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Bob Jaeger

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AN EXPERIMENTAL STUDY OF INTERFERENCE COMPETITION AMONG TERRESTRIAL SALAMANDERS¹

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Abstract. Previous studies showed that the terrestrial salamander *Plethodon cinereus* competitively excludes a sibling species, *P. shenandoah*, from optimal habitats in Virginia. However, the mode of competition (interference or exploitation) was not well understood. In the present study, pairs of congeners and pairs of conspecifics were maintained in experimental enclosures in the laboratory under food-limited conditions. Mass changes and behavioral interactions during feeding periods were monitored over 2 mo. Behavioral data were compared both between species and between "winners" and "losers." (The winning salamander gained more or lost less mass than the cohabiting loser.)

Winners exhibited more aggressive activity than losers among interspecific pairs, suggesting that aggressive superiority and foraging superiority are associated. However, *P. cinereus* did not win more often than *P. shenandoah*, although it was on the average more aggressive. Males of both species were more aggressive than conspecific females. The data suggest that interference competition occurs both within and between the two species. We suggest that interference may be involved in competition for space, rather than for food items per se.

Key words: aggression; agonistic behavior; interference competition; *Plethodon cinereus*; *Plethodon shenandoah*; salamanders.

INTRODUCTION

Competition between individuals for the use of one or more limited resources is generally believed to be mediated through exploitation (differential utilization of a resource once organisms have gained access to it), interference (one organism limiting another's access to the resource), or a combination of the two (Miller 1967, Colwell and Fuentes 1975). However, evidence for competition in natural settings is difficult to assess, since inferences are often drawn from the relative spatial distributions of congeners or from observations of competitive release. Wiens (1977) criticized much of the empirical literature in this area of research because of the dearth of quantitative data on the behavioral and morphological mechanisms facilitating competition.

One means of investigating the processes of competition is to conduct manipulative tests under controlled laboratory conditions. In this way one can expose the relationships between the variables of interest and more clearly elucidate the underlying mechanisms of the system. Such designs are costly in terms of artificiality, but they can yield crucial information on the potential behavioral modes of interaction between organisms in a complex community. When laboratory experiments are combined with field evidence, ecologists have a powerful means of establishing a more complete mechanistic view of community dynamics.

This approach was followed in the present study in which we attempted to measure behavioral aspects of interference competition within and between two species of terrestrial salamanders.

Plethodon cinereus and the morphologically similar *P. shenandoah* maintain parapatric distributions in forests in Virginia (Jaeger 1970). The parapatry is apparently maintained by competition for a limited food supply, with *P. cinereus* excluding its congener from habitats preferred by both species (Jaeger 1971, 1972). Both intra- and interspecific competition were thought by Jaeger (1972) to be a consequence of differential exploitation of the food resource. More recent studies, however, suggest that some sort of behavioral interference occurs (Jaeger 1974a, Fraser 1976, Thurow 1976, Gergits 1977, Kaplan 1977, Jaeger and Gergits 1979).

In the present experiment, we maintained intra- and interspecific pairs of salamanders in experimental chambers. Food was limited such that both individuals within a pair could not maintain their metabolic requirements (see below), although one presumably could do so at the expense of the other if it were a superior competitor. Mass change served as the monitor of competitive success for each individual. Concomitant behavioral interactions were recorded at intervals during the test. Members of each pair were designated as "winner" or "loser." A winner was defined as the individual within each pair that gained more or lost less mass over the 2-mo test period; the loser was then the cohabiting salamander that lost more mass. We then looked for associations between winners and any of the recorded behavior patterns. An individual could be a winner through a superior

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exploitation efficiency or through an interference mechanism preventing complete access by the other individual to the food resource. An association between winning and one or more of the recorded behavior patterns would indicate a possible mechanism for the interference process, although the causal relationship cannot be unequivocally assumed. Lack of any such associations would provide some evidence for exploitation efficiency differentials as the mediator of competition.

We made two predictions: (1) Winners will exhibit more aggressive behavior than losers. (2) *P. cinereus* will be a winner more often than *P. shenandoah* in the interspecific test. The underlying assumption is that aggressive superiority by one individual or species will directly interfere with the foraging success, and thus competitive ability, of the other individual or species.

We consider this research a preliminary study of the relationships between agonistic behavior (King 1973) and competition for food. The chemical and visual signals used by salamanders during encounters are now being investigated. Future refinement and elaboration of our technique may lead to a practical means of directly assessing the mechanisms of competitive interactions.

METHODS

Experimental procedures

Salamanders were collected during October 1976 on Hawksbill Mountain, Shenandoah National Park, Virginia, USA. Individuals were placed in separate 15 cm diameter petri dishes lined with moist filter paper until initiation of the experiment in February 1977. The salamanders were fed *Drosophila melanogaster*.

Individuals were partitioned into three groups of 13 pairs of salamanders each. Paired individuals were approximately equal in mass, as determined immediately prior to the experiment on an analytical balance (± 0.01 g precision). The groups (with mean masses ± 1 SD) were: (1) interspecific experimental group, *P. cinereus* ($x = 1.16 \pm 0.28$ g) and *P. shenandoah* ($x = 1.16 \pm 0.31$ g); (2) *P. cinereus* intraspecific control group ($\bar{x} = 1.16 \pm 0.14$ g); (3) *P. shenandoah* intraspecific control group ($x = 1.20 \pm 0.33$ g). Therefore, any differences in foraging or agonistic behavior could not be attributed to differences in initial sizes of salamanders. Both control groups were reduced to 12 pairs due to escapes during the experiment. Unfortunately, determination of sexes of individuals was not possible until after the experiments, because we could not reliably sex the salamanders from external morphology.

Paired salamanders remained together in experimental chambers for 58 d during the course of the experiment. Experimental chambers consisted of 24 x 16 cm glass jars. These remained sealed except for a small hole in the cover used to introduce food. A cot-

ton plug prevented the escape of fruitflies (prey) and salamanders, and permitted entry of fresh air. A moistened sand-loam soil served as the substrate. The chambers were kept at 18°C in a controlled temperature room at 80% relative humidity and a photoperiod of L10:D14.

We performed the following test to determine mass changes of paired salamanders under food-limited conditions. Fruit flies (*Drosophila melanogaster*) were the limited food resource. Using data from R. Jaeger (*personal observation*) we calculated the average metabolic requirement per gram salamander for *P. cinereus* to be 5.3 flies/d at 18°C. We assumed that the requirement of *P. shenandoah* was similar. Knowing the summed masses of each pair of salamanders, we determined the approximate number of flies required every 3 d for each pair to maintain its summed body mass. The number of flies actually given to each pair of salamanders was arbitrarily reduced to 75% of the original determination. This number was assumed to be a limited food supply for each pair such that both salamanders could not maintain their initial body masses. All salamanders were fed every 3 d, with each pair receiving the predetermined number of flies each feeding. Flies were placed in glass tubes and counted before being injected into the experimental chambers with a jet of compressed air.

Salamander mass was determined, with both urinary bladders and stomachs empty, immediately preceding and following the 58-d experiment. Utilizing the calculated mass changes, we were able to determine the winner and loser for each pair. Paired salamanders that differed <5% in mass change were omitted from the winner-loser data set.

Behavioral interactions

Behavioral interactions were observed for one-third of the total pairs on every feeding day, with each control and interspecific group represented equally. Observations of a pair were made immediately after feeding. Each pair was thus observed every 9 d for a total of six observation periods during the 2 mo. Each observation period lasted 10 min. An Esterline-Angus event recorder was used to record frequencies of behavior patterns. Individuals within a pair were readily identified by unique patterns of dorsal pigmentation.

We recorded four types of behavior patterns: (1) Approach: one salamander moves toward another such that a continued line of movement in that direction would intersect the body of the second salamander. (2) Body contact: any part of the body of one salamander touches any part of the body of the other salamander (but see head attack below). This was recorded only for the individual that initiated the contact. (3) Head attack: this category was divided into three parts: (a) bite: one salamander opens its jaws and grasps the other salamander; (b) snap: one salamander faces the other, opens and closes its jaws with-

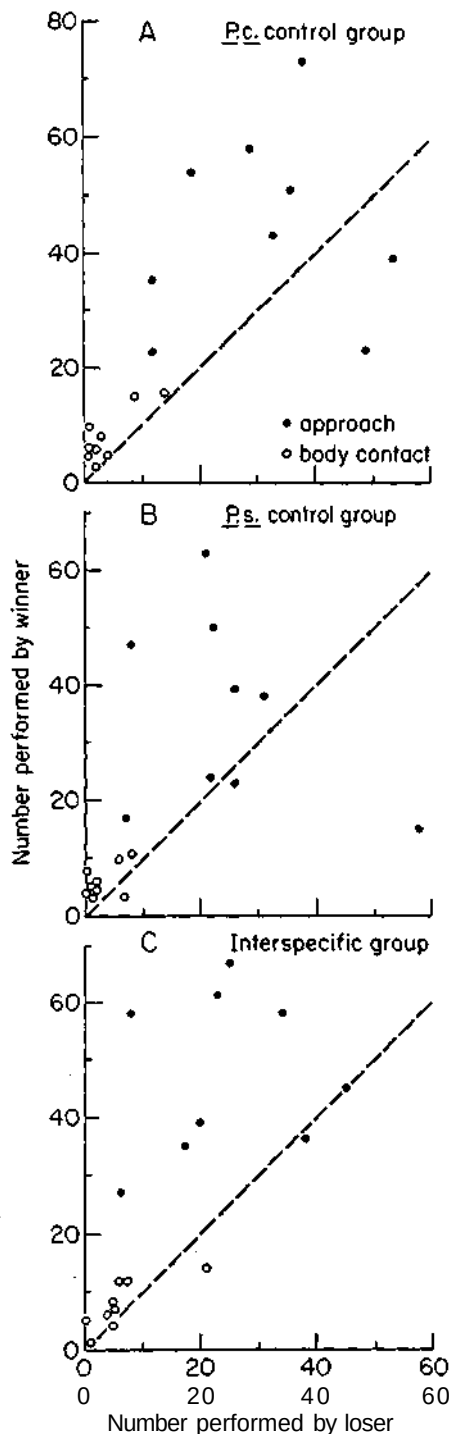


FIG. 1. Number of approaches (solid circles) and body contacts (open circles) performed by members of each pair of salamanders during six 10-min observation periods just after feeding. Total number of approaches and body contacts, respectively, of each winner is plotted against the corresponding total for the cohabiting loser of every pair in (A) the *P. cinereus* control group, (B) the *P. shenandoah* control group, and (C) the interspecific group. ($N = 9$ for all groups.) The broken lines indicate equal numbers of responses; winners acted more frequently for circles above the lines, losers more frequently for circles below the lines.

TABLE 1. Comparison of mean percent mass changes of paired salamanders within the interspecific group and between interspecific (int) and control groups. *Pc* = *P. cinereus*; *Ps* = *P. shenandoah*; N = sample size.

Test (A x B)	N	Changes in mass (% change)	
		A	B
<i>Pc</i> (int) x <i>Ps</i> (int)	13, 13	-.70	-2.99*
<i>Pc</i> (int) x <i>Pc</i> (control)	13, 24	-.70	.40t
<i>Ps</i> (int) x <i>Ps</i> (control)	13, 24	-2.99	-6.59t

* One-sided probability, not significant, Wilcoxon matched-pairs signed-ranks test.

t Two-sided probability, not significant, Mann-Whitney U test.

out grasping the other salamander; (c) tongue flick: one salamander opens its jaws and contacts the other salamander with its tongue. Behavior patterns 3a-c were pooled because it was frequently impossible to differentiate among them under the experimental conditions. (4) Withdrawal: a salamander breaks body contact and moves away from the other salamander. Other behavior patterns, such as pursuit and grappling, were observed too infrequently for statistical analysis.

RESULTS

Behavioral interactions: winners vs. losers

We partitioned the data on interactive behavior patterns by winner vs. loser within each pair of salamanders as a test of prediction 1 above. There was no significant difference (at $\alpha = .05$) in the number of approaches between winners and losers in either control group (Figs. 1A and B). However, winners approached significantly more often than did losers in the interspecific group (Fig. 1C, $P < .01$ Wilcoxon matched-pairs signed-ranks test).

P. cinereus winners initiated significantly more body contacts than did losing conspecifics (Fig. 1A, $P < .005$) in the control group. No such difference occurred between *P. shenandoah* conspecifics or in the interspecific group (Figs. 1B and C).

No significant difference occurred between winners and losers in any group for two other behavior patterns: head attack and withdrawal.

Percent mass changes: *P. cinereus* vs. *P. shenandoah*

We then tested prediction 2 above, that *P. cinereus* will more often be a winner than will *P. shenandoah* in the interspecific group. The data do not support the prediction. Individuals within interspecific pairs did not differ significantly in percent mass change (Table 1). Also, neither species in the interspecific pairings differed significantly from its corresponding control group (Table 1).

TABLE 2. Comparison of mean number of approaches per six 10-min bouts of paired salamanders within the interspecific group, between interspecific (int) and control groups, and between *P. cinereus* (*Pc*) control group and *P. shenandoah* (*Ps*) control group.

Test (A x B)	N	Number of approaches	
		'A	'B
<i>Pc</i> (int) x <i>Ps</i> (int)	13, 13	46.8	33.2*t
<i>Pc</i> (int) x <i>Pc</i> (control)	13, 24	46.8	35.2*t
<i>Ps</i> (int) x <i>Ps</i> (control)	13, 24	33.2	32.8t
<i>Pc</i> (control) x <i>Ps</i> (control)	24, 24	35.2	32.8t

* Significant differences at $\alpha = .05$.

t Wilcoxon matched-pairs signed-ranks test.

t Mann-Whitney U test.

Behavioral interactions: *P. cinereus* vs. *P. shenandoah*

We considered the hypothesis that *P. cinereus* was more aggressive than its congener. Paired individuals of the two species did not differ significantly ($\alpha = .05$) in frequency or duration of any behavior recorded, with one important exception: number of approaches. *P. cinereus* approached significantly more than *P. shenandoah* in the interspecific test (Table 2). *P. cinereus* in the interspecific test also approached significantly more than its conspecific control group. However, *P. shenandoah* in the interspecific test did not differ significantly from its conspecific control. When all *P. cinereus* controls were compared with *P. shenandoah* controls, there also was no significant difference in number of approaches. One-sided probabilities were used in Table 2 due to a priori predictions based on data by Gergits (1977) concerning the direction of changes in behavior between intra- and interspecific tests.

Behavioral interactions: males vs. females

Since Gergits (1977) found that males are more aggressive than conspecific females, we partitioned the control groups for each species by sex. Males and females of neither species differed significantly in number of approaches (Table 3). However, males of both species performed head attacks significantly more often than conspecific females.

DISCUSSION

Interference competition

Parapatric distributions between species are often thought to be a consequence of interference competition (Jaeger 1974b, Colwell and Fuentes 1975). Consequently, Jaeger's (1972) conclusion, that the parapatry maintained by *P. cinereus* and *P. shenandoah* was due to exploitation competition, was not very satisfactory. Subsequent laboratory studies indicated that individuals of the two species could influence each

TABLE 3. Comparison of mean number of approaches and head attacks per six 10-min bouts for male and female *P. cinereus* (*Pc*) and *P. shenandoah* (*Ps*) in control groups.

Test	<i>N</i>	χ^2	
Number of approaches			
$\delta Pc \times \delta Pc$	16, 8	35.0	35.6
$\delta Ps \times \delta Ps$	13, 11	34.2	31.2
Number of head attacks			
$\delta Pc \times \delta Pc$	16, 8	4.1	1.1*
$\delta Ps \times \delta Ps$	13, 11	5.9	2.4*

* Significant differences at $\alpha = .05$, Mann-Whitney U test.

other's positions in space (Jaeger 1974A, Thurow 1976) through aggressive interactions (Thurow 1976, Gergits 1977). The present study provides preliminary evidence that an aggressively superior salamander can depress the foraging success of an aggressively inferior salamander, though the outcomes are not clearly species dependent.

Behavior patterns relevant to agonistic encounters are difficult to categorize for salamanders. Some information, transmitted by chemical cues (Tristram 1977, McGavin 1978), seems to facilitate spacing among individuals (Jaeger and Gergits 1979), but visual displays also appear to be important. An encounter begins by one salamander approaching another, which initiates a sequence of agonistic behavior patterns. Whether approach is stimulated by visual or chemical cues or both is unknown. The approach may be broken off or may result in an active aggressive encounter: body contact, head attack, or grappling. Head attacks were relatively frequent for both species (Table 3). Any of the above behavior patterns may result in withdrawal by the salamander being "attacked" and, occasionally, pursuit by the "attacker." It is sufficient here merely to state that all of these behavior patterns are components of agonistic behavior, and we leave to later papers a detailed analysis of the agonistic behavior displays.

All behavioral interactions were recorded during periods of feeding. These are the periods during which agonistic behavior would have the greatest influence on the foraging success of the interacting salamanders.

Winners vs. losers

Frequency of approach, the initial phase of an agonistic encounter, was associated significantly with winning in the interspecific group. We suggest that the most parsimonious possibility is that a series of approaches by one salamander somehow acted to inhibit the feeding of the approached congener and thus led to differential, long-term changes in body mass. However, other explanations, such as the presence of uncontrolled factors leading to a secondary association of mass loss and behavioral submissiveness, cannot be entirely ruled out. In natural habitats, agonistic be-

havior could lead to a reduction of the long-term fitness of the loser. This might be manifested through a reduction in growth rate, lower lipid storage deposition, higher mortality, and eventually a decrease in fertility.

Since conspecific winners and losers in the control groups did not differ in frequency of approach, we suggest that the approach component of aggression was more effective interspecifically than intraspecifically. Within the *P. cinereus* control group, the second phase in an aggressive sequence (body contact) proved effective in separating winners from losers. Within the *P. shenandoah* control group, no recorded behavior pattern separated winners from losers.

However, inspection of Fig. 1 reveals that in all three graphs most of the points (for both approaches and body contact) lie on the winner side of the equal response line, although significant differences are achieved in only two cases. We conclude, then, that winners were winners because they were more aggressive than losers and, consequently, they acquired more of the limited food supply.

P. cinereus vs. *P. shenandoah*

Contrary to prediction, *P. cinereus* was not a winner more often than *P. shenandoah* in the interspecific group and neither species differed in mass change from its conspecific control group. However, *P. cinereus* was the more aggressive species (by approach) in the interspecific group and showed an increase of approach behavior over conspecific controls. In short, *P. cinereus* "raised its level of passive aggression" when interacting with a congener. Yet this higher level of aggression did not lead to consistent "winning" over *P. shenandoah*. These apparently contradictory results lead us to suggest several hypotheses.

First, species recognition occurs between the two congeners, since *P. cinereus* was more aggressive toward its congener than toward conspecifics. This agrees with data in Jaeger and Gergits (1979), which demonstrated that individuals of both species tend to avoid substrates chemically marked by congeners.

Second, the level of active aggression (head attack) is partly dependent on the sex of the individual. Males of both species were more actively aggressive than conspecific females. Since frequency of head attack and winning were directly associated (in the *P. cinereus* control group), the pattern of sexual pairing may have influenced the competitive outcome in certain cases. We were unable to test statistically for sexual differences between winners and losers due to small sample sizes when data were partitioned by sexual combinations. However Jaeger and Gergits (1979) also showed for *P. cinereus* that both males and females tend to avoid male-marked but not female-marked substrates. Consequently, males may be more actively aggressive than females but there may be more avoidance of contact with males.

Third, while *P. cinereus* is more aggressive, it is not necessarily more successful in capturing food (as indicated by mass changes) than *P. shenandoah*, as proposed by Kaplan (1977). We hypothesize that differential interspecific aggression may primarily result in partitioning of space by salamanders, as suggested by Thurow (1976), rather than in differential capture of prey items per se. Since our experimental chambers were small closed systems, possible emigration of the aggressively inferior salamanders could not occur.

We emphasize that these laboratory results cannot be directly extended to an understanding of the nature of the interspecific interactions of *P. cinereus* and *P. shenandoah* under natural conditions. The data do hint at a potential mode of these interactions, and at the very least they demonstrate that interference occurs even under laboratory conditions. Observations of behavioral interactions of salamanders in the field (W. Gergits, *personal observation*) will aid in corroborating our evidence. With this reservation in mind, this preliminary study leads us to the following general conclusions: (1) Interference competition (through agonistic behavior) does occur between *P. cinereus* and *P. shenandoah*; (2) It is often expressed in passive aggression (approach) rather than active aggression (head attack, etc.); (3) Between individuals, aggressive superiority can lead to foraging superiority; (4) Between species, *P. cinereus* is more aggressive.

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