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RESEARCH PAPER

Ectoparasite load increase in reproductively active sand lizards

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Abstract. Sexual reproduction imposes risks on participating adults through increased probability of injury, predation pressure, or parasite exposure. Evolutionary theory predicts that animals will tolerate parasite infection during reproduction at the expense of increased parasite load, resulting in individual trade-offs between the temporary costs of current reproduction against the long-term evolutionary benefits in the form of life-long production of viable offspring. We tested this hypothesis, predicting that participation in sexual reproduction increases parasite exposure by investigating ectoparasite load on sand lizards (*Lacerta agilis*). Using generalized additive models to correct for bimodal seasonal dynamics of ectoparasite activity, site and year, we found that ectoparasite load is higher in adults (animals that overwintered at least twice) than in subadults that overwintered once only. Between sexes of adult sand lizards, males had a higher number of blood-sucking ectoparasites than females. Our results indicate that both sexually-motivated extensive locomotion associated with territory defence and mate search in males, and increased energy uptake during gestation in females, contribute to elevated ectoparasite exposure. Increased host mobility associated with increased ectoparasite exposure leads to collateral burden of reproduction on sand lizard populations.

Key words: host-parasite interaction, parasite exposure, sexual behaviour, tick, *Ixodes*, *Lacerta*, reptile

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Introduction

Parasitism influences host life-history. In addition to investing resources in maintenance and reproduction, the infected host must mount defence against the parasite, and repair damage suffered (McNew et al. 2020). The resulting cumulative energetic requirements may exceed the individuals' capabilities, imposing a trade-off between the health and reproduction of the host. By defending against a parasite and coping with the damage incurred now, hosts are predicted to increase their probability of survival and future reproduction. Whether the infected host invests resources into growth or reproduction instead of defence and repair depends on its recent *vs.* future reproductive prospects (Sorci et al. 1996, Agnew et al. 2000). When current reproduction is unlikely, such as when experimental individuals are kept in separated housing, infected animals reduce their

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activity (Main & Bull 2000). The situation is more complex when future, postponed reproduction is an option. For example, infected female lizards prioritise health by changing their appearance to resemble the nuptial colouration of males. By mimicking visual signalling of males, infected females avoid mating attempts, and instead of energetically costly reproduction they can allocate metabolic resources into coping with infection (Václav et al. 2007). On the other hand, when opportunities for current reproduction increase and future reproductive opportunities are uncertain, hosts tolerate parasitism and reproduce at a possible expense of decreased survival (Kutzer & Armitage 2016, Taggart et al. 2018). Consequently, young animals have greater prospects of future reproduction, and thus are predicted to make a greater investment in responding to pathogenic agents.

We studied sand lizards (*Lacerta agilis*) in orchards in Central Europe to investigate how sexual maturity and behaviour associated with reproduction influenced ectoparasite exposure. Sand lizards are a small (up to 200 mm), sexually dimorphic lizard that occupies open, grassland habitats in the Palaearctic. In Central Europe sand lizards reproduce once each year starting at the age of two years and living for up to five years, although older individuals have been recorded (Guarino et al. 2010). Reproduction onset begins shortly after emergence from hibernation, when males emerge in March or April, followed several weeks later by females. The animals are promiscuous, with forced coupling by males of females in their territory. Males search for mates in their territory, which they defend both actively (involving fights) and through deterring competitors by visual displays (Olsson 1994). Females lay eggs to loose soil in June, with juveniles hatching in mid-summer.

In this study we focused on ectoparasites. While endoparasite infections are important to health (Dunlap & Mathies 1993), accurate diagnosis of infection by viruses, bacteria, or endoparasites is technically more demanding. Ectoparasite infections are more visible and their investigation is thus less invasive for the host (Jacobson 2007). Ectoparasites attach to hosts to obtain a blood meal, draining host resources and contributing to pathogen transmission (Bull et al. 2012). In reptiles, infestation by ectoparasites affects the host through higher risk of predation (Oppliger & Clobert 1997), or lower possibility of mating (Olsson et al. 2005, Václav et al. 2007). Some studies show that tick load has no significant effect on immediate short-burst locomotor performance or escape success from predators (Ekner-Grzyb et al. 2013), but a long-term influence on host performance in an individual's lifetime is understudied (Taggart et al. 2018, Otero et al. 2019). Infestation by ticks could be connected to infection of erythrocystic parasites, and distinguishing the effect of each on the host separately is challenging (Dunlap & Mathies 1993, Godfrey et al. 2010).

High prevalence of ticks on sand lizards makes them the greatest parasite vector for this reptile (Majláthová et al. 2010, Ekner et al. 2011a), and tick prevalence varies seasonally in the Palaearctic (Pérez et al. 2012). In Europe, tick activity has two seasonal peaks: one in the spring and the second at the end of the summer and beginning of the autumn, with a decrease during the hottest summer months. In years with higher precipitation during summer, the activity of ticks can remain high, without the mid-summer depression (Pérez et al. 2012, Žákovská et al. 2013).

We investigated the hypothesis that ectoparasite load on sand lizards differs between age cohorts as a result of increased host spatial activity related to reproduction. Adult males defend territories and search for mates resulting in larger home ranges than those occupied by females (Nicholson & Spellerberg 1989, Galán 1999). We hypothesised that the increased movement of males will facilitate the chance of an encounter with mites and ticks. We predicted adult males to have the highest ectoparasite loads. In adult females, gestation imposes energy costs and pre-partum females spend a greater time searching for prey, thereby increasing movement and increasing ectoparasite exposure. In contrast, subadults of both sexes provide a baseline ectoparasite load that is independent of elevated exposure due to reproductive behaviour.

Material and Methods

Simulation

We simulated a process in which host mobility influences ectoparasite exposure to validate the reasoning in our hypothesis. We used a two-dimensional random walk Markov chain on a plane of 5,000 cells to simulate host mobility, where visiting each cell constituted ectoparasite exposure and size of the plane reflected landscape with suitable habitat. The Markov chain started at a random location within the plane at coordinates **c** and ran for 1,000 steps. The number of steps represents the length of activity of the host. Each *i*th step was calculated as $\mathbf{c}_i = \mathbf{c}_{i-1} + \mathbf{s}\ \forall\ i \in [2,1000]$ where **s** is a vector with two elements drawn from a normal distribution $N(0, \sigma^2)$. The variance σ^2 constituted host mobility. If a value $c_{i-1} + s$ exceeded the borders of the plane, the respective coordinate of the step was calculated as $c_{i-1} - s$. We ran 200 simulations for each of 25 values of σ^2, and smoothed the results with a Loess regression.

Data collection

We sampled two different sand lizard populations during the months when the animals were active (Dračková et al. 2020). In the population from an orchard in Unín (48.72 N, 17.24 E) in Slovakia, the active period, when animals were sampled, extended from April to September 2007, while in an orchard in Hustopeče (48.93 N, 16.72 E) in the Czech Republic, it was between May and August 2018 and May and September 2020. At weekly intervals we caught lizards by hand or by noosing and marked each individual using toe clipping in 2007-2018 (Waichman 1992) or heat branding in 2020 (Winne et al. 2006, Ekner et al. 2011b). We sexed the animals, photographed them on a photographic grey card and counted ectoparasites attached to each individual. In 2020, during two trapping sessions, we collected ectoparasites from randomly selected individuals for another study. At other trapping sessions, ectoparasites were not removed from the hosts. The majority of ectoparasites belonged to the order Ixodida (Gwiazdowicz & Filip 2009), but as most of these were larval instars, identification to species was not possible.

To estimate the age cohort of individual animals, we used tpsDig v.2.02 (Rohlf 2005) software to measure body length from rostrum to anus from the digital images. Lizards over 60 mm were assigned as adults, individuals of 47 to 60 mm were considered subadults that had over-wintered once but had not yet reproduced (Dračková et al. 2020).

Statistical analysis

To reduce the influence of outliers on the statistical analyses, we removed individuals with the number of ectoparasites exceeding the Tukey's fences (Tukey 1977). The outlier detection method with Tukey's fences means that the dataset for further analyses satisfied the condition $m_i \leq Q_3 + 1.5 (Q_3 - Q_1)$, where m_i is the number of ectoparasites counted on a sand lizard at the capture *i*, and Q_1 and Q_3 are first and third quartile of all recorded values of m_i, respectively.

We calculated the season of capture as date of the year (ordinal date). To evaluate the seasonal component of ectoparasite activity from the comparison between age cohorts of hosts, we detrended the number of the ectoparasites using a generalized additive model (GAM). The GAM extends generalized linear models and applies quadratically penalized regression splines to smooth model terms to estimate complex, non-linear relationships between explanatory and response variables. We related the number of ectoparasites to season at the first capture of each individual. We evaluated overdispersion of the model errors from Q-Q plots and tested the Poisson error structure with a dispersion test (Cameron & Trivedi 1990). The model was considered overdispersed, when $\sigma^2(\boldsymbol{\varepsilon}) = \mu(\boldsymbol{\varepsilon})(1 + \alpha)$ and $\alpha > 0$, where σ^2 is the variance of the model residuals $\boldsymbol{\varepsilon}$, μ is the mean and α is the dispersion parameter. When the model was overdispersed, we used a negative binomial error structure that allows different mean and variance of $\boldsymbol{\varepsilon}$. We estimated the smoothing parameter of GAM with the REML method. We selected the optimal number of knots of the smoother with the Akaike Information Criterion (AIC). For further analyses, we used the GAM model to obtain the seasonally detrended ectoparasite load as the difference between the model prediction and ectoparasite load detected on the day of capture of each individual.

We estimated the differences in the predicted, seasonally detrended ectoparasite load between sexes and age cohorts with a Mann-Whitney test. To assess complex influences of sand lizard age, sex, their interaction, site of capture, year, and season, we modelled ectoparasite load with a GAM on first captures of each animal, using REML for parameter estimation. For the complex GAM analysis, we discarded the recaptures to avoid non-independence of the samples. Implementing a mixed model with the individual animals treated as a random factor was not possible, because our dataset did not contain a sufficient number of recaptures.

We ran all analyses in R (R Core Team 2019) using packages mgcv (Wood 2011), AER (Kleiber & Zeileis 2008) and RColorBrewer (Neuwirth 2014).

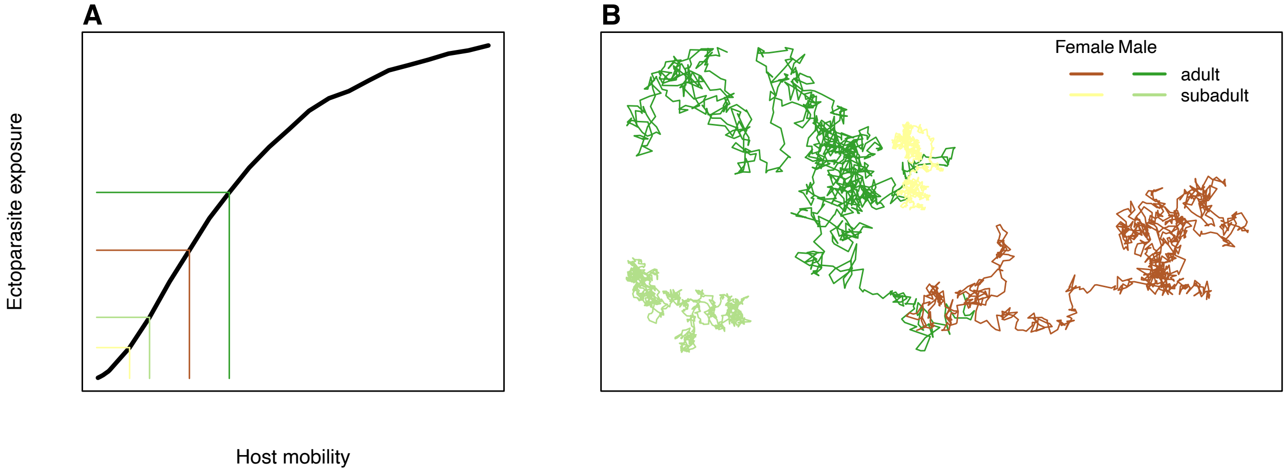

Fig. 1. Simulation of a hypothetical influence of increased host mobility linked with sexual maturity on ectoparasite exposure in sand lizards (*Lacerta agilis*). A) Ectoparasite exposure correlated with host mobility from 5,000 simulations; B) Examples of random walk Markov chains simulating the influence of sexually-dependent host mobility on ectoparasite exposure. Adult animals are expected to have increased ectoparasite loads due to increased movement in relation to behaviour associated with reproduction. Adult females will have increased energy uptake due to gestation, and adult males will move more to defend their territories and to search for mates.

Ethics statement

Sampling was based on permits 2579/2007-2.1 and 1323/527/05-5.1 issued by The Ministry of the Environment of the Slovak Republic, and JMK 38000/2018 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

Simulations showed that host mobility positively correlated with ectoparasite exposure (Fig. 1). With increasing host mobility, ectoparasite exposure increased non-linearly in an S-shaped curve. The saturation of ectoparasite exposure was dependent on the length of the simulation (Fig. 1A).

We captured 477 sand lizards (200 in 2007, 81 in 2018, and 196 in 2020) with 0 to 239 ectoparasites (Fig. 2). Estimating the threshold for outlier detection at 59 ectoparasites, we removed 23 records, resulting in the final dataset of 454 captures of 335 individuals. All hyper-parasitized individuals were adults (20 males and three females). The ectoparasite load did not differ between sites in the final dataset (Mann-Whitney test: U = 27,461, $P = 0.110$). Median ectoparasite load was 11 (Table 1), and 24 individuals did not have any ectoparasites at the time of capture.

The GAM to model the seasonal aspect of ectoparasite activity with a Poisson error structure was overdispersed (dispersion test: $\alpha = 8.99$, $z = 9.61$, $P < 0.001$) and the model was fitted with a negative binomial distribution. The GAM that best fitted the data had six knots according to AIC comparison (Fig. 3A). The model had a significant intercept ($\beta_0 = 2.65$, $z = 55.3$, $P < 0.001$) and smoothing term (EDF = 4.66, $\chi^2 = 93.4$, $P < 0.001$), and explained 18.1% of deviance observed in the data (Fig. 3B). The smoothing term was meaningful for interpretation because there was no monotone response possible within the 95% confidence interval of the smooth.

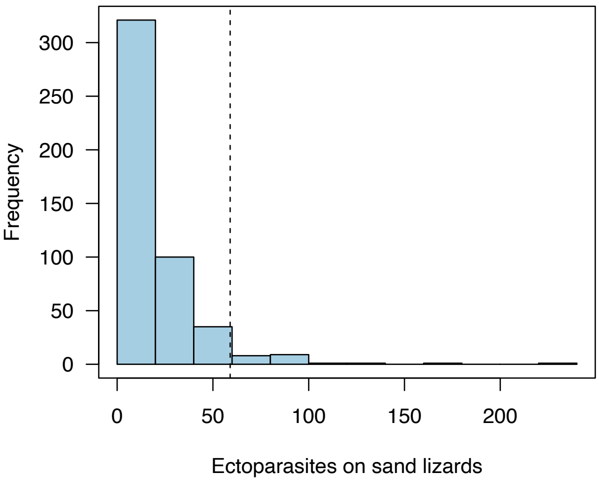

Fig. 2. Histogram of the ectoparasite load on sand lizards (*Lacerta agilis*). Vertical line indicates the threshold of 59 ectoparasites estimated for outlier detection. Animals with more than the threshold number of ectoparasites were removed from further analyses.

Table 1. Sex, age cohort and ectoparasite load of sand lizards.

	Sand lizard	Ectoparasite load per host		
Sex, age	captures	median	IQR	range
Female				
subadult	27	9	14.5	[0,40]
adult	211	10	16.5	[0,57]
Male				
subadult	19	6	11.0	[0,21]
adult	197	13	22.0	[0,59]

Having corrected for the ectoparasite load with respect to seasonal variation, we found no differences in ectoparasite load between sexes of subadult sand lizards (Mann-Whitney test: U = 251, *P* = 0.911), but we observed significant differences in adults (Mann-Whitney test: U = 16,024, *P* < 0.001). The difference in ectoparasite load is also present in both sexes, as adult males host more ectoparasites than subadult males (Mann-Whitney test: U = 2,851.5, *P* < 0.001), and adult females host more ectoparasites than subadults of the same sex (Mann-Whitney test: U = 3,549.5, *P* = 0.038). When data were not seasonally detrended, the significance of the tests remained stable in all comparisons except the female age cohorts (Fig. 4A). Observed ectoparasite load in adult females was statistically identical to that

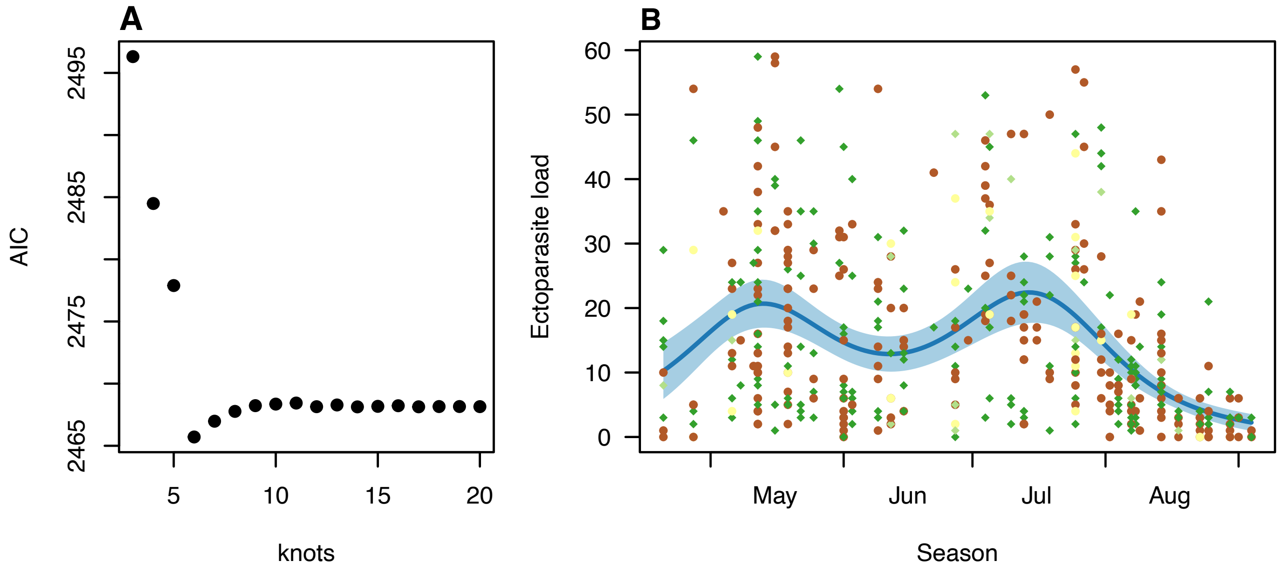

Fig. 3. Seasonal trend in observed ectoparasite load on sand lizards. A) Selection of the number of knots for the smoothing term of the generalized additive model, six knots were selected based on AIC; B) Bimodal distribution of ectoparasite load on sand lizards with peaks in May and July. Blue line – prediction from the generalized additive model with negative binomial distribution of the residuals relating season to ectoparasite load on sand lizards; shaded area – 95% confidence interval on the model prediction; circles – females, brown for adults and beige for subadults; diamonds – males, dark green for adults and light green for subadults. Some observations overlap.

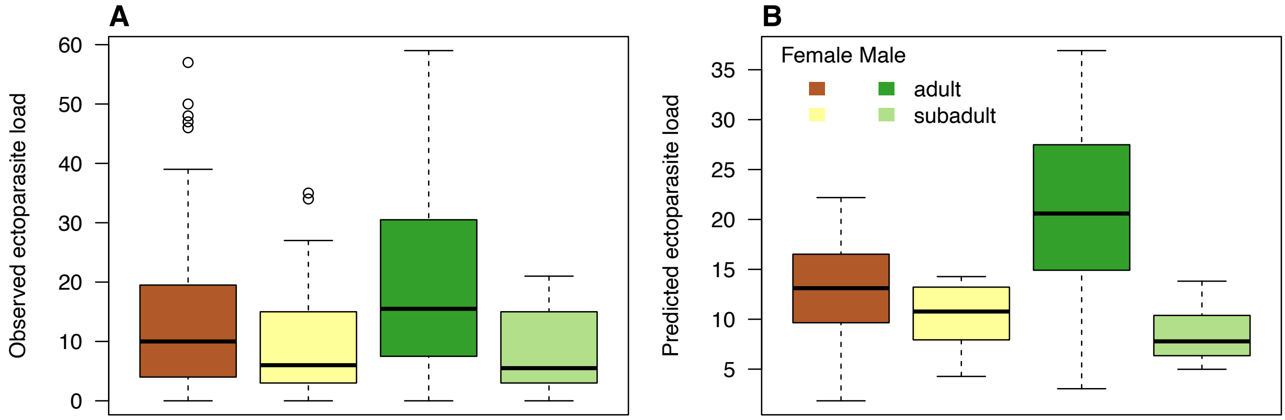

Fig. 4. Ectoparasite load on sand lizards differentiating sex and age cohorts. A) Observed ectoparasite load; B) Predicted ectoparasite load. The values are predicted from a generalized additive model correcting the observed ectoparasite load for sex, age, their interaction, capture site, year and the non-linear effect of season (Table 2).

Table 2. Generalized additive model of ectoparasite load on sand lizards. Covariates with significant effects are in bold.

Parametric terms	Estimate	SE	z	*P*
Intercept	136.82	140.10	0.98	0.329
Sex (male)	**0.51**	**0.10**	**5.24**	**< 0.001**
Age (subadult)	**–0.41**	**0.19**	**–2.16**	**0.031**
Site (Unín)	–1.14	0.85	–1.33	0.182
Year	–0.07	0.07	–0.96	0.338
Sex (male) : age (subadult)	**–0.55**	**0.28**	**–1.96**	**0.050**
Smooth term	knots	EDF	χ^2	*P*
Season	**6**	**4.65**	**100.2**	**< 0.001**

observed in subadult females (Mann-Whitney test: U = 3,035.5, $P = 0.580$).

In a complex GAM that evaluated sex, age, and their interaction on ectoparasite load, correcting for site, year, and the non-linear relationship with season, we confirmed the significant influence of sex and age (Table 2). The model used a negative binomial error structure, as the Poisson structure was overdispersed (dispersion test: $\alpha = 7.02$, $z = 9.94$, $P < 0.001$). Including the additional covariates in the GAM increased the explained deviance to 28.3%. Predicted ectoparasite load was highest in adult males, followed by adult females. Subadults of both sexes had low predicted ectoparasite load, with males having fewer ectoparasites than females in the model predictions (Fig. 4B).

Discussion

Our simulation study showed that increased host mobility can increase ectoparasite exposure. In the simplified scenario with evenly distributed ectoparasites and a random walk of hosts, we observed an increase of ectoparasite exposure in hosts that covered longer distances (Fig. 1). This outcome is biologically feasible, as ticks quest on vegetation for passing hosts. In fact, tick infection has been linked to host foraging movement in birds (Fecchio et al. 2020) and to territory size in mammals (Wanelik et al. 2017).

We found a bimodal distribution of ectoparasite load on sand lizards with progressing season. The peaks, when sand lizards suffer from highest ectoparasite infestation, are in mid-May and mid-July (Fig. 3). The tick activity as inferred from flagging is known to be unimodal or bimodal in different years. The bimodal activity of questing ticks has peaks in early summer (May-June) and early autumn (September-October; Pérez et al. 2012, Žákovská et al. 2013, Hauck et al. 2020). The autumn peak inferred from flagging is desynchronized with our observation of a mid-summer peak in ectoparasite load on sand lizards. Changes in the activity of parasites are a product of parasite adaptation to the environment and the temporal presence of its primary host (Žákovská et al. 2013, Lewis et al. 2002).

In generalist parasites, their seasonal activity reflects environmental requirements (temperature, moisture, vegetation cover, etc.) rather than activity patterns of the host. When temporal changes in tick load on the inspected host do not align with the temporal activity of questing ticks, ticks are either generalist parasites, or the host under survey might not be their primary target. If the parasite load aligns in time with the activity of the host better than with environmental cues, the parasite load modality is likely caused by the host activity (Lewis et al. 2002). We did not flag questing ticks from vegetation, but as ticks infect multiple vertebrate hosts (Matuschka et al. 1991), we assume that the bimodal host infestation of sand lizards observed herein is driven by local life cycle of the hosts. The highest spatial activity of male sand lizards in Central Europe is in mid-May, when mating peaks, while females experience their highest energetic demand during the final phases of gestation, when they most likely hunt extensively (Opatrný 1992).

We show that subadults had fewer ectoparasites than either sex of the adult animals (Fig. 4). This finding is not the effect of subadults being alive for insufficient time to encounter as many ectoparasites as the adults, because the subadult age cohort consists of sand lizards that have already overwintered and their seasonal phenology is similar to that of the adults (Krütgen et al. 2018). We interpret the lower ectoparasite load found on subadult sand lizards as being partially confounded by difference in host resource requirements. Whereas subadults require nutrients for growth and maintenance, adults also invest energy in reproduction.

Adult sand lizards had more ectoparasites than subadults of both sexes, with adult males exceeding any other category (Fig. 4). Correcting the observations for seasonality, spatial differences between sites and differences in biological dynamics of any given year confirmed the conclusion that ectoparasite load differed between sexes and age cohorts. This result contrasts with previous findings, where no correlation between sexes and parasite load was found in sand lizards in Poland (Gryczyńska-Siemiątkowska et al. 2007, Wieczorek et al. 2020). In our observations, differences in ectoparasite load between sexes was less pronounced, albeit still significant, when data were not statistically corrected for seasonal trends (Fig. 4A). The excess of ectoparasites on males compared to that on females became pronounced once confounding effects influencing the observations, in particular the non-linear seasonal trends in ectoparasite load, were accounted for (Fig. 4B). The discrepancy between our results and those found in Poland shows the importance of assessing modality of temporal fluctuations of all biota involved in the interaction, the hosts as well as the parasites.

Experimental manipulations and natural observations with parasite loads differing by orders of magnitude show a negative effect of parasites on host locomotion. For example, haemogregarine infection influences predator avoidance/escape (Oppliger & Clobert 1997), tick infestation decreases locomotion speed or travelling distance (Main & Bull 2000), or maternal parasite load projects into offspring life-history traits (Sorci et al. 1996). In the wild, ectoparasites, such as ticks, aggregate on hosts through environment-to-host transmission and detach after feeding, with adult ticks reproducing in vegetation not on their hosts. Environment-to-host transmission of parasites depends strongly on host home range size (Wanelik et al. 2017, Wieczorek et al. 2020) and thus on the activity of the host in its territory. Our results show that the increased spatial activity related to sand lizard reproduction increases ectoparasite exposure. Sexually active sand lizards are exposed to more ectoparasites, increasing the cost of reproduction.

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