Effect of body size on the abundance of ectoparasitic mites on the wild rodent Oligoryzomys nigripes

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ORIGINAL PAPER

Effects of sex and locality on the abundance of lice on the wild rodent *Oligoryzomys nigripes*

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Abstract Various factors can affect the parasite distribution on a host. In this study, the influence of sex, body size, and locality of a rodent host, *Oligoryzomys nigripes*, on lice abundance was investigated. A generalized linear model indicated that the sex and locality of *O. nigripes* significantly contributed to the variation in lice abundance on the host. The male bias of lice parasitizing the rodent host *O. nigripes* may be associated with intersexual differences in physiology and behavior, while locality differences in lice abundance may be associated with differences in host density and diversity between the two localities sampled. Studies of host–parasite associations improve the understanding of the ecology of infectious diseases, as well as the evolution of these host–parasite interactions.

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Introduction

The parasite abundance in a host population may differ between host sexes. Sex bias towards males in parasitism occurs in several groups of mammals (Krasnov et al. 2005; Zuk 2009), and the proximal causes include body mass, suggesting that larger individuals can support more parasites (Moore and Wilson 2002) and reduced immunocompetence, suggesting a hormonal mechanism mediating sex differences in parasite susceptibility (Zuk and McKean 1996; Klein 2004). The causes are not mutually exclusive and may interact in the formation of sex bias parasitism. In polygynous mating systems, intersexual competition for females favors larger males and compromises male immune systems due to higher testosterone levels compared with monogamous systems (Klein 2000a; Fernandes et al. 2010; Barcelar et al. 2011).

Gender differences in parasite abundance may also be the result of intersexual differences in behavior leading to greater parasite exposure of one sex (Zuk and McKean 1996; Hillegass et al. 2008). In some mammal groups, males have greater mobility than females, facilitating contact with other infected individuals and parasite infective stages (Bordes et al. 2009). In these situations, males can be responsible for parasite transmission within host populations (Durden 1983; Ferrari et al. 2004; Krasnov et al. 2011).

In addition to host traits having a strong effect on parasite composition and abundance, the environment outside the host may also have an impact on ectoparasites (Lareschi and Krasnov 2010). Local variation in host density may influence the frequency of intraspecific and interspecific contacts and thus the rate of parasite transmission by infected individuals (Ryder et al. 2007), which may also be influenced by differences in host species composition between localities if different species share the same ectoparasites (Krasnov et al. 2006).

Anoplura is a group of obligate parasites of eutherian mammals that are quite common in rodent species (Light et al. 2010). *Hoplopleura* is a cosmopolitan genus of sucking lice comprising over 136 species worldwide and its members parasitize rodent hosts almost exclusively (Kim 2006; Smith et al. 2008). However, published studies with Anoplura are mainly descriptions of new species (e.g., Castro et al. 2001; Durden and Timm 2001; Durden and Raush 2007; Weaver and Barton 2008) or of species assemblages on a particular host (e.g., Durden and Wilson 1991; Durden et al. 1997; Weaver and Smales 2009). In this study, we gathered data on *Hoplopleura* lice (Insecta: Anoplura) parasitizing the rodent *Oligoryzomys nigipres* (Mammalia: Rodentia) at two localities in the same geographical area of southeastern Brazil to test the hypothesis that host sex, body mass, and locality affect lice abundance.

Material and methods

Study area

The study was performed at two localities, 70 km apart, in the Cerrado of Southeast Brazil in São Paulo State: Mogi Guaçu Experimental Station (22°24' S, 47°15' W) and Itirapina Experimental Station (22°24' S; 82°47' W). The Itirapina Experimental Station has an area of 3,212 ha and covers altitudes ranging from 700 to 827 m, while the Mogi Guaçu Experimental Station has an area of 3,050 ha and covers altitudes ranging from 600 to 730 m. The Cerrado is a Neotropical savannah formation comprising different vegetation physiognomies that differ in the density and composition of woody and ground layer plants, forming a continuum from open and dry grasslands to dense forests (Goodland 1971). The sample sites in both areas consist of a physiognomy known as “Cerradão” which is characterized by a dense forest with high trees and a totally closed canopy (Oliveira-Filho and Ratter 2002).

Data sampling

Fieldwork was conducted from February 2009 to June 2010. The data were obtained from rodents captured on five consecutive days per month in each study area. To capture the rodents, 80 *Sherman* traps (dimensions 7.5×9.0×23.5 cm) were used; four traps, baited with sweet potato and peanut butter, were placed on the ground in each capture station. Therefore, the total capture effort was 6,800 trap nights. Each rodent captured was placed in a glass container with a small hole on the lid and a piece of cotton soaked in acetate inside to anesthetize the rodent, facilitating its handling. Each rodent was marked with a numbered leg band, its weight was recorded with the Pesola® scale (precision=1 g), and its sex was identified and recorded. The hair of each rodent was brushed several times with a toothbrush over a white plastic tray. The ectoparasites from each host were collected from the plastic tray and were placed in a glass jar containing 70 % alcohol with an inner and outer label containing the following information: host species, host sex, host identification (number of the leg band), date of capture, and capture site. After each use, the plastic tray was thoroughly inspected and cleaned before receiving another anaesthetized rodent. The rodents captured were released after the parasite collection procedure. The ectoparasites collected (Anoplura) were identified by Professor Pedro Marcos Linardi and his team from the Federal University of Minas Gerais. This research was authorized by the System of Authorization and Information in Biodiversity (SISBio number 17669).

Statistical analyses

Two discrete distribution models, Poisson and negative binomial, were fitted to the lice abundance data using maximum likelihood, and the chi square goodness-of-fit test was used to determine if the observed data fit one of these distributions. The Poisson distribution indicates a pattern of random distribution of parasite abundance among hosts, while the negative binomial distribution indicates a default aggregate distribution (overdispersion data), with many hosts harboring few parasites and a few hosts harboring many parasites (Poulin 2007). In this study, the distribution of lice abundance was fitted to a negative binomial distribution (χ^2=18.25; d.f. = 14; P value=0.19). Even though the Poisson regression is the classic model used to count data, its use is limited when the data show overdispersion and/or excessive zeros (Cameron and Trivedi 1998). The generalized linear model of the negative binomial regression models the overdispersion data (Zeileis et al. 2008) and was used in this study with the response variable being the lice abundance per host and the explanatory variables being the body size (weight), the gender (sex), and the location of occurrence (locality) of the host species.

A Cochran–Mantel–Haenszel chi square test (CMH test) was used to test the null hypothesis that the explanatory variables “sex” and “locality” are conditionally independent in relation to lice abundance. The test showed that the variables are conditionally independent (CMH test=20.85; d.f. = 16; P=0.184), i.e., there is no interaction between the variables, excluding from consideration interactions between the variables in the procedure of adjusting the models. The variables “gender” and “weight” also do not interact because *O. nigripes* does not display sexual size dimorphism (Eisenberg and Redford 1999). Therefore, the body weight in this case is only an indication of the age of the host. Like all generalized linear models, the negative binomial regression allows estimates of significant parameters for the factors to be interpreted in terms of rate ratio (Dobson 2002) to assess the magnitude of the variance between the classes of the significant factors. For model validation analysis, the Pearson residual patterns were used to generate a normal probability plot of residuals. In this method, simulated bands with a 90 % confidence interval (or confidence envelopes) were built using 1,000 simulations to help to better interpret the graph. If the model is well adjusted, most of the points representing the residuals must be distributed within these bands (Atkinson 1987). All statistical procedures were performed using the R environment 2.12.2 (R Development Core Team 2010). The adjustments of regression models were made using the *pscl* extension 1.03.6 (Zeileis et al. 2008).

Results

A total of 91 individuals of *O. nigripes* was captured in both areas, Mogi Guaçu (n=33) and Itirapina (n=58), during the fieldwork period. In Mogi Guaçu, only one species of louse, *Hoplopleura travassosi* (n=61) was found parasitizing *O. nigripes*, while in Itirapina, two species of lice, *H. travassosi* (n=348) and *Hoplopleura imparata* (n=42), were found on the same host species.

The negative binomial regression model indicated that the explanatory variables “sex” and “locality” significantly influenced the abundance of lice per individual host (Table 1). The lice abundance in males was greater than in females (rate ratio=1.8), and in Itirapina, the lice abundance was greater than in Mogi Guaçu (rate ratio=2.6). The graph of the probability of the residuals shows that most of the points representing the residual are distributed within the confidence bands, indicating that the model is valid (Fig. 1).

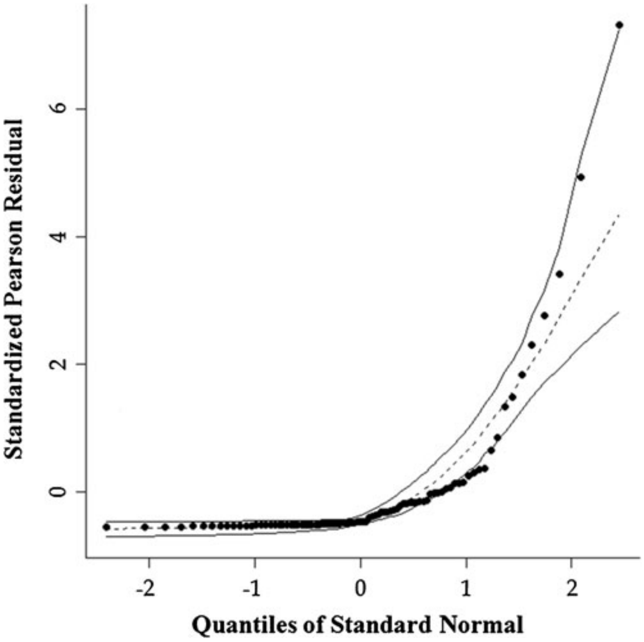

Fig. 1 Quantiles of standard normal plots based on the negative binomial model

Discussion

The abundance of lice parasitizing *O. nigripes* was influenced by gender and location of occurrence of the host. Males have a significantly larger abundance of parasites compared with females. The sexual bias in parasitic infestation of vertebrate hosts is found both for endoparasites (Poulin 1996; Ferrari et al. 2004) and for arthropod ectoparasites (Harrison et al. 2010; Matthee et al. 2010).

Table 1 Best fit regression model to describe lice abundance on *O. nigripes* hosts from two localities in Brazil (α=0.05)

Coefficients	Estimate	S.E.	z	*P*
Intercept	2.133	0.801	2.662	0.008
Weight	−0.054	0.037	−1.461	0.144
Sex	0.961	0.448	2.148	0.032[a]
Locality	−1.255	0.460	−2.725	0.006[a]

[a] Significant factor

Intersexual differences in morphology, physiology, and behavior are the factors responsible for sexual bias in parasitism (Klein 2000a; Moore and Wilson 2002; Hillegass et al. 2008; Krasnov et al. 2011). In mammal systems, males tend to be larger than females (Lindenfors et al. 2007), making it difficult to separate the effects of “body size” and “sex” in analyses. However, the rodent species studied here does not show sexual dimorphism in size (Eisenberg and Redford 1999), which excludes the influence of morphological sex differences on the preferential tendency of parasitism for males by the lice species of this study. Thus, physiological and behavioral intersexual differences may be the factors influencing this trend of parasitism.

The influence of physiology on the sexual difference of parasitism is based on a negative relationship between the levels of male hormone, testosterone, and the performance of the immune function. High levels of testosterone have negative effects on the immune function and thus males may be more susceptible to infection than females (Klein 2000b, 2004). Additionally, selective pressures that influence differences in reproductive strategy between males and females contribute to the intersexual variance in immunity and susceptibility to parasites (Zuk 2009; Negro et al. 2010). Males in monogamous mating systems are subject to weaker sexual selection than promiscuous species (Zuk and McKean 1996) and the corresponding lower level of stress can be an advantage with respect to susceptibility to parasites.

Some studies on the use of space by Sigmodontinae rodents (which *O. nigripes* is included) suggest that these rodents have a promiscuous mating system (Püttker et al. 2006; Blondel et al. 2009; Steinmann et al. 2009; Pires et al. 2010). The male competition for access to females results in increased levels of testosterone, which is associated with aggressive interactions and produces a severe physiological stress, increasing the susceptibility of males to parasitic infection (Negro et al. 2010; Ostner et al. 2011).

In addition to physiological differences between sexes, behavioral differences may also play an important role in sexual bias of parasitism. Males of *O. nigripes* traverse greater distances than females, most likely as a consequence of the promiscuous mating system (Püttker et al. 2006), where males have greater mobility, which increases the chances of finding sexual partners (Fernandes et al. 2010; Pires et al. 2010; Perdue et al. 2011).

Reproduction of this species in southeastern Brazil occurs all year round, showing two peaks, from September to November and from February to April (Eisenberg and Redford 1999), and it is assumed there is no difference in the pattern of mobility throughout the year. The high male mobility facilitates intraspecific and interspecific contact with infected individuals and with infective stages of parasite (Krasnov et al. 2005; Bordes et al. 2009).

The abundance of lice parasitizing *O. nigripes* also differed between the two localities of Cerrado sampled, with Itirapina showing an abundance of lice per host significantly higher than in Mogi Guaçu. The difference between the localities in the abundance of parasites can be a reflection of the difference in density of host species in both areas, which influences the frequency of intraspecific contacts (Krasnov et al. 2006; Ryder et al. 2007). In Itirapina, individuals of *O. nigripes* were always caught in traps, while in Mogi Guaçu, sometimes no individuals were caught in the traps.

The difference in host species diversity between locations may also be responsible for the variation in the abundance of ectoparasites because interspecific contacts promote host shift when different species share the same parasite (Krasnov et al. 2006; Lareschi and Krasnov 2010). In Mogi Guaçu, no other species of rodent was found to be parasitized by lice, whereas in Itirapina, it was observed that *Necromys lasiurus* (*n*=17), which was only captured in this locality, shares the two species of lice with *O. nigripes*. However, while *O. nigripes* harbors more individuals of *H. travassosi* (n=348) than individuals of *H. imparata* (*n*=42), the *N. lasiurus* species harbors more individuals of *H. imparata* (*n*=381) than individuals of *H. travassosi* (*n*=9).

Other studies in South America indicate a similar pattern: *H. travassosi* parasitizing rodents from the genus *Oligoryzomys* (Oryzomyini) and *H. imparata* parasitizing *N. lasiurus* or species of the genus *Akodon* (both Akodontini) (e.g., Barros-Batesti et al. 1998; Lareschi and Krasnov 2010). In this study, the presence of *H. imparata* in 20 % of *O. nigripes* individuals parasitized and *H. travassosi* in 17 % of *N. lasiurus* individuals parasitized is indicative of the occurrence of the horizontal transfer of lice between host species through interspecific contacts.

Agosta et al. (2010) proposed in a review that host switch or colonization of novel hosts in an evolutionary–ecological context is possible when the parasite is pre-adapted to the novel host because the novel host shares important characteristics with the current host or was a host in the past, or when the parasite displays phenotypic plasticity that enables the use of the novel host.

Sucking lice have a very high level of parasite–host specificity (Smith et al. 2008). More than 87 % of all known species of sucking lice are associated with one, two, or three host species. Sixty-two percent (62 %) of the Hoplopleuridae family is specific to a single host species (Kim 2006), and the transmission between individual hosts occurs by contact (Durden 1983). The composition of host species and their relative abundance have an important role in the exchange of parasites transmitted directly. Higher density and a higher number of host species in a locality increase the chances of intraspecific and interspecific parasitic exchange between individuals (Arneberg et al. 1998; Krasnov et al. 2002; Valera et al. 2003).

To conclude, we found that sex and locality were the important factors affecting lice abundance, most likely because male hosts show greater mobility and physiological stress as a result of the promiscuous mating system of the species and because the increased number and density of host species found at one location, Itirapina, associated with the mobility of the hosts facilitates the intraspecific and interspecific exchange of lice between individuals.

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