Dead and alive parasites: sexual ornaments signal resistance in the male fish, *Rutilus rutilus*

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ABSTRACT

The Hamilton and Zuk hypothesis proposed that male sexual ornaments could signal resistance against local co-evolving parasites. We examined the ornamentation – the breeding tubercles – of roach from five populations in relation to (a) parasite load (intensity/prevalence; five species), (b) host resistance (proportion of dead parasites; two species), (c) immune function (spleen size) and (d) somatic condition. The gill endo-parasite *Rhipidocotyle campanula* was locally the most prevalent and abundant among the five parasite species studied. Ornamentation correlated positively with the proportion of dead *R. campanula*, but not with the other parameters or the other parasite species. This suggests that ornamentation may signal a male's ability to eliminate local parasites as expected by the hypothesis. Furthermore, we propose that the proportion of dead parasites in a host may provide a useful measure of its resistance, since it might be a species-specific, direct, long-term measure of host immunological response.

Keywords: co-evolution, expression of secondary sexual characters, Hamilton and Zuk, sexual selection.

INTRODUCTION

Hamilton and Zuk (1982) proposed that secondary sexual characters could signal genetically based parasite resistance and may have evolved via mate choice. Since their proposal, the role of parasites and immunological defence in host sexual selection has been a subject of growing interest. Many hypotheses based on physiological regulations and trade-offs with respect to mating, reproduction, sexual signalling and immune function have been suggested (for a review, see Braude *et al.*, 1999). These hypotheses focus on the relationships between (a) sexual hormones, ornaments and immunocompetence (Folstad and Karter, 1992), (b) hormonally regulated resource reallocation between the immune system and reproduction (Wedekind and Folstad, 1994), (c) sperm quality, ornamentation, sex hormones and immunity (Folstad and Skarstein, 1997; Hillgarth *et al.*, 1997), and (d) stress, testosterone and allocation to different components of the immune system (Braude *et al.*, 1999). Empirical studies testing the above relationships have shown some evidence for

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each of the hypotheses proposed (e.g. Skarstein and Folstad, 1996; Liljedal *et al.*, 1999; Verhulst *et al.*, 1999).

The original hypothesis by Hamilton and Zuk (1982) has been tested by examining male ornamentation in relation to parasite resistance by using parasite load or immune function as a measure of parasite resistance. In general, studies based on measures of immune function have generally provided stronger evidence for the hypothesis than those based on measures of parasite load (Møller *et al.*, 1999). However, to date, a male's ability to directly eliminate its natural parasites has not been used as a measure of resistance. This approach would be useful, since the original hypothesis suggests co-adaptation cycles between the host and parasite are an underlying force in the evolution of sexual selection (Hamilton and Zuk, 1982). Co-adaptation cycles are most probable among local host and parasite populations (Ebert, 1994; Lively, 1999).

The aim of this study was to test Hamilton and Zuk's (1982) hypothesis using a new method to examine host resistance: separation of dead and alive parasites. We used the lekking fish *Rutilus rutilus* (roach) as a model organism. Male roach develop sexual ornaments (breeding tubercles) during the breeding season. We examined ornamentation of the fish from five populations in relation to (a) host resistance (proportion of dead parasites; two parasite species), (b) parasite load (intensity/prevalence; five parasite species), (c) immune function (spleen size) and (d) somatic condition. The hypothesis predicts that host resistance should be higher in highly ornamented males. More specifically, parasite loads should be lower, and spleen size and the proportion of dead parasites should be higher, among high-ornamented males.

MATERIALS AND METHODS

We chose roach as a study organism because it was used successfully to examine the relationships between male ornamentation and parasite load by Wedekind (1992) and because we knew its parasites well (e.g. Taskinen *et al.*, 1991, 1994; Valtonen *et al.*, 1997). Roach display lek-like spawning behaviour, whereby females choose between males (Wedekind, 1996). Male roach develop sexual ornaments during spawning (Wiley and Collette, 1970; Wedekind, 1992).

We chose five parasites of roach to study the relationship between ornamentation and parasite resistance or parasite load: three gill parasites – *Rhipidocotyle campanula* (Digenea, Bucephalidae), *Paradiplozoon homoion* (Monogenea) and *Myxobolus* sp. (Protozoa) – and two liver parasites – *Raphidascaris acus* (Nematoda) and *M. mülleri* (Protozoa). They fulfilled the following criteria: (1) they were abundant among the roach in the study areas (Brummer-Korvenkontio *et al.*, 1991; Koskivaara and Valtonen, 1991; Taskinen *et al.*, 1991; Valtonen *et al.*, 1997); (2) they were expected to be harmful (see, for example, Bauer and Zmerzlaja, 1973; Hoffmann *et al.*, 1990; Shul'man, 1990; Valtonen *et al.*, 1994); and (3) they occurred in different tissues. In addition, Wedekind (1992) had previously shown that male ornamentation could reveal *P. homoion* and *R. acus* infections in roach. We chose *R. campanula* and *R. acus* to study the proportion of dead parasite individuals as a measure of host resistance. We chose the former based on our previous experience in separating dead and alive larvae in tissues of roach, and the latter because Valtonen *et al.* (1994) reported that both dead and alive larvae were present in the liver of roach through-out the year in the study area. Furthermore, the transmission of *R. campanula* to a roach is temporally limited to occur between June and September (Taskinen *et al.*, 1994; Taskinen,

1998). Therefore, the proportion of dead *R. campanula* measured at the time of breeding in May should indicate the extent of defensive host responses against the parasite during the previous 8–11 months.

We chose spleen size as an immunological variable since it was used in previous immune function studies (e.g. Møller *et al.*, 1999) and the spleen is assumed to be an essential secondary lymphatic organ in fish (Manning, 1994).

Using nets, dip nets or angling, we collected sexually mature male roach from five populations close to the city of Jyväskylä, Finland (Lake Konnevesi, Lake Päijänne, Lake Lahnajärvi, Lake Jyväsjärvi and Lake Saravesi) during the spawning period, between 19 and 26 May 1999 (Table 1). The fish were transported and stored at 4°C. Each day, we caught the fish in the late evening and examined them during the next morning. In the laboratory, we classified the fish into three categories based on their sexual ornamentation, breeding tubercles on the body sides and operculum, using hand examination: (1) no tubercles, smooth skin; (2) slightly or moderately rough skin; and (3) very rough skin. The last group is comparable to rough sandpaper. It is worth noting that all the males studied, including the ones with no breeding tubercles, were sexually mature and ready to spawn. Hereafter, we refer to the groups as 'low-ornamented', 'medium-ornamented' and 'high-ornamented', respectively. One person performed ornament classifications throughout the study. The same person prepared fish tissues for parasitic examination and provided them in random order to the person that studied the parasites, so that the latter was blind with respect to breeding tubercles. To verify the repeatability of this categorization method, an extra group of fish ($n = 74$) was sampled and several persons conducted the classification. The repeatability was tested using the kappa measure of agreement. The agreement between measurers was highly significant (kappa = 0.916, $P < 0.001$). We also examined another sexual ornament, the number of breeding tubercles in the front of the head, and the stress-induced skin disease epidermal papillomatosis. These results will be reported elsewhere.

Measurements were made for fish length, total weight, somatic weight (gonads and internal organs removed) and spleen weight. We then examined parasites from the gills and liver microscopically using transmitted light, by pressing the tissues between two large glass plates. We counted a number of dead and alive *R. campanula* and *R. acus*. Alive *R. campanula* were moving inside the metacercarial cyst. Dead *R. campanula* were motionless and more or less brownish in colour due to variable amounts of melanization, and often clearly degenerated. Dead *R. acus* were motionless, partly or totally encysted, and at various stages of degeneration, while alive worms were moving vigorously. The repeatability, R (see Krebs, 1989), of the ratio of dead to alive parasites was high ($R = 0.964$, $F_{19,20} = 53.829$, $P < 0.001$), calculated from counts of *R. campanula*. The somatic condition of fish (condition factor, K) was calculated using the equation $K = \text{constant} \times \text{somatic weight (g)}/(\text{length (cm)})^3$ (Bolger and Connolly, 1989).

We used analysis of covariance (ANCOVA), with the length of the fish as a covariate, to analyse the relationships between ornamentation, population, spleen size, condition, proportion of dead and alive *R. campanula* and *R. acus*, as well as intensity of *R. campanula* and *R. acus* infection. Details of the statistical analysis are given in Table 2 and Table 3. Population was used as a random factor and ornamentation as a fixed factor. Length was used as a covariate to control for possible age-dependent immunity and ornamentation. If it was not possible to use population as a factor due to violation of the assumptions of ANCOVA, the populations were analysed separately. However, Lake Jyväsjärvi was

always analysed separately, since high-ornamented males were only found in that lake (Table 1).

To analyse the proportion of dead *R. campanula* and *R. acus* in relation to ornamentation, we selected males that were infected with at least three individuals. For *R. campanula*, populations from which sufficient numbers of fish were available were Lakes Konnevesi, Jyväsjärvi and Saravesi and, for *R. acus*, Lakes Konnevesi, Päijänne, Jyväsjärvi and Saravesi (see Table 1). To meet the assumptions of ANCOVA, proportions of dead parasites were arcsin transformed:

$$\sqrt{\frac{X + \frac{3}{8}}{n + \frac{3}{4}}}$$

where X = number of dead parasites and n = number of dead plus alive parasites (see Anscombe, 1948; Zar, 1999).

We used logistic regression to analyse the relationships between parasite load of the less abundant parasites and ornamentation, population and fish length. In the logistic regression, we used infection (infected *vs* non-infected) as a dependent variable, ornamentation and population as categorical factors, and fish length as a continuous factor. We used an automated, forward stepwise variable selection procedure to select the model that fit the data best. By comparing hierarchical sets of regression models, the significance of each interaction and main effect was calculated using likelihood ratio statistics (Forward LR) (Norušis, 1997). Then, we repeated the variable selection using an automated backward stepwise elimination procedure (Backward LR). If the above procedures did not result in the same model, the simplest of the statistically adequate models was selected. In other words, the terms that were different in the two models were tested for their significance using an improvement χ^2-test. If a term was significant, it was included in the model.

We performed all statistical analyses using SPSS (SPSS Inc., Chicago, IL, USA).

RESULTS

General patterns

There was considerable variation between the five roach populations in ornamentation, proportion of dead parasites, spleen size, prevalence and intensity of parasitism, and mean fish size (Table 1). The gill trematode *Rhipidocotyle campanula* was the locally most prevalent and abundant parasite in three of the five study populations: Lake Konnevesi, Lake Jyväsjärvi and Lake Saravesi. In those lakes, the prevalence (proportion of infected) of *R. campanula* infection in male roach was 1.00, which was significantly higher than that of the second most prevalent parasite, the liver nematode *Rhapidascaris acus*, in two of the populations: Lake Konnevesi and Lake Jyväsjärvi (binomial test, $P < 0.001$ for both populations). In addition, the mean intensity of *R. campanula* (from 9 to 88 parasites per infected host, Table 1) was significantly higher than that of *R. acus* (from 5 to 11) (ln-transformed numbers of parasites, paired *t*-tests: Lake Konnevesi, $t_{17} = -3.982$, $P = 0.001$; Lake Jyväsjärvi, $t_{36} = -4.339$, $P < 0.001$; Lake Saravesi, $t_{29} = -7.295$, $P < 0.001$). The prevalence and intensity of the other parasites were lower than those of *R. campanula* or *R. acus* in each lake (Table 1).

Table 1. Male roach collected from five lake populations during spawning in 1999: method and date of collection, mean length of fish, prevalences and mean intensities of infection for gill and liver parasites, and immunocompetence parameters (relative spleen size and proportions of dead parasites)

	L. Konnevesi	L. Päijänne	L. Lahnajärvi	L. Jyväsjärvi	L. Saravesi
Method of collection[a]	Net	Net	Net	Gill netting	Hook and line
Date	19 May	25 May	23 May	26 May	21 May
Numbers of fish					
Low-ornamented	15	22	21	0	16
Medium-ornamented	14	14	31	32	14
High-ornamented	0	0	0	13	0
Total	29	38	52	45	30
Length (mm)	154 ± 3	155 ± 3	148 ± 2	189 ± 3	142 ± 2
Gill parasites					
Myxobolus sp.					
prevalence[b]	0.38	0.16	0.04	0.16	0.67
intensity	2.9 ± 0.7	1.0 ± 0.0		2.6 ± 1.1	2.6 ± 0.5
Paradiplozoon homoion					
prevalence[b]	0.17	0.0	0.16	0.02	0.0
intensity	1.4 ± 0.2		1.0 ± 0.0		
Rhipidocotyle campanula					
prevalence[b]	1.00	0.26	0.02	1.00	1.00
intensity	14 ± 1	2 ± 1		9 ± 1	88 ± 19
Liver parasites					
Myxobolus mülleri					
prevalence[b]	0.17	0.10	0.04	0.11	0.13
intensity	4.8 ± 1.4	2.3 ± 1.3		1.8 ± 0.6	3.3 ± 0.8
Raphidascaris acus					
prevalence[b]	0.62	0.81	0.64	0.84	1.00
intensity	5 ± 1	9 ± 2	5 ± 1	6 ± 1	11 ± 3
Immune function					
Relative spleen size	129 ± 8	214 ± 9	158 ± 7	187 ± 5	151 ± 10
Proportion of dead parasites					
Rhipidocotyle campanula	0.32 ± 0.3			0.67 ± 0.4	0.46 ± 0.4
Raphidascaris acus	0.91 ± 0.4	0.71 ± 0.6	0.97 ± 0.1	0.83 ± 0.4	0.93 ± 0.3

[a] Method of data collection: by net from river during migration to spawning grounds, by gill netting from the lake or by hook and line from the lake. [b] Proportion of sample infected.
Note: Mean (± standard error of the mean) given when at least three fish were found for each cell.

Immune function and somatic condition

The measure of immune function – spleen size (spleen weight to somatic weight ratio) – did not differ between low- and medium-ornamented males in Lakes Konnevesi, Päijänne, Lahnajärvi and Saravesi, or between medium- and high-ornamented males in Lake Jyväsjärvi (Table 2). Similarly, the condition of fish did not differ between low- and

medium-ornamented males in Lakes Konnevesi, Päijänne, Lahnajärvi and Saravesi, or between medium- and high-ornamented males in Lake Jyväsjärvi (Table 2).

Proportion of dead parasites

The proportion of dead *R. campanula* was 1.4 times higher among medium-ornamented males than low-ornamented males in Lake Konnevesi and Lake Saravesi, as indicated by the significant main effect of 'ornamentation' ($P < 0.001$; Table 3, Fig. 1). The same trend was also found in the third of the three populations inhabited by *R. campanula*, Lake Jyväsjärvi, but the effect of ornamentation was not significant ($P = 0.091$; Table 3, Fig. 1). Moreover, the effect of fish length as a covariate was non-significant in Lake Konnevesi and Lake Saravesi, and in Lake Jyväsjärvi (Table 3).

We found no statistically significant relationship between the proportion of dead *Raphidascaris acus* and ornamentation in Lake Konnevesi, Lake Päijänne and Lake Saravesi, or in Lake Jyväsjärvi (Table 3).

Parasite loads

We found no significant relationship between ornamentation and intensity or prevalence for any of the parasites. To analyse the relationship between ornamentation and intensity of *R. campanula* infection, we used ln-transformations, and performed separate analyses for each population because of heterogeneity of variances. The effect of ornamentation on the intensity of *R. campanula* infection was not significant in Lake Konnevesi, Lake Saravesi or Lake Jyväsjärvi (Table 3). In addition, we found no significant relationship between *R. acus*

Table 2. Results of analyses of covariance for the length, spleen size and condition of the roach collected from five lake populations during spawning in 1999

Parameter	Lake	Details of test	P
Spleen size	Konnevesi	ornamentation $F_{1,121} = 1.139$	0.359
	Päijänne	population $F_{3,121} = 24.84$	0.009
	Lahnajärvi	ornamentation × population $F_{3,121} = 0.555$	0.646
	Saravesi	the covariate length $F_{1,121} = 0.062$	0.803
	Jyväsjärvi	ornamentation $F_{1,42} = 1.117$	0.297
		the covariate length $F_{1,42} = 0.020$	0.899
Condition	Konnevesi	ornamentation $F_{1,126} = 4.069$	0.137
	Päijänne	population $F_{3,126} = 4.851$	0.102
	Lahnajärvi	ornamentation × population $F_{3,126} = 0.674$	0.570
	Saravesi	the covariate length $F_{1,126} = 0.286$	0.598
	Jyväsjärvi	ornamentation $F_{1,42} = 0.042$	0.838
		the covariate length $F_{1,42} = 4.584$	0.038

Note: Ornamentation is for low- *vs* medium-ornamented males in Lake Saravesi, Lake Konnevesi, Lake Päijänne and Lake Lahnajärvi and medium- *vs* high-ornamented males in Lake Jyväsjärvi.

Table 3. Results of analyses of covariance for proportion of dead parasites and parasite loads (*R. campanula* and *R. acus*) for the roach collected from five lake populations during spawning in 1999

Parameter	Lake	Details of test	*P*
Proportion of dead *R. campanula*	Konnevesi Saravesi	ornamentation $F_{1,53} = 32.018$	< 0.001
		population $F_{1,53} = 63.341$	< 0.001
		ornamentation × population $F_{1,53} = 0.057$	0.812
		the covariate length $F_{1,53} = 2.459$	0.123
	Jyväsjärvi	ornamentation $F_{1,34} = 3.017$	0.091
		the covariate length $F_{1,34} = 0.108$	0.745
Proportion of dead *R. acus*	Konnevesi Päijänne Saravesi	ornamentation $F_{1,148} = 3.022$	0.229
		population $F_{2,148} = 22.99$	0.003
		ornamentation × population $F_{2,148} = 0.206$	0.815
		the covariate length $F_{1,148} = 0.259$	0.365
	Jyväsjärvi	ornamentation $F_{1,27} = 0.004$	0.952
		the covariate length $F_{1,27} = 0.443$	0.511
Intensity of *R. campanula* infection	Konnevesi	ornamentation $F_{1,26} = 1.539$	0.226
		the covariate length $F_{1,26} = 5.041$	0.033
	Saravesi	ornamentation $F_{1,27} = 1.742$	0.198
		the covariate length $F_{1,27} = 0.749$	0.484
	Jyväsjärvi	ornamentation $F_{1,41} = 0.104$	0.749
		the covariate length $F_{1,41} = 3.024$	0.090
Intensity of *R. acus* infection	Konnevesi Päijänne Lahnajärvi Saravesi	ornamentation $F_{1,93} = 2.152$	0.231
		population $F_{3,93} = 3.299$	0.135
		ornamentation × population $F_{3,93} = 0.549$	0.650
		the covariate length $F_{1,93} = 0.476$	0.492
	Jyväsjärvi	ornamentation $F_{1,37} = 0.378$	0.543
		the covariate length $F_{1,37} = 1.439$	0.238

Note: Ornamentation is for low- *vs* medium-ornamented males in Lake Saravesi, Lake Konnevesi, Lake Päijänne and Lake Lahnajärvi and medium- *vs* high-ornamented males in Lake Jyväsjärvi.

intensity (ln-transformed data) and ornamentation in populations in Lake Konnevesi, Lake Päijänne, Lake Lahnajärvi and Lake Saravesi, or in Lake Jyväsjärvi (Table 3).

The results of the logistic regression indicated that not ornamentation, population or fish length affected the risk of infection by *Paradiplozoon homoion*, as the logistic model included the constant only. When analysing the risk of infection by the protozoan gill parasite *Myxobolus* sp. in Lake Konnevesi, Lake Päijänne, Lake Lahnajärvi and Lake Saravesi, the logistic regression model included the term 'population' (change in log likelihood if term removed = − 80.2, likelihood ratio = 40.03, d.f. = 1, *P* < 0.001), but not 'ornamentation' or 'fish length', suggesting that the effect of ornamentation and fish length on *Myxobolus* sp. infection was non-significant in those populations. In Lake Jyväsjärvi, neither ornamentation nor fish length affected *Myxobolus* sp. infection, as the model
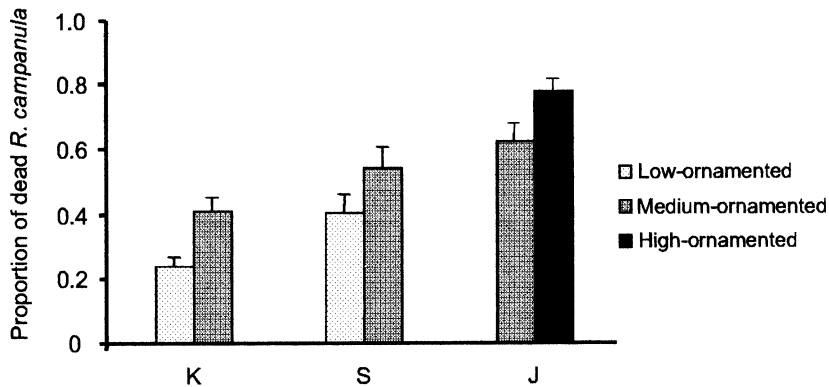
Fig. 1. Mean proportions of dead *Rhipidocotyle campanula* among differentially ornamented males in Lake Konnevesi (K), Lake Saravesi (S) and Lake Jyväsjärvi (J).

included the constant only. Similarly, logistic regression for the liver protozoan, *M. mülleri*, also indicated that the risk of infection was not related to ornamentation, population or fish length in Lakes Konnevesi, Päijänne, Lahnajärvi and Saravesi, or by ornamentation or fish length in Lake Jyväsjärvi.

DISCUSSION

The main result of the present study is that the resistance against *R. campanula* was positively correlated with ornamentation in male roach in all of the three populations where this parasite occurred in sufficient numbers for statistical analyses (Lakes Konnevesi, Jyväsjärvi, Saravesi). In all of these populations, all fish were infected by *R. campanula*, which was the most abundant parasite species studied. This suggests that ornamentation may signal parasite resistance in general, or specific resistance against *R. campanula* in male roach in the present system, which is in accordance with the prediction of the hypothesis by Hamilton and Zuk (1982). Wild roach have been shown to produce specific antibodies against *R. fennica* (Aaltonen *et al.*, 1997), a close relative of *R. campanula*. Therefore, a specific humoral immune response and specific resistance against *R. campanula* are possible. However, it is also possible that the ornaments do not signal parasite resistance as such, but a general good condition. However, this is unlikely, since the present results indicate no relationship between ornamentation and fish condition (Table 2).

Rhipidocotyle campanula was the locally most prevalent (100% infection) and abundant (on average 14, 9 and 88 parasite specimens per host in Lakes Konnevesi, Jyväsjärvi and Saravesi, respectively) parasite in the study populations. *Rhipidocotyle campanula* is assumed to be harmful to roach, since the larvae migrate to the gills (Taskinen *et al.*, 1991) where they interfere with blood circulation (Baturo, 1977). Heavy infections by bucephalid digeneans like *R. campanula* have been reported to cause considerable mortality in roach (e.g. Hoffmann *et al.*, 1990). If ornaments signal specific resistance against *R. campanula*, this is in line with the idea that host–parasite co-evolutionary cycles would drive the evolution of sexual selection (Hamilton and Zuk, 1982), since such cycles are most likely to be found in locally abundant and virulent parasites (Ebert, 1994; Lively, 1999).

We did not find a significant relationship between ornamentation and resistance against any parasite species in populations where the prevalence of *R. campanula* was low (Lake Päijänne and Lake Lahnajärvi). It is possible that we did not study the right parasite species in those populations, since a total of 51 parasite taxa have been reported from roach in the present study area (Koskivaara *et al.*, 1991a,b; Halmetoja *et al.*, 1992; Valtonen *et al.*, 1997), not including bacteria or viruses. It is also possible that we did not examine the right character of ornamentation to reveal such relationships in those populations, since Wedekind (1992) found breeding tubercles on the lateral line to signal different parasite species in male roach than the tubercles on the operculum. However, both of the species that were related to ornamentation in the study of Wedekind (1992), *Paradiplozoon homoion* and *Raphidascaris acus*, were included in the present study.

Roach have been shown to mount a humoral (antibody-mediated) response against *Rhipidocotyle* metacercaria (Aaltonen *et al.*, 1997). Another defence mechanism in fish is a cellular response, a non-specific granulocytic inflammatory reaction resulting in encapsulation, death and eventually disappearance of the parasite (e.g. Poole and Dick, 1984; Ramakrishna and Burt, 1991). A more detailed description of the cellular response of roach against *Raphidascaris acus*, and the resulting death of the parasite, is given by Valtonen *et al.* (1994). In histological examinations, we found a corresponding response in roach against *Rhipidocotyle campanula*. Moreover, Aaltonen *et al.* (1997) found that *Rhipidocotyle* antibodies increased with repeated exposure in roach. For these reasons, it is reasonable to assume that the host immune response is a significant mortality factor of the parasites in host tissues, at least for *R. campanula*.

The present study is the first to use the proportion of dead parasites to study the hypothesis of Hamilton and Zuk. By using this novel method, we found that the proportion of dead *R. campanula* was positively and significantly correlated with ornamentation, whereas total *R. campanula* load and spleen size were not. This indicates that the proportion of dead parasites could serve as a valuable measure of host resistance, in addition to parasite load or traditional immune function measures. The proportion of dead parasites is a long-term measure of host immune function. For instance, roach are infected by *R. campanula* annually from June to September in the present study area (Taskinen *et al.*, 1994; Taskinen, 1998). Thus the parasites examined while breeding in late May had been exposed to host immune defence for at least 8 months. Finally, the proportion of local parasites eliminated by the host is a measure of host resistance that is connected to the co-evolutionary cycle between a host and a parasite. Indeed, it is reasonable to presume that it is exactly the most abundant virulent local parasite against which the resistance is needed. For these reasons, we suggest that the proportion of dead parasites would be a useful measure of host resistance in the context of parasitism and sexual selection. To conclude, the present study has shown that sexual ornamentation of male roach could signal resistance against a locally abundant parasite, which is in accordance with the hypothesis of Hamilton and Zuk (1982).

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