parasitism in red deer are modulated by sex

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Background & hypothesis

Ticks are frequently aggregated in their hosts; that's few hosts carry high tick burdens[1]. This tick-host interaction feature conditions pathogen transmission patterns[2].

Host physiological traits[3], host activity traits[4], body mass[5] or tick spatial distribution patterns[6] modulate macroparasite burdens on hosts. Sexual dimorphism in size (**Fig. 1**) and in life history traits, and sexual segregation may trigger different tick-encounter rates of red deer (*Cervus elaphus*) males and females. This could have an effect on patterns of tick-borne pathogen transmission since the red deer is a relevant host for ticks and pathogens in Europe.

We hypothesized that tick parasitism on males and hinds would be differentially influenced by host individual, host population and environmental factors.

Figure 1. Sexual size dimorphism of the red deer; male (left), female (right).

Results

The 59.5% of deer were parasitized by ticks, mainly by adults (**Table 2**); 1772 ticks were collected (1761 adults and 11 nymphs). Adults belonged to *Hyalomma lusitanicum* (98.8%), *Rhipicephalus bursa* (0.5%), *Rh. sanguineus* (0.05%), and *Dermacentor marginatus* (0.05%), and nymphs belonged to *Hy. lusitanicum* (0.5%) and *Rh. bursa* (0.1%).

Sex	Age class	PosT/N	PrevT	Cou-AvT	Cou-AvA
Male	Fawn (1)	2/20	10.0	0.2 (0-2)	0.1 (0-2)
	Yearling (2)	21/24	87.5	14.5 (0-50)	14.4 (0-50)
	Subadult (3)	10/11	90.9	15.6 (0-60)	14.8 (0-60)
	Adult (4)	104/118	88.1	24.0 (0-125)	23.6 (0-125)
	Old (5)	9/9	100.0	39.3 (0-140)	39.0 (0-140)
	Subtotal male	*146/182*	*80.2*	*20.4 (0-140)*	*20.0 (0-140)*
Female	Fawn (1)	2/16	12.5	0.3 (0-2)	0.2 (0-2)
	Yearling (2)	2/10	20.0	1.2 (0-11)	1.2 (0-11)
	Subadult (3)	4/13	30.8	1.7 (0-12	1.7 (0-12)
	Adult (4)	22/72	30.6	2.2 (0-36)	2.2 (0-36)
	Old (5)	6/12	50.0	8.5 (0-49)	8.5 (0-49)
	Unknown	0/1	0.0	0.0 (0-0)	0.0 (0-0)
	Subtotal female	*36/124*	*29.0*	*2.4 (0-49)*	*2.4 (0-49)*
TOTAL		182/306	59.5	13.1 (0-140)	12.9 (0-140)

Table 2. No. of tick parasitized deer (PosT), sampling size (N), prevalence (PrevT), average number of counted ticks/deer (Cou_AvT) as well as counted adult ticks (Cou_AvA) throughout deer sex and age class. Minimum and maximum collected and counted ticks is shown within brackets.

Deer males were the primary target for ticks (**Table 2**), the weight of each factor differed between sexes, and each sex specific model was not able to accurately predict burdens on the animals of the other sex (**Fig. 4**). That is, results support for sex-biased differences.

The higher weight of host individual and population factors in the model for males (**Fig. 5**) show that intrinsic deer factors more strongly explain tick burden than environmental host-seeking tick abundance. In contrast, environmental variables predominated in the models explaining tick burdens in hinds.

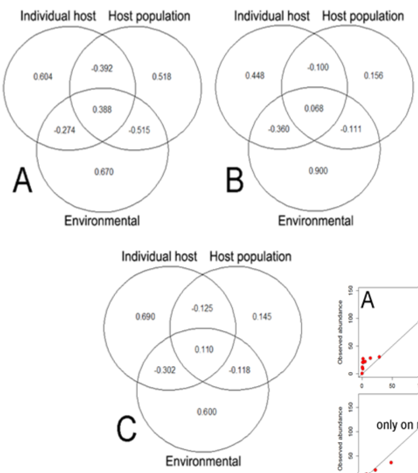

Figure 5. Variation partitioning of the deviance explained by final models: A) males; B) hinds; and C) males & hinds. Values in diagrams are the proportions of variation of each model that can be explained exclusively by individual host, host population and environmental factors, and by the combined effect of these factors.

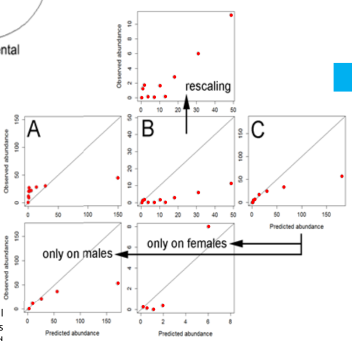

Figure 4. Calibration's assessment of the three models: A) predictions from the model for hinds on the dataset for males; B) predictions from the model for males on the dataset for hinds (also rescaling the observed abundance axis); and C) predictions from the model for males and hinds on the validation dataset, also independently for males and females (only five intervals were used in these last cases due to sample size).

Methodology

Study area and host individual traits

To test the hypothesis, ticks from 306 red deer - 182 males and 124 females - were collected during 7 years (2004-2010) in a red deer population in south-central Spain (**Fig. 2**). The whole body was surveyed for ticks (**Fig. 3**), which were counted, collected and identified to species level[7-9]. Every deer was weighed, aged, sexed, and biometrically characterized. Kidney fat index (KFI) was calculated.

Figure 2. Summer aspect of the landscape in the study area (38º55'N, 4º16'O; 600–850 m a.s.l.).

Host population traits

Annual censuses for red deer and wild boar were used as predictors for tick burden models. Censuses were performed by counting individuals approaching feeders in the red deer rut season[10].

Environmental variables

Meteorological data at the short time scale, in 30 days before each animal was surveyed, were considered as a proxy of climatic constraints of tick activity. The actual evapotranspiration - a measure of hydric stress experienced by ticks in its off-host period - was calculated.

Figure 3. Counting and collection of ticks from a stag.

Factor	Predictor	Description
Host individual	Sex	Deer sex (male, female)
	Age class	Age class (1: 0–1 year old; 2: 1–2 years old; 3: 2–3 years old; 4: 4–10 years old; and 5: >10 years old)
	KFI	Kidney fat index (%)
	TL	Total length (cm)
Host population	Deer_C	Deer counts in year *t-1* (No. of animals)
	Deer_C t-2	Deer counts in year *t-2* (No. of animals)
	Wild boar_C t-2	Wild boar counts in year *t-2* (No. of animals)
Environmental	AET_M	Actual evapotranspiration (mm) of 30 days before sampling (dbs)
	AvT_M	Average mean daily temperature (°C) of 30 dbs
	AP_M	Accumulated precipitation (mm) of 30 dbs
	Year	Sampling year

Table 1. Predictors employed for tick burden modelling.

Statistical modelling and analytical design

By using generalized linear models, with a negative binomial error distribution and a logarithmic link function, we modelled tick abundance on deer with potential predictors (**Table 1**). Three models were developed: one for males, another for hinds, and one combining data for males and females and including "sex" as factor.

Variation partitioning procedures[11] were used to estimate the variation of the final models explained independently by each factor (pure effects) and the variation explained simultaneously by two or more factors[12]. Cross-validation was employed to assess whether the results of the model developed on the dataset for a given sex can be used to explain variation in the response variable on the dataset for another sex[13].

Discussion

Parasites benefit from host conditions[14], which vary less in hinds than in stags[15]. Sex-related resource allocation traits can be behind the higher dependence of tick parasitism in males on intrinsic factors. Innate genetic resistance could also be behind; red deer with major histocompatibility complex class II DRB-2 haplotype 2 had lower tick burdens[16] and haplotype 2 is more frequent in hinds in the study population[17].

Host density was related to tick burden, probably because host densities regulate densities of host-seeking ticks[18]. Host population variables explained a much higher amount of variation in males, likely related to behavioural differences between sexes.

The effect of climate, with positive influences of average temperature and AET and negative influence of precipitation, maybe related to the preponderance of the xerophilic *Hyalomma lusitanicum* in the study estate.

Conclusion

Intrinsic factors more strongly explain tick burden than host-seeking tick abundance in red deer males. In contrast, environmental variables predominated in the models explaining tick burdens in hinds.

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