Behav Ecol Sociobiol (1984) 15:35–37

Behavioral Ecology and Sociobiology

Parasites determine a predator's optimal feeding strategy

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Received June 13, 1983 / Accepted November 12, 1983

Summary. The diet selected by three-spined sticklebacks (*Gasterosteus aculeatus*) depends on the degree of parasitization by one or both of two parasite species (*Schistocephalus solidus, Glugea anomala*). Uninfested fish prefer the more profitable of two different size classes of prey (*Daphnia magna*). Fish parasitized by *Glugea* or *Schistocephalus* attack both prey types equally often, whereas sticklebacks infested by both parasite species prefer to attack the less profitable prey. The diet selected is optimal under the condition that parasites decrease their host's competitive ability.

Introduction

To be parasitized is normal for many animal species and parasites often strongly affect their host's physical condition. Therefore natural selection should have favoured strategies or learning rules which incorporate the constraints imposed by inevitable parasites.

It is not unusual that up to 50% of a stickleback population is infested either by cysts of the microsporidian sporozoan *Glugea anomala* or by larvae of the cestode *Schistocephalus solidus* (Arme and Owen 1967; Wootton 1976). Parasitized fish have a lower health condition and achieve a lower swimming speed than uninfested ones (Arme and Owen 1967; Lester 1971; Pennycuick 1971). Although reproduction is reduced, infested sticklebacks can spawn successfully (Arme and Owen 1967; Pennycuick 1971) and therefore even minor genes mitigating the effects of infestation are exposed to natural selection. Optimal foraging theory (MacArthur and Pianka 1966; Krebs and Davies 1981) predicts how an animal should proceed to feed most efficiently. If, for example, its food consists of two prey types that differ in profitability, the animal should concentrate only on the more profitable type if its abundance is above a certain threshold; otherwise the predator should feed upon both prey types unselectively. Because of their lower swimming speed, parasitized fish are not quick enough in intraspecific competition with healthy fish to catch a profitable item as often as the uninfested competitors. Therefore they should avoid waste of energy in attempting to attack the more profitable prey and prefer instead the less profitable but less contested type; the more they are infested, the more this is likely. This prediction was tested with 100 sticklebacks of which 36 had no apparent parasite, 21 were infested by *Glugea*, 23 by *Schistocephalus*, and 20 by *Glugea* plus *Schistocephalus*.

Materials and methods

Three-spined sticklebacks (*Gasterosteus aculeatus*) were caught in October 1982 from a pond where nearly all sticklebacks came from broods of that year. There was a high population density, and 40% had no apparent parasite. Fish were tested singly on the second day after capture. They were not fed in the laboratory. The experimental tank (25.5 × 12.5 × 17 cm) had in front of the back wall a transparent Plexiglas cell containing the prey; this cell was divided into seven adjacent compartments, each with a base of 1 × 1 cm. These contained 0, 4 large, 4 large, 0, 4 small, 4 small, and 0 water fleas (*Daphnia magna*) (water level 1.5 cm), respectively. Large water fleas were those passing through a sieve with 1.8 mm holes but not through one with 1.7 mm holes; for small water fleas sieve holes were 1.2 mm and 1.1 mm. Near the wall vis-à-vis the cell containing prey there were two plants (*Vallisneria* sp.) and an aerating stone. A 'dither' (Barlow 1968) stickleback was in the test tank during all trials in order to decrease the nervousness of the test fish which were not accustomed to the laboratory. Since the dither fish was satiated and its reaction to the experimental cell had been completely habituated before the experiments it stayed mostly in the planted part of the tank. After a test fish had been transferred to the planted part it began, after some hesitation, biting at the cell containing prey. Bites at compartments with small *Daphnia* and at those with large ones were counted for 5 min starting with the first attack. Each stickleback was used only once.

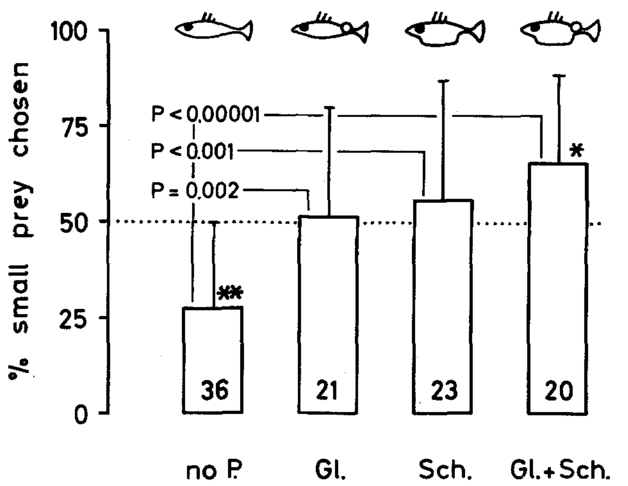

Fig. 1. Percentage of small prey chosen by fish infested with no parasite, with *Glugea anomala*, with *Schistocephalus solidus*, and with *Glugea* plus *Schistocephalus*; lengths of fish were 2.8 ± 0.2, 2.8 ± 0.2, 2.9 ± 0.3, 2.8 ± 0.2 cm, respectively (mean ± SD); numbers of fish are given in the columns; bars give SD; P after Mann-Whitney U-test, two-tailed; * $P < 0.03$, ** $P < 0.001$ after Wilcoxon-test, two-tailed

Results

Since parasitized and unparasitized sticklebacks caught and swallowed the large water fleas as quickly as the small ones in control experiments and the large water fleas had a dry weight three times that of the small ones (Milinski 1982), the small water fleas were the less profitable prey. Parasitized sticklebacks conducted a higher percentage of their attacks towards the small water fleas than fish without parasites (Fig. 1) which supports the hypothesis that parasitized fish switch to less profitable prey because of their decreased competitive ability. This result could be an artefact if unparasitized fish attack less often than the parasitized ones during a trial and therefore stop biting before they would switch to smaller prey. This hypothesis must be rejected because unparasitized fish bit more often than the infested ones during a trial ($P < 0.002$, Wartmann and Wette's combined probability test (Lienert 1973) of three Mann-Whitney U-tests, one-tailed).

Could the modified choice behaviour of the infested fish be due simply to differences in hunger? There is considerable evidence that when choosing prey animals are less selective the hungrier they are (refs. in Heller and Milinski 1979). Possibly the parasitized fish were hungrier than the unparasitized ones and therefore attacked also small prey whereas the uninfested sticklebacks selectively chose large *Daphnia*. It is impossible to exclude hunger differences between the experimental groups but at least those fish which were infested with *Glugea* plus *Schistocephalus* significantly preferred small *Daphnia* over large ones whereas the uninfested fish preferred the large prey items (Fig. 1). The parasitized fish were not unselective, as they should have been because of the effect of hunger, but they were selective for small prey. I see no theoretical reason for a preference for unprofitable prey with increasing hunger.

Discussion

Since there are theoretical reasons why one individual cannot be equally resistant to every possible parasite (Hamilton and Zuk 1982), natural selection should have favoured host strategies mitigating *similar* effects of several parasite species, e.g. a decreased competitive ability. Such a strategy would be the selection of a diet not preferred by healthy fish. The sticklebacks which were infested most heavily preferred the less profitable prey which was avoided by the uninfested ones. That this is profitable has been shown with groups of two healthy sticklebacks each of which were given large and small *Daphnia*; whereas the better competitors consumed a higher proportion of the more profitable prey, their less successful companions concentrated increasingly on the less profitable prey thereby enhancing their net energy intake (Milinski 1982). Therefore the parasitized fish chose a diet which has proved to be a profitable one for poor competitors.

It is an open question how the change in preference came about in the infested fish. Since the strategy should depend not only on the degree of parasitization but also on the frequency of competitors and the abundance of profitable prey, learning (Milinski 1982) is more likely to have produced the test fishes' preference according to the conditions in the pond they came from than a pre-programmed link between the degree of parasitization and diet selection.

Parasites as agents of natural selection are impressive and very diverse (Price 1980). We must consider this fact when we test predictions of optimal foraging theory. We should be prepared to find the animal's solution of the foraging task to be different from the predicted one because constraints from parasites or another illness have shifted the optimum.

Acknowledgements. I thank Prof. E. Curio and K. Regelmann for reading the manuscript, and K. Regelmann also for computer work. The Deutsche Forschungsgemeinschaft (Az. Cu. 4/25-3) is thanked for financial support.

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