

*Department of Biology, Southwest Missouri State University, Springfield*

## **Parasitized Salamanders are Inferior Competitors for Territories and Food Resources**

Daria S. Maksimowich & Alicia Mathis

Maksimowich, D. S. & Mathis, A. 2000: Parasitized salamanders are inferior competitors for territories and food resources. *Ethology* **106**, 319–329.

### **Abstract**

Parasites have been shown to impair the behaviour of their hosts, compromising the host's ability to exploit and compete for resources. We conducted two experiments to determine whether infestation with an ectoparasitic mite (*Hannemania eltoni*) was associated with changes in aggressive and foraging behaviour in the Ozark zigzag salamander, *Plethodon angusticlavius*. In a first experiment, male salamanders with high parasite loads were less aggressive overall than males with low parasite loads during territorial disputes. In addition, males with high parasite loads were more aggressive toward opponents with high parasite loads (symmetric contests) than toward opponents with low parasite loads (asymmetric contests). In contrast, males with low parasite loads did not adjust their level of aggression according to the parasite load of the opponent. In a second experiment, foraging behaviour of females was tested in response to 'familiar' (*Drosophila*) prey and 'novel' (termite) prey. Latency to first capture was significantly longer for parasitized than non-parasitized females when tested with 'familiar' prey, but not for 'novel' prey. Our results suggest that parasite-mediated effects may have profound influences on individual fitness in nature.

Corresponding author: Alicia Mathis, Department of Biology, Southwest Missouri State University, Springfield, MO 65804-0095, USA. E-mail: sam477f@mail.smsu.edu

### **Introduction**

Parasites can have a wide range of effects on the behaviour of their hosts (e.g. Moore 1995; Levri & Lively 1996; Robb & Reid 1996). Some parasites directly manipulate host behaviour, which may facilitate parasite transmission. Parasites can also indirectly affect host decisions, for example by imposing energetic constraints on the host (Milinski 1985; Polak 1996; Tripet & Richner 1997). Physiological stress on the host can influence energetically costly behaviour associated

with male–male competition, such as running stamina (Schall et al. 1982) and activity patterns (Schall & Sarni 1987). Nutritive demands imposed on the host by the parasite also may influence host foraging behaviour (Crowden & Broom 1980). For instance, infested individuals may be unable to compete for superior feeding grounds, or may become less discriminating in their food source.

Salamanders of the genus *Plethodon* (family Plethodontidae, the lungless salamanders) are completely terrestrial, occupying moist patches located under rocks and logs on the forest floor (Jaeger 1980). Competition may be intense during dry periods, and can result in spacing (i.e. territoriality) among individuals (Mathis 1990). Resources may be patchily distributed, and individuals may compete for higher quality areas (Jaeger et al. 1982; Gabor 1995; Townsend & Jaeger 1998). Territoriality of terrestrial salamanders is widespread, although not ubiquitous (review by Mathis et al. 1995).

Populations of several species of plethodontid salamanders have been reported to be infested with an ectoparasitic mite (Rankin 1937; Anthony et al. 1994). The parasitic larva of the trombiculid chigger mite, for example, completely embeds itself into the host tissue (Hyland 1961). Because chigger mites are extremely cryptic, little is known about their biology, let alone their influence on host behaviour. The presence of the larva causes a local host reaction, in which connective tissue encapsulates the larva. The parasite increases in size while feeding on lymph and blood. It is not known how long mites will remain on the host, or what stimulates them to emerge from it. Attachment near the snout of plethodontid salamanders can damage the tissue of the nasolabial grooves, and it has been suggested that these mites may interfere with a salamander's ability to detect prey, or pheromones of territorial rivals or potential mates (Anthony et al. 1994).

The present study is the first to investigate the role of parasites in the behaviour of caudates. Our objective was to determine whether parasitism is associated with altered behavioural patterns in individuals from a population of the Ozark zigzag salamander, *Plethodon angusticlavius*, naturally infested with the mite *Hannemania eltoni*.

Our first experiment was designed to determine whether agonistic behaviour is associated with level of parasitism. Game theory (Maynard Smith 1982) provides a useful framework for examining the influence of differences ('asymmetries') between contestants on the outcome of aggressive contests. According to game theoretic models, one factor that should influence an individual's level of aggression is its fighting ability or 'resource holding potential' (RHP) (Maynard Smith & Parker 1976). RHP may be influenced by characteristics intrinsic to the individual (body condition, absolute size, experience) and factors that are context dependent (condition relative to opponent, size relative to opponent, residency status). Escalations of contests are predicted to occur when perceived asymmetries in RHP are small; otherwise, the asymmetry should be used to settle the contest quickly (Maynard Smith & Parker 1976; Parker & Rubenstein 1981; Hammerstein & Parker 1982). In this experiment, we considered parasite load ('low' levels or 'high' levels of infestation) to be an indicator of body condition, and therefore RHP. Symmetric contests were between individuals with approximately the same parasite

load (i.e. low vs. low, or high vs. high), and asymmetric contests were between individuals with different parasite loads (low vs. high). We tested the following hypotheses: (1) males exhibit higher levels of aggression in symmetric contests than in asymmetric contests, and (2) males with low parasite loads exhibit greater levels of aggression than males with high parasite loads, regardless of the parasite load of their opponents.

The goal of our second set of experiments was to determine whether parasitism was associated with altered foraging behaviour in females when foraging on 'familiar' (*Drosophila*) and 'novel' (termite) prey. We tested the hypotheses that (1) latency to first capture is greater for parasitized females than for non-parasitized females, and (2) parasitized females capture fewer prey in total than non-parasitized females.

## Methods

### Collection and Maintenance of Salamanders

Adults of *P. angusticlavius* were collected by hand in Newton County, north-western Arkansas in Mar. and Apr. 1997. Salamanders (snout-vent length  $\bar{x} \pm SD$ :  $38.6 \pm 4.1$  mm) were housed individually in clear, plastic Petri dishes (8.5 cm diameter, 1.3 cm depth) lined with moist filter paper. Petri dishes are commonly used as holding chambers for small plethodontid salamanders, and salamanders perform apparently normal behavioural patterns in these chambers (i.e. feeding, pheromonal marking, aggressive behaviour, e.g. Mathis 1990; Mathis & Britzke 1999). Salamanders were maintained on a 12 L: 12 D light regime at  $14 \pm 2^\circ\text{C}$  and fed *Drosophila hydei* approximately once weekly ad libitum until tested.

Mites were visible under the skin of the limbs, snout, trunk and tail of infested individuals, and were approximately 1 mm in length. There were few uninfected males in our sample; the proportion of infected males (83%) was higher than the proportion of infected females (60%), although the difference was not statistically significant ( $\chi^2 = 2.571$ ,  $df = 1$ ,  $p = 0.054$ ; one-tailed). Males with less than the median number of parasites were categorized as having low parasite loads (0–2 mites,  $\bar{x} \pm SD = 0.7 \pm 0.82$ ;  $n = 11$ ), and males with the median number of parasites or higher were categorized as having high parasite loads ( $\geq 3$  mites, range = 3–12;  $\bar{x} \pm SD = 5.2 \pm 1.86$ ;  $n = 13$ ). Females were categorized as either parasitized (presence of one or more mites, range = 1–12,  $\bar{x} \pm SD = 3.2 \pm 2.81$ ;  $n = 37$ ) or non-parasitized (no visible mites;  $n = 42$ ).

### Test 1: Male–Male Competition

Trials were conducted in Aug. and Sep. 1997. Each male was tested twice, once in a symmetric contest and once in an asymmetric contest, with the order of testing determined randomly. Symmetric contests were between males within the same parasite-load category (either both contestants with a low parasite load or both with a high parasite load). Asymmetric contests were between males with

different levels of parasitism (low vs. high). Because body size influences aggression in this species (Mathis & Britzke 1999), males were paired for snout-vent length (difference of  $\leq 2$  mm; mean difference in SVL =  $0.54 \pm 0.114$  mm) to eliminate asymmetries in body size. Due to the small pool of males available for testing, four individuals were used as partners for additional males, and so were tested twice in one of the conditions. To maintain statistical independence, data for these four individuals were averaged over the two tests. Each male was fed five *Drosophila* 1 day prior to the setting up of the experimental chambers. The following day, males were placed in separate pre-test holding chambers (23 × 23 × 2 cm). Each half of the chamber was lined with a separate moist paper towel. Males were allowed to establish a territory by marking the chamber with pheromones (e.g. Mathis 1990) for 6 days and were tested on the 7th day.

The experimental chambers were identical to the pre-test holding chambers. Immediately prior to each trial, individuals in each pair of test salamanders were placed under separate opaque habituation dishes (9 cm diameter, 1.5 cm depth), while half of the paper towel lining from their respective pre-test chambers was transferred to either side of an experimental chamber. Any faecal pellets that were present on the substrate were removed. Thus, during testing, individuals were exposed to both their own substrate and that of their opponents, thereby eliminating possible effects of residency status (Mathis et al. 1999). The position of the paper towels (left or right side) was determined randomly for each trial.

Once the paper towels were in place, the salamanders were placed at opposite ends of the experimental chamber under separate opaque habituation dishes. Each male was placed on the paper towel with its own substrate markings. After 5 min, the habituation dishes were removed simultaneously, and the behaviour of both test males was recorded for 20 min.

We quantified two patterns of threat behaviour previously described for *P. cinereus* by Jaeger (1984) and observed for many other species of plethodontids, including *P. angusticlavius* (Mathis & Britzke 1999). 'All trunk raised' (ATR) is considered an aggressive posture, in which the salamander raises its entire trunk, head and sometimes tail off the substrate. 'Biting' is an overt aggressive behaviour that occurs when one salamander grasps another with its mouth. In each trial, we recorded the total number of bites and the total time spent in ATR for each male. Use of duration of aggression as a response variable is appropriate for this study because the 'winner' of the contest is determined as the individual that is willing to persist the longest in the asymmetric war of attrition model (Maynard Smith & Parker 1976; Hammerstein & Parker 1982).

Because each salamander was tested twice (once per treatment), data were analysed using the Wilcoxon matched-pairs signed-ranks test in the following comparisons: (1) 'low' males: symmetrical vs. asymmetrical contests; and (2) 'high males': symmetrical vs. asymmetrical contests. Because disputes are predicted to escalate when the contest is symmetrical (Maynard Smith & Parker 1976), we used one-tailed tests ( $\alpha = 0.05$ ). We also performed a post-hoc test to determine whether males with high parasite loads exhibited overall lower levels of ATR than males with low parasite loads. For this test, we averaged time spent in ATR in asym-

metrical and symmetrical contests for each male, and performed a Mann–Whitney U-test.

### Test 2: Foraging Behaviour of Females

Females were fed *Drosophila hydei* approximately once weekly *ad libitum* until tested. Trials were conducted in Sep. and Oct. 1997. Thus, all females had a minimum of 6 mo of experience feeding solely on *Drosophila* in the laboratory prior to testing. Each female was tested twice in separate experiments, once with a ‘familiar’ prey type (*Drosophila*) and once with a ‘novel’ prey type (termites: *Reticulitermes*). Salamanders undoubtedly had experience with termites prior to capture, but because this experience occurred at least 6 mo prior to the experiment, we refer to termites as a ‘novel’ prey. All females were tested in the first experiment with fruit-flies, and approximately 3 wks later were tested in the second experiment with termites ( $\bar{x} \pm \text{SD}$ : 21.08  $\pm$  6.37 days).

To standardize hunger levels, each female was fed *Drosophila* to satiation in her Petri dish prior to testing. After 24 h, all uneaten flies were removed. Plethodontids use chemical cues to detect prey (David & Jaeger 1981); thus to remove possible odours of previous prey items, salamanders were placed in clean Petri dishes lined with fresh filter paper. Because *P. cinereus* feed inefficiently in unmarked/unfamiliar territories (Jaeger 1981), females were allowed to mark a new territory for 3 days. On the 4th day, five flies were introduced into the Petri dish via a hole in the centre of its lid. When a prey item was consumed, it was immediately replaced to maintain a constant density of 5 prey items in the testing chamber at all times. Females that made no attempt to strike a prey item (58% of *Drosophila* trials and 5% of termite trials) were eliminated from the comparisons of latencies and number of captures.

Each test ran for 10 min, with the following behavioural patterns recorded: (1) latency to first capture, quantified as time elapsed before the female successfully consumed a prey item; (2) total number of prey items consumed, and (3) total number of nose-taps (chemosensory behaviour). Parasitized and non-parasitized females were compared using a Mann–Whitney U-test (two-tailed;  $\alpha = 0.05$ ).

## Results

### Test 1: Male–Male Competition

For males with low parasite load, time spent in ATR during symmetrical contests was not significantly different from that during asymmetrical contests (Fig. 1;  $T = 26$ ,  $p > 0.40$ ). However, males with high parasite loads spent significantly more time in ATR in symmetrical contests than in asymmetrical contests (Fig. 1;  $T = 14$ ,  $p = 0.05$ ). In the post-hoc test, males with low parasite loads ( $n = 11$ ) spent significantly more time in ATR ( $\bar{x} \pm \text{SE} = 686.7 \pm 73.4$  s) than males with high parasite loads ( $\bar{x} \pm \text{SE} = 556.9 \pm 34.9$  s;  $U = 172$ ,  $p < 0.03$ ).

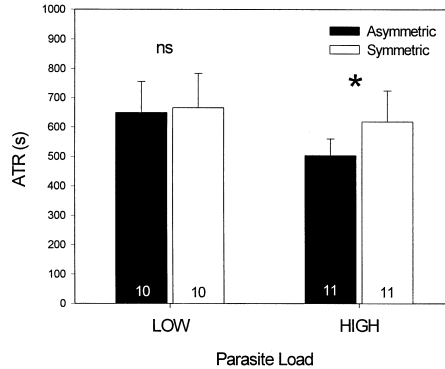


Fig. 1: Time spent in ATR (aggressive posture) during asymmetrical and symmetrical contests for males with low parasite loads ('LOW') and high parasite loads ('HIGH'). In symmetrical contests, the two males had similar parasite loads. In asymmetrical contests, one male had a high parasite load and the other had a low parasite load. Bars indicate  $\bar{x} + SE$ ; numbers within bars indicate sample size. The asterisk denotes a significant difference

Overt aggression in the form of bites was observed only occasionally. A total of four bites were recorded over all trials. Three of the four bites occurred in symmetrical contests, but the number of bites was insufficient for statistical analysis.

### Test 2: Foraging Behaviour of Females

In tests with *Drosophila*, latency to first capture was significantly different between non-parasitized and parasitized females (Fig. 2a;  $U = 280.5$ ,  $p = 0.015$ ), with non-parasitized females consuming their first fruitfly approximately 3 min faster than parasitized females. Neither the total number of flies consumed (Fig. 2b;  $U = 494$ ,  $p > 0.40$ ) nor the total number of nose taps (Fig. 2c;  $U = 509$ ,  $p > 0.20$ ) was significantly different between parasitized and non-parasitized females, although parasitized females tended to consume fewer flies and perform fewer nose-taps than non-parasitized females.

In tests with termites, there were no significant differences between non-parasitized and parasitized females for any of the behavioural patterns recorded (Fig. 2a:  $U = 1148.5$ ,  $p > 0.20$ ; Fig. 2b:  $U = 1412.5$ ,  $p > 0.20$ ; Fig. 2c:  $U = 1345$ ,  $p > 0.70$ ), although the trends were consistent with those seen in the tests with fruit-flies. The proportion of unresponsive females (females that made no attempt to consume prey) was greater when females were tested with flies (58.23%) than when they were tested with termites (5.13%) ( $\chi^2 = 36.99$ ,  $p < 0.001$ ).

## Discussion

### Male–Male Competition

For males with low parasite loads ('good condition'), levels of aggression were relatively high regardless of the condition (parasite status) of their opponents. In

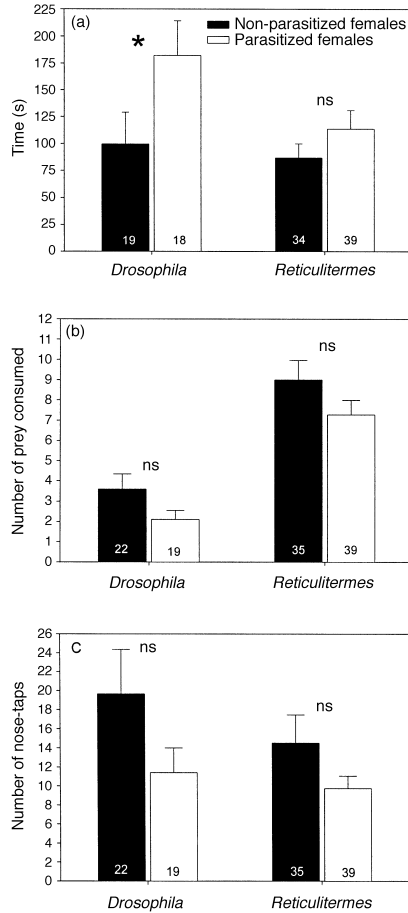


Fig. 2: Response of parasitized and non-parasitized females to fruit-flies (*Drosophila*) and termites (*Reticulitermes*). Responses are (a) time to first capture, (b) number of flies consumed, and (c) number of nose-taps (chemosensory behaviour). Bars indicate  $\bar{x} + SE$ ; numbers within bars indicate sample size. The asterisk denotes a significant difference

contrast, the level of aggression for males in relatively poor condition (high parasite load) was generally lower, but depended on the condition of their opponents. These data suggest that high levels of parasitic infestation are associated with decreased agonistic behaviour in *P. angusticlavius*, and that asymmetries in parasite load may be used to settle territorial disputes for infested males.

A prediction from game theory is that contests should be settled quickly when perceived asymmetries between two opponents are large (Maynard Smith & Parker 1976). This prediction was supported by results of a previous study (Mathis & Britzke 1999) in which males of *P. angusticlavius* decreased their levels of aggression when opponents differed in body size (an indicator of RHP). The results of the

present study also support this game theory prediction, but only for males with high parasite loads. Males with high parasite loads were more aggressive during symmetric contests, where opponents were other highly parasitized males, than in asymmetric contests where opponents were males with low parasite loads. In contrast, males with low parasite loads responded aggressively regardless of the opponent's parasite load. Therefore, a male's level of aggression may be based on its own condition, the condition of the opponent, or possibly the opponent's level of aggression.

In the present study, males with low parasite loads maintained relatively high levels of aggression in both symmetric and asymmetric contests, while males with high parasite loads exhibited somewhat lower levels of aggression. Similar results have been reported for the lizard *Sceloporus occidentalis*; males infected with malarial parasites displayed less often than non-infected males in agonistic encounters, presumably by assessing their relative ability to compete in male–male interactions (Schall & Dearing 1987). None of the infested males in our study were noticeably unhealthy. However, aggressive displays are likely to be energetically costly, and males in poor condition may thus be unable to expend the energy necessary to maintain the threat posture for prolonged periods. In one contest, a male infested with at least 12 mites (concentrated on front limbs) appeared unable to maintain the ATR posture. In a different study with *P. angusticlavius*, larger males (measured in snout-vent length: SVL) were more aggressive than smaller males in territorial disputes (Mathis & Britzke 1999). This was observed regardless of the difference in relative SVL between opponents, further supporting the hypothesis that resource holding potential affects the level of aggressive displays.

#### Foraging Behaviour of Females

Despite long-term experience with *Drosophila*, parasitized females of *P. angusticlavius* took longer to react to the presence of familiar prey than non-parasitized females. The increased response time may reflect an impaired ability to detect or respond to prey items by infested females, and may indicate that parasitized females are inferior foragers. Attachment of parasites on or near the snout can occlude the nasolabial grooves (Anthony et al. 1994) and impair chemosensory function. However, the number of nose-taps did not differ significantly between the two groups of females, suggesting that possible effects of infestation on this chemosensory behaviour are weak if they occur at all.

The difference in foraging behaviour between parasitized and non-parasitized females was less pronounced when females were tested with the novel prey type (termites). In general, females consumed termites more readily than fruit-flies. In a different study (Jaeger et al. 1995), males of *P. cinereus* also struck more frequently at termites than ants, regardless of previous training. There are several possible explanations for the observed preference for termites in this study. Since termites are high in lipids and low in chitin content (Walls et al. 1989; Jaeger 1990; Gabor & Jaeger 1995), this food source may be considered a high-quality prey type by salamanders. Additionally, females may benefit by varying their food types to

obtain a more nutritionally balanced diet. A preference for foods that have not been recently consumed also has been observed in other generalist foragers, such as the land hermit crab *Coenobita compressus* (Thacker 1998). Finally, termites are less mobile than fruit-flies, and may simply be easier to capture.

Although parasitized females responded more slowly to prey items, the number of prey items captured and consumed was not significantly different between the infested and non-infested females. Similar results have been reported for dace, *Leuciscus leuciscus*, in which the total number of prey consumed also was not correlated with parasite load, although infested individuals were less efficient foragers (Crowden & Broom 1980). These individuals compensated for decreased foraging efficiency by increasing the total time spent feeding. Other studies likewise indicate that parasitism can alter host foraging behaviour qualitatively, for example by changing choice of food source (Karban & English-Loeb 1997).

While this altered response time did not affect the total number of prey items captured in our laboratory study, a delay in attack may have more serious consequences in nature. Reduced reaction time could be costly in a complex environment and where prey are mobile and more likely to escape predators. The lack of an effect on number of prey captured in our experiment may have been an artefact of the small size of our testing chambers and the lack of hiding places for prey. Furthermore, in nature, encounter rates with prey items are low during dry periods; thus failure to quickly detect and respond to prey may increase the risk of starvation.

### Conclusions

Among plethodontid salamanders, asymmetries in body size (Mathis 1990, 1991), territorial ownership (Jaeger 1984; Mathis et al. 1998), resource quality (Gabor & Jaeger 1995) and resource quantity (Nunes 1988) affect levels of agonistic behaviour. Our results suggest that infestation by parasitic mites also may mediate competitive ability. Furthermore, decreased foraging efficiency also was associated with parasitism. Negative effects on aggression and foraging clearly are correlated with parasite load, but the design of our study does not allow determination of causation. Parasite load may be only an indirect indicator of other aspects of condition that may be the direct cause of the negative effects. For example, individuals in poor condition may be more susceptible to parasitic infections. Subtle alterations in behaviour either directly or indirectly associated with parasitic infestation could compromise an individual's ability to compete for resources, resulting in an overall reduction in fitness.

### Acknowledgements

We thank William Wrenn at the University of North Dakota for identifying *H. eltoni*. Financial support was provided by the Department of Biology at Southwest Missouri State University.

## Literature Cited

- Anthony, C. D., Mendelson, J. R. & Simons, R. R. 1994: Differential parasitism by sex on plethodontid salamanders and histological evidence for structural damage to the nasolabial groove. *Am. Midl. Nat.* **132**, 302—307.
- Crowden, A. E. & Broom, D. M. 1980: Effects of the eye fluke, *Diplostomum spathaceum*, on the behaviour of dace (*Leuciscus leuciscus*). *Anim. Behav.* **28**, 287—294.
- David, R. S. & Jaeger, R. G. 1981: Prey location through chemical cues by a terrestrial salamander. *Copeia* **1981**, 435—440.
- Gabor, C. R. 1995: Correlational test of Mathis' hypothesis that bigger salamanders have better territories. *Copeia* **1995**, 729—835.
- Gabor, C. R. & Jaeger, R. G. 1995: Resource quality affects the agonistic behaviour of territorial salamanders. *Anim. Behav.* **49**, 71—79.
- Hammerstein, P. & Parker, G. A. 1982: The asymmetric war of attrition. *J. Theor. Biol.* **96**, 647—682.
- Hyland, K. E. 1961: Parasitic phase of chigger mite, *Hannemania hegeneri*, on experimentally infested amphibians. *Exp. Parasitol.* **11**, 212—225.
- Jaeger, R. G. 1980: Fluctuations in prey availability and food limitations for a terrestrial salamander. *Oecologia* **44**, 335—341.
- Jaeger, R. G. 1981: Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.* **117**, 962—974.
- Jaeger, R. G. 1984: Agonistic behavior of the red-backed salamander. *Copeia* **1984**, 309—314.
- Jaeger, R. G. 1990: Territorial salamanders evaluate size and chitinous content of arthropod prey. In: *Behavioural Mechanisms of Food Selection*. NATO ASI Series, Subseries G: Ecological Sciences. (Hughes, R. N., ed.). Springer-Verlag, Heidelberg, pp. 111—126.
- Jaeger, R. G., Kalvarsky, D. & Shimizu, N. 1982: Territorial behavior of the red-backed salamander: Expulsion of intruders. *Anim. Behav.* **30**, 490—496.
- Jaeger, R. G., Schwarz, J. & Wise, S. E. 1995: Territorial male salamanders have foraging tactics attractive to gravid females. *Anim. Behav.* **49**, 633—639.
- Karban, R. & English-Loeb, G. 1997: Tachinid parasitoids affect host plant choice by caterpillars to increase caterpillar survival. *Ecology* **78**, 603—611.
- Levri, E. P. & Lively, C. M. 1996: The effects of size, reproductive condition, and parasitism on foraging behaviour in a freshwater snail, *Potamopyrgus antipodarum*. *Anim. Behav.* **51**, 891—901.
- Mathis, A. 1990: Territorial salamanders assess sexual and competitive information using chemical signals. *Anim. Behav.* **40**, 953—962.
- Mathis, A. 1991: Large male advantage for access to females: Evidence for male-male competition and female discrimination in a territorial salamander. *Behav. Ecol. Sociobiol.* **29**, 133—138.
- Mathis, A. & Britzke, E. 1999: The roles of body size and experience in agonistic displays of the Ozark zigzag salamander, *Plethodon angusticlavius*. *Herpetologica*, **55**, 344—352.
- Mathis, A., Deckard, K. & Duer, C. 1998: Laboratory evidence for territorial behavior by the southern red-backed salamander, *Plethodon serratus*: Influence of residency status and pheromonal advertisement. *Southwest. Nat.* **43**, 1—5.
- Mathis, A., Jaeger, R. G., Keen, W. H., Ducey, P. K., Walls, S. C. & Buchanan, B. W. 1995: Aggression and territoriality by salamanders and a comparison with the territorial behaviour of frogs. In: *Amphibian Biology*, Vol. 2. Social Behaviour (Heatwole, H. & Sullivan, B. K., eds). Surrey Beatty & Sons, Chipping Norton, NSW, Australia, pp. 633—676.
- Mathis, A., Schmidt, D. W. & Medley, K. A., in press: The influence of residency status on aggressive behavior of male and female Ozark zigzag salamanders, *Plethodon angusticlavius*. *Am. Midl. Nat.*, in press.
- Maynard Smith, J. 1982: *Evolution and the Theory of Games*. Univ. of Chicago Press, Chicago.
- Maynard Smith, J. & Parker, G. A. 1976: The logic of asymmetric contests. *Anim. Behav.* **24**, 159—175.
- Milinski, M. 1985: Risk of predation of parasitized sticklebacks, *Gasterosteus aculeatus* L. under competition for food. *Behaviour* **93**, 203—216.
- Moore, J. 1995: The behavior of parasitized animals. *Bioscience* **45**, 89—96.
- Nunes, V. 1988: Feeding asymmetries affect territorial disputes between males of *Plethodon cinereus*. *Herpetologica* **44**, 386—391.

- Parker, G. A. & Rubenstein, D. I. 1981: Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav.* **29**, 135—162.
- Polak, M. 1996: Ectoparasitic effects on host survival and reproduction: The *Drosophila-Macrocheles* association. *Ecology* **77**, 1379—1389.
- Rankin, J. S. 1937: An ecological study of parasites of some North Carolina salamanders. *Ecol. Monogr.* **7**, 169—269.
- Robb, T. & Reid, M. L. 1996: Parasite-induced changes in the behaviour of cestode-infested beetles: adaptation or simple pathology? *Can. J. Zool.* **74**, 1268—1274.
- Schall, J. J. & Dearing, M. D. 1987: Malarial parasitism and male competition for mates in the western fence lizard, *Sceloporus occidentalis*. *Oecologia* **73**, 389—392.
- Schall, J. J., Bennett, A. F. & Putnam, R. W. 1982: Lizards infested with malaria: Physiological and behavioral consequences. *Science* **217**, 1057—1059.
- Schall, J. J. & Sarni, G. A. 1987: Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia* **1987**, 84—93.
- Thacker, R. W. 1998: Avoidance of recently eaten foods by land hermit crabs, *Coenobita compressus*. *Anim. Behav.* **55**, 485—496.
- Townsend, V. R., Jr & Jaeger, R. G. 1998: Territorial conflicts over prey: Domination by large male salamanders. *Copeia* **1998**, 725—729.
- Tripet, F. & Richner, H. 1997: Host responses to ectoparasites: Food compensation by parent blue tits. *Oikos* **78**, 557—561.
- Walls, S. C., Mathis, A., Jaeger, R. G. & Gergits, W. F. 1989: Male salamanders with high-quality diets have faeces attractive to females. *Anim. Behav.* **38**, 546—548.

*Received: February 9, 1999*

*Initial acceptance: May 17, 1999*

*Final acceptance: September 16, 1999 (J.-G. Godin)*