SALAMANDRA **56**(1): 75–77
15 February 2020 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

Correspondence

The causes of extremely low tick prevalence in European legless squamates remain an unanswered question

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Manuscript received 24. May 2019
Accepted: 30. November 2019 by Stefan Lötters

Parasitism substantially impacts fitness-related traits, such as body condition, survival and reproductive success (e.g., Lanciani 1975, Lehman 1993). Among the parasites known from free-ranging vertebrates, ticks (Ixodida) are particularly important as potent vectors of pathogens with a high capacity to infect domestic animals and humans. Recently, the spread of tick-borne diseases and the abundance of ticks have increased, or are predicted to increase, in response to global warming (Gray et al. 2009). Similarly, the strong impact of climatic change affects reptiles, a group that represent important host and vector organisms for ticks with prevalence reaching up to 100% (Eisen et al. 2001). Infestations can even exceed 50 ticks per individual (Dudek et al. 2013), as has been observed across many species and populations (e.g., Delfino et al. 2011, Ra et al. 2011).

For these reasons, detailed data on the association of reptiles and ticks are highly relevant. The majority of studies on ticks concern lizards. Snakes, the group with the second highest species richness and worldwide distribution, have remained less recognized with regard to ticks, except as far as captive specimens are concerned (e.g., Nowak 2010). However, recent studies on tropical snakes have revealed a high prevalence, exceeding 50% in Australian species (Natush et al. 2018) and up to 30% in Indian snakes (Pandit et al. 2011). In contrast, in temperate North America, despite tick prevalence reaching 36% in lizards, no ticks were detected in snakes (Apperson et al. 1993). In the mentioned study, sampling involved 16 species, but sample sizes did not exceed 10 individuals per population, so that a lower prevalence may have remained undetected. Clearly, the body of data on tick occurrence in snakes, especially in temperate zones, is still full of gaps and does not provide any consistent picture, which highlights the need for further research.

We studied the correlates of tick prevalence and infestation across a set of species and populations in central European snakes and, additionally, other legless reptiles, the slow worms. Specifically, we predicted that the intensity of tick infestation negatively correlates to the condition of specimens. Also, we expected that prevalence and infestation exhibits a seasonal and spatial pattern, reaching their highest levels in lowland rather than highland/montane habitats and in spring, after the first annual ecdysis, when the density of ticks in the environment is highest (Gray 2008).

We gathered data collected within the framework of several field projects on six species of legless reptiles belonging to four families native to Poland and common throughout Europe, i.e., Natricidae – grass snake (*Natrix natrix*), Viperidae – common European adder (*Vipera berus*), Colubridae – smooth snake (*Coronella austriaca*) and Aesculapian snake (*Zamenis longissimus*), and Anguidae – slow worms (*Anguis fragilis*, *A. colchica*). In ca. half of the populations (16 out of 33), we surveyed reptiles throughout their whole activity season, while in the remaining 17 popula-

Table 1. Tick prevalence in populations of six species of legless reptiles from Poland.

Species	N of examined populations	N of captured individuals	N of individuals with ticks	Years of surveys
Natrix natrix	10	669	0	2001–2017
Vipera berus	8	179	0	2003–2018
Coronella austriaca	6	159	3	2003–2018
Zamenis longissimus	1	137	1	2009–2013
Anguis fragilis	1	100	0	2015–2017
Anguis colchica	7	89	0	2003–2018
Total	33	1,333	4	

tions, only spring, summer or autumn surveys were performed. The latter populations were also included in this study to obtain as detailed an insight as possible into local variation of tick prevalence. Each individual was examined for the presence, location and the number of ticks. In most specimens, body size and sex were recorded, excluding only those juveniles whose sexual identity could not be established with certainty. Also, we did not remove ticks from reptiles, except in one instance. The tick collected from the cloaca of a female Aesculapian snake was, however, damaged during removal so that further identification was not possible.

In total, we examined 1,333 specimens from 33 populations in 18 localities (Table 1). Ticks were detected in four specimens, three in smooth snakes and one in an Aesculapian snake. Detailed information on all studied populations and localities (Sites I–XVIII) are provided in Supplementary data 1.

In the smooth snake, three cases of tick infestation were recorded, with one tick per individual: in the mouth corner of one adult female (10 May 2018; body mass: 64 g; SVL: 48 cm; site III); on the neck of one adult male (18 June 2015; body mass: 41 g; SVL: 48 cm; site VI); and on the neck of one juvenile (4 June 2016; body mass: 4.5 g; SVL: 17 cm; site VI). In the Aesculapian snake, one tick was observed on the internal, scaleless side of the cloaca in an adult female (20 July 2011; body mass: 225 g; SVL: 104 cm; site XII).

Figure 1. Behavior of females Aesculapian snake (*Zamenis longissimus*) having cloaca infested with a tick (photographed by Ryszard Babiasz). Position of the tick is marked with a red circle.

This snake was noteworthy for displaying an as yet unknown behaviour, which probably constituted an attempt to rid itself of the tick by keeping the cloaca everted (Fig. 1). None of the infested snakes exhibited any signs of lowered body condition, such as emaciation or dysecdysis.

The single instances reported here may indicate that ticks prefer the anteriormost body parts, as has previously been noted in Australian snakes (Natush et al. 2018), except for the one case in which the cloaca was parasitized, possibly during oviposition. As expected, in three out of four cases, ticks were observed in two lowland populations and in spring/early summer. However, the extremely low prevalence of ticks did not allow us to test for seasonal and spatial patterns of prevalence and infestation or their relation to the host's condition. Most importantly, the dataset reported here is the largest for temperate legless reptiles, and the extreme rarity of ticks in the examined populations (0.3%) strongly indicates their high resistance towards tick infestations. This pattern is strikingly contrary to published records on European lacertids that revealed very high prevalences, reaching as much as 82% in sand lizards, *Lacerta agilis* (Bauwens et al. 1983) and 35–37% in the same species in western Poland (Dudek et al. 2013). We propose two, non-mutually exclusive, explanations for this phenomenon.

Firstly, there is an obvious contrast between tick occurrence in tropical snakes (Pandit et al. 2011, Kho et al. 2015, Natush et al. 2018) as opposed to temperate species. This indicates that climatic conditions are likely to contribute to the discrepancies observed in tick prevalence. Specifically, we propose that short hibernation periods or their entire absence in the tropics lead to a prolonged period of exposure to the risk of tick infestation. A similar effect was reported in another host-parasite system, i.e., mite infestation in snails was shown to be reduced after experimentally induced hibernation (Haeussler et al. 2012). Accordingly, the shortening of the winter season through ongoing climate change could be anticipated to gradually increase tick prevalence in temperate snakes populations.

Secondly, ticks can reach high prevalence in squamates in temperate zones, but apparently inflict mostly species with legs, which has been observed not only in Europe (Dudek et al. 2013), but also in North America (Apperson et al. 1993). This suggests that the climatic conditions postulated here may not be the sole cause underlying the low prevalence of ticks in snakes and slow worms, but rather they interact with at least one more factor. We suggest that a legless body, with the consequent reduction of easily penetrable sites, such as armpits and groins (Dudek et al. 2013), may greatly limit the attachment of ticks to potential hosts. Also, the duration of tick attachment is likely to be reduced in legless reptiles as a result of routine movements and a different mode of ecdysis, as both slow worms and snakes typically moult in one piece, unlike lizards (Vitt & Caldwell 2013).

Overall, our observations point to temperate legless reptiles having a strong capacity of avoiding tick infestation. We do not exclude the possibility that infestation rates may be higher than our observations suggest, but if this is the case, then removal rates during hibernation and/or ecdysis are probably even higher. However, due to the extremely low prevalence of ticks, field studies are bound to fail to provide sufficient resolution to test such a hypothesis, and an experimental approach is now the necessary next step to explain the enigma of negligible tick prevalence in temperate legless reptiles. Additionally, the low density of ticks suggests they play only a minor role in spreading haemoparasites amongst temperate snakes and slow worms and that other modes of transmission may be of much greater importance, such as the vertical transmission recently described in garter snakes (Kauffman et al. 2017), but this aspect also requires further studies.

Acknowledgements

Surveys were conducted based on the permits from Regional Directorates for Nature Conservation: WPN.6401.21.2015.TB, WPN.6401.183.2017.AJ, WPN.6401.88.2015.Msz, WPN.6401.281.2017.MK, 132/2016, DOPozgiz-4200/II-12/1040/09/ed; and WOP.6401.4.24.2018.MO. Our study was supported by a grant from the National Science Centre (No. UMO-2016/21/N/NZ8/00959) and the NATRIX Herpetological Association. We thank Ryszard Babiasz for sharing his photograph of an Aesculapian snake infested with tick. We also thank Stefan Lötters for his comments on an earlier version of the text that substantially improved the manuscript.

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Supplementary data

The following data are available online:

Supplementary document 1. Detailed list of all studied species, populations, numbers of individuals, and timing of survey.

Supplementary document 2. Map of Poland with site numbers.