warm up. Thermal performance of ectotherms will be critical in their ability to escape an attack by an en-

dotherm or an ectotherm that has reached its thermal optimum. During the reproduction season, sand lizards cannot escape the ecological niche of the endotherm predator due to the physiological demands of mating and gravidity. The trade-off between participating in reproduction and avoiding predation risk seems to be skewed towards prioritizing reproduction, leading to low survival rate in season phase I in female sand lizards. Interestingly, tail length is a poor predictor of sand lizard survival at our site (Table S1).

When developing our model, (1), (3) and (4), we considered only mortality attributable to predation (m_P), setting mortality due to other causes at zero. While the solution reduced dimensionality of the problem, it deviated the model from reality. Mortality unrelated to predation contributes to the estimated survival rates, and could be sex- and season-dependent. The projected dates of tail autotomy events (Fig. 1B) support the conclusion that predation contributes to low survival in the sand lizard active season.

Reproduction is a costly endeavour. The behavioural and morphological changes during reproduction attract attention of non-target receivers, the predators. Our results show that tail autotomy events, likely attributable to an escape from a predator attack, improve survival of sand lizard by about 5%. Tail autotomy events are most frequent in late spring and late summer, and males have a slightly higher predation risk. Gravid females do not lose their tail but their lives during a predator attack.

Higher mortality in males is one of the established realities in ecology, where males suffer from higher predation, higher conspecific aggression, risky

exploratory behaviours. Assuming that the primary and secondary sex ratio is 1:1, the selective removal of one sex from the population should result in sex ratio shifting in favour of females. According to Fisher (1930), sex ratio 1:1 benefits populations, giving rise to mechanisms that compensate faster loss of males. For example, in humans, more boys are born and the secondary sex ratio is greater than 1. Our results demonstrate seasonal ecological mechanisms that balance losses of both sexes in such a way that the sex ratio remains 1:1.

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Competing interests

The authors declare that they have no competing interests.

Author contributions

RS, ZH, NM conceptualised and designed the study; RS, ZH, MŠ, NM collected data; RS and MŠ performed investigation; ZH curated the data; ŠM and PŠ designed and implemented the algorithm for sexing lizards; NM per-

formed statistical analyses; RS, PŠ, NM wrote the manuscript, which all authors reviewed.

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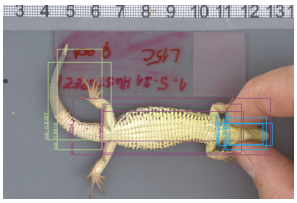
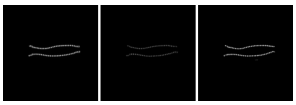
Supplementary material

1. Photograph of sand lizard ventral side

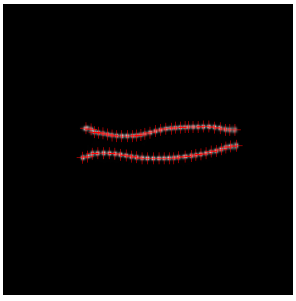


2. Detection of lizard head, body and tail with the YOLO detector

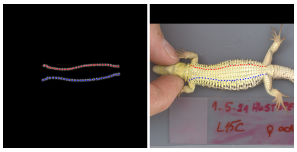
3. Oriented and cropped photograph centered at the detected body; added zeros (black region) to allow a square crop



4. Three size- and shape-specific U-Net models detecting ventral scales in the second row from the medial line as circle gradients centered on the scale



5. Localization map of scale gradient centers, result of the first U-Net model that returned a valid answer (found 26–35 scales on each side)



6. Identification of the sides of the rows of scales based on their relative distance (left), and overlay of the detected scales localization map on the photograph (right)

Figure S1: Scheme of the ScalesCounter algorithm

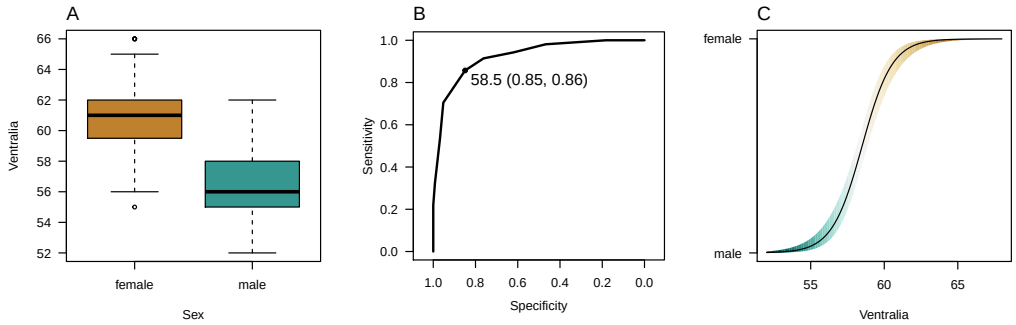


Figure S2: Sex determination in adult sand lizards, *Lacerta agilis*, using morphological isometry. A. Number of scales in the second row from the ventral medial line (ventralia) in sand lizards shows statistically significant sexual differences. B. Receiver operating characteristic curve, indicating threshold number of ventralia scales that differentiate the sexes of sand lizards. At 58.5, the specificity of sex determination is equal to 0.85 and sensitivity to 0.86. C. Logistic regression model indicating probability of sex determination of sand lizards based on the number of ventralia scales. At 58.4, $p = 0.5$.

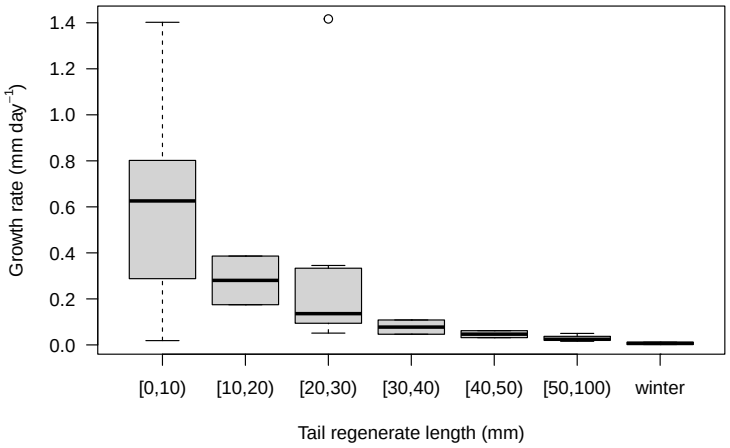


Figure S3: Individual seasonal growth rates of the tail regenerate in sand lizards (*Lacerta agilis*) conditional on tail regenerate length. winter – seasonal growth rate during hibernation.

Table S1: Model selection of capture-recapture data of sand lizards (*Lacerta agilis*) analysed based on the CJS model. The models used group covariates sex (female, male), age (0young, 2adult), season (phase1, phase2), and individual covariates tailL (tail length corrected for body length) and aged (approximate age of the animal at first capture in days), Phi – survival rate, p – recapture probability.

Model	n_{par}	AIC_c	ΔAIC_c	Weight	Deviance
Phi(∼ −1 + sex:season)p(∼1)	5	1341.576	0.000	3.390e-01	971.277
Phi(∼ −1 + sex:season)p(∼age)	6	1342.979	1.402	1.681e-01	970.630
Phi(∼ −1 + sex:season)p(∼sex)	6	1343.393	1.817	1.366e-01	971.044
Phi(∼ −1 + sex:season)p(∼season)	6	1343.542	1.966	1.268e-01	971.193
Phi(∼ −1 + sex:age:season)p(∼tailL)	10	1345.318	3.742	5.219e-02	1324.865
Phi(∼ −1 + sex:age:season)p(∼sex)	10	1345.327	3.751	5.197e-02	964.697
Phi(∼ −1 + sex:age:season)p(∼age)	10	1345.841	4.265	4.019e-02	965.211
Phi(∼ −1 + sex:age:season)p(∼season)	10	1345.887	4.311	3.927e-02	965.257
Phi(∼ −1 + sex:age:season)p(∼ −1 + sex:season)	12	1347.151	5.575	2.088e-02	962.329
Phi(∼ −1 + sex:season)p(∼ −1 + sex:season)	8	1347.218	5.642	2.019e-02	970.746
Phi(∼ −1 + sex:season)p(∼ −1 + sex:age:season)	12	1352.393	10.817	1.518e-03	967.571
Phi(∼ −1 + sex:age:season)p(∼ −1 + sex:age:season)	16	1352.707	11.131	1.298e-03	959.396
Phi(∼season)p(∼1)	3	1355.358	13.782	3.447e-04	989.132
Phi(∼season)p(∼sex)	4	1356.888	15.312	1.604e-04	988.629
Phi(∼season)p(∼tailL)	4	1357.057	15.481	1.474e-04	1348.975
Phi(∼season)p(∼age)	4	1357.072	15.496	1.463e-04	988.813
Phi(∼season)p(∼season)	4	1357.213	15.637	1.364e-04	988.954
Phi(∼aged)p(∼age)	4	1357.478	15.902	1.194e-04	1349.396
Phi(∼aged)p(∼1)	3	1357.585	16.009	1.132e-04	1351.536
Phi(∼aged)p(∼tailL)	4	1358.941	17.365	5.747e-05	1350.859
Phi(∼aged)p(∼sex)	4	1359.126	17.550	5.239e-05	1351.044
Phi(∼1)p(∼1)	2	1359.375	17.799	4.627e-05	995.173
Phi(∼aged)p(∼season)	4	1359.427	17.851	4.507e-05	1351.346
Phi(∼age)p(∼1)	3	1360.327	18.751	2.874e-05	994.101
Phi(∼sex)p(∼1)	3	1360.782	19.206	2.289e-05	994.556
Phi(∼1)p(∼season)	3	1360.873	19.297	2.187e-05	994.647
Phi(∼1)p(∼tailL)	3	1360.918	19.342	2.139e-05	1354.869
Phi(∼1)p(∼sex)	3	1361.001	19.425	2.052e-05	994.775
Phi(∼tailL)p(∼1)	3	1361.038	19.462	2.014e-05	1354.988
Phi(∼1)p(∼age)	3	1361.301	19.725	1.766e-05	995.075
Phi(∼age)p(∼age)	4	1361.336	19.760	1.735e-05	993.077
Phi(∼age)p(∼tailL)	4	1361.746	20.170	1.413e-05	1353.664
Phi(∼age)p(∼sex)	4	1361.932	20.356	1.288e-05	993.673
Phi(∼age)p(∼season)	4	1361.982	20.406	1.256e-05	993.723
Phi(∼1)p(∼ −1 + sex:season)	5	1362.089	20.514	1.190e-05	991.790
Phi(∼sex)p(∼tailL)	4	1362.274	20.698	1.085e-05	1354.193
Phi(∼sex)p(∼season)	4	1362.312	20.736	1.065e-05	994.054
Phi(∼tailL)p(∼season)	4	1362.587	21.011	9.287e-06	1354.505
Phi(∼tailL)p(∼sex)	4	1362.707	21.131	8.745e-06	1354.625
Phi(∼sex)p(∼age)	4	1362.709	21.133	8.734e-06	994.451
Phi(∼tailL)p(∼tailL)	4	1362.864	21.288	8.084e-06	1354.782
Phi(∼tailL)p(∼age)	4	1363.000	21.424	7.553e-06	1354.918
Phi(∼aged)p(∼ −1 + sex:age:season)	10	1363.156	21.580	6.984e-06	1342.703
Phi(∼season)p(∼ −1 + sex:age:season)	10	1363.287	21.711	6.542e-06	982.657
Phi(∼age)p(∼ −1 + sex:season)	6	1363.336	21.760	6.385e-06	990.987
Phi(∼tailL)p(∼ −1 + sex:season)	6	1363.762	22.186	5.161e-06	1351.590
Phi(∼age)p(∼ −1 + sex:age:season)	10	1366.996	25.420	1.024e-06	986.366
Phi(∼sex)p(∼ −1 + sex:age:season)	10	1367.087	25.511	9.786e-07	986.457
Phi(∼1)p(∼ −1 + sex:age:season)	9	1367.117	25.541	9.642e-07	988.570
Phi(∼tailL)p(∼ −1 + sex:age:season)	10	1368.953	27.377	3.850e-07	1348.500
Phi(∼ −1 + sex:season)p(∼tailL)	6	1419.548	77.972	0.000e+00	1407.376