Original article

Distribution pattern and number of ticks on lizards

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ABSTRACT

The success of ectoparasites depends primarily on the site of attachment and body condition of their hosts. Ticks usually tend to aggregate on vertebrate hosts in specific areas, but the distribution pattern may depend on host body size and condition, sex, life stage or skin morphology. Here, we studied the distribution of ticks on lizards and tested the following hypothesis: occurrence or high abundance of ticks is confined with body parts with smaller scales and larger interscalar length because such sites should provide ticks with superior attachment conditions. This study was performed in field conditions in central Poland in 2008–2011. In total, 500 lizards (Lacerta agilis) were caught and 839 ticks (Ixodes ricinus, larvae and nymphs) were collected from them. Using generalised linear mixed models, we found that the ticks were most abundant on forelimbs and their axillae, with 90% of ticks attached there. This part of the lizard body and the region behind the hindlimb were covered by the smallest scales with relatively wide gaps between them. This does not fully support our hypothesis that ticks prefer locations with easy access to skin between scales, because it does not explain why so few ticks were in the hindlimb area. We found that the abundance of ticks was positively correlated with lizard body size index (snout-vent length). Tick abundance was also higher in male and mature lizards than in female and young individuals. Autotomy had no effect on tick abundance. We found no correlation between tick size and lizard morphology, sex, autotomy and body size index. The probability of occurrence of dead ticks was positively linked with the total number of ticks on the lizard but there was no relationship between dead tick presence and lizard size, sex or age. Thus lizard body size and sex are the major factors affecting the abundance of ticks, and these parasites are distributed nearly exclusively on the host's forelimbs and their axillae.

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1. Introduction

Most ectoparasites have specific niches on the host body (e.g. Andrews and Petney, 1981; Andrews et al., 1982; Chilton et al., 1992). Of primary importance, from the parasites' perspective, is a good attachment site on the host body, to allow efficient feeding. For example, blood-sucking parasites like ticks, fleas and lice prefer places with easy access to skin, e.g. hairless parts of the rodent's body with a thin skin and dense vascular system (Weallers and Marganeidge, 1971; Pilosof et al., 2012; White, 1976). Another important feature of a good attachment site is that it should be

outside the reach of the animal's mouth and claws because some animals have a well-developed antiparasitic behaviour, e.g. birds can brushing and scratching their body to dispose Phthiraptera parasites (Nelson and Murray, 1971; Reiczigel and Rozsa, 1998). Also, the attachment place should be secured from tearing by vegetation.

Some species of lizards from five families (Iguanidae, Chamaeleonidae, Gekkonidae, Lacertidae and Scincidae) have special skin invaginations called nuchal or mite pockets. The probable role of these pockets is the effective controlling of infestation by their major ectoparasites – ticks (Arnold, 1986; Salvador et al., 1999). The skin inside pockets is more resilient and hyperplastic, which allows quick repair of damage caused by ticks (Arnold, 1986). Moreover, under the skin there are aggregations of lymphoid cells, which probably alleviate tick-borne infections (Arnold,

1986). Experiments of Salvador et al. (1999) have shown that *Ixodes ricinus* ticks prefer feeding in mite pockets of *Psammodromus algirus* lizards. Lizards that have these pockets blocked and have ticks attached in different parts of the body have a low survival rate (Salvador et al., 1999). However, the majority of lizard species do not have special sites on their skin where ectoparasites are attached. There are a few studies about tick attachment sites on lizards and certain patterns in tick distribution on lizard bodies have been reported. Ixodidae ticks usually prefer attaching to fore-limbs and their axillae in various species of lizards (Bauwens et al., 1983; Apperson et al., 1993; Ra et al., 2011) but some species preferably engorge on flanks, e.g. *I. asanumai* on *Eumeces okadae* lizards (Hayashi and Hasegawa, 1984a,b) or hindlimbs, e.g. *Ambly-omma* sp. on monitor lizards (Nowak, 2010). Thus there are clear preferences in feeding places, which are dependent on species of lizard and tick (Burridge and Simmons, 2003). In the case of lizards that are hosts for two or more ticks species, this topic is more complicated because parasites may compete for the host (Holmes, 1973). Also Ixodidae ticks may compete for the host with mites parasites what is known in case of *Sceloporus occidentalis* lizard (Prendeville and Hanley, 2000). Recent studies have shown that tick communities on lizard hosts are niche-segregated and lizard males and females as well young and adult lizards may differ in tick distribution (Andrews and Petney, 1981; Andrews et al., 1982; Chilton et al., 1992; Tälleklint-Eisen and Eisen, 1999; Prendeville and Hanley, 2000). For example, males sand lizards (*Lacerta agilis*) should have a larger number of ticks than females because males are more mobile (Olsson et al., 1996) and thus more prone to contact with ticks. Also, it can be expected that young sand lizards individuals may have a higher tick load because they colonise new territories during post-natal dispersal (Ryberg et al., 2004).

Parasite–host interactions are dynamic, with consequences for fitness in both host and parasite (Carius et al., 2001; Lambrechts et al., 2006; Tryjanowski et al., 2007). Studies on birds shown that parasite fitness may depend on host quality (Tschirren et al., 2007). Theoretically, when the host is in good condition, the parasite may gain more than when the host is of poor quality. Fitness of animal is often correlated with body size (Brown et al., 1993) and larger body size of a parasite may indicate more resources found on its host. Thus, paradoxically, it is possible that fitness of a parasite may be positively correlated with fitness of its host (Tseng and Myers, 2014). This may lead to a situation where larger parasites might be attached to larger hosts. For the same reason, larger numbers of ectoparasites may be found on larger hosts.

The host body size and condition are not constant in time, though. There are numerous abiotic and biotic factors that may deteriorate the condition of animals and thus may shape the host-parasite interactions. Especially, sub-lethal effects of predators may greatly worsen the condition of the host (Vermeij, 1982; Bowerman et al., 2010). One of the best examples of this phenomenon is auto-tomy in some lizards species. Lizards drop a part of the tail during an attack by a predator and in this way avoid deadly consequences. However, the long-term effect of autotomy is that lizards have to rebuild the tissue and replenish lipid reserves (Wilson, 1992; Maginnis, 2006). This is costly and involves substantial foraging effort and mobility, which may lead to more contacts with ectopar-asites. Thus it is possible that the presence of an injured tail may be correlated with a higher number of ectoparasites than in non-autotomized lizards.

The aim of this study was to examine the distribution of ticks and the factors affecting their number on the lizard body. Specifi-cally, we tested the hypothesis: The occurrence or high abundance of ticks is confined to the body parts with smaller scales and larger interscalar length because such sites should provide ticks with superior attachment conditions.

2. Materials and methods

2.1. Study area and study species

The study was carried out in April–June in 2008–2011 in the Barycz valley in Poland (51°34′N, 17°40′E, elevation 110–170 m). This study area is characterised by extensively farmed land with a mosaic of arable fields, meadows, small woodlots, and scattered trees and shrubs of various ages, dominated by crack willow *Salix fragilis*, silver birch *Betula pendula*, black poplar *Populus nigra*, and Scots pine *Pinus sylvestris*. It includes both dry sandy areas and moist sites (for details, see Ekner-Grzyb et al., 2013).

The sand lizard (*L. agilis* Linnaeus, 1758; Lacertidae) is a short-legged, rather robust, small to medium-sized lizard (Dudek et al., 2014). It is a ground-dwelling and diurnal species, with one of the widest geographical distribution ranges of all reptiles (Bischoff, 1984). In the study area the sand lizard is a common species, with average population densities of 9.25 individuals/ha (Ekner et al., 2008).

Lizards used for measurements of scales were preserved speci-mens from the Poznan University of Life Sciences collection.

Castor bean tick (*I. ricinus*; Ixodidae, Linnaeus, 1758) is a species with the widest distribution among European ticks. In some regions of Central Europe it commonly infests the sand lizard (Bauwens et al., 1983; Matuschka et al., 1991; Gryczyńska et al., 2007; Majláthová et al., 2008). There are only few studies about tick com-munities on sand lizards in Europe (Bauwens et al., 1983).

2.2. Study procedures

Lizards were captured using special herpetological nets (fab-ric net attached to the end of a metal stick with a metal circle) or by hand. Next, the lizards were aged by measuring snout-vent length (Gvozdik, 2000) and classified as: adult (>45 mm), subadult (35–45 mm) or juvenile (<35 mm). Juveniles were lizards in the 1st calendar year of life, subadults in the 2nd calendar year of life, and adults were in the 3rd year or older. We used snout-vent length as the body size index instead of total body length because some lizards had signs of autotomy, but for lizards that had a fully developed tail, the total body length was strongly positively cor-related with snout-vent length ($r = 0.798$, $P < 0.001$, $n = 348$). Then, the lizards were sexed based on the presence of femoral pores in males (which are larger and more distinct than in females) and the expanded gonadal area in the tail base in males. Also, males have larger heads and during the mating season males have green body colouration (Borczyk et al., 2014). Animals were examined for the presence of ticks, which were removed with forceps and stored in 70% ethanol for other studies (Ekner et al., 2011a; Ekner-Grzyb et al., 2013). The part of the body where each tick was feeding was recorded as presence in one of the following body locations: abdomen, back, forelimb, hindlimb, ear, head, neck or flank. Ticks were identified to species level and life stage using a stereomicro-scope, according to Siuda (1993), and scutum length and width of some of the collected ticks were measured. During the study, all ticks from one lizard were put together to the same test-tube (for logistical reasons) so we have not collected data about the distri-bution of ticks at various life stages in relation to the lizard body part where they engorged. All the ticks were identified as *I. ricinus*. The presence of dead ticks was also noted (dead ticks were dry, flat, and easily detached from the skin).

In lizards after tail autotomy, both original and regenerated parts of the tail were measured. To avoid pseudoreplication, lizards were permanently marked using electrical heating devices called Medical Cautery Units (for method description, see: Ekner et al., 2011b), so each individual was used only once in the study.

Measurements of scales were conducted on eight adult specimens (four females and four males). Lizards were placed on a flatbed scanner (HP Scanjet 3800) and scanned with a ruler at 1200 dpi. These pictures were analysed with ImageJ software. On each specimen, we drew a 4 mm^2 square in four body locations (forelimb, hindlimb, neck, and flank) and counted scales within it and measured the length of the interscalar region.

To test possible correlation between tick size and lizard body size, the width of the scutum of all ticks from 67 randomly chosen lizards was measured using a stereomicroscope and Zeiss LSM Browser software.

2.3. Statistics

Counts of ticks from different body parts of the same lizard can be treated as repeated measures. Thus, we used generalised linear mixed models (GLMMs) to account for the dependency of body parts in one individual. A GLMM with a Poisson error distribution and log-link function was used to analyse factors affecting the number of ticks on lizard bodies. Tick numbers were divided into body parts to analyse differences in tick abundance between the head, ear, neck, flanks, back, abdomen, forelimbs, and hindlimbs. Other explanatory variables were: sex, age, body size index, presence of autotomy, and date in the season. Lizard identity and year of study were assigned as random factors. As sex is unidentifiable in juveniles and subadults, we built two GLMMs. In the first GLMM, we analysed only adults and we omitted the effect of age. In the second GLMM we used all the data but we did not analyse the effect of sex. Age was measured for almost all lizards, so here we present results from the GLMM with the effect of age. The GLMM with the effect of sex is presented in Supplementary material.

A GLMM with Gaussian error distribution and identity-link function was used to analyse scutum width in ticks – a proxy of tick size. The explanatory variables included tick age (larvae vs. nymphs), age and sex of the lizard host, presence of autotomy, body size index, and date in the season. Lizard identity and year were random factors in this analysis. Again, as age was measured for a larger sample of lizards than sex, here we present results from GLMMs with the effect of age. The GLMM with the effect of sex is presented in Supplementary material. A GLMM with binomial error distribution and logit-link function was used to analyse factors affecting the probability of occurrence of dead ticks on lizards. For this purpose we used the presence (not number) of dead ticks because in most lizards only single dead ticks occurred. The explanatory variables included the number of live ticks, age, and sex of the lizard, autotomy, body size index, and date in the season. Study year was a random factor. As the number of dead ticks was low, we did not include their location on the lizard body in the model. Similarly to the GLMM for the total number of ticks, we built two separate models: one including lizard age (with a larger sample size) and a second model with the effect of sex (presented only in Supplementary material).

A GLMM with Gaussian error distribution and identity-link function was used to analyse the density of scales and length of interscalar region in different body parts in adult lizards. Other explanatory variables included sex and date in the season. Lizard identity was a random factor in this analysis.

In all GLMMs, paired contrasts were calculated to find statistically significant differences between levels (if larger than two) of categorical explanatory variables. We also calculated the McFadden pseudo R^2 to approximate variance explained by each model (Menard, 2000). The significance level was set at $\alpha = 0.05$.

Statistical analyses were performed with SPSS 21.0 for Windows.

3. Results

A total of 500 individual sand lizards were captured, but several individuals escaped during measurements. Consequently, we collected complete data about autotomy for 497 individuals (348 individuals had intact tails and 149 had autotomized ones) and we were able to identify sex in 291 adult lizards (136 females and 155 males).

In total, 839 ticks were found on 182 (37%) out of the 500 examined lizards (Table A.1). Only tick larvae (63.7%) and nymphs (26.3%) of *I. ricinus* were found. On average ($\bar{x} \pm$ SD), 4.61 ± 6.96 ticks were on an infested host. The maximum number of ticks living on a lizard (an adult male) was 66. In total, 25 dead ticks were found attached to 19 sand lizards. Probability of occurrence of dead ticks on the host was positively related to the number of live ticks on the host (estimate = 0.063 ± 0.029, Table 1). However, the occurrence of dead ticks was not related to lizard sex, age, autotomy, and date in the season or body size (Table 1). All dead ticks but one were attached to the forelimb area.

3.1. Factors affecting tick abundance

The effect of body part on infestation rate was significant (Table 2) and most parasites concentrated around the forelimbs in their axillae on the trunk (but not directly on legs or toes), with other body parts much less infested (Table 3 and S3, Figs. 1a and 2). Tick abundance increased also with progress of the season and with the body size index (Tables 2 and 3). Adult lizards had higher numbers of ticks than juveniles had (Figs. 1b and 3) and the number of ticks on males was twice as high as on females (Fig. 1c). Tail autotomy had no significant influence on tick infestation (Table 2).

The scutum of 272 ticks (larvae and nymphs) from 67 lizards was measured. Scutum width was larger in nymphs (0.350 ± 0.005 mm) than in larvae (0.239 ± 0.006 mm) but the effects of lizard age, sex, body size index, tick load, and date in the season were statistically non-significant (Table 4).

Table 1
The generalised linear mixed model with binomial error variance and logit-link function with factors affecting the presence of dead ticks on lizards – variant with the effect of age ($n = 500$ lizards). McFadden pseudo R^2 for the model = 0.11.

Source of variation	F	$df1, df2$	P
Age	1.833	2, 490	0.161
Autotomy	0.167	1, 490	0.846
Body size index	0.162	1, 490	0.687
Date	0.623	1, 202	0.431
Number of live ticks	4.603	1, 490	0.032
Random effect	Estimate ± SE	Z	P
Year	0.762 ± 1.064	0.716	0.474

Table 2
The generalised linear mixed model with Poisson error variance and log-link function with factors affecting the abundance of ticks on lizards – variant with the effect of age ($n = 500$ lizards). McFadden pseudo R^2 for the model = 0.35. Statistically significant differences are marked in bold.

Source of variation	F	$df1, df2$	P
Age	8.798	2, 782	**<0.001**
Autotomy	0.109	1, 406	0.897
Body size index	4.057	1, 411	**0.045**
Date	11.660	1, 690	**0.001**
Body part	166.896	7, 3970	**<0.001**
Random effect	Estimate ± SE	Z	P
Lizard identity	1.749	0.187	**<0.001**
Year	0	0	–

Table 3
Estimates of parameters from the generalised linear mixed model presented in Table 1. Explanations: see also Table 2.

Source of variation	Estimate	SE	P
Intercept	−4.548	0.609	**<0.001**
Age = adults	0.479	0.394	0.226
Age = juveniles	−1.597	0.426	**<0.001**
Age = subadults	0[a]		
Autotomy = no	0.024	0.128	0.899
Autotomy = yes	0[a]		
Body size index	0.024	0.012	**0.045**
Date	0.008	0.002	**0.001**
Body part = abdomen	−2.686	0.422	**<0.001**
Body part = back	−2.531	0.393	**<0.001**
Body part = ear	−1.769	0.279	**<0.001**
Body part = flanks	−0.764	0.189	**<0.001**
Body part = forelimbs	2.027	0.113	**<0.001**
Body part = head	−2.079	0.320	**<0.001**
Body part = hindlimbs	−3.784	0.715	**<0.001**
Body part = neck	0[a]		

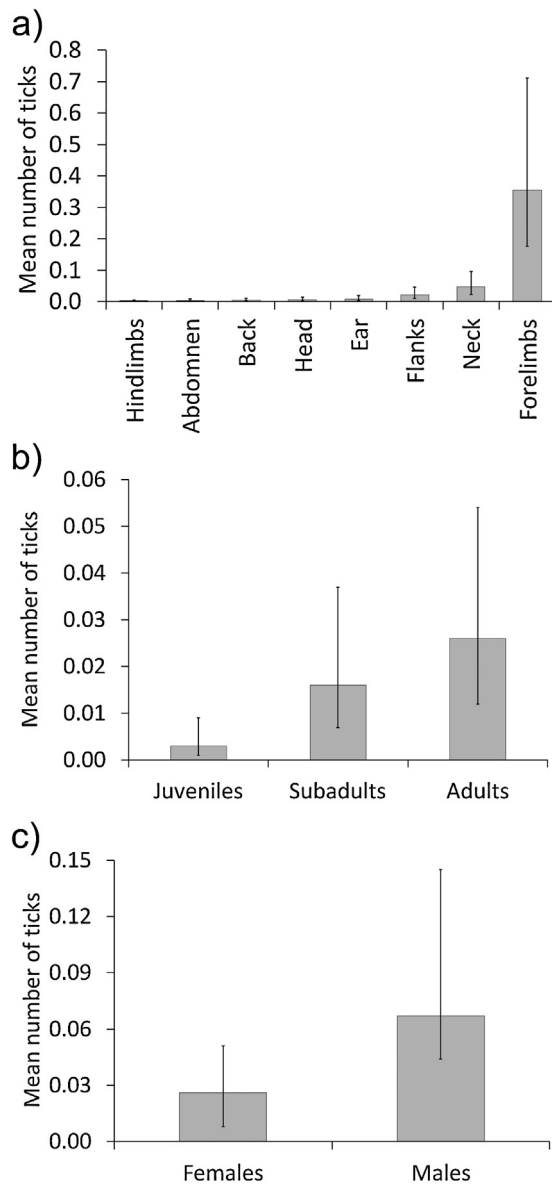[a] The reference category.

a)

b)

c)

Fig. 1. The effect of body part (a), age (b) and sex (c) on the mean number of ticks on lizard bodies. The means are estimates from generalised linear mixed models. Whiskers are 95% confidence intervals.

Table 4
The generalised linear mixed model with Gaussian error variance and identity-link function, testing factors affecting scutum width in ticks – a variant with the effect of lizard age (n = 67 lizards and 270 ticks). McFadden pseudo R^2 for the model = 0.12. Explanations: see Table 2.

Source of variation	F	df1, df2	P
Age of ticks	444.856	1, 262	**<0.001**
Age of lizards	2.404	2, 261	0.092
Autotomy	0.009	1, 262	0.923
Body size index	3.012	1, 262	0.084
Date	0.329	1, 262	0.566
Number of live ticks	0.199	1, 262	0.656
Random effect	Estimate ± SE	Z	P
Lizard identity	0.211 ± 0.323	0.603	0.510
Year	0	–	–

3.2. Lizard skin scales morphology

The effect of body part on scale number per 4 mm² was significant but the effect of sex was not (Tables 5 and 6). There were significant differences in number of scales between all body parts, with the exception of the forelimb-hindlimb pair (Table 7; Fig. 4a). Similarly, the effect of length of the interscalar region was significantly related to body location but not to sex. There were significant differences in length of the interscalar region among all body locations except the forelimb-hindlimb pair (Fig. 4b). We also measured the gap width between scales behind limbs and it was at most 0.13 mm. This gap was not present in other body parts because scales fitted close to each other, so statistical analysis was not feasible.

Table 5
The generalised linear mixed model with Gaussian error variance and identity-link function testing factors affecting the density of scales on different parts of the lizard body (n = 8 adult lizards). McFadden pseudo R^2 for the model = 0.32.

Source of variation	F	df1, df2	P
Sex	3.606	1, 6	0.106
Body part	48.360	3, 21	**<0.001**
Random effect	Estimate ± SE	Z	P
Lizard identity	3.473 ± 9.313	0.373	0.709

Table 6
Estimates of parameters from the generalised linear mixed model presented in Table 7.

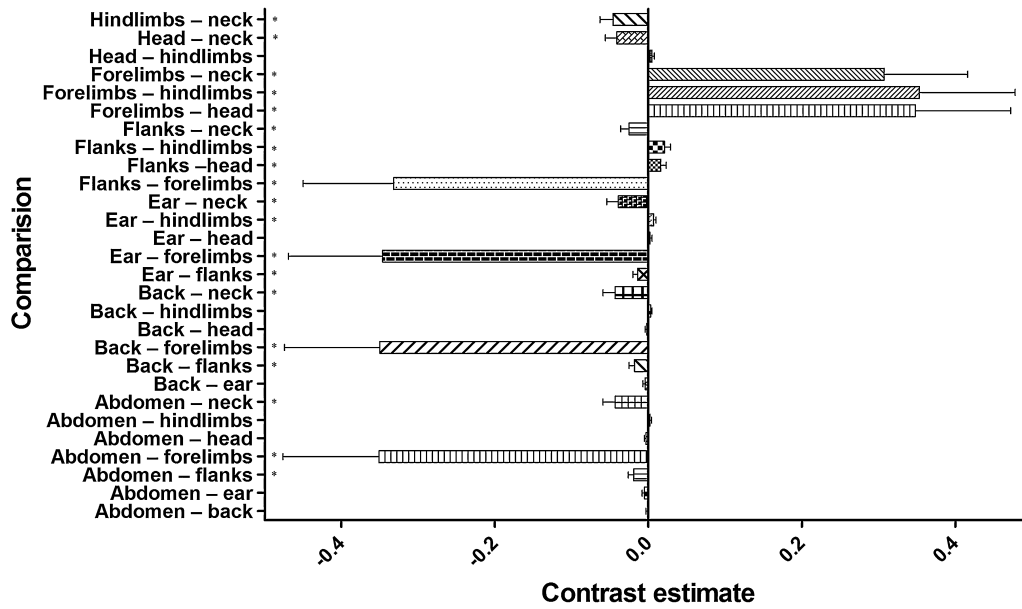| Source of variation	Estimate	SE	P
Intercept	25.583	7.425	**0.011**
Sex = female	5.188	2.732	0.106
Sex = male	0[a]		
Body part = flank	−13.250	3.384	**0.001**
Body part = forelimbs	23.250	3.384	**<0.001**
Body part = hindlimbs	17.375	3.384	**<0.001**
Body part = neck	0[a]		

[a] The reference category.

Table 7
Estimated paired contrasts for the effect of body part in the generalised linear mixed model presented in Table 6. Statistically significant differences are in bold.

Comparison	Contrast estimate	SE	P
Flank – forelimbs	−36.500	3.384	**<0.001**
Flank – hindlimbs	−30.625	3.384	**<0.001**
Flank-neck	−13.250	3.384	**0.001**
Forelimbs – hindlimbs	5.875	3.384	0.097
Forelimbs – neck	23.250	3.384	**<0.001**
Hindlimbs – neck	17.375	3.384	**<0.001**

Fig. 2. Estimated paired contrasts for the effect of body part in the generalised linear mixed model presented in Table 1. Statistically significant differences are marked with asterisks.
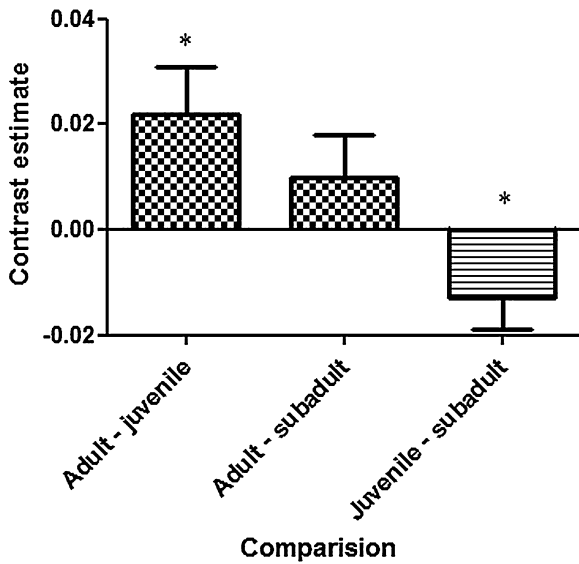

Fig. 3. Estimated paired contrasts for the effect of age in the generalised linear mixed model presented in Table 1. Statistically significant differences are marked with asterisks.

Fig. 4. Mean number of scales (a) and mean length of interscalar region (b) in different parts of lizard bodies. Means are estimated from generalised linear mixed models. Explanations: see Fig. 1.

4. Discussion

Our results revealed a specific distributional pattern of ticks on the lizard body but did not fully support the hypothesis that the specific distribution pattern of ticks on lizards was linked with size of scales and length of interscalar region. However, the analyses supported the hypothesis that host body size is positively correlated with tick loads and that males have higher numbers of ticks. We did not find evidence that lizard size, age or tail autotomy affect the number of ticks.

The infestation rate of sand lizards by *I. ricinus* ticks recorded in our research is similar to other studies (Bauwens et al., 1983; Gryczyńska et al., 2007) and it is typical for areas with average infestation level. Our research has shown that ticks prefer to attach to the lizard trunk in the forelimb area, where almost all ticks (90%) were found. This finding is similar to the results of another study on
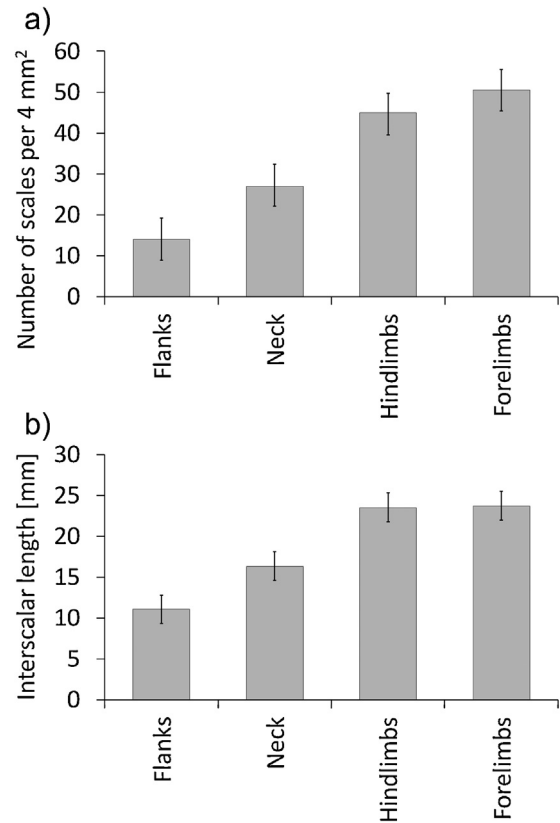
sand lizards (Bauwens et al., 1983). The area around the forelimbs is out of reach by lizards and it is secure from scratching by vegetation. However, hindlimbs are also probably secure from tearing by vegetation but ticks were very scarce there, with only two ticks found. This suggests that there must be another explanation why these ectoparasites prefer engorging in the forelimb area.

We hypothesised that a good attachment site for ticks should provide effortless access to the host skin between scales. Our results indicate that the largest interscalar regions were in the forelimb and hindlimb regions because in these body parts scales are small and do not fit tightly against each other. In other parts of lizard body, scales lie close together and there are no gaps with accessible skin. This supports the expectation that ticks prefer the parts of the body with easy access to skin but does not solve the problem of why so few ticks are in the hindlimb area. We suppose that this may be linked with the surface structure of this area. Behind the hindlimbs there is the tail with the largest and closely connected scales. In fact the area of small scales around the hindlimbs is much smaller than the area around the forelimbs. Another possible explanation is that lizard forelimbs have thinner skin and a denser vascular system than the skin behind the hindlimbs, which was described in other studies (Weallers and Marganeidge, 1971; White, 1976). Yet another reason for the absence of ticks in the hindlimb area is that lizards may scratch or chew ticks from this part of the body. It is also possible that ticks prefer limbs because they favour low temperature and low insolation. In temperate climates heliothermic lizards must bask in sunny places most of the day (House et al., 1979), whereas studies of preferable microhabitats of ticks have shown that these animals are sensitive to high temperature and dry environments (Randolph and Storey, 1999). Thus tick preferences for forelimb regions of lizards may be related to the suitable microclimate (Mead-Briggs et al., 1975). However feeding ticks not suffer from lack of water which obtain with blood, but they might avoid direct sunshine. The axillae of forelimbs are perhaps better secured from sunrays than on the hindlimbs but this hypothesis requires further studies.

We have found that tick infestation level is linked with lizard body length. This supports the idea of positive correlation between fitness of the host and ectoparasite. Body size is usually positively correlated with fitness, as this determines competitive abilities and mating success of *L. agilis* (Olsson et al., 1996). The mechanistic explanation might be that adult and bigger lizards provide a larger available surface for tick attachment (Bauwens et al., 1983). That might explain why, contrary to expectations, juvenile lizards had a lower tick load than mature lizards. Of course, the effect of a large tick load in larger individuals should be investigated in detail, as very large numbers of ectoparasites may, eventually, diminish survival and performance of infested lizards. However, we have not found any relationship between tick size and lizard size. This result may be explained also by the fact that Ixodidae ticks are not be able to actively choose the host and thus tick morphometric characteristics on hosts are probably a random sample from the tick population (Pollock et al., 2012).

Larger numbers of ticks found in male lizards may be explained by the higher mobility of this sex than of females and thus the larger area visited (Olsson et al., 1996; Scali et al., 2001). Males of majority of lizards species have large home ranges as compared with females (Perry and Garland, 2002), which is related to active searching for females during the mating season and to defending a territory (Olsson, 1979). Thus males may be more prone to contact with ticks. Moreover, male lizards, which inhabit larger areas, have higher testosterone levels and this inhibits the immunological system and might contribute to higher infestation levels (Saad et al., 1990; Uller and Olsson, 2003; Belliure et al., 2004; Oppliger et al., 2004).

In the study area the number of autotomized lizards was relatively high, which was probably linked with high predatory pressure, especially by shrikes (Antczak et al., 2005). We did not find any evidence that tick load is related to autotomy, though. Theoretically, autotomized specimens of *P. algirus* have smaller territories (Salvador et al., 1995) and consequently are less exposed to contacts with ticks. On the other hand, after the autotomy, insects usually have a handicapped immune system and thus are more threatened by parasites (Slos et al., 2009). These two contrary factors might counteract and, consequently, obliterate the relationship between tail autotomy and tick load in sand lizards.

Date in the season was not attributed to any of the above hypotheses and was only included as a covariate in models. However, it was positively correlated with tick load and this may be explained by the phenology of ticks, which start to appear in early April and their abundance in the environment increases with time and, therefore, the infestation follows this trend (Tälleklint-Eisen and Eisen, 1999; Prendeville and Hanley, 2000; Randolph et al., 2002).

We also found several dead ticks on lizards. The reason why ectoparasites sometimes died during engorging is not clear. Some authors suggest that this may be caused by the response of the immune system of the host (Wikel et al., 1996; Wikel and Bergmann, 1997; Willadsen and Jongejan, 1999). We did not find any differences in occurrence of dead ticks between females and males. There was also a significant correlation between the probability of dead tick occurrence and the total number of live ticks on lizards. This suggests that there might be (competitive) interactions between ticks on one host because such a phenomenon is observed in some other ectoparasites, e.g. Phthiraptera lice (Tryjanowski et al., 2009; Vas et al., 2012). However, another explanation related to simply larger sample size is possible. When dead ticks are a rare phenomenon, then lizards that have more ticks also have a higher probability of finding some dead ticks because it is known in the literature that some ticks cannot successfully engorge and die in situ (Randolph, 1979).

5. Conclusion

In our study we have shown that *I. ricinus* ticks attach mostly to the area of forelimbs and exceptions from this rule are rare. We conclude that the reason for this pattern may be linked with skin scales morphology (scales size and length of interscalar region), because ticks have easier access to skin in axillae region and can easily attach and engorge there. Another reason for the preference for this place may be protection from sun rays and brushing vegetation. However, we cannot explain why ticks avoid areas behind the hindlimbs, where skin scales morphology is similar to that in the forelimb region. Most likely, lizards can scratch ticks from hindlimbs but this question requires more behavioural studies. These results suggest that niche selection on a host body is not only a consequence of interspecific competition in parasites.

Appendix A.

See Table A.1.

Table A.1
Summary table with the distribution and number of ticks on different parts of lizard body with regard to lizard sex and age categories.

Sex[a]	Abdomen	Back	Ears	Head	Hindlimbs	Neck	Flanks	Forelimbs	Total
Females ($n = 136$)	1	0	8	3	0	23	16	193	244
Males ($n = 155$)	4	5	7	8	2	59	18	427	530
Total	5	5	15	11	2	82	34	620	774

Age	Abdomen	Back	Ear	Head	Hindlimbs	Neck	Flanks	Forelimbs	Total
Adults ($n = 291$)	5	5	15	11	2	82	34	620	774
Subadults ($n = 80$)	1	1	0	0	0	2	6	42	52
Juveniles ($n = 122$)	0	1	0	0	0	4	1	7	13
Total	6	7	15	11	2	88	41	669	839

[a] Sex identified only in adults.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ttbdis.2015.10.014.

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