



Disassortative parasitic infestation by larval mites of the genus *Trombidium* (Acari: Trombidiidae) influences mate choice in a population of the cantharid beetle *Rhagonycha fulva* SCOPOLI, 1763 (Coleoptera: Cantharidae)

A. LACINY & H.L. NEMESCHKAL

Abstract: Observations on a population of *Rhagonycha fulva* in Lower Austria revealed an infestation with ectoparasitic larval mites of the genus *Trombidium* (Trombidiidae). Taking into account the ambiguous results of previously published works on sexual selection in connection with parasitism, the aim of this study was to determine (1) if and how the presence, abundance and location of ectoparasites on the host's body coincide with mating status in this particular host, and furthermore to determine (2) if parasitic load correlates with additional characters such as sex and body-size.

Microscopic assessment of the number and location of mites on the host's body as well as measurements of the right metathoracic femur led to the following results: Significant differences were found in the distribution and abundance of ectoparasites between mated male and female host as well as a disassortativity of parasite presence within mated couples. Larger mated males were observed to carry fewer parasites than smaller male specimens. While female size alone did not directly influence parasitic load, the cumulative number of larval mites in a mated couple decreases significantly with increasing female size. These findings and their putative biological implications for the species are discussed in light of existing theories.

Keywords: Ectoparasitism, *Trombidium*, Cantharidae, sexual selection, immunocompetence handicap

Citation: LACINY A. & NEMESCHKAL H.L. 2015: Disassortative parasitic infestation by larval mites of the genus *Trombidium* (Acari: Trombidiidae) influences mate choice in a population of the cantharid beetle *Rhagonycha fulva* SCOPOLI, 1763 (Coleoptera: Cantharidae). – Entomologica Austriaca 22: 75–89.

Introduction

Species portraits of host and parasite

The red soldier beetle *Rhagonycha fulva*, a member of the cantharid family, is one of Austria's most common beetles. The yellowish-red imagines range from 7 to 10 mm in size and are active from May to August. During this time they can frequently be found on Apiaceae, where they prey on smaller arthropods, feed on pollen and mate for remarkably long periods of time (HARDE & SEVERA 2000). However, despite their conspicuous appearance and striking abundance in Central Europe very little research has been previously conducted on the species' biology, life-cycle and mating behaviour.

Observations on a population of *R. fulva* in Oberpiesting (Lower Austria) in 1999 revealed an infestation of the adult soldier beetles with ectoparasitic larval mites of the genus *Trombidium* (Trombidiidae). The larval stages of these members of the suborder Parasitengona have been found to occur on a large number of arthropod hosts including Lepidoptera, Coleoptera, Diptera, Orthoptera, Hemiptera and Homoptera, Hymenoptera, Araneae, Pseudoscorpiones and Opiliones (ZHANG 1998, CONRADT et al. 2002). Trombidiid larvae emerge from eggs laid into the soil in synchrony with the activity of their hosts, usually during spring and summer in temperate regions. Hosts are presumably found through positive phototactic and/or negative geotactic movement on the soil surface and on plants, though the exact mechanisms are unknown. After acquisition of an arthropod host, an ectoparasitic larva can remain attached for up to two weeks before it moves into the soil to complete its development (ZHANG 1998). The attachment process is accompanied by formation of a feeding tube, the stylostome, at the site of cheliceral penetration where the host's hemolymph is extracted by the parasite (MOHAMED & HOGG 2004). Depending on the volume of hemolymph extracted from the host, the larvae increase in size over time (PETERSON et al. 1992). The parasitic larval stage is followed by a calyptostatic protonymph, a predatory deutonymph, a calyptostatic tritonymph and free-living, predatory imago (ZHANG 1998).

Assortative Mating

Assortative mating – i.e., a type of non-random mating in which the mated partners show greater phenotypic or genotypic similarities than would be expected in a random mating situation – has been observed across a variety of taxa including humans, beetles and other arthropods (ALCOCK & HARDLEY 1987, CRESPI 1989, HARARI et al. 1999, ALVAREZ & JAFFE 2004, MCLAIN 2005).

With respect to arthropods in particular, CRESPI (1989) postulates three main causes for assortative mating: Mate choice, mate availability and mating constraints. Which of these best explains the observed assortativity of mated couples differs among taxa. For example, HARARI et al. (1999) found support for the mating constraints hypothesis and an overall preference for larger mates in the curculionid beetle *Diaprepes abbreviatus* (LINNAEUS, 1758). However, most studies focus on assortative mating by size alone which is insufficient to explain many mating systems in the Coleoptera (ALCOCK & HARDLEY 1987).

Parasitism and sexual selection

Perhaps the most widely known hypothesis attempting to link parasitic infestation and sexual selection is that of William D. Hamilton and Marlene Zuk formulated in 1982. The Hamilton-Zuk hypothesis of parasite-mediated sexual selection suggests that a male's trait (e.g. bright colours) can serve as a signal indicating resistance to diseases and parasites, thereby allowing females to choose the most resistant mates (HAMILTON & ZUK 1982). However, while further examination showed a significant negative effect of parasites on males' showy characters, the magnitude of the effects varied greatly across host and parasitic taxa, thus yielding highly ambiguous results that indicate the immense complexity of sexual selection and male advertising (HAMILTON & POULIN 1997). Consequently, a wide array of studies has been conducted since the initial publication of the Hamilton-Zuk

hypothesis, leading to the postulation of other possible connections between parasitism and mate-choice.

Among the most important aspects of this topic was the question addressed by FOLSTAD & KARTER (1992), who stated that in some species a negative feedback loop between signal intensity of male sexual characters and resistance to parasites may take effect. This is supposedly due to the fact that hormones such as testosterone, while enhancing the formation of showy male sexual characters, may have negative effects on immunocompetence, thus making the showiest males also the ones most susceptible to infection (FOLSTAD & KARTER 1992). Since the development of showy sexual characters can be detrimental to the immune-system, these characters can function as costly and honest signals similar to those postulated in Zahavi's "Handicap Principle" (ZAHAVI 1975). However, further examinations concerning this so-called "immunocompetence handicap" yielded results that found the correlations between parasite burden and sexual characters to be significantly positive, negative or without any significant correlations (FOLSTAD & KARTER 1992, GETTY 2002).

Aim and research questions

Based on the ambiguous results of previous research and the competing theories aiming to explain possible correlations between an individual's resistance to parasitic infections and its mating success, we wanted to explore the relationship between ectoparasitic load and mate-choice in *Rhagonycha fulva*. The aim is to clarify if and how the presence, abundance and location of ectoparasites influence mate-choice in this species and whether parasitic load is correlated with other traits such as sex and body-size.

Microscopic assessments of parasitic load, distribution of the parasites on the host's body as well as the measurement of a size parameter on mated and unmated specimens of the cantharid beetle *Rhagonycha fulva* were used to address the following questions:

- Is there a sexual dimorphism concerning the abundance and / or distribution of ectoparasites on hosts?
- Does parasitic load and distribution of ectoparasites on hosts differ significantly between mated and unmated host individuals?
- Is there evidence for size assortative mating in hosts?
- Does host body-size influence infestation with ectoparasitic mites?
- How do ectoparasitic loads of mated individuals correlate with the loads of their respective partners?
- Are ectoparasites a factor in mate-choice of the host species and can they be considered to influence mating success?

Material and methods

This study was conducted on specimens of *R. fulva* (see figure 1) collected by H.L. Nemeschkal in July of 1999 in Oberpiesting, Lower Austria (N47° 52' 21", E16° 6' 30"). Mated pairs were picked in copula. "Unmated" specimens were not observed to be engaged in mating but were all picked from the direct vicinity of copulating couples. All animals

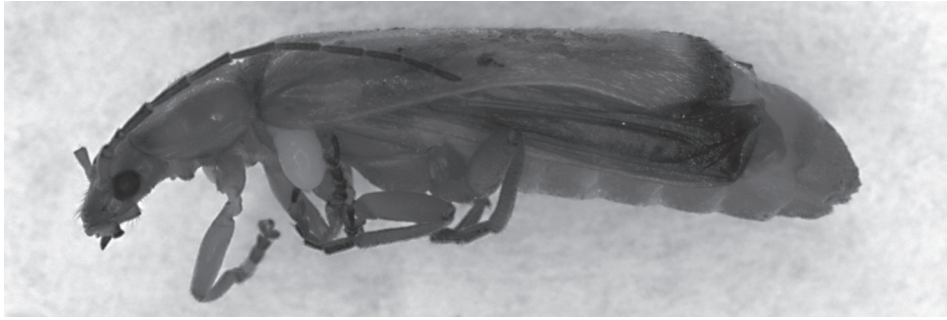


Fig.1: Mated female host beetle in lateral view with a larval *Trombidium* under its left elytron.

Abb.1: Verpaartes Weibchen der Wirtsart in Lateralansicht mit Trombidienlarve unter dem linken Deckflügel.

were killed and conserved in 70% ethanol immediately after collection and identified using the identification key after FREUDE et al. (1979).

The material used for experimentation consisted of 34 unmated males and 11 unmated females as well as 198 pairs of mated beetles.

Ectoparasitic larval mites were identified as members of the genus *Trombidium* by Ao. Univ.-Prof. Mag. Dr. Manfred G. Walzl (Department of Integrative Zoology, University of Vienna) and confirmed as Trombidiidae via DNA-barcoding at the Department of Parasitology of the Veterinary University of Vienna (unpublished data).

The investigation of parasitic loads was achieved by observing each host-specimen under a binocular microscope (Olympus SZ 30) to assess the locations of larval mites on hosts. Each larval *Trombidium* found on the host was assigned to one of five regions on the host's body: thorax (lateral or ventral, excluding subelytral space and coxae), abdomen (lateral or ventral, excluding subelytral space), leg-bases (ventrolateral or ventral, between or at coxae), dorsal subelytral space (between elytra and thoracic or abdominal tergites) and the interstice between elytron and ala.

The length of the right metathoracic femur of each individual was measured using a measuring microscope (Nikon MM-40) to obtain a size-parameter for each specimen.

To test for significant differences between the observed groups of *R. fulva* hosts (male, female, paired, unpaired) in the distribution of larval mites on the hosts, a *G*-test (goodness of fit test) was performed. The *G*-test as well as mean and standard deviation were calculated in MS Excel (Windows 7).

To calculate linear regression coefficients with bootstrap randomizations ($n=5000$), the program MUREG (NEMESCHKAL 1999) was used. For this purpose, all length measurements were logarithmized (\ln) and the raw numbers of larval mites present were transformed subsequently by a square-root transformation. The regression method was applied to determine if and how mating status, sex, size and parasitic load of the specimens influence one another and also whether the data indicate assortativity within pairs regarding size and parasite-infestation. In all cases where binary observations were of interest (i.e. mated/unmated, male/female, parasitized/non-parasitized), dummy-coded variables (1/0) were used.

To construct a path diagram illustrating the respective influences of male (x_1) and female (x_2) femur length on the total parasitic load of the mated couple (y), a multiple linear regression analysis was conducted in MUREG. The obtained regression coefficients and the standard deviations of the variables were then used to calculate the path coefficients using the following formula (PC_{xi} path coefficient; b_{xi} partial regression coefficient; s_{xi} standard deviation of a predictor variable; s_y standard deviation of the criterion variable):

$$PC_{xi} = b_{xi} * (s_{xi} / s_y).$$

To determine whether mating between paired *R. fulva* couples was assortative regarding size, the correlation coefficient (Pearson's r) of logarithmized femur-lengths was calculated in MS Excel.

Results

Location of ectoparasites on hosts

Microscopic assessment of the mites' location on the host-body revealed characteristic distributional patterns for the observed groups. In all male beetles as well as in the unmated females, the highest number of ectoparasites was found in the dorsal subelytral space, followed by the base of the legs (table 1). However, while mated and unmated males had roughly half of their ectoparasites located under the elytra (56% and 48% respectively, table 1) the percentage of subelytral parasites was even higher in mated females (77%). Thorax, abdomen and the interstice between elytron and ala each held 2–12% of the observed parasites in all males and mated females. In unmated females only two parasites were found, one located on the thorax, one at the leg-base (table 1).

The results of the G-test revealed a significant difference in the distribution of ectoparasites between mated males and mated females (d.f. = 4, G -value = 16.44327, p = 0.00248) and no difference between mated and unmated males (d.f. = 4, G -value = 4.19562, p = 0.38018). Due to small sample size, unmated females were excluded from statistical testing.

Parasitic loads

For the total parasitic loads of each of the four groups, mean and standard deviation of the number of parasites found within the respective group were calculated for the entire group including parasitized as well as non-parasitized hosts. Additionally, mean ectoparasitic loads within the group of the individuals infested with at least one ectoparasite were assessed separately. Rates of infestation denote the percentage of individuals in each of the four groups infested with a minimum of one larval *Trombidium* (table 2).

The highest mean ectoparasitic load was found on mated females (0.924 ± 1.574 in total, 2.033 ± 1.789 in the infested group only), the lowest average number of mites per individual was observed in unmated females (0.182 ± 0.405 total, 1.0 ± 0 among infested individuals) with mated and unmated males ranging in between. The highest observed total count was 13 mites per individual (mated female). The rates of parasitism ranged from 18.2% for unmated females to 47.1% for unmated males. The percentage of infested mated females was found to be only slightly lower than that of the unmated males (45.5%), the rate of parasitism for mated males was 39.4%.

Table 1: Distribution of ectoparasitic larval mites along the five body-regions of mated and unmated male and female specimens of *R. fulva*; absolute and relative frequencies.

Tabelle 1: Verteilung ektoparasitischer Milbenlarven über fünf Körperregionen von verpaarten und unverpaarten männlichen und weiblichen Exemplaren von *R. fulva*; absolute und relative Häufigkeiten.

	thorax	abdomen	leg-base	ala	subelytral	sum
male mated (n=198)	8.33% (10)	5% (6)	25.83% (31)	5% (6)	55.83% (67)	120
female mated (n=198)	3.31% (6)	2.21% (4)	15.47% (28)	1.66% (3)	77.35% (140)	181
male unmated (n=34)	12% (3)	12% (3)	28% (7)	0%	48% (12)	25
female unmated (n=11)	0%	50% (1)	50% (1)	0%	0%	2

Linear regression analyses

When testing whether mated and unmated males differ concerning the presence of ectoparasites on the host-animals (table 3, regression 1), no significant difference could be detected between mated and unmated males. An identical result was obtained when calculating with the number of ectoparasites on mated and unmated male host-specimens (table 3, regression 2).

The regression analysis testing whether the presence or absence of parasites differ significantly between mated male and mated female beetles (table 3, regression 3) revealed that mated females have a significantly higher parasite-presence than mated males ($P=0.03$). When incorporating the numbers of parasites found on mated male and female hosts (table 3, regression 4), mated females were found to have significantly higher parasitic loads than mated males ($P=0.001$).

The assessment of the relationship of parasite presence within mated couples (table 3, regression 5) revealed a negative regression coefficient ($b=-0.111111$) indicating a disassortativity of parasite presence on mated individuals. In this disassortative relationship concerning the presence of parasites on mated partners the females have a significantly greater amount of parasitic infestation than the males they mate with ($P=0.007$).

When assessing the relationship of ectoparasitic loads within mated couples regarding the number of ectoparasites (table 3, regression 6) only a non-significant trend towards disassortativity within the mated couples was found ($P=0.094$), whereby the females were infested with more parasites than their male partners.

When comparing the lengths of right metathoracic femora of mated and unmated male beetles to answer the question whether mated and unmated males differ significantly with respect to this size parameter (table 3, regression 7), the analysis revealed that unmated males possess significantly longer femora than mated males ($P=0.024$).

The assessment of the relationship of femur lengths within the mated couples (table 3, regression 8) reveals a slightly non-significant trend toward assortativity with respect to femur length ($P=0.058$).

When attempting to determine how size (represented by femur length) and parasitic load coincide in mated males (table 3, regression 9), the results of the regression analysis indicate a significant negative relationship between femur length and parasitic load

Table 2: Means and standard deviations (SD) of parasitic infestation by ectoparasitic larval mites on mated and unmated males and females of *R. fulva* for the total sample and for parasitized individuals; rates of parasitism.

Tabelle 2: Mittelwerte und Standardabweichungen (SD) der Parasitenlast durch ektoparasitische Milbenlarven an verpaarten und unverpaarten Männchen und Weibchen von *R. fulva* für die gesamte Stichprobe sowie für parasitierte Individuen; Parasitierungsraten.

	male mated	female mated	male unmated	female unmated
mean (total)	0.616	0.924	0.735	0.182
SD (total)	0.994	1.574	1.024	0.405
mean (parasitized)	1.013	2.033	1.563	1.000
SD (parasitized)	1.014	1.789	0.964	0.000
rate	39.4%	45.5%	47.1%	18.2%

($b = -0.00995442$), indicating that larger males have fewer ectoparasites ($P = 0.033$).

When assessing the same relationship between size and parasitic load in unmated male specimens (table 3, regression 10) and in mated females (table 3, regression 11), no significant relations were found.

Path analysis

According to the results of the regression analysis, a non-significant weak positive correlation (Pearson's $r = 0.084$) between the femur lengths of mated males and females was observed.

The influence of the male's body-size (represented by femur length) on the total parasitic load of the mated pair was shown to be non-significant ($P = 0.157$). In contrast, the path analysis showed a significant negative effect of increasing female body-size on the cumulative ectoparasitic load of the mated couple (Pathcoeff. $x_2 = -0.13$; $P = 0.002$; see Fig. 2).

Discussion

Assessment of the distribution of parasites among the host-animals' body-regions shows that the highest parasitic load is in the subelytral space for the three largest of the four host-groups (mated males and females, unmated males). Similarly, other studies investigating parasitism by trombidid larvae in Coleoptera (PETERSON et al. 1999, MOHAMED & HOGG 2004) have shown that the subelytral dorsal abdominal tergites are the most suitable place for mite-attachment because the intersegmental membranes are soft and therefore easy to penetrate and the forewings provide protection against detachment (e.g. by the host's cleaning behaviour). In *R. fulva* the base of the legs also seems to be a relatively safe and easily accessible place for the parasites, since it proved to be the second most frequently occupied region in all groups of the studied sample. The distribution of ectoparasites was shown to be significantly different between mated males and females with the most striking difference being the infestation of the subelytral cavity that held 56% of the mites in males, but 77% in females. This dissimilarity in the infestation of the subelytral space may be explained by behavioural differences between male and female soldier beetles (pers. observation). While females tend to be generally sessile, males perform fast and frequent flights, which may lead to difficulties for the parasites to remain attached near the moving

Table 3: Results of linear regression analyses including regression coefficients (b), coefficients of determination (r^2) and P -values as well as model significances. P -values and their corresponding levels of significance for a one-sided test were set as follows: $P > 0.1$ no significance (n.s.), $0.1 \geq P > 0.05$ no significance but a trend (n.s./tr.), $0.05 \geq P > 0.01$ significant (*), $0.01 \geq P > 0.001$ very significant (**), $P \leq 0.001$ highly significant (***).

Tabelle 3: Ergebnisse der linearen Regressionsanalysen mit Regressionskoeffizienten (b), Bestimmtheitsmaß (r^2) und P -Werten, sowie Modellsignifikanzen. P -Werte und ihre korrespondierenden Signifikanzen für einen einseitigen Test wurden wie folgt festgelegt: $P > 0.1$ nicht signifikant (n.s.), $0.1 \geq P > 0.05$ nicht signifikant aber Trend (n.s./tr.), $0.05 \geq P > 0.01$ signifikant (*), $0.01 \geq P > 0.001$ hoch signifikant (**), $P \leq 0.001$ höchst signifikant (***).

regr.	dependent variable	independent variable	b	r^2	P	signific.
1	mated vs. unmated males (dummy variable)	parasitized vs. non-parasitized (dummy variable)	-0.039778	0.003049	0.139	n.s.
2	mated vs. unmated males (dummy variable)	number of ectoparasites (square-root transformed)	-0.029232	0.002697	0.130	n.s.
3	mated males vs. mated females (dummy variable)	parasitized vs. non-parasitized (dummy variable)	-0.062030	0.003759	0.030	*
4	mated males vs. mated females (dummy variable)	number of ectoparasites (square-root transformed)	-0.070981	0.009587	0.001	***
5	mated males, parasites present/absent (dummy variable)	mated females, parasites present/absent (dummy variable)	-0.111111	0.012821	0.007	**
6	parasites on mated male (square-root transformed)	parasites on mated female (square-root transformed)	-0.052432	0.003886	0.094	n.s./tr.
7	mated males vs. unmated males (dummy variable)	femur length of mated and unmated male (ln)	-0.428600	0.005606	0.024	*
8	femur length of mated male (ln)	femur length of mated female (ln)	0.087924	0.007133	0.058	n.s./tr.
9	femur length of mated male (ln)	parasites on mated male (square-root transformed)	-0.009954	0.009700	0.033	*
10	femur length of unmated male (ln)	parasites on unmated male (square-root transformed)	-0.023018	0.000003	0.482	n.s.
11	femur length of mated female (ln)	parasites on mated female (square-root transformed)	-0.004251	0.002711	0.197	n.s.

wings. This could lead to the parasite being more evenly distributed along the male hosts' body than on their female conspecifics.

In this study average ectoparasitic loads for *Rhagonycha fulva* were found to be between 2.03 ± 1.79 (mated females) and 1.0 (unmated females) larval mites per infested individual. Even considering that the average load for unmated females may not be representative due to very small sample size of the group ($n = 11$), these numbers are relatively low compared to the findings of other studies. PETERSON et al. (1992) found a similar average number

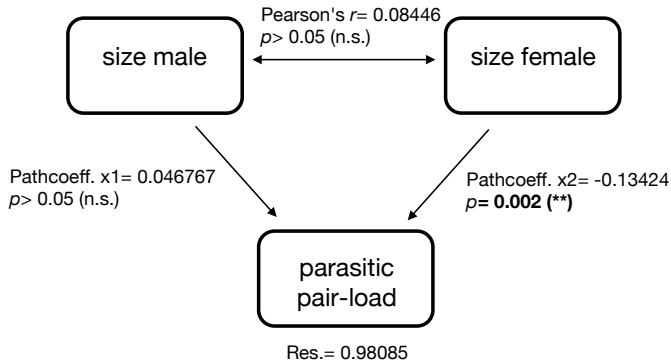


Fig. 2: Path-diagram illustrating the effects of male and female body size of the hosts on the total parasitic pair-load. Path coefficients for x_1 (male femur length) and x_2 (female femur length) are shown, as well as correlation (Pearson's r) between paired male and female femur lengths, significances and residual.

Abb. 2: Pfaddiagramm zur Illustration der Effekte männlicher und weiblicher Körpergröße der Wirtstiere auf die Gesamtparasitenlast des Paares. Pfadkoeffizienten für x_1 (Femurlänge des Männchens) und x_2 (Femurlänge des Weibchens) sowie die Korrelation (Pearson's r) zwischen den Femurlängen verpaarter Individuen, Signifikanzen und Residuum sind dargestellt.

of 1.88–2.88 *Trombidium* larvae per individual of the bean-leaf beetle *Cerotoma trifurcata* (FORSTER, 1771). However, larger arthropods such as Lepidoptera were observed to be infested by up to 15 larval mites (ROBAUX 1974) and female grasshoppers with up to 175 ectoparasites per individual (SEVERIN 1944).

Excessive parasitism by trombidiid larvae is thought to be detrimental to the host's survival and reproduction (CONRADT et al. 2002) with the severity of the effect depending on the relative size of host and parasite in addition to the total parasitic load (ZHANG 1998).

The rates of parasitism observed in this study ranged from 18–47%. This percentage is high compared to the findings of PETERSON et al. (1992), who found infestation rates of 1–5% on *C. trifurcata*, but seems consistent with the results of other studies (for a complete review, see ZHANG 1998): Parasitism rates ranged from 90% in the buzzing grasshopper *Sphingonotus savignyi* SAUSSURE, 1884 parasitized by *Allothrombidium* sp. (CHANDRA 1984) to 0–3% in cereal leaf beetles (*Oulema* spp.) infested by *Eutrombidium trigonum* (HERMANN, 1804) (HEYER 1992). In Lepidoptera, CONRADT et al. (2002) found 11–50% parasitized individuals within the studied populations.

Rates of parasitism by trombidiid larvae can fluctuate greatly between years or seasons (PETERSON et al. 1992, ZHANG 1998), therefore without comparable data from other years, the results obtained in this study can merely be considered a snapshot of the observed population for a specific time and place.

When interpreting the results of the linear regression analysis, it appeared noteworthy that the rate of parasitism in mated females in relation to mated males was significantly higher. Taking into account the assumptions of the immunocompetence-handicap hypothesis, one would assume that the male specimens – especially those with high mating success – would be more susceptible to parasitic infections due to the trade-off between showy male characters and an optimally functioning immune-system (FOLSTAD & KARTER 1992).

Fittingly, CONRADT et al. (2002) found male butterflies with higher rates of infestation than females. This is not the case for the observed population of *R. fulva*. However, PETERSON et al. (1992) also found significantly higher rates of parasitism in female specimens and pointed out that ecological and behavioural factors, such as sex-dependent differences in intracanalopy and soil-surface distribution patterns may account for the differences in infestation. A similar explanation seems likely for the species in question: As female soldier-beetles tend to be larger in overall body-size and much less mobile than their male conspecifics, it may be easier for larval mites to access and latch on to female hosts.

Due to the prolonged mating time the assumption seems logical that the larval mites may switch from one host to another during copula. However, Trombidiidae tend to avoid leaving a healthy and suitable host once they are attached and have formed a stylostome (ZHANG 1998). While other mites – mainly of the family Podapolipidae – are prone to change hosts during mating (HURST et al. 1995), trombidiid larvae are currently not known to be sexually transmitted between arthropod hosts (KNELL & WEBBEREY 2004).

Another interesting finding in this respect is the fact that no significant difference in parasitic load could be found between mated and unmated males. Since so little is currently known about the mating habits of *R. fulva* in the wild, there can be no absolute certainty, that the “unmated” animals of this study have never engaged in mating prior to being collected. As all unmated specimens were picked from the direct vicinity of mating couples the assumption was made that they had had less success in acquiring a mate than other conspecifics at the time of their collection. However, more biological data about the species would be necessary to safely interpret these results.

According to the Hamilton-Zuk hypothesis, a female should be able to choose the most parasite-resistant mate based on phenotypic characters, such as showy colouration. However, the size of this effect varies depending on the type of parasite involved, with endoparasites having a greater effect on male showiness than ectoparasites (HAMILTON & POULIN 1997). Furthermore, some studies have even shown higher mating-success for individuals with parasitic infections (GETTY 2002, KERSTES et al. 2013). Explanations for these phenomena include behavioural manipulation by the parasite itself (McLACHLAN 1999, DE CRESPIGNY et al. 2006) and adaptive behaviour such as augmented mating-eagerness in the hosts (KERSTES et al. 2013). Additionally, most biological mating-systems seem to depend on a far more complex array of characters than immunocompetence and showiness alone. GETTY (2002) stresses the need to distinguish between traits connected to viability and those linked to the susceptibility to parasitic infection:

“Immunity and parasites might play a fundamental role in many biological signalling systems, but viability-indicating traits are not necessarily parasite-load-indicating traits. Theory allows for the possibility that high-quality big signallers have greater health and more parasites than low-quality small signallers (and the data suggest that in many systems they do).” (GETTY 2002)

He also points out that large – and therefore high-quality – signallers may be hosts to more parasites with less impact to their viability. In a system in which fitness is more sensitive to predators than to parasites, this could lead to sexual selection for larger body-size, higher

steroid levels, and – in accordance with the immunocompetence handicap hypothesis – lower anti-parasite competence in desirable males (GETTY 2002)

In the studied sample a significant disassortativity regarding the presence of parasites was detected within the mated pairs: Mated couples frequently consisted of one individual heavily infested and the other nearly or completely parasite-free, in most of these cases the female was the more heavily parasitized mate.

The analysis of the influence that body-size of parasite infestation revealed that while mated male specimens are on average smaller in size than unmated ones, the larger mated males tended to have fewer ectoparasitic mites. The mating status of males as well as the size of mated females alone does not seem to have a significant effect on parasitic load. However, when interpreting the results of the path analysis, it becomes evident that increasing size of the female partner contributes negatively to the total parasitic load of mated couples, while male size plays no significant role in that matter.

Since the exact mechanisms of mate choice, courtship and sexual selection in *R. fulva* are not sufficiently studied at this point, only tentative conclusions can be made about the complex connections discovered in this study: Assuming a system with female choice and persistent courtship by males as in the related cantharid species *Chauliognathus pennsylvanicus* (DE GEER, 1774) (McLAIN 2005), one could draw the conclusion that parasite-infested female beetles tend to choose a male partner with few or no parasites, as shown by the disassortativity of parasitic loads. The negative effect of increasing female body-size on total parasitic pair-load may be caused by the fact that while there was no significant correlation of size within the mated pairs, a slight trend toward positive size assortative mating was discovered. Since the larger mated males were shown to have fewer parasites, by choosing a relatively large mate, a large female would indirectly lower the ectoparasitic load of the mated pair, though its own size does not correlate with the number of parasites it carries. It is not known whether members of the studied species can directly assess the parasitic load of their prospective partners (e.g. via chemical cues) or whether size, colouration or other traits serve as optical indicators but the evidence strongly suggests a form of mate choice that involves disassortative mating regarding ectoparasitic load. With a residuum of over 98% for the variance of total ectoparasitic load of a mated pair, the results of the path analysis can only serve to explain a small portion of what contributes to the cumulative amount of parasites on a couple. While the size of the female partner certainly plays a significant role, many other – so far unknown – factors undoubtedly have influence on that matter.

Among arthropods in general the most common form of assortative mating is assortativity regarding size, often with the largest individuals of both sexes being the ones with the highest mating-success (CRESPI 1989). This also holds true for many species of the Coleoptera in particular (McLAIN 1981, BERNSTEIN & BERNSTEIN 1998, HARARI et al. 1999). Possible advantages that suggest the adaptive value of this “self seeks like” mechanism of mate choice are the reduction of excessive genetic variance, a stabilizing effect on population genetics and the possibility to simultaneously choose for good genes and minimize inbreeding, thus making assortative mating itself evolutionarily beneficial and therefore widespread across various species (ALVAREZ & JAFFE 2004).

However, in many species other factors seem to play more important roles in mate choice, e.g. amount and quality of nuptial gifts, operational sex ratio of the population (ALCOCK & HARDLEY 1987) as well as the local frequency of selectively favoured phenotypes (McLAIN 2005). These are just a few of many possible factors that can influence mate choice independent of mere body size. In biological systems involving parasites with a detrimental effect on viability or fecundity individuals face additional challenges when it comes to choosing a mate: Due to their physiological dissimilarities, males and females often respond differently to parasitic infections with males often being the more susceptible sex (FOLSTAD & KARTER 1992, KERSTES et al. 2013). However, infected individuals of both sexes do not necessarily have a lower chance of finding a mate in populations that have coevolved with parasites. In certain species of Coleoptera, parasitized animals were shown to display a higher willingness to mate and experience no trouble finding a partner. This is thought to increase the offspring's genetic diversity and thereby its fitness in an environment with a constant threat of parasitism (KERSTES et al. 2013).

A similar mechanism might be at work in the studied case of *Rhagonycha fulva*, however further research regarding the biology of host and parasite and the details of sexual selection and mating behaviour in the red soldier beetle is necessary in order to understand the role trombidiid parasites play in the process of mate choice in this common but poorly studied beetle.

Though exact taxonomic identification of the larval mites was not possible in the course of this study due to lack of comparable sequences in the used databases, further investigation of this subject may yield results that could help address the open questions of host-specificity and determine whether specimens of *Rhagonycha fulva* show infestation of one host by multiple species of ectoparasites, as observed in other species of Coleoptera (PETERSON et al. 1992).

Zusammenfassung

Untersuchungen einer niederösterreichischen Population von *Rhagonycha fulva* ergaben einen Befall zahlreicher Individuen mit ektoparasitischen Milbenlarven der Gattung *Trombidium* (Trombidiidae). In Anbetracht der ambivalenten Ergebnisse vorangegangener Studien zum Thema Parasitenbefall und Paarungserfolg war das Hauptziel der hier durchgeführten Untersuchung, festzustellen, (1) ob und wie das Vorhandensein, die Anzahl und die Verteilung der Ektoparasiten auf den Wirtstieren den Paarungserfolg beeinflussen, und (2) ob ein Parasitenbefall mit anderen Merkmalen, wie etwa dem Geschlecht und der Körpergröße, korreliert.

Mikroskopische Analysen sowie Längenmessungen am rechten Metaferm lieferten folgende Ergebnisse: Die Untersuchungen ergaben signifikante Unterschiede in der Anzahl und der Verteilung der Ektoparasiten zwischen verpaarten Männchen und Weibchen, sowie eine Disassortativität im Vorhandensein von Ektoparasiten innerhalb der Paare. Für verpaarte Männchen zeigte sich ein negativer Zusammenhang zwischen Körpergröße und Parasitenbefall. Obwohl die Größe des Weibchens keinen direkten Einfluss auf die Parasitenlast hatte, verringerte sich die Parasitenanzahl eines Paares signifikant mit zunehmender Größe des weiblichen Partners. Diese Ergebnisse und ihre möglichen

biologischen Implikationen für die untersuchte Art werden im Lichte bereits bestehender Theorien diskutiert.

Acknowledgements

We wish to thank the staff of the Department of Theoretical Biology, University of Vienna, for their helpful support throughout the entire project and especially Dr. Brian Metscher for his technical advice. We further wish to thank Dr. Hans-Peter Führer and his colleagues Mag. Carina Zित्रa, Walpurga Wille-Piazzai and Barbara Eigner (Institute of Parasitology, Veterinary University of Vienna) for their assistance with the genetic analysis, as well as Josef Harl for designing the PCR-protocol. Special thanks also go out to the first author's family and friends for their unwavering support during the entirety of her studies.

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Authors' addresses

Alice Laciny MSc, 2nd Zoological Department, Museum of Natural History,
Burgring 7, 1010 Vienna, Austria. E-Mail: a.laciny@gmx.at

Ao. Univ.–Prof. Dr. Hans Leo Nemeschkal, Department of Theoretical Biology,
Faculty of Life Sciences, University of Vienna, Althanstraße 14,
1090 Vienna, Austria. E-Mail: hans.leo.nemeschkal@univie.ac.at

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Zeitschrift/Journal: [Entomologica Austriaca](#)

Jahr/Year: 2015

Band/Volume: [0022](#)

Autor(en)/Author(s): Laciny Alice, Nemeschkal Hans

Artikel/Article: [Disassortative parasitic infestation by larval mites of the genus Trombidium \(Acari: Trombidiidae\) influences mate choice in a population of the cantharid beetle Rhagonycha fulva SCOPOLI, 1763 \(Coleoptera: Cantharidae\) 75-89](#)