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FORAGING TACTICS OF A TERRESTRIAL SALAMANDER: COSTS OF TERRITORIAL DEFENCE

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Abstract. Red-backed salamanders, *Plethodon cinereus*, established territories in laboratory chambers. Their foraging tactics, on two types of prey differing in caloric profitability and defence behaviour, were observed under a series of experimental conditions in which competitive threat was increased: no competitor present < familiar conspecific's pheromones present < unfamiliar conspecific's pheromones present < familiar conspecific intruder present < unfamiliar conspecific intruder present. As the degree of competitive threat increased, more time was devoted to territorial defence (displays and biting) at the expense of foraging. Simultaneously, the territorial residents gradually shifted from a specialized diet on the more profitable prey type to an indiscriminate diet, even though prey densities and the residents' encounter rates with each prey did not change. The presence of unfamiliar pheromones and both intruders led to approximately a 50% decrease in the residents' rates of net energy gain, about 80% of which was due to the time withdrawn from foraging and 20% due to change in diet. Changes in foraging time and diet both reflected the costs of territorial defence.

Introduction

Intra- or interspecific competition for a scarce resource may cause animals to establish territories (defended areas), wherein an individual or family group has exclusive or nearly exclusive access to food or other limiting resources (Morse 1980). The adaptive advantage of a territory is contingent upon the benefit obtained by the defender exceeding the cost of defence (Brown 1964). Ideally, the benefit should be measured in terms of the increase in fitness that accrues from preferential access to the critical resource. Similarly, cost may be assessed by measuring the loss of fitness due to injuries sustained during territorial defence as well as the time and energy subtracted from exploitation of the resource. To understand the 'decision rules' (sensu Krebs 1978) used by an individual when forming and maintaining a territory, one must quantify the benefits and costs involved. Although it has been difficult to measure benefit and cost in terms of fitness, several studies have succeeded in measuring them in units of time and energy, particularly for birds that utilize feeding territories (Wolf & Hainsworth 1971; Gill & Wolf 1975; Carpenter & MacMillen 1976).

We have attempted to measure some energetic costs and benefits for the red-backed salamander (*Plethodon cinereus*), individuals of which establish terrestrial feeding territories on the forest floor of eastern North America (Jaeger et al. 1982b). These territories apparently protect patches of prey from conspecific and congeneric competitors during dry periods when food is limited in availability (Jaeger 1980a, b). Although foraging occurs throughout the diel cycle, prey availability depends on rainfall. During periods of rain, salamanders forage in the leaf litter on the forest floor where prey are abundant and available. As the leaf litter dries after a rain, salamanders retreat to patches of moisture under rocks and logs where prey are scarce. Both males and females apparently establish territories under these cover objects.

Our eventual goal is to understand how variability in competitive pressure and food abundances in forest habitats influence the spatial and temporal patterns of territories and the tenacity with which they are defended. In the laboratory experiment reported here, we report the costs (in terms of changes in rate of net energy gain) to territorial salamanders that are exposed to a gradation of conspecific interference competition.

The benefit to *P. cinereus* from possessing a feeding territory is a high sustained yield while foraging. Laboratory experiments (Jaeger et al.

1981) demonstrated that salamanders foraging within an established territory had a considerably higher rate of net energy gain than those foraging in the absence of an established territory. Field studies (Jaeger 1980a) provided complementary information, suggesting that salamanders lacking territories obtained less food per day than those with territories.

The costs of territoriality to a salamander are more obscure. First, there is the obvious cost of an escalated aggressive contest with an intruder (Rubenstein 1981). Aggressive contests over territorial ownership between individuals of *P. cinereus* often result in injury to the chemosensory structures (nasolabial grooves) of one of the combatants. Laboratory and field studies showed that injury to the nasolabial grooves leads to lower capture rates, and thus lower caloric yield (Jaeger 1981). However, the risk of this cost seems to be low for a territorial defender, since intruders seldom attack a defender, although defenders frequently initiate attacks (Jaeger et al. 1982b).

Second, Schoener (1974) argued that a competitor can depress the abundance of the preferred food type by exploitation competition (see also Pulliam 1974). If this occurred, the optimally foraging territorial owner would have to expand its diet to include less profitable prey types (Pyke et al. 1977) or to change foraging sites (MacArthur & Pianka 1966). This cost also is probably low for salamanders. Laboratory studies showed that territorial salamanders quickly expel intruders (Jaeger et al. 1982b) or force them into a submissive posture that inhibits foraging (Jaeger 1981; Jaeger et al. 1981); field observations support this concept (Jaeger 1979).

The third cost is the time that a territorial owner must subtract from foraging in order to observe or to evict intruders. Such a reduction in foraging time would very likely decrease the rate of net energy gain for the defender. This cost has been demonstrated in several species where territorial or dominance interactions occur (Johnson & Hubbell 1974; Carpenter & MacMillen 1976; Morse 1981). Below we test the hypothesis that when a potential competitor increases its threat, the defender will increasingly subtract time from foraging as a consequence of defending its territory; thus, the rate of net energy gain decreases.

A fourth cost involves the 'mistakes' (sensu Hughes 1979) that a foraging salamander might make in its choice of diet during interference from a competitor. Other studies indicate that interference competition can affect the foraging behaviour of individuals of diverse species (Johnson & Hubbell 1974; Morse 1974; Blaustein 1980). Optimal foraging theory predicts (Pyke et al. 1977), and previous experiments have shown (Jaeger & Barnard 1981), that an unmolested territorial salamander would specialize on a more profitable prey type when that prey is abundant. We predicted that this would not be true (i.e. the salamander would switch to a more indiscriminate diet) under pressure of interference competition, when the territorial animal would be forced to monitor the activity of both prey and competitor simultaneously. We test this prediction below, monitoring changes in choice of diet and rate of net energy gain by a territorial individual with increasing threat from a potential competitor.

Methods

Experimental Chambers

Adult *P. cinereus* were collected from the Catskill Mountains, Greene County, New York, in autumn 1979. Gravid females were eliminated from the sample to reduce the possibility of courtship during the experiment, but it was impossible to distinguish between males and non-gravid females from external morphology. Each of 23 salamanders was placed in an experimental chamber, 31 × 16 × 9 cm, that contained 7 cm of damp soil covered with moist paper towels and was topped with a transparent lid (see Fig. 1 in Jaeger & Rubin 1982). The chambers were kept in a controlled temperature room at 15C with a 12L:12D light cycle and a light intensity ≃ 3 lx. Twice weekly for five months the salamanders were fed a mixture of two species of flies, *Drosophila melanogaster* and *D. virilis*, so that they would become experienced with feeding on these prey types. The paper towels were changed weekly, and the salamanders readily established territories in these chambers (Jaeger et al. 1981).

Experimental Conditions

After the five month training period, each salamander was tested for its choice of diet (see below) under each of six conditions, performed in random sequence over six weeks. Conditions 2–6 increased the threat of competitive interference to the territorial salamander (see Discussion).

Condition 1—general control. On day 1, clean paper towels were placed in the salamander's chamber. This standardized the length of time that pheromones could be deposited, and a territory advertised, before a foraging test was performed. On day 3, the salamander was fed to satiation with a mixture of the two types of flies and excess flies were removed 24 h later. This standardized the hunger level among salamanders at test time. On day 7, 22 flies of each type were blown into the salamander's chamber and the salamander's choice of diet was monitored (see below). This condition replicated the high prey density test in Jaeger & Barnard (1981) and established the percentage of each type of fly in the salamander's diet in the absence of competition or other treatments.

Condition 2—surrogate control. This was the same as condition 1, except that a surrogate salamander was placed in the centre of the chamber on day 1. The surrogate was constructed by rolling absorbent paper to the length and width of a salamander and wetting it. It was replaced with a fresh surrogate each day thereafter, and the foraging test on day 7 was performed in the presence of a surrogate. This served as a control for subsequent conditions where either surrogates marked with pheromones or live salamanders were introduced into the chamber.

Condition 3—familiar surrogate. This was the same as condition 2, except that each day, prior to being placed in the chamber, the surrogate was rolled on the substrate of a conspecific, impregnating it with the conspecific's pheromones (Jaeger & Gergits 1979); these conspecifics were kept in separate chambers lined with damp filter paper. The test animal then had the opportunity to become familiar with a particular conspecific's pheromones. On day 7, the foraging test was conducted in the presence of the familiar surrogate. This condition tested for the effect of a familiar conspecific's pheromones on the foraging tactics of a salamander.

Condition 4—unfamiliar surrogate. Each day an unmarked surrogate was placed in the chamber, as in condition 2. However on test day 7 a surrogate impregnated with an unfamiliar conspecific's pheromones was introduced. This condition tested for the effect of unfamiliar pheromones on the salamander's foraging tactics.

Condition 5—familiar intruder. As in condition 3, a familiar surrogate was introduced on days 1–6. On test day 7 however the conspecific, whose pheromones had been used to mark the surrogates, was placed into the chamber. The chamber then contained a territorial resident and a familiar intruding salamander. A 5 min habituation period was allowed between introduction of the intruder and the flies. This condition tested for the effects of the presence of a familiar intruder on the foraging tactics of the resident salamander.

Condition 6—unfamiliar intruder. As in condition 4, an unmarked surrogate was placed in the chamber on days 1–6. On test day 7 an unfamiliar conspecific was introduced and 5 min were allowed for habituation before introducing the flies. This condition tested for the effects of the presence of an unfamiliar intruder on the foraging tactics of the resident.

Prey Types and Feeding Techniques

Details of methods can be found in Jaeger & Barnard (1981). The two species of flies, *Drosophila virilis* ($\bar{X} = 2.9 \pm 0.4$ mm^3, 3 cal/fly) and *D. melanogaster* ($\bar{X} = 0.9 \pm 0.2$ mm^3, 1.2 cal/fly), are hereafter referred to as large and small flies respectively. On test day 7, 22 large and 22 small flies were placed in a plastic tube. The foraging test was begun by blowing the flies into the chamber by a jet of air through a hole in the lid. Each time that a salamander (resident or intruder) ingested a fly it was immediately replaced by another fly of the same size. Thus a constant density and equal ratio of large and small flies were maintained throughout the foraging test. The above density of flies was known to induce a specialized diet on the larger species in the absence of competition; large and small flies did not induce different pursuit or handling times for *P. cinereus* (Jaeger & Barnard 1981). The resident salamander was allowed to eat 10 flies during the test; a pilot study showed that 10 large flies would only half fill an adult salamander's stomach, thereby avoiding satiation effects (Jaeger & Barnard 1981). The test was terminated after 45 min if a resident salamander had not ingested 10 flies, but this seldom occurred. Jaeger & Barnard (1981) provided estimates of the energetic costs of handling large and small flies and gave a rationale for why individuals of *P. cinereus* judge large flies to be more profitable.

Foraging and Agonistic Behaviour

During each foraging test we monitored the number of large and small flies that the resident ingested. We also recorded the percentage of encountered flies of each size that was eaten. A salamander was assumed to have encountered a fly if the salamander moved to ≤ 3 cm from the fly or the fly moved to ⩽3 cm from the salamander. This encounter distance is essentially the striking range of the salamander (Jaeger & Barnard 1981). Intercapture intervals were measured with a stopwatch.

The rate at which the resident bit the intruder was recorded, and the total time that it spent in threat and submissive displays (Jaeger 1981) was estimated with a stopwatch. All paired salamanders were about equal in size (38–42 mm snout–vent length).

Rate of Net Energy Gain

The rate of net energy gain for each territorial resident was estimated by the equation given in Jaeger & Barnard (1981). The rate incorporates information about calories assimilated (the number of large and small flies ingested, the caloric value of each fly, the salamander's assimilation efficiency), the calories metabolically expended (weight of the salamander, time spent moving and stationary, and the caloric cost of each), and the foraging time required to ingest 10 flies.

Data Analysis

Each salamander was tested once under each of the six experimental conditions. Therefore we compared the responses of individuals among conditions using Friedman two-way analysis of variance by ranks tests and between conditions using Wilcoxon matched-pairs signed-ranks tests (Siegel 1956). All tests were two-sided with α significance level set at one of three values (see Tables I and II below), determined in each case by dividing 0.05 by the number of statistical tests in which a particular data set was used.

Results

Change in Choice of Diet

We use two methods to investigate choice of diet under the six experimental conditions of increasing competition. First we compare the sum of the large flies eaten by all of the salamanders with the sum of the small flies eaten (Fig. 1A). Since the two types of flies were present in equal abundance, we compare the observed numbers eaten with an expected ratio of 1:1, using two-sided binomial tests (Siegel 1956). The salamanders ate significantly more large than small flies under conditions 1–5, but they did not significantly specialize under condition 6 (Table I). However this analysis assumes that the foraging salamanders had an equal probability of encountering the two types of prey. To account for possible differential encounter rates, our second method compares the percentage of the encountered large flies eaten against the percentage of the encountered small flies eaten by each salamander (Fig. 1B). This analysis reveals that salamanders ate significantly more encountered large than small flies under conditions 1–4, but not under conditions 5 and 6 (Table I). The second method provides more reliable information about choice of diet, so we conclude that the salamanders specialized on the more profitable prey type

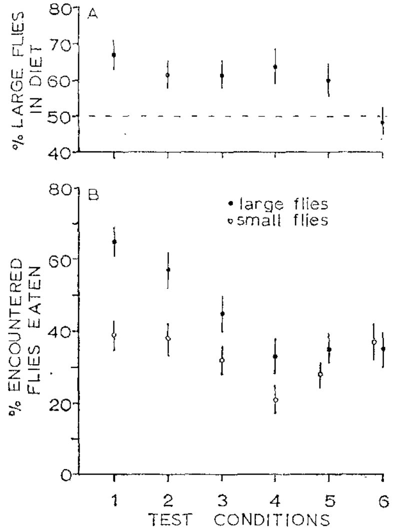

Fig. 1. Mean percentage (± 1 SE) (A) of the salamanders' diet composed of large flies and (B) of the encountered large and small flies that were eaten. Test conditions are: 1, general control; 2, surrogate control; 3, familiar surrogate; 4, unfamiliar surrogate; 5, familiar intruder; 6, unfamiliar intruder.

Table I. Choice of Diet under Six Testing Conditions

Test condition	No. large vs small flies eaten *P*†	% large vs small encountered flies eaten *P*‡
1	< 0.0006*	0.00006*
2	< 0.001*	0.0014*
3	< 0.003*	0.025*
4	< 0.018*	0.0006*
5	< 0.0036*	0.26
6	> 0.80	0.85

*Significant difference at $\alpha = 0.05$.

†Equiprobable binomial tests of the total number of large vs small flies eaten.

‡Wilcoxon tests of the percentage of large vs percentage of small flies that were encountered and eaten.

except when either a familiar or unfamiliar intruder was present.

We now ask to what extent choice of diet varied among the six experimental conditions. Encounter rates did not differ significantly, across the six conditions, either for small flies (Friedman test, $P > 0.50$) or for large flies ($P > 0.50$). The percentages of encountered small flies eaten also did not vary significantly (Fig. 1B; Friedman test, $P > 0.05$). However the percentages of the encountered large flies eaten did vary significantly (Fig. 1B; $P < 0.005$), and pair-wise Wilcoxon tests between selected conditions locate these changes in specialization on large flies (Table II). The presence of a familiar surrogate (condition 3) did not alter the residents' specialization on large encountered flies, compared to control conditions (1 and 2). However, specialization decreased in the presence of the unfamiliar surrogate (condition 4) and with the appearance of either intruder (conditions 5 and 6).

Thus, a threat of competition can cause a territorial salamander to alter its choice of diet even when encounter rates with prey do not change.

Time Subtracted from Foraging

Mean intercapture intervals (Fig. 2) varied significantly among the six experimental conditions (Friedman test, $P = 0.005$). Pair-wise Wilcoxon tests (Table II) show that the territorial residents did not significantly increase their intercapture intervals from control conditions (1 and 2) to when a familiar surrogate (condition 3) was present. Intercapture intervals did increase significantly in the presence of the unfamiliar surrogate (condition 4) or either type of intruder (conditions 5 and 6). Therefore, the salamanders increasingly subtracted time from foraging as competitive threat escalated.

Table II. Probabilities from Wilcoxon Tests Comparing Responses of Territorial Salamanders between Selected Paired Test Conditions

Test conditions compared	% encountered large flies eaten P	$\bar{X}$ intercapture interval P	Rate of net energy gain P
1 vs 2	0.10†	0.87†	0.98†
2 vs 3	0.06†	0.11†	0.76†
2 vs 4	0.005†*	0.001†*	0.002†*
2 vs 5	0.003†*	0.002†*	0.008†*
2 vs 6	0.004†*	0.009†*	0.005†*
3 vs 4	0.014§*	0.006§*	0.014§*
5 vs 6	0.79§	0.44§	0.68§

†$\alpha = 0.01$ because one data set was used in 5 different Wilcoxon tests.
§$\alpha = 0.025$ because each data set was used in 2 different Wilcoxon tests.
*Significant difference at stated α, two-sided test.

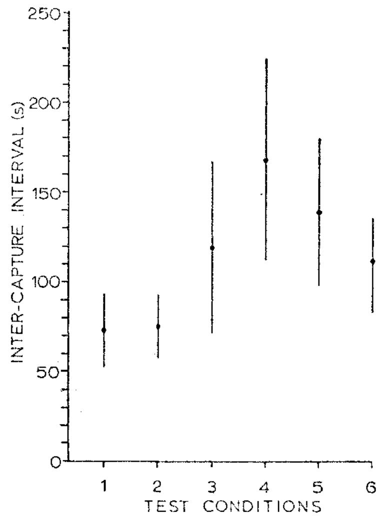

Fig. 2. Mean intercapture intervals (± 1 SE) during each of six test conditions. Means were computed by averaging all intervals of the 23 salamanders.

Time Added to Defence

Agonistic behaviour was recorded for conditions 2–6. The rate of biting varied significantly across these conditions (Friedman test, $P < 0.005$). The territorial salamanders never bit the surrogates, and they bit the familiar intruder ($\bar{X} = 0.07$ bites/min) significantly less frequently than the unfamiliar intruder ($\bar{X} = 0.23$ bites/min): Wilcoxon test, $P = 0.01$. Only one intruder attacked a resident. No courtship behaviour was observed between males and females paired in conditions 5 and 6.

The percentage of foraging time that residents spent in threat plus submissive displays (Table III) differed significantly among conditions 2–6 (Friedman test, $P < 0.01$). The control surrogate (condition 2) induced significantly fewer displays than all other conditions ($P < 0.01$ in each case), and the familiar surrogate (condition 3) caused significantly less displaying ($P < 0.0005$) than the familiar intruder (condition 5). No other comparisons showed significant differences.

Generally the residents subtracted time from foraging (Fig. 2) in the presence of competitive

Table III. Percentage of the Foraging Time* during Which Territorial Salamanders Performed Agonistic Displays

Test condition	Time threatening $\bar{X}$% (± 1 SE)	Time submissive $\bar{X}$% (±1 SE)	Total time displaying $\bar{X}$% (± 1 SE)
2	0.0	0.0	0.0
3	3.0 (1.8)	5.2 (2.2)	8.2 (2.8)
4	2.1 (1.6)	15.9 (4.2)	18.0 (5.1)
5	28.6 (7.5)	21.5 (8.0)	50.1 (8.4)
6	17.3 (6.6)	12.0 (6.0)	29.3 (7.8)

*Time required to capture 10 flies.

threats and added this time to territorial defence in the form of agonistic displays (Table III) and biting. Although the rank order between the mean values in Fig. 2 and Table III is not perfect, territorial defence exacted an obvious cost in foraging time.

Change in Rate of Net Energy Gain

Rate of net energy gain (Fig. 3) was significantly different among the six conditions (Friedman test, $P < 0.005$). Wilcoxon tests (Table II) show that the rate did not significantly change between control conditions (1 and 2) and the familiar surrogate (condition 3). Both the unfamiliar surrogate (condition 4) and the intruders (conditions 5 and 6) induced a lower rate of net energy gain in the resident salamander. Therefore, the presence of a potential competitor produced a reduction in the net energy obtained by the territorial salamander.

Discussion

Jaeger (1981) found that individuals of *P. cinereus* are less aggressive (threat display and biting) toward familiar conspecifics than toward strangers. This 'dear enemy recognition' seems to be a function of territoriality (Fisher 1954); familiar territorial neighbours pose little threat to an individual's own possession of a territory whereas strangers may be seeking a territory and are therefore a threat. Based on previous work with *P. cinereus* (Jaeger 1981), we predicted that experimental conditions 2–6 would represent an increasing threat of competition: surrogate control < familiar surrogate < unfamiliar surrogate < familiar intruder < unfamiliar intruder.

None of the parameters of foraging showed a significant difference between the two control conditions. Therefore any disturbance caused by introducing the control surrogate per se had no appreciable effect on the behaviour of the resident salamanders. As predicted by optimal foraging theory, and as found by Jaeger & Barnard (1981) and Jaeger et al. (1981), the salamanders specialized on the more profitable prey type at high prey density, although small flies were not completely eliminated from the diet.

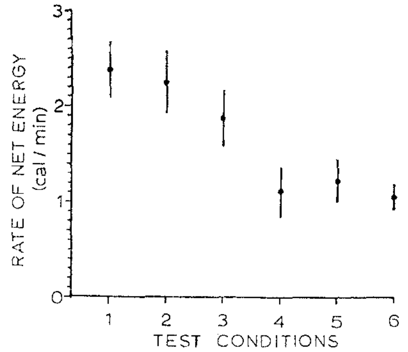

Fig. 3. Mean rate of net energy gain (± 1 SE) for the territorial salamanders during each of six test conditions: 1 cal = 4.184 J.

The familiar surrogate also caused no change in foraging tactics, but the resident did respond to it with an increase in agonistic displays. The unfamiliar surrogate elicited a further increase in agonistic displays and a decrease in the resident's specialized diet. Aggression by the resident increased again, in the form of occasional biting, with the appearance of the familiar intruder, and the resident switched to an indiscriminate diet. Aggression escalated still further, with frequent biting, in the presence of the unfamiliar intruder, and the resident's diet remained indiscriminate. We conclude, then, that the territorial salamanders did view conditions 2–6 as an increase in competitive threat and that they varied both their foraging tactics and their agonistic behaviour in response to that increasing threat.

One cost of territoriality, then, was subtraction of time from foraging and addition of time to defence when potential competitors intruded (cf. Fig. 2 and Table III). This behaviour is not surprising, as it has been observed in many territorial species. What is surprising is that choice of diet should have changed (specialist on the profitable prey type to generalist). We suggest two possible explanations for the observed change in diet choice.

First, interference competition induced relatively long intercapture intervals, and thus low capture rates, because of the time invested in agonistic behaviour. If capture rates were used by the salamanders to census prey density, as suggested by Krebs et al. (1974) for chickadees, then low rates in conditions 4–6 may have been falsely interpreted by the salamanders as meaning 'low prey density'. This explanation seems unlikely, since Jaeger & Barnard (1981) and Jaeger et al. (1982a) found that individuals of *P. cinereus* use visual encounter rates (not capture rates) to estimate changing densities of flies, and encounter rates did not vary significantly among test conditions in the present experiment. Also intercapture intervals differed little between conditions 3 and 6 (Fig. 2), yet the salamanders specialized on large flies in the former condition and fed indiscriminately in the latter (Fig. 1B).

Second, the salamanders may have made 'mistakes' in visually assaying encounter rates with the flies while simultaneously visually watching potential competitors in conditions 4–6. This may also have led to the false interpretation of 'low prey density', leading to the indiscriminate diet. The assumption here is that salamanders could not accurately monitor prey and competitors at the same time and that they opted to sacrifice 'optimal' foraging (prey specialization) in order to watch and interact with the competitors. In the absence of further evidence, we tentatively pose this as a hypothesis.

Subtracting time from foraging and abandoning a specialized diet both contributed to the significant decline in rates of net energy gain in conditions 4–6 (Fig. 3). We partitioned out the time (based on intercapture intervals) and diet (based on numbers of large and small flies eaten) components and compared conditions 4–6 with condition 2 (surrogate control). In condition 4, time subtracted from foraging accounted for 82.0% of the decrease in rate of net energy gain, and a decreasingly specialized diet accounted for 18.0% of the decline; in condition 5, time accounted for 87.0% and the absence of a specialized diet accounted for 13.0%; in condition 6, time accounted for 80.3% and absence of a specialized diet accounted for 19.7%. Therefore, time devoted to defence exacted the larger cost in net energy to the foraging territorial salamander and change in diet added considerably to that cost.

These data indicate that the choice of diet of a territorial predator can change because of interference competition, even in the absence of prey depletion caused by exploitation competition or in the absence of changing encounter rates with prey. This change in diet can impose a cost on the rate of net energy gain of the foraging predator. Werner & Mittelbach (1981) noted that optimal foraging models falsely assume that predators have perfect information about the environment. Interference competition between salamanders seems to have reduced the information about prey density needed for the foraging resident to choose a specialized diet.

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REFERENCES

Blaustein, A. R. 1980. Behavioral aspects of competition in a three species rodent guild of coastal southern California. *Behav. Ecol. Sociobiol.*, **6**, 247–255.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.*, **76**, 160–169.

Carpenter, F. L. & MacMillen, R. E. 1976. Threshold model of feeding territoriality and test with a Hawaiian honeycreeper. *Science, N.Y.*, **194**, 639–642.

Fisher, J. 1954. Evolution and bird sociality. In: *Evolution as a Process* (Ed. by J. Huxley, A. C. Hardy & E. B. Ford), pp. 71–83. London: Allen and Unwin.

Gill, F. B. & Wolf, L. L. 1975. Economics of feeding territoriality in the golden-winged sunbird. *Ecology*, **56**, 333–345.

Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. *Am. Nat.*, **113**, 209–221.

Jaeger, R. G. 1979. Seasonal spatial distributions of the terrestrial salamander *Plethodon cinereus*. *Herpetologica*, **35**, 90–93.

Jaeger, R. G. 1980a. Fluctuations in prey availability and food limitation for a terrestrial salamander. *Oecologia*, **44**, 335–341.

Jaeger, R. G. 1980b. Microhabitats of a terrestrial forest salamander. *Copeia*, **1980**, 265–268.

Jaeger, R. G. 1981. Dear enemy recognition and the costs of aggression between salamanders. *Am. Nat.*, **117**, 962–974.

Jaeger, R. G. & Barnard, D. E. 1981. Foraging tactics of a terrestrial salamander: choice of diet in structurally simple environments. *Am. Nat.*, **117**, 639–664.

Jaeger, R. G., Barnard, D. E. & Joseph, R. G. 1982a. Foraging tactics of a terrestrial salamander: assessing prey density. *Am. Nat.*, **119**, 885–890.

Jaeger, R. G. & Gergits, W. F. 1979. Intra- and interspecific communication in salamanders through chemical signals on the substrate. *Anim. Behav.*, **27**, 150–156.

Jaeger, R. G., Joseph, R. G. & Barnard, D. E. 1981. Foraging tactics of a terrestrial salamander: sustained yield in territories. *Anim. Behav.*, **29**, 1100–1105.

Jaeger, R. G., Kalvarsky, D. & Shimizu, N. 1982b. Territorial behaviour of the red-backed salamander: expulsion of intruders. *Anim. Behav.*, **30**, 490–496.

Jaeger, R. G. & Rubin, A. M. 1982. Foraging tactics of a terrestrial salamander: judging prey profitability. *J. Anim. Ecol.*, **51** 167–176.

Johnson, L. K. & Hubbell, S. P. 1974. Aggression and competition among stingless bees: field studies. *Ecology*, **55**, 120–127.

Krebs, J. R. 1978. Optimal foraging: decision rules for predators. In: *Behavioural Ecology: An Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 23–63. Sunderland, Mass.: Sinauer Associates.

Krebs, J. R., Ryan, J. C. & Charnov, E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.*, **22**, 953–964.

MacArthur, R. H. & Pianka, E. R. 1966. On optimal use of a patchy environment. *Am. Nat.*, **100**, 603–609.

Morse, D. H. 1974. Niche breadth as a function of social dominance. *Am. Nat.*, **108**, 818–830.

Morse, D. H. 1980. *Behavioral Mechanisms in Ecology*. Cambridge, Mass.: Harvard University Press.

Morse, D. H. 1981. Interactions among syrphid flies and bumblebees on flowers. *Ecology*, **62**, 81–88.

Pulliam, H. R. 1974. On the theory of optimal diets. *Am. Nat.*, **108**, 59–74.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, **52**, 137–154.

Rubenstein, D. I. 1981. Combat and communication in the Everglades pygmy sunfish. *Anim. Behav.*, **29**, 249–258.

Schoener, T. W. 1974. The compression hypothesis and temporal resource partitioning. *Proc. Nat. Acad. Sci. U.S.A.*, **71**, 4169–4172.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill.

Werner, E. E. & Mittelbach, G. G. 1981. Optimal foraging: field tests of diet choice and habitat switching. *Am. Zool.*, **21**, 813–829.

Wolf, L. L. & Hainsworth, F. R. 1971. Time and energy budgets of territorial hummingbirds. *Ecology*, **52**, 980–988.

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