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THE RELATIVE PALATABILITY OF
" MIMETIC SALAMANDERS
(*NOTOPHTHALMUS VIRIDESCENS*, *PSEUDOTRITON*
RUBER, *PLETHODON JORDANI*, *DESMOGNATHUS* SPP.)
TO GARTER SNAKES (*THAMNOPHIS SIRTALIS*).

A Thesis
by
J. Ann Berry

Submitted to the Graduate Faculty of
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ABSTRACT

The Relative Palatability of Mimetic Salamanders
(*Notophthalmus viridescens*, *Pseudotriton ruber*,
Plethodon jordani, *Desmognathus* spp.) to Garter Snakes
(*Thamnophis sirtalis*).

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In feeding experiments, seven garter snakes showed decided preferences in species of mimetic salamanders eaten and not eaten. These preferences formed a graded series, from the most to the least preferred:
Desmognathus spp. > *P. jordani* > *P. ruber* > *N. viridescens*
efts (none eaten). Relative size was not a factor in the snakes' choice of salamander species. Snakes consistently rejected more *P. ruber* than either *Desmognathus* spp. or *P. jordani*. There is no evidence of change in the responses of garter snakes to the salamanders over the course of the investigation. There were no significant differences between times to attack among the species of salamanders. There was no significant difference between ingestion times for *P. ruber* and *Desmognathus* spp., but ingestion times for *P. jordani* were significantly shorter.

There was no significant relation between size of salamander and ingestion time. No significant relation was found between ingestion time of a type of salamander and subsequent acceptance or avoidance of the next salamander offered whether of the same or different type. Evidence supports the hypothesis that *Pseudotriton* is involved in a Müllerian mimicry complex rather than Batesian with red eft. Evidence indicates that *P. jordani* is slightly protected from garter snake predation, and supports the hypothesis that it acts as a model for the palatable *Desmognathus*.

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INTRODUCTION

The English naturalist, Henry W. Bates, collected butterflies in the Brazilian Amazon region in the mid 1800's and discovered a phenomenon he called mimicry. Although it may take many forms, mimicry can be said to exist when one species, the mimic, is avoided by a predator because it resembles another inedible species, the model.

The concept of mimicry and the evolution of warning coloration has stimulated scientists ever since Bates' discovery. A truly repulsive species (the model) gains an advantage by making itself obvious to predators with displays which advertise its distasteful qualities. This is called aposematism and may take the form of coloration, odors, behavior, etc. The idea that another, less repulsive species (the mimic) can gain a selective advantage by "miming" the truly repulsive one by a false warning signal (pseudoaposematism) has many evolutionary implications. Like many other discoveries, mimicry raises many questions. Scientists have debated such subjects as: the relative advantages and disadvantages for model and mimic, selective factors

involved, the degree of effectiveness, predator responses and many others. Ideally, careful examination of mimicry allows us to learn a great deal about the interrelationships among species, in particular that between predator and prey.

Two types of mimicry are pertinent to the present research. Batesian mimicry involves a model with some form of aposematism announcing its undesirable quality and an inoffensive mimic with a similar warning. (The mimic, therefore, is protected to some degree from predation because it is mistaken for the model). Mullerian mimicry is when both species are undesirable (co-models) and exhibit warning signals which are similar and mutually beneficial against predation.

So far, two cases of suspected mimicry in salamanders are known. The first involves *Plethodon jordani* (model) and *Desmognathus imitator* (mimic) (Dunn, 1927; Brimley, 1944; Huheey, 1960; Huheey and Brandon, 1961; Orr, 1967, 1968; Cody, 1969; Brodie and Howard, 1973). Three other species of *Plethodon* (models) as well as the polymorphic *Desmognathus ochrophaeus* (mimics) may be involved in this complex (Brodie and Howard, 1973; Dodd, et al., 1974). The second case involves the red eft stage of *Notophthalmus viridescens* (model) and the

red salamanders *Pseudotriton ruber*, *P. montanus* and perhaps other mimics (Brodie, 1968a, 1976; Brodie and Howard, 1972; Howard and Brodie, 1973; Huheey and Brandon, 1974, 1977; Pough, 1974; Brandon, et al., 1979a; Brodie and Brodie, 1980).

The Order Caudata (salamanders, etc.) reaches its highest density and diversity in the southern Appalachians, and all known mimetic species occur in western North Carolina. They are subject to a variety of vertebrate and invertebrate predators. In response to these predator pressures, salamanders have developed a variety of anti-predator strategies. These defenses can be grouped as morphological and behavioral. Morphological defense mechanisms include tail autotomy, toxic skin secretions, coloration and odor. Behavioral defenses include motionlessness, escape, biting, posturing, and, in some species, vocalization. Noxious skin secretions which repel the predator are probably the most important adaptation of terrestrial salamanders with other defensive adaptations dependent upon these secretions (Brodie, 1977). A combination of toxicity and aposematic coloration could lead to a mimetic system.

Considering the variety of predators which use salamanders as a food source, it is important to see if predators apply differential selective pressures on salamander species. Most palatability studies thus far have concentrated on visually oriented avian predators (Howard and Brodie, 1971, 1973; Brodie and Howard, 1973; Dodd, et al., 1974; Brandon, et al., 1979a, b; Brodie and Brodie, 1980) which would be affected by the combined stimuli of coloration and toxicity. Birds who are known to eat salamanders, seem to be logical subjects to use in testing the effectiveness of mimetic systems involving coloration. Since birds are not the only predators of salamanders, it is also important to use other predators in palatability tests. Only this broader view will allow an understanding of the mechanisms at work in the evolution and maintenance of such systems.

One predator which probably applies considerable pressure on salamander populations is the eastern garter snake, *Thamnophis sirtalis*. This species has been used but sparingly in palatability studies (Huheey, 1960; Orr, 1967; Brodie, 1968a) despite several favorable attributes which include being a known natural predator of salamanders and being easily maintained in the laboratory. They are small, require little space and usually adjust well to captivity.

In this study, feeding experiments were conducted to determine the responses of seven garter snakes to four types of salamanders: *Pseudotriton ruber*, the red eft stage of *Notophthalmus viridescens*, *Plethodon jordani* and *Desmognathus* spp. The *Desmognathus* were used as a control and without regard to species because of their known palatability to predators (Howard and Brodie, 1971, 1973; Brandon et al., 1979b).

This research was designed to investigate the following null hypotheses:

- Ho₁: There is no significant difference between the numbers of salamanders of different species eaten by garter snakes.
- Ho₂: Previous response to a salamander species by a garter snake does not influence the numbers of salamanders subsequently eaten by garter snakes.
- Ho₃: There is no significant difference among salamander species over the time of this investigation in the numbers killed or eaten and those not eaten by a garter snake.
- Ho₄: There is no significant effect of salamander size on attack rate by garter snakes.

- Ho₅: There is no significant difference between attack times by garter snakes among the salamander types.
- Ho₆: There is no significant difference between ingestion times by garter snakes for the different salamander types.
- Ho₇: Ingestion time of a salamander by a garter snake is not significantly related to the size of the salamander.
- Ho₈: There is no significant difference between ingestion time by a garter snake and subsequent acceptance or avoidance of the same type of salamander.
- Ho₉: There is no significant difference between ingestion time and subsequent acceptance or avoidance of the next salamander offered.

REVIEW OF THE LITERATURE

Several aspects of this study benefit from a review of the current literature. These include: 1) Mimicry as it relates to salamanders, 2) Relative toxicity of salamanders used in this experiment, 3) An evaluation of garter snakes as predators on salamanders.

The oldest reference to mimicry in salamanders is Dunn's (1927) use of the term *imitator* for a new montane race of *Desmognathus fuscus* from the Smoky Mountains. The red cheeked morph of this form was thought to "mimic" the red cheeks of sympatric *Plethodon jordani*. Dunn called this "a clear case of mimicry." The *Desmognathus* form has recently been shown to be a separate species, *D. imitator*, by electrophoretic analysis (Tilley, et al., 1978). In this system, *P. jordani* is the presumed model and *D. imitator* the mimic. Later, Bishop (1947) extended the mimicry argument to the red legged form of *P. jordani* and sympatric red legged *D. ochrophaeus*. He said the observations "would seem to strengthen Dunn's contention."

Hairston (1949) remarked on the fact that large percentages of the "imitator" individuals occur only in populations sympatric with brightly marked *Plethodon jordani*. Huheey (1960) suggests that such a distribution

could not be due to random mutation alone, and must have "positive survival value, directly or indirectly."

Some investigators have looked at other explanations rather than mimicry. Brimley (1944) recognized that the "imitator" form had only been reported from regions where the red legged or red cheeked *Plethodon* occur. He commented that the similarity could be a manifestation in the *Desmognathus* of causes which had produced color patches in *P. jordani* or perhaps both salamanders "exhibit traces of an old color pattern which has long since disappeared in their relatives but still persists in the *Plethodon* and turns up once in a while in this form (*Desmognathus*) also."

Noble (1931) concluded that the red coloration could be the by-product of some unknown physiological mutation having survival value, yet have no apparent survival value in itself. Huheey (1960) argues that this does not explain why it appears to benefit the *Desmognathus* only in regions where a colored subspecies of *P. jordani* occurs rather than over a larger portion of its range. Nor, he claims, does it "explain the exact parallelism" with the *Plethodon* in both bases.

Since Huheey (1960), all authors except Cody (1969), have discussed the relationship of these two salamanders in terms of Batesian mimicry. To be considered a Batesian mimicry complex certain criteria must be met:

1. There must be an undesirable quality in the model.
2. There must be some form of advertisement to predators.
3. At least one natural predator must discriminate between model and nonmimetic.
4. That predator must associate the mimic with the model.

Assuming that coloration has survival value, the benefit in this case must fall into one of four categories (Huheey, 1960).

1. Advantages with respect to the physical environment.
An advantage is bestowed upon the salamander in relation to some nonbiological factor or combination of factors. Huheey states that this is little more than remotely probable.
2. Advantages with respect to intraspecific relations.
This assumes that the color pattern is an advantage in recognition of one another. This idea is also dismissed because of the lack of sexual dimorphism and the apparent colorblindness of the animals.

3. Advantages with respect to prey. The red color on the head of *jordani* may have the advantage of attracting insects so they may be easily captured. This still does not explain the red on the rear legs of the red legged *Plethodon* nor does it explain the occurrence of the red colored *Desmognathus* only in regions where the similarly colored *Plethodon* occurs.
4. Advantages with respect to predators. The redness would be considered either cryptic or warning coloration. Huheey states here that although "coloration might serve a deceptive or illusionary purpose, it is again difficult to see why the 'imitator' forms occur only in those regions where *jordani*...occurs." Assuming that the model-mimic theory is correct, Huheey goes on to say, then at least one of the predators from which the model is protected by its aposematic coloration would be color sensitive. The pattern could be of value with respect to colorblind predators and the color a refinement for the color sensitive predator.

Huheey thought Hypothesis Four to be correct and performed an experiment to test the hypothesis. *P. jordani* and *Desmognathus* were fed to a garter snake (*Thamnophis sirtalis*), an adult sparrow hawk (*Falco sparverius*), and a pair of shrikes (*Lanius ludovicianus*).

He concluded that *P. jordani* has a "lower degree of acceptability" than *Desmognathus* and that color patterns serve aposematic and pseudoaposematic functions in the two species. The undesirable quality which is advertised by the color on the model is the "slime exuded copiously from the tail of the larger specimens, and to a lesser degree, the entire body of all specimens." He admits that the efficiency of the warning coloration is probably not 100%."

Huheey and Brandon (1961) reported red cheeked *Desmognathus* in the range of red legged *Plethodon jordani*. Brimley (1928) had previously reported specimens of *Desmognathus* with red cheeks, and specimens with red cheeks and red legs from Tusquitee Bald, N. C. where legged *P. jordani* are found. Huheey and Brandon (1961) suggest that if the aposematic *jordani* is of recent origin no contradiction appears in the mimicry interpretation. Evidence for this is the fact that only two of the seven subspecies of *jordani* exhibit apparent aposematic coloration, and the high variability in the pseudoaposematic coloration of *D. carolinensis*.

Orr (1967) worked with what "were considered to be the most frequent natural predators upon this supposed mimetic complex." Among the predators were the eastern garter snake (*Thamnophis sirtalis*) and the short tailed shrew (*Blarina brevicauda*). Feeding experiments followed Brower (1958a,b,c), in which an experimental group of garter snakes and shrews were offered *P. jordani* and normal *D. ochrophaeus*. Controls were given red cheeked and normal *D. ochrophaeus*. Salamanders, *Gyrinophilus porphyriticus* and *Desmognathus quadramaculatus*, were tested for their discrimination ability between *P. jordani* and normal *D. ochrophaeus*. The salamander predators were placed on the forest floor in cages with both *P. jordani* and normal *D. ochrophaeus* and checked at regular intervals to determine the numbers of salamanders eaten. The predators did not discriminate between *P. jordani* and *D. ochrophaeus* but Orr suggested that infrequent predators such as birds might lead to more fruitful research.

The numbers of mimics in an area should be in direct proportion to the number of models (Sheppard, 1959). To test this hypothesis in the *D. ochrophaeus* (= *D. imitator*)-*P. jordani* complex, Orr (1968) sampled eight belt transects in the Great Smoky Mountains National Park. He

found a positive correlation between *P. jordani* and red cheeked *D. ochrophaeus*. The correlation coefficient between the frequencies of *P. jordani* and red cheeked *D. ochrophaeus* were significantly different from zero, while that between *P. jordani* and normal were not, suggesting "some factor other than the suitability of the collection site is operating." Orr concluded that the factor could be mimicry, but stated that "confirmation of this is dependent upon the finding of a natural predator that does discriminate between models and non-mimetics."

Cody (1969) attempted to explain the color pattern similarities by calling it aggression-associated convergence. The function of this convergence would be interspecific territories and reduced competition. A strong rebuttal of this explanation was made by Brodie and Howard (1973) and accepted by Huheey and Brandon (1974).

Brodie and Howard (1973) tested the hypothesis that the similarity in color pattern is the result of Batesian mimicry and followed Orr's suggestion that using birds might lead to more fruitful research. One brown thrasher and four blue jays were used in feeding trials. Those birds found *P. jordani* distasteful but edible, and avoided mimics after having been conditioned to avoid models.

In cases of mimicry where the model is not inedible but is distasteful to predators, the evolution of warning coloration and false warning coloration is dependent upon an alternate food source. When alternate food is available unpalatable prey may be avoided (Alcock, 1970a, b).

Brodie and Howard (1973) noted the similarity of other morphs of *D. ochrophaeus* with several other species of *Plethodon* (*P. cinereus*, *P. nettingi* and *P. welleri*) which have bright dorsal pigmentation and could be aposematic coloration. In 1974 Dodd and co-workers investigated this idea. A lizard (*Cordylus giganteus*), hedgehog (*Hemiechinus auritis collaris*), and three turtles (one *Chelydra serpentina*, two *Kinosternon sonoriense*) all ate *Desmognathus* readily, but when fed *Plethodon nettingi* experienced such symptoms as gagging, regurgitation, difficulty in swallowing and swollen tongues. It was determined that the small *P. nettingi* contained noxious qualities resulting from the slimy secretions which could serve as a defensive mechanism and that *P. nettingi* could serve as a model for a palatable animal such as *D. ochrophaeus*.

The distasteful qualities of *P. jordani* to birds has been established (Huheey, 1960; Brodie and Howard, 1973).

The red cheek patches or red legs on *P. jordani* would be considered aposematic coloration, thus advertising the distasteful, slimy secretion exuded from the skin (mainly tail) of *Plethodon*. Experiments and observations have established birds as natural predators on salamanders (Huheey, 1960; Orr, 1967; Howard and Brodie, 1970, 1971, 1973; Brodie and Howard, 1973; Brandon and Huheey, 1975; Brodie and Brodie, 1980). Birds will eat *P. jordani* but suffer discomfort and will learn to avoid them. They will also be repelled from the mimic, once conditioned to avoid the model, while still accepting the non-mimetic form (Brodie and Howard, 1973).

Since predators do eat *P. jordani*, the advantage gained from aposematic coloration may be slight, and the advantage gained by the mimic from pseudoaposematic coloration even slighter. But, any genetically determined advantage, however slight, which enables an organism to live to reproduce, should in time become established in the gene pool of that population (Dobzhansky, 1951).

The second presumed case of Batesian mimicry in salamanders involves *Pseudotriton ruber* as the palatable mimic of the noxious red eft, *Notophthalmus viridescens*. The noxiousness of the red eft is well known (Noble, 1931; Conant, 1975). Tetrodotoxin (TTX), found in the skin of

red efts, is among the most toxic non-protein substances known (Fuhrman, 1967) and few predators are known to eat them (Conant, 1975). Brodie (1968a) demonstrated the susceptibility of vertebrates to this toxin by intraperitoneal injections and forced feedings. Animals tested were white mice, salamanders (*Gyrinophilus porphyriticus*, *Desmognathus quadramaculatus*) frogs (*Rana clamitans*, *R. catesbeiana*), toads (*Bufo americanus*, *B. cognatus*, *B. terrestris*, *B. valliceps*, *B. woodhousi*), and snakes (*Thamnophis sirtalis*, *Nerodia sipedon*). Experimental animals experienced such symptoms as muscular weakness, gasping, gaping and regurgitation, loss of fighting reflex, convulsions, Haxoid paralysis, and continued heartbeat after cessation of respiration. Brodie concluded that there are individual and ontogenetic variations in the amount of toxin present in the efts, but that the aposematic red eft stage of *N. viridescens* is well protected by skin toxins.

In 1971, Howard and Brodie produced evidence that *P. ruber* is a Batesian mimic of *N. viridescens* efts. They found no difference in the numbers of mimics and non-mimics eaten by chickens before conditioning with the model and a significant difference after conditioning.

They concluded that "the palatable mimic (*Pseudotriton ruber schencki*) derives a selective advantage over non-
aposematically colored salamanders due to their
similarity in color to the noxious model (*Notophthalmus viridescens viridescens*) and that this relationship is
clearly the result of Batesian mimicry."

In 1972, Brodie and Howard made a case for behavioral mimicry in the defensive displays of *P. ruber* which, they claim, closely paralleled those of *N. viridescens* efts. They said "it is logical to postulate that behavioral traits shared by members of this mimetic complex but not by other sympatric salamanders will enhance the selective advantage enjoyed by the mimic."

Later, Howard and Brodie (1973) again tested birds for their reaction to these salamanders, but used wild natural predators (nine blue jays, *Cyanocitta cristata* and one brown thrasher, *Toxostoma rufum*) in addition to chickens which were used as naive subjects. Eight of ten wild birds exhibited some degree of initial rejection of *Pseudotriton*, and only 15% of eighty-four *Pseudotriton* were eaten. There was a significant difference in the mean seizure times of control *Desmognathus* and *Pseudotriton* of four jays before contact with efts. No difference in seizure times were observed for the other wild birds or

chickens. None of the efts were killed or eaten. Chickens once again readily ate mimics and non-mimics before conditioning with the model. After they were taught to avoid models, they began avoiding mimics. All predators that ate *Pseudotriton* did so without apparent distaste or deleterious effects.

Howard and Brodie (1973) noted the size difference between *Pseudotriton* and its eft model.

The black spots on *Pseudotriton* are larger than those on efts, and the color brighter. *Pseudotriton* may function as a "supermimic" in that the larger spots imposed on a brighter color may convey a stronger warning signal to predators than the "normal" pattern of the model. *Pseudotriton* are commonly larger than efts.

To explain the rejection of the *Pseudotriton* by the wild birds before conditioning, Howard and Brodie (1973) suggest that the wild birds were conditioned to avoid efts when trapped and therefore avoided the palatable mimic when initially tested in the laboratory. They suggest that since the range of *P. ruber* is completely contained within the range of *N. viridescens* and the color patterns of both vary geographically, changes in color pattern should be examined.

Pough (1974) did such an examination and offered indirect evidence that red salamanders are palatable, Batesian mimics of red efts. He reported that

Pseudotriton which was found in regions without a sympatrically occurring red eft (the eft stage is shortened or absent) are cryptically colored throughout life, while those that occur sympatrically with red efts are red at some stage of life. In regions where red salamanders never grow larger than efts they are red throughout life and the red salamanders which do grow larger than efts are red as juveniles and become cryptically colored as adults.

Huheey and Brandon (1974) commented on the 'presumed' eft-*Pseudotriton* mimetic complex. They disagree with the Howard and Brodie suggestion that *Pseudotriton* acts as a "supermimic" of red efts, and accept Pough's (1974) statement that *Pseudotriton* darkens as it grows larger than efts. "An effective mimic cannot safely outgrow its model; if it does indeed become larger, a switch to cryptic coloration is advantageous." They agree that "the greater the deterrent, the less discriminating the predator becomes overlooking differences between model and mimic... In view of the toxicity of the eft, there is no need for perfect mimicry by *Pseudotriton* though we doubt any advantage occurs from being a supermimic." They agree that *P. ruber* and *P. montanus* act as simple Batesian mimics of red efts.

Brodie (1976) defended his idea that the red salamanders are supermimics of red efts:

Even the small *Pseudotriton* from this area (Highlands Biological Station, N. C.) are as large or larger than efts...Newly metamorphosed *P. ruber* are lighter red than adults. Some individuals have more dark pigmentation than others but in this population, most adults are bright red-orange regardless of size. It seems unlikely that any of the red salamanders in the Highlands area are cryptic rather than aposematic.

However, in 1977, Huheey and Brandon reported that a new high molecular weight toxin had been isolated from the skin of *N. viridescens*, different from the potent low molecular weight TTX long known to protect efts. Also a high molecular weight non-TTX poison had been isolated from the skin of salamanders of the genus *Pseudotriton*. Because of these findings, they felt the mimetic relationship, usually thought to be Batesian, needed reexamination.

In 1979 they conducted a study to examine this relationship (Brandon et al., 1979a). Five domestic chickens found *P. ruber* and *P. montanus* to be intermediate in palatability between highly unpalatable efts and highly palatable dusky salamanders (*D. ochrophaeus*). Defensive behaviors of *Pseudotriton* were judged to be more similar to hemidactyline phethodontid relatives

than to red efts. They concluded that *Pseudotriton* has a "reduced palatability of their own that is reinforced by their skin color and defensive posture."

They further conclude:

...where they are sympatric, red efts, species of *Pseudotriton*, and perhaps *Gyrinophilus porhyriticus* form a Müllerian mimetic complex sharing the cost of teaching predators that brightly reddish salamanders have reduced palatability, with red efts having the most noxious and *G. porhyriticus* the least noxious skin secretions.

So it now appears that the eft-*Pseudotriton* mimetic complex is of the Müllerian type rather than Batesian, with both species possessing distasteful qualities and repelling predators to their mutual benefit.

Most palatability studies that produced results demonstrating avoidance of mimetic salamanders used visually oriented avian predators. Dodd and co-workers (1974) found that other animals which eat salamanders could be used to demonstrate noxiousness of different species. Several experimenters have used the eastern garter snake, *T. sirtalis* (Huheey, 1960; Orr, 1967; Brodie, 1968a), in studies concerning the noxiousness of salamanders.

T. sirtalis ranges from 1,000 to 6,000 ft. in the Great Smoky Mountains (King, 1939). These snakes are known to eat salamanders and stomach content analyses have shown that salamanders account for 31.37% of the diet of garter snakes in George Washington National Forest, Virginia (Uhler et al., 1939) and 23.08% of their diet in Harlan County, Kentucky (Barbour, 1950).

Carpenter (1952) found garter snakes in Michigan had a distinct preference for earthworms (80%), but had a secondary preference for amphibians (15%). He states that the common garter snake will eat all amphibians small enough to be swallowed. He concluded that food records indicate that garter snakes have little individual food preference but will take any type available within the range of food preference for that species. Lagler and Salyer (1945) also conclude that availability is a factor in determining the food habits of *T. sirtalis*. They found amphibians composed 55.4%, earthworms 35.3% and fish 6.2% of the food of garter snakes from about the natural waters on Michigan. Those collected from about fish rearing stations ate 43.8% fish, 41.4% amphibians and 11.3% earthworms. This clearly indicates that availability is a factor in garter snake food choice.

In the mountains of North Carolina, where all known mimetic forms of salamanders occur, salamanders are abundant and available, although not obvious. In North America there are more species of salamanders than any other part of the world. The southern Appalachians exhibit a higher concentration of both species and individuals than any other part of the United States, most of which occur in North Carolina (Brimley, 1944).

Since garter snakes are known to be natural predators of salamanders, several investigators have tried to determine their reactions to the species involved in mimetic relationships. Huheey (1960) experimentally fed two specimens of *P. jordani* to one garter snake and reported:

It ate both, evidencing no sign of distaste, although it did acquire a certain amount of slime on its head from the salamanders. Hence it appears that there is no "undesirable" factor in *jordani* as far as the garter snake is concerned.

Orr (1967) found no discrimination between *P. jordani* and *D. ochrophaeus* when fed to eight garter snakes. He reported the snakes:

...rather consistently ate all salamanders presented to them... One can conclude with certainty that *Thamnophis* does not discriminate between the supposed models, mimics and non mimetics. Thus if mimicry does exist between these two species of salamanders, the mimicry is not effective when salamanders are fed upon by *Thamnophis sirtalis sirtalis*.

Brodie (1968a) tested predators for susceptibility to *N. viridescens* skin toxin. Reptiles were tested by forced feedings. Brodie concluded, "*Thamnophis s. sirtalis* and to a lesser degree *Natrix s. sipedon* were found to be resistant to *Notophthalmus* toxin, but neither was resistant enough to feed consistently on newts."

From the available evidence it seems that garter snakes will eat salamanders rather indiscriminantly when available as a food source, but will perhaps avoid *N. viridescens* even though they show natural resistance to the toxins of that salamander.

This investigation was designed to determine if garter snakes do, indeed, show preference for certain species of mimetic salamanders. It is assumed that if the snakes are selective, they should be most discriminating when an alternate food source is available. Preferences on the part of garter snakes should be considered a measure of relative palatability and/or relative noxiousness of these prey species and should supplement our present knowledge of selective pressures on salamander communities.

MATERIALS AND METHODS

Four types of salamanders were used in this research: *Notophthalmus viridescens* efts, *Pseudotriton ruber*, *Plethodon jordani* and drab colored *Desmognathus* spp. *Desmognathus* was used without regard to species because their palatability is well accepted by the scientific community (Howard and Brodie, 1971, 1973; Brandon, et al., 1979b). Specimens were collected from northwest North Carolina, primarily Watauga County. Salamanders were separated by species and housed in plastic shoe boxes measuring 8 X 15 X 30 cm. They were offered food, but not tended individually.

Predators were common garter snakes, *Thamnophis sirtalis*, housed individually in plastic shoe boxes and maintained at room temperature, approx. 20-26°C. Preliminary feeding experiments were run with fourteen snakes caught in the Fall of 1979. Of those fourteen, two died and three large snakes weighing over eighty-seven grams were eliminated because of size. Seven ate salamanders readily and were used in the actual experiment.

Testing was done once every 6-8 days over a seven month period from January 1980 to July 1980. One day prior to testing snakes were placed in clean boxes with

damp paper substrate and fed their favorite non-salamander food item (frog parts, tadpoles, fish or earthworms) until food was refused. Feeding simulated natural situations where food is abundant. Eighteen to twenty-four hours later each snake was placed in the feeding box and allowed a few minutes to adjust before introduction of the salamander. A stopwatch was started when the snake noticed the salamander, as determined by a head turn or tongue flick in the direction of the prey or by following the prey species. Attack time was measured from notice time until actual attack. Ingestion time was recorded as time from first attack until the salamander completely disappeared. All activities were recorded to the nearest 0.01 minute.

Snakes were fed salamanders in a circular sequence, *P. ruber*, *N. viridescens* efts, *P. jordani*, *Desmognathus* spp., unless availability made this impossible. Sequence began with different salamanders for different snakes. If the snake refused one of the species of salamanders it was immediately offered the next species until all had been tried, or one had been eaten by the snake. If the snake ate a salamander it was returned to its box until the next week when the sequence was

continued from where it had previously stopped. Salamanders were removed if they had not been attacked after five minutes from notice time. Since all snakes consistently avoided efts, they were eliminated from later sequences except for periodic trials.

No attempt was made to quantify visual discrimination powers of the snakes between species, because while sight may play an important role in the feeding behavior of garter snakes (Fox, 1952) the vomeronasal system seems to be the most important system in the sensory discrimination of prey items (Wilde, 1938; Halpern and Frumin, 1979).

Reactions of snakes were recorded as "killed or eaten" and "not eaten." Since a large part of the data is nominal data, contingency tables were the main statistical tools used for interpretation of data. Yates's correction for continuity was used when appropriate. For the continuous measures, parametric correlation analysis, analysis of variance (ANOVA) and t-tests were used for analysis. Primary statistical sources were Siegel (1956) and Scheffler (1979).

RESULTS AND OBSERVATIONS

In approximately 15% of the one hundred thirty-one trial runs snakes rejected all salamanders offered. Since data obtained on these days reveal nothing about relative palatability of the salamanders to garter snakes, the "no eat" days were eliminated from analysis. A "no eat" day was defined as a day when a snake refused at least two non-eft salamanders.

The results of this experiment will be used to examine the hypotheses presented in the Introduction. Each of these null hypotheses will be posed in turn, and relevant data presented.

Ho₁: There is no difference between the number of salamanders of different species eaten by garter snakes.

The salamander species used in this experiment were not attacked at the same rate (Table 1). Rather, the snakes showed decided preferences which form a graded series from the most palatable dusky salamanders (*Desmognathus* spp.) to the least palatable eft (*N. viridescens*). The palatability sequence was *Desmognathus* spp. *P. jordani* *P. ruber* *N. viridescens* (Table 2).

Table 1. Responses of Seven Garter Snakes to Offered Salamanders.¹

	Offered	Eaten	Not eaten but Killed	% Eaten	% Survival
<i>N. viridescens</i> efts	31	0	0	0	100
<i>P. ruber</i>	51	14	2 ²	27	69
<i>P. jordani</i>	49	39	0	80	20
<i>Desmognathus</i> spp.	64	60	0	94	6

¹Includes preliminary and actual timed trial data.

²Both salamanders fully ingested and regurgitated.

Efts were highly unpalatable to the snakes (Table 1). Only one eft was eaten by a garter snake. This was during the preliminary experiment so neither the time to attack nor the ingestion time was recorded. The ingestion was followed by long periods of yawning and hiccup-like movements by the snake. That snake refused to eat another eft. It died nine weeks later, after four more feedings. Of the other twelve snakes, four bit efts when first exposed to them, but none of the efts were harmed or eaten. No snake attacked more than one eft. Snake behavior make it impossible to use "time to attack" or "ingestion time" for further comparisons with other species. It was concluded that red efts are highly unpalatable to garter snakes, much more so than any other species tested (Table 2).

Red salamanders (*Pseudotriton*) were found to be less repulsive than red efts, but less palatable than the other types studied. Very highly significant differences were found between numbers of *P. ruber* and both *P. jordani* and *Desmognathus* spp. killed or eaten and those not eaten (Table 2). Six of eleven snakes initially avoided *P. ruber*, four of twelve initially avoided *P. jordani* and one of thirteen avoided *Desmognathus* spp.

Table 2. Chi-square (X^2) values from 2 X 2 contingency tables comparing the palatability of two different salamander species to seven garter snakes. Degrees of freedom equal one in each case.

Less Palatable	More Palatable		
	<i>P. ruber</i>	<i>P. jordani</i>	<i>Desmognathus</i> spp.
Red efts	12.36** N = 81	48.14** N = 80	70.58** N = 85
<i>P. ruber</i>		21.70** N = 100	46.83** N = 115
<i>P. jordani</i>			5.13* N = 113

*P < .05
**P < .001

Significant differences were also found between numbers of *P. jordani* and *Desmognathus* killed or eaten and those not eaten (Table 2), indicating that *P. jordani* is less palatable than the dusky salamanders.

It can be concluded that there is a difference between numbers of salamanders of different species eaten by garter snakes. The null hypothesis (H_{01}) of no difference between numbers of salamanders of different species eaten by garter snakes is rejected.

H_{02} : Previous response to a salamander species by a garter snake does not influence the numbers of salamanders subsequently eaten by garter snakes.

Comparisons of rates of attack after previous rejection with rates of attack after previous acceptance for each species are all insignificant (*Pseudotriton*, $P=.12$; *P. jordani*, $P=.16$; *Desmognathus*, $P=.80$). The previous response of a snake to a salamander species apparently does not affect subsequent responses to that species. Null hypothesis (H_{02}) is accepted.

H_{03} : There is no significant difference over the time of the experiment in the numbers of a salamander species eaten by garter snakes.

The numbers of *Pseudotriton* killed or eaten during the first half of the experiment were not significantly different than those in the second half of the experiment ($X^2= 2.29$, $df= 1$, NS). The same was true for *P. jordani* ($X^2= .47$, $df= 1$, NS) and *Desmognathus* spp. ($P= .39$, NS). The null hypothesis (H_{04}) stating that responses of garter snakes to salamander species do not change over time must be accepted.

H_{04} : There is no significant effect of salamander size on attack rate by garter snakes.

Since all efts are rejected, the size of these salamanders was unimportant to the snakes. To eliminate size as a probable factor influencing the snakes' choice of other salamanders, the variable of relative size (salamander snout vent length (SVL)/wt. of snake) was used. Relative size was used instead of actual size because the snakes were of various sizes.

There were no differences found among salamanders eaten in each size grouping (Table 3). Since the *Pseudotriton* were generally larger than the other types offered, these data were extracted and analyzed separately. There were no differences among the size categories of *P. ruber* ($X^2= .02$, $df= 2$, NS). Seemingly, the relative size of all salamanders offered was

Table 3. Contingency table of relative sizes (snout vent length (SVL) of salamander/weight of snake) of salamanders killed or eaten and those not eaten by seven garter snakes.

Relative size	Killed or eaten	Not eaten	Total
1.96 + (Large)	O= 13 E= 16.4	O= 11 E= 7.6	24
1.27 - 1.95 (Medium)	O= 30 E= 31.5	O= 16 E= 14.5	46
.75 - 1.26 (Small)	O= 50 E= 45.1	O= 16 E= 20.5	66
Total	93	43	136 $X^2= 4.13, df= 2, NS$

Observed (O), Expected (E), not significant (NS).
E= total of column X total of row/total N.

unimportant to the snakes. Null hypothesis (Ho5) predicting no difference between the size categories of salamanders eaten by garter snakes must be accepted.

Ho5: There is no significant difference between attack times by garter snakes among the salamander types.

There were no significant differences in the times to attack among the three species, *P. ruber*, *P. jordani*, and *Desmognathus* spp. ($F_{3,112} = .394$, NS). There were no times recorded for efts. Null hypothesis (Ho6) is accepted.

Ho6: There is no significant difference between ingestion times by garter snakes for the different salamander types.

Ingestion times of the three (non-eft) types of salamanders by the garter snakes are significantly different (Table 4).

Two tailed t-tests reveal no difference between ingestion times of *P. ruber* and *Desmognathus* spp. ($t_{(50)} = 1.25$, NS). Ingestion times of *P. jordani* were significantly shorter than those of *P. ruber* ($t_{(50)} = 3.35$, $P < .01$) and of *Desmognathus* ($t_{(76)} = 2.31$, $P < .05$). The null hypothesis (Ho7) of no difference among ingestion times for the three species of salamanders must be rejected.

Table 4. Analysis of variance of ingestion times for the three (non-eft) salamander types.¹

Source	SS	df	MSS	F	P
between	350.70	2	175.35	9.44	<.01
within	1653.23	89	18.58		

¹There were no ingestion times recorded for efts.

These results are interesting considering the relative palatability of the different types of salamanders. The most interesting variable to look at here would be behavior, since none of the salamanders were anesthetized.

Salamander Behavior

As is often the case with cryptically colored species, *Desmognathus* would remain motionless and alert when introduced into the snake cage. Once frightened by discovery, the salamander vigorously fled from the predator. At times, the dusky salamanders perceived the oncoming attack and turned to face and attack the predator, biting the snake's upper jaw. They would show great stamina and strength in their attempts to free themselves from their predators and did escape occasionally. It was easy for the snake to recapture the dusky salamander within the confines of the cage. If the predator made contact towards the posterior end of the salamander, the *Desmognathus* (depending on size) often turned and attacked again biting the upper jaw of the snake. In such incidences, ingestion time was prolonged, hence the large variation in ingestion times of *Desmognathus*.

Brightly colored, unpalatable species will often boldly display themselves to predators. Such behavior was exhibited by *P. ruber*. These red salamanders would

commonly walk around the cage, at times on and underneath the snake. Occasionally, they would show a flight reflex if frightened and make quick attempts towards escape. Once bitten, they would thrash about and push with their feet but would not fight back in the manner described for *Desmognathus*. Only one (60 mm SVL) showed real fighting behavior. Ingestion in this case took 38.85 min.

P. jordani showed similar motionlessness and flight behavior to the dusky salamanders, yet never fought back once attacked. Instead, they would curl their tails around the predators face, exuding their slime. This did not seem to discourage the snakes.

The variation in ingestion times for *Desmognathus* can be accounted for in behavior. However, once bitten, *P. ruber* and *P. jordani* showed similar behavior. Since *P. ruber* is generally larger and bulkier than *P. jordani*, size was examined to see if there was a correlation between size of a salamander and ingestion time.

Ho7: Ingestion time of a salamander by a garter snake is not significantly related to the size of the salamander.

A correlation (Pearson's r) was used to determine the relationship between actual size of salamander (SVL) and ingestion time. The correlation obtained for each of the three salamander types were not significantly different from zero ($-.201$ to $.208$). Actual size of salamander is not significantly correlated with ingestion time in this study.

Since snakes were of various sizes, it seemed logical to look at the relationship between salamander size, relative to snake size and ingestion time for the three species. The correlations (Pearson's r) were not significant for the three salamander types ($-.193$ to $.404$). Relative size of salamander is not significantly correlated with ingestion time in this study. Null hypothesis (H_0) is accepted.

H₀: There is no significant difference between ingestion time by a garter snake of a type of salamander and subsequent acceptance or avoidance of the same type of salamander.

H₀: There is no significant difference between ingestion time and subsequent acceptance or avoidance of the next salamander offered.

A correlation (point biserial) between ingestion time and response to the next salamander offered of the same type was not significantly different from zero ($r = -.111$, $df = 91$). There was no significant correlation between ingestion time and acceptance or avoidance of the next salamander offered, same or different ($r = -.061$, $df = 91$). Garter snakes do not avoid salamanders because of recent experiences of ingestion times involving the same or different type of salamander. Null hypotheses H_{08} and H_{09} are accepted.

The results seem to support the following:

1. Garter snakes show decided preferences for certain types of salamanders when an alternate food source is available.
2. Red efts are highly unpalatable to garter snakes and will be avoided by them consistently.
3. *Pseudotriton ruber* is unpalatable to garter snakes but they are not completely avoided.
4. *Plethodon jordani* is eaten less by garter snakes than the most palatable *Desmognathus* spp.
5. In this type of experiment garter snakes do not change responses to a salamander species over time.

6. When the unpalatability of a species is not 100%, a garter snake will "forget" and accept that species periodically.
7. Garter snakes will occasionally avoid all salamanders when an alternate food source is available.
8. Time to attack by a garter snake is not a reflection of the palatability of a salamander species to the snake.
9. There are differences in ingestion times of different salamander species by garter snakes.
10. Size is an unimportant source of variation in ingestion time of a salamander species by a garter snake.
11. Longer ingestion times do not deter garter snakes from subsequent acceptance of salamanders, of the same or different species.
12. Shorter ingestion times do not encourage subsequent acceptances by garter snakes of salamanders of the same or different species.

DISCUSSION

Analysis of any mimetic system must include information about models and mimics, their predators, and their interactions with those predators. The present experiment was initiated to determine if one predator, the eastern garter snake, *Thamnophis sirtalis*, could tell us anything about the palatability of several salamander species thought to be mimetic.

The presumed model in the present study is the red eft stage of *Notophthalmus viridescens*. It has long been known to be highly toxic (Noble, 1931; Fuhrman, 1967; Conant, 1975) and brightly colored. Previous work (Brodie, 1968a; Howard and Brodie 1971, 1973) indicates clearly that it is toxic and aposematic.

The presumed mimic is *Pseudotriton ruber*, the red salamander. It is sympatric with red efts and is brightly colored in a pattern reminiscent of the efts. All researchers explained the color similarity in terms of Batesian mimicry (Howard and Brodie 1971, 1973; Brodie and Howard, 1973; Pough, 1974; Huheey and Brandon, 1974; Brodie, 1976) until Brandon and co-workers suggested that the mimetic relationship might be Müllerian (Huheey and Brandon, 1977; Brandon et al., 1979).

In this investigation the eastern garter snake was used to determine if these salamanders are of equal palatability to such a predator. If so, the salamanders derive no advantage from their morphological defense mechanisms and the mimetic system would fail where those reptilian predators are concerned. However, if the snakes do discriminate among salamanders, choices can be considered a reflection of different levels of palatability and/or noxiousness. Information resulting from palatability studies using natural predators is vital to our understanding of mimetic systems. At the heart of this is the study of the interrelationships among predator and prey and the consequences of these relationships, which is one of the most interesting subjects available to the evolutionary biologist.

Results of this investigation clearly indicate that red eftts enjoy protection from garter snake predation since none were eaten. Information from past experiments have shown that *T. sirtalis* is resistant to the toxins found in the skin extracts of members of the Salamandridae (Brodie, 1968a, b). However, it is clear that garter snakes will avoid eftts completely when other prey are available.

Are *Pseudotriton* palatable mimics of the red efts, noxious co-models with the efts, or neither? The status of this salamander is becoming clearer. The garter snakes in this experiment found them to be of intermediate palatability between the efts and the palatable control *Desmognathus*. The red salamanders were accepted less often than the other two salamander types (27% eaten), regardless of past feeding history of the snakes. These results are in agreement with recent findings that specimens of *Pseudotriton* repel predators by their own skin secretions (Brandon, et al., 1979a). Presumably, this unpalatability is a result of the high molecular weight toxin found in skin extracts of *Pseudotriton* (Huheey and Brandon, 1977).

Another presumed model studied in this investigation is *Plethodon jordani*. This species is black over most of its range, but has bright red coloration in some areas. It is known to exude a sticky slime from its skin. Also, two species of *Desmognathus* have been found which have a high incidence of similar coloration within the range of the red marked *P. jordani*.

The presumed mimics are *Desmognathus ochrophaeus* and *Desmognathus imitator*. *D. ochrophaeus* is a polymorphic species which has a high incidence of red legged

coloration where it is sympatric with the red marked *Plethodon*. *D. imitator* is found primarily in areas sympatric with red marked *P. jordani*.

Several explanations of the similar coloration have been offered in the past, ranging from coincidental (Noble, 1931; Brimley, 1944) to Batesian mimicry (Dunn, 1927; Hairston, 1949; Huheey, 1960; Huheey and Brandon, 1961, 1974; Orr, 1967; Brodie and Howard, 1973) to aggression-associated convergence (Cody, 1969).

Results of this experiment indicate that *P. jordani* were eaten significantly less than the control *Desmognathus* ($X^2 = 5.13$, $P < .05$), although significantly more than the unpalatable *Pseudotriton* ($X^2 = 21.70$, $P < .001$). Former investigators have concluded that *P. jordani* is readily and consistently eaten by garter snakes as are *Desmognathus* (Huheey, 1960; Orr, 1967). However, in those experiments no mention was made of an alternate food offered to the snakes. Since the undesirability of *P. jordani* in this experiment is slight (80% eaten), the snakes would be likely to accept these salamanders more readily if hungry. It has been shown that in times or areas of abundant prey, predators will avoid unpalatable prey (Cott, 1940; Alcock, 1970a,b).

The unpalatability of *P. jordani* must be slight because ingestion times for this species were significantly shorter than the other two groups, indicating that the slime exude is not a deterrent to garter snakes. This information seems to contradict the earlier evidence that they are of reduced palatability. Perhaps the deterrent might be something other than their slime.

The only conclusion which can be drawn here is that if *P. jordani* is protected from garter snake predation by some undesirable quality, the advantage gained would be only marginal. However slight, any genetically determined quality which allows an individual to live to reproduce is an advantage (Dobzhansky, 1951).

One aspect of mimicry not addressed by the present design concerns learning. Learning and forgetting are important components of mimicry (Huheey, 1964; Emlen, 1968). Although results indicate that snakes did not react differently to the salamanders over the course of this experiment, some interesting observations can be made.

Snakes avoid the repulsive salamanders (efts) and avoided other unpalatable species (*Pseudotriton*) for periods of time when fed an alternate food. The less

noxious of these probable Müllerian comrades (*Pseudotriton*) was accepted periodically and was again avoided by the snakes. Since it is impossible to evaluate what effect experience with one species has on the snakes' responses to the other species by this experimental design, some other avenues of research are needed.

An experiment similar to this one where snakes are fed an alternate food supply but offered only *Pseudotriton* at strictly controlled intervals would give more insight into exactly how much time is required for the snakes to "forget" the distasteful qualities and accept that species again. Brower's design (1958a,b,c) could also be used to investigate if learning takes place when snakes are offered a controlled series of salamanders with varying degrees of palatability. Orr (1967) performed such an experiment on garter snakes using *P. jordani* and *D. ochrophaeus* and got no change in behavior. However, the palatability of these species seems to be only slightly different. If salamanders of known palatability were used (*Pseudotriton* and red efts) more fruitful research might ensue concerning snake learning.

SUMMARY

It can be concluded from this experiment that *Notophthalmus viridescens* efts enjoy protection from garter snakes when fed an alternate food since none were eaten. Results also indicate that *Pseudotriton ruber* is intermediate in palatability between red efts and species of *Desmognathus*. This supports the Müllerian mimicry hypothesis proposed by Brandon and co-workers (1979a). There also is evidence that *Plethodon jordani* is slightly unpalatable to garter snakes, which might allow this salamander species to act as a model for highly palatable *Desmognathus*.

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