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PARASITE-INDUCED CHANGES IN BEHAVIOR AND COLOR MAKE *GAMMARUS PULEX* MORE PRONE TO FISH PREDATION

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Abstract. The acanthocephalan parasite *Pomphorhynchus laevis* is transmitted by crustaceans such as *Gammarus pulex* to its paratenic or final hosts, fish. The conspicuous orange-yellow parasite is visible through the transparent cuticle of *G. pulex.* Infected gammarids are significantly less photophobic than uninfected ones. When hungry three-spined sticklebacks (*Gasterosteus aculeatus*), one of the hosts of this parasite, were offered equal numbers of uninfected and infected prey, *G. pulex* infected with *P. laevis* were eaten significantly more often. We tested experimentally whether parasite color and parasite-induced changes in host behavior affected the predation rate of *G. pulex.* Color effects were tested with uninfected *G. pulex* by painting an orange spot on their cuticle that simulated infection. Behavioral effects were tested with infected *G. pulex* by covering the place through which the orange parasite was visible with inconspicuous brown paint. We showed for the first time that both parasite color and changed intermediate host behavior promote the transmission of *P. laevis* to its next host. The evolution of orange parasite color, and why sticklebacks do not avoid infected prey, are discussed.

Key words: behavioral changes; coloration; Gammarus pulex; Gasterosteus aculeatus; *intermediate host; parasite transmission;* Pomphorhynchus laevis; *predation risk.*

INTRODUCTION

Parasites with a complex life cycle involving several hosts are faced with problems of transmission from one host to the next. There is a wealth of solutions to this problem (e.g., Moore and Gotelli 1990, Moore 1995). Well known are the parasite-induced changes in the behavior of intermediate hosts of Acanthocephala, a group of parasitic worms in vertebrates, especially in fish and birds. The behavior of the intermediate hosts of Acanthocephala, arthropods, may show various changes when infected, including changes in activity, photoreaction, escape behavior, substrate color choice, and vertical distribution (e.g., Moore 1984, Poulin 1994). These behavioral changes increase the exposure of the intermediate host to the next host of the parasite.

The timing of behavioral changes was studied in one system, that of *Gammarus lacustris* infected with *Polymorphus paradoxus.* Changes in behavior coincided with the onset of infectivity of the parasite for the next host (Bethel and Holmes 1973, 1974). There is some evidence that the behavioral changes in *G. lacustris* are caused by parasite-induced modifications in serotonergic neuromodulatory activity (Harris-Warrick et al. 1989, Helluy and Holmes 1990, Thompson and Kavaliers 1994). Intermediate hosts that harbor the infective stage of acanthocephalans, the cystacanth stage, may show physiological changes such as reduced O_2 consumption (Rumpus and Kennedy 1974) and increased hemocyanin concentration, the respiratory pigment for most crustaceans (Bentley and Hurd 1993).

Several studies have shown increased predation of intermediate hosts that are infected by acanthocephalans (reviewed by Moore 1984 and Nickol 1985). It is tempting to ascribe this increased predation risk to parasite-induced changes in behavior that make the intermediate host more vulnerable. Although cystacanths of most Acanthocephala species are colorless, some of those using aquatic crustaceans as intermediate hosts are bright orange colored, or cause changes in the pigmentation of their intermediate hosts (Nickol 1985). Almost all cases (five out of six) for which an increase of predation risk of infected intermediate hosts was shown concern aquatic crustaceans with marked color effects of their acanthocephalan parasites: *Gammarus lacustris* infected by *Polymorphus paradoxus* (Holmes and Bethel 1972, Bethel and Holmes 1977) or by *Polymorphus minutus* (Hindsbo 1972); *Hyalella azteca* infected by *Corynosoma constrictum* (Bethel and Holmes 1977); *Gammarus pulex* infected by *Pomphorhynchus laevis* (Kennedy et al. 1978); and *Asellus intermedius* infected by *Acanthocephalus dirus* (Camp and Huizinga 1979). In all these systems, the parasite not only induces behavioral changes, but at the same time increases the conspicuousness of the intermediate hosts by color effects.

It is well established that conspicuously colored prey suffer enhanced predation, called oddity selection (e.g., Curio 1976). In the interpretation of increased predation risk of intermediate hosts infected by acanthocephalans, parasite-induced behavioral changes may

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thus be confounded by parasite-induced changes in appearance. There has been one attempt to experimentally separate these causes. Bethel and Holmes (1977) painted oval marks, about the size and color of cystacanths of *P. paradoxus,* on the carapaces of uninfected *G. lacustris.* They were exposed to Mallards (*Anas platyrhynchos*) together with equal numbers of uninfected but unpainted prey. Unfortunately, Mallards are surface feeders and did not appear to feed actively on the gammarids. It is therefore not surprising that the proportions of marked and unmarked gammarids that were eaten were not different.

In our study, we used a different acanthocephalan system: *Pomphorhynchus laevis,* which uses *Gammarus pulex* as intermediate host. Three-spined sticklebacks, *Gasterosteus aculeatus,* a visually hunting fish, served as predator. The aim of our study was to disentangle the effects of parasite color and changed host behavior on the predation risk of *G. pulex* infected with *P. laevis.* The separate effects of color and behavior were studied experimentally by painting an orange spot that simulated infection on the cuticle of uninfected *G. pulex,* and covering the place through which the orange parasite was visible in infected *G. pulex* with a neutral color, respectively.

Methods

The prey Gammarus pulex *and the parasite* Pomphorhynchus laevis

Gammarus pulex (Amphipoda) that were uninfected or visibly infected by the spiny-headed worm *Pomphorhynchus laevis* (Acanthocephala) were freshly collected with a long hand net for each set of the experiments (24 September 1995–09 October 1995). They were sampled from the Wohlensee near Berne, Switzerland (46°57′ N, 7°28′ E), at sites where sticklebacks had been breeding during April–July 1995. After collection, they were acclimatized over a few hours to room temperature. Only *G. pulex* of a total length between 0.5 and 1.0 cm were used in the experiments. Infected *G. pulex* are easily recognized, because the yellow-orange cystacanth stage of *P. laevis* is clearly visible through the cuticle of the intermediate host. The prevalence of infection in *G. pulex* was assessed on 14 and 18 September 1995 at three different breeding sites (Eymatt, Aumatt, Hasli) which are a few hundred meters apart. *G. pulex* were always handled with insect forceps.

In part of the experiments, an orange or brown spot of about the size of a single *P. laevis* cystacanth was painted on the cuticle of *G. pulex. G. pulex* were dabbed on absorbing tissue to remove attached water, picked up with an insect forceps, and a spot of paint consisting of about a 1:1 mixture of oil paint (''Marie's oil colours,'' Shanghai, China; colors ''orange'' and ''raw sienna'') and Tipp-Ex (a white typographic correction fluid manufactured by the Tipp-Ex Company of Frankfurt, Germany) (P. I. Ward, *personal communication*) was applied with a toothpick. The paint dried quickly after blowing. The whole procedure took <2 min. The painted *G. pulex* were put in a beaker with water at room temperature and allowed at least 15 min to recover before they were offered as prey to sticklebacks. The particular oil colors were selected on the basis of matching the hue of the parasite color and the gammarid body color, respectively, although both oil colors had a somewhat greater brightness.

In order to check whether *G. pulex* in our population showed a changed photoreaction when infected by cystacanths of *P. laevis,* we used a similar setup to that used by Kennedy et al. (1978). The distribution of *G. pulex* in response to light was quantified in clear water in a small plastic tank (32.5 × 17.5 cm, water level 14 cm) providing a choice between light and dark zones. The bottom and sides as well as the top of one half of the tank were covered with opaque dark gray plastic. The tank was divided in two halves by an opaque, dark gray, plastic partition positioned 4 cm above the bottom of the tank. The uncovered half was lit by a 33 W fluorescent tube mounted 10 cm above the water surface. The light intensity was 3630 lx, 3 cm above the water surface. The tank was filled with Wohlensee water at room temperature, which was exchanged after every second test and aerated between but not during tests.

G. pulex were caught in July 1996 from the Wohlensee, 2 d before the tests. Infected and uninfected gammarids were stored separately in buckets filled with aerated Wohlensee water at room temperature and leaf litter. The gammarids were used only once. Ten infected and 10 uninfected *G. pulex* were put into a petri dish with water, which was placed at the bottom in the middle of the tank. They were allowed to leave the petri dish, after which it was removed. After 1 h of acclimatization, the numbers of infected and uninfected gammarids in the light half of the tank were recorded at 5-min intervals for 30 min. The ratio of total numbers of infected or uninfected gammarids in light to those in dark was used in the analysis. At the end of the experiments, the water temperature in the light half was 0.1°C higher than in the dark half (mean ± 1 SD was 19.0° ± 0.5° and 18.9° ± 0.5°C, respectively).

The predator Gasterosteus aculeatus

Sticklebacks *Gasterosteus aculeatus,* which were used as predators in the experiments, had been caught in the Wohlensee shortly before the start of the 1995 breeding season. *P. laevis* is the prevalent parasite in this stickleback population: about 75% of the sticklebacks are infected (T. C. M. Bakker and B. Mundwiler, *unpublished data*). The sticklebacks were stocked in a group of several hundred fish in an outside storage tank of ≈200 L. The temperature in the tank was kept below 20°C by a continuous inflow of cool water (10°–15°C) from a well. Day length was artificially prolonged to

16 h. The fish were fed frozen blood worms and live *Tubifex* worms.

The stored sticklebacks had not experienced gammarids for more than 6 mo and were thus inexperienced in catching *G. pulex.* Because gammarids are relatively difficult prey to catch, experience will influence the ease with which these prey are caught (e.g., Ibrahim and Huntingford 1992, Mackney and Hughes 1995). As the *G. pulex* used in the experiments will have been exposed to fish predators in the field, the combination of inexperienced predators and experienced prey will probably maximize differential predation.

Female sticklebacks that were not reproductively active and around 5 cm standard length were used in the experiments in order to reduce the effects of confounding variables on prey selection. They were used only once. In order to standardize the hunger level of the sticklebacks and to make them willing to eat gammarids, the sticklebacks were not fed for 3 d before the start of the experiments. They were acclimatized for a few hours to room temperature before they were introduced into the experimental tanks. The standard length and wet mass of the fish were assessed shortly before introduction. After the experiments the wet mass was measured again. The fish were given at least 1 h to become familiar with the experimental tank before the start of the experiment.

Experiments

In a pilot experiment, we determined predation rates under the conditions later used in the main experiments. The fish consumed about one *G. pulex* every 9 h. The duration of the experiments was therefore set at 47 h, so that most sticklebacks would not consume more than half of the 20 prey items offered.

The experiments were performed in small plastic tanks (35 × 18 cm, water level 13 cm). The outer walls of the tanks were covered with gray, opaque partitions to prevent interactions between fish in neighboring tanks. The tanks were filled with tap water that was renewed every second experiment. The water was at room temperature (18°–21°C) at the start of the experiment. Each tank was aerated through an airstone except during the experiment. During the experiment the airstone was removed, because *G. pulex* that clung to the white stone were easily detected. Each row of six tanks was lit by a 33 W fluorescent tube, mounted 37 cm above the water surface. The light : dark schedule was 14L:10D. Each tank was provided in its center with a *Vallisneria* plant planted in a plastic cup (height 7 cm, diameter 5 cm) filled with coarse gravel, and at the bottom with an almost black tree leaf of roughly 14 cm^2 that we had collected from leaf litter in the Wohlensee. The plant, gravel, and leaf offered *G. pulex* hiding places and food.

At least 1 h after the introduction of hungry fish into the experimental tanks, one in each tank, water containing 20 selected *G. pulex* was poured into each tank in such a way that the gammarids were divided over the whole tank. During the 47 h of the experiment the tanks were left undisturbed.

We performed three kinds of experiments in order to study the effects of parasite color and changed host behavior on the predation risk of *G. pulex* infected with *P. laevis.* In the first experiment, 10 infected and 10 uninfected *G. pulex* prey were exposed to sticklebacks. Gammarids in the two prey classes were matched for size by eye. Differential predation on the two prey classes can be due to effects of parasite color and/or host behavior. These two effects were experimentally separated in two further experiments.

The second experiment investigated the effect of parasite color on the predation risk of its intermediate host. Sticklebacks were again offered 20 *G. pulex.* These were all uninfected by *P. laevis* cystacanths. In half of the gammarids, an infection was simulated by painting dorsally on the cuticle of *G. pulex* an orange spot of similar color and size as a *P. laevis* cystacanth. The other half of the prey were treated similarly, but with brown paint that matched the body color of *G. pulex.* They served as a control for the effects of the paint. Gammarids in the two prey classes were matched for size by eye. Possibly differential effects of the two colors on *G. pulex* were checked in a pilot experiment. The fate of 20 uninfected *G. pulex* was assessed after 47 h in the experimental tank, but without a predator. They were either all painted with an orange or a brown spot. The mortality rate was equal for gammarids treated with the different colors (1 out of 20), as was the loss of the paint (4 of out 20), which was due to molting in half of the cases.

The third experiment investigated the effect of parasite-induced changes in host behavior on predation risk. Sticklebacks were again offered 20 *G. pulex.* Half of them were infected, but the parasite was masked by applying brown paint dorsally and laterally on the area where the cystacanth was visible. The other half of the prey were uninfected but treated similarly, and served as a control for effects of the paint. Gammarids in the two prey classes were matched for size by eye. Forty-seven hours after introduction of the prey, sticklebacks were removed and the tanks carefully checked for remaining prey.

Cases in which sticklebacks did not eat a single prey (6 times out of 70) and those in which more than half of the prey items were consumed (15 times out of 70) were left out of the analyses of predation rate. The actual number of infected prey eaten was compared with the expected number of infected prey eaten when sticklebacks do not discriminate. The expected numbers were corrected for the numbers of dead prey that we found at the end of the experiments, because sticklebacks do not eat dead prey items. The number of prey items that had not been consumed in Experiment 2 and that had lost their paint (a total of 37 prey items out of 233 left in 15 experiments) were assumed to be

TABLE 1. The outcomes of predation by *G. aculeatus* on a mixture of 10 *G. pulex* infected by *P. laevis* and 10 uninfected *G. pulex.*

Experiment	Replicates	Number of *Gammarus pulex* eaten		*P*
		Infected	Uninfected	
1) Effects of color and behavior	24	91 (211)	57 (226)	<0.006
2) Effect of color	15	50.5 (146)	11.5 (149)	<0.002
3) Effect of behavior	10	30 (90)	13 (99)	<0.03

Note: In Experiment 2 the infection was simulated, while in Experiment 3 the visible parasite was masked. The total number of infected and uninfected *G. pulex* in each experiment after correction for unavailable (dead) prey is given in parentheses. *P* values are two-tailed according to the Wilcoxon one-sample test of infected prey eaten.

equally divided among the two classes of prey (orange and brown).

RESULTS

G. pulex infected by *P. laevis* showed a changed photoreaction: in behavioral tests without predators, infected gammarids were significantly less often in the dark half of the tank than uninfected ones (Wilcoxon matched-pairs signed-ranks test on the ratio of light to dark per replicate, $N = 7$, $T = 1$, $P < 0.05$, two-tailed). Median ratios of numbers in light to those in dark were 0.67 (range 0.37–1.12) and 0.37 (range 0.27–0.79) for infected and uninfected *G. pulex,* respectively.

Sticklebacks consumed significantly more infected *G. pulex* than uninfected ones (Experiment 1 in Table 1). Experimental exclusion of behavioral (Experiment 2) or color effects (Experiment 3) of the parasite on its intermediate host showed that both parasite color and parasite-induced changes in *G. pulex* behavior significantly increased their vulnerability to predation by sticklebacks (Table 1).

The proportion of prey eaten that was infected (naturally or simulated) was different among experiments (median proportion in Experiments 1, 2, and 3 was 0.65 (range 0–1), 1.0 (range 0.5–1), and 0.69 (range 0–1), respectively (Kruskal-Wallis ANOVA, df = 2, $H = 6.82$, $P = 0.033$). A multiple comparison between experiments showed that Experiment 1 and 2 differed significantly at the 5% level in this respect.

Infected *G. pulex* suffered higher mortality during the experiments than uninfected ones. At the end of Experiment 1, in which unpainted gammarids were used, the median number of dead *G. pulex* was 1 (range 0–4) and 0 (range 0–3) for infected and uninfected gammarids, respectively (all replicates including those in pilot experiments and those not used in further analyses, Wilcoxon matched-pairs signed-ranks test, $N = 22$, $z = 3.22$, $P = 0.0013$, two-tailed). In Experiment 3, in which brown paint was applied, the median numbers were 1 (range 0–5) and 0 (range 0–1), respectively (Wilcoxon matched-pairs signed-ranks test, $N = 9$, $T = 4.5$, $P = 0.033$, two-tailed). The total number of gammarids that died in Experiments 1 (unpainted gammarids) and 3 (painted gammarids) was not significantly different (Mann Whitney *U* test, $N = 13$ and 34, $z = 1.47$, $P = 0.14$, two-tailed).

The fish used in the different experiments had a comparable body size, body mass, and condition factor (Table 2). The total number of *G. pulex* eaten differed among experiments and therefore so did the mass lost by sticklebacks (Table 2). In Experiment 1, more prey were eaten and the fish lost less mass than in Experiments 2 and 3 (post-hoc Fisher PLSD tests on the number of prey eaten, 1 vs. 2 $P < 0.05$, 1 vs. 3 and 2 vs. 3 $P > 0.05$; Fisher PLSD test on mass loss, 1 vs. 2 and 1 vs. 3 $P < 0.05$, 2 vs. 3 $P > 0.05$). These results suggest that painted prey were less attractive to sticklebacks. The results were similar when the total number of prey eaten and the mass loss were standardized for differences in fish body size using residual values from linear regression.

The prevalence of *P. laevis* infection in *G. pulex* in the Wohlensee, as determined shortly before the experiments, was 11.8% ($N = 356$), 7.8% ($N = 655$), and

TABLE 2. Means ± 1 SD of standard body length (in centimeters), body mass (in grams), condition factor (CF = mass × 100/length^3; Bolger and Connolly 1989), mass loss (in grams) during the experiments, and number of *G. pulex* eaten in Experiments 1, 2, and 3.

Experiment	*N*	Body size	Body mass	CF	Mass loss	Number eaten
1	24	4.88 ± 0.25	1.56 ± 0.22	1.34 ± 0.09	0.04 ± 0.03	6.62 ± 2.93
2	15	5.05 ± 0.26	1.68 ± 0.17	1.31 ± 0.06	0.09 ± 0.07	4.13 ± 2.47
3	10	4.97 ± 0.32	1.67 ± 0.32	1.35 ± 0.09	0.08 ± 0.03	4.30 ± 2.45
F (df)		1.75 (2, 46)	1.18 (2, 40)	0.46 (2, 40)	5.27 (2, 40)	3.24 (2, 46)
P		0.18	0.32	0.64	0.0093	0.048

Note: Differences among the experiments were tested with ANOVA; given are *F* statistics, degrees of freedom, and *P* values. Note that in Experiment 2 the masses of six fish were lacking.

20.8% ($N = 424$) at the sites Eymatt, Aumatt, and Hasli, respectively; the mean prevalence being 14.4% ($N = 1435$). A sample of 214 *G. pulex* caught at the same sites in September 1993 showed a similar prevalence (i.e., 19.6%). The intensity of infection (mean number of *P. laevis* per *G. pulex*) in this sample was 1.29; 73.8% ($N = 31$) had one, 23.8% ($N = 10$) had two, and 2.4% ($N = 1$) had three cystacanths.

Discussion

We have experimentally shown for the first time that parasite-induced changes in behavior as well as coloration promoted the transmission of the acanthocephalan *Pomphorhynchus laevis* from its intermediate host *Gammarus pulex* to its next host, the three-spined stickleback *Gasterosteus aculeatus.* Our experiments cannot give information about the relative extent of these two causes. The paint that we used to mimic cystacanths of *P. laevis* and to hide visible orange cystacanths, respectively, worked well in the sense that it did not seem to affect the gammarids' behavior or survival. Athough we tried to match the parasite color and gammarids' body color as well as possible, natural colors are variable. Additionally, the odor and taste of painted and unpainted gammarids may have been different. Sticklebacks ate somewhat less of the painted prey. However, they found the gammarids with simulated infection more attractive than naturally infected gammarids. For these reasons, the magnitude of the effects of parasite color and changed host behavior on the susceptibility of gammarids to fish predation cannot be compared. Additionally, the ratio of infected prey eaten to uninfected prey eaten in the various experiments slightly underestimates the actual degree of differential susceptibility, because the sticklebacks were sampling gammarids without replacement. The actual differential susceptibility depends on the experimental setup and performed manipulations, and may be different under natural conditions.

Why is *P. laevis* so conspicuously colored? Does this parasite need to give its intermediate host a more conspicuous appearance, in addition to behavioral changes, in order to guarantee its transmission to the next host? Or does the conspicuous orange color of the parasite have other functions? It may be significant that the orange cystacanths belong to Acanthocephala species which use aquatic crustaceans as intermediate hosts. In other aquatic parasite systems, intermediate hosts also undergo parasite-induced changes in behavior, but these are not accompanied by color effects of the parasite, e.g., *Cyclops vernalis* (Copepoda) infected by *Eubothrium salvelini* (Cestoda) (Poulin et al. 1992); and cyclopoid copepod species (*Cyclops abyssorum* and *Macrocyclops albidus*) infected by *Schistocephalus solidus* (Cestoda) (Urdal et al. 1995, Wedekind and Milinski 1996). In these cestode systems, the main parasite-induced change in behavior is an increase in swimming activity of the infected copepods. Poulin et al. (1992) could not detect differences in time spent near the surface of infected and uninfected copepods in a water column of 14 cm, but in Wedekind and Milinski's (1996) experiments, more infected copepods moved to the water surface than uninfected ones when transferred to a water column of only 2 cm. In a meta-analysis of parasite-induced behavioral changes, Poulin (1994) found that cestodes have a greater influence on host activity than acanthocephalans, while the reverse was true for host microhabitat choice.

For some of the intermediate hosts of orange Acanthocephala, the changes in photoreaction as a result of parasitization have been studied (reviewed in Nickol 1985). Uninfected *Gammarus lacustris, Hyalella azteca,* and *Gammarus pulex* are photophobic and negatively phototactic, but infection with various orange Acanthocephala species reversed their photoreaction: they became photophilic and positively phototactic. We found similar changes in *G. pulex* infected by *P. laevis.* The exception is *G. lacustris* infected by *Polymorphus marilis*: the host became photophilic but stayed negatively phototactic (Bethel and Holmes 1973, 1977). However, the main host for this parasite is a diving bird, the Lesser Scaup. Thus, the behavioral changes may be adequate for transmission of *P. marilis.* There is one obvious consequence of the changes in photoreaction induced by the orange Acanthocephala species: an increase in exposure of their intermediate hosts and themselves to the deleterious effects of solar UV-B radiation (280–320 nanometers) (e.g., Williamson 1995).

The orange color of the above-mentioned Acanthocephala species is made up of carotenoids (e.g., Barrett and Butterworth 1968, 1973). Numerous beneficial metabolic and nutritional functions have been suggested for carotenoids (e.g., Goodwin 1986, Segner et al. 1989), one of these being photoprotection. In zooplankton there is convincing evidence that carotenoids protect against the damaging effects of UV-B radiation (e.g., Hairston 1976, 1979, 1980, Ringelberg 1980, Luecke and O'Brien 1981, Byron 1982, Ringelberg et al. 1984). Experiments showed that more pigmented zooplankton pay a cost in terms of increased predation by visually selective predators (e.g., Byron 1982). The orange color of some acanthocephalans may thus be an adaptation to cope with increased levels of UV-B radiation caused by parasite-induced changes in the behavior of their intermediate hosts, aquatic crustaceans. The additional benefit of orange cystacanth color to the enhancement of transmission to the next host may have further facilitated the evolution of conspicuous parasite coloration. It would be interesting to test this idea with comparative data of aquatic Acanthocephala systems. Are intermediate hosts of orange-colored acanthocephalans (or alternatively, parasite-induced dark colored intermediate hosts [see Nickol 1985]; melanin is another photoprotective pigment [Luecke and O'Brien 1983]) more exposed to UV-B

radiation than intermediate hosts of colorless acanthocephalans (or alternatively, parasite-induced light colored intermediate hosts [caused by pigmentation dystrophy, see Nickol 1985])?

It would be an easy task for sticklebacks to avoid gammarids infected by *P. laevis.* Why don't they do so? Often there will be no selective pressure to avoid parasitized prey, because the benefits of ingesting parasitized prey are higher than the costs of avoiding them (Lafferty 1992). We showed that infected gammarids are more frequently preyed upon than uninfected ones. The parasite-induced changes in both prey behavior and coloration make them more profitable prey. Infected gammarids made up a significant proportion of the gammarid population in our field site, at least at some times of the year. Gammarids are beneficial to sticklebacks because they are an important source for carotenoids (e.g., Simpson et al. 1981, Boonyaratpalin and Unprasert 1989; T. C. M. Bakker and B. Mundwiler, *personal observation*). The orange-red breeding coloration of stickleback males, which is made up of carotenoids (e.g., Brush and Reisman 1965, Czeczuga 1980), plays an important role in sexual selection: redder males are preferred as mates by females (e.g., Milinski and Bakker 1990, Bakker 1993, Bakker and Mundwiler 1994) and have greater chances to establish territories (e.g., Bakker and Sevenster 1983). *G. pulex* infected with *P. laevis* showed increased mortality under our laboratory conditions. There are conflicting reports about the damaging effects of this parasite in fish (e.g., Chubb 1965, Hine and Kennedy 1974). In small fish species like the stickleback, it is likely that the parasite reduces the fitness of its host: the intensity of infection in sticklebacks found dead in the field was greater than that in sticklebacks which were reproductively active at the same time (T. C. M. Bakker and B. Mundwiler, *personal observation*). Additionally, the parasite affects physical condition and secondary sexual traits (eye color and relative pectoral fin size) in reproductively active males (T. C. M. Bakker and B. Mundwiler, *personal observation*), thereby probably decreasing reproductive success. On the other hand, sticklebacks of our Wohlensee population reproduce only during one breeding season and then die. Thus, they have to cope with the negative effects of *P. laevis* only for a short period of time.

In our experiments, there was individual variation in the extent to which infected gammarids were preferentially eaten. We have indications that there exists genetic variation in the susceptibility to *P. laevis* in Wohlensee sticklebacks (T. C. M. Bakker and B. Mundwiler, *personal observation*). It will be a challenge to link this to variation in prey choice.

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