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The Possibility of the Existence of Mimicry Between Two Species of Southern Appalachian Salamanders

Lowell Preston Orr

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To the Graduate Council:

I am submitting herewith a dissertation written by Lowell Preston Orr entitled "The Possibility of the Existence of Mimicry Between Two Species of Southern Appalachian Salamanders." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in .

J.T. Tanner, Major Professor

We have read this dissertation and recommend its acceptance:

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

March 12, 1962

To the Graduate Council:

I am submitting herewith a dissertation written by Lowell Preston Orr entitled "The Possibility of the Existence of Mimicry Between Two Species of Southern Appalachian Salamanders." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

James T. Tanner
Major Professor

We have read this dissertation and
recommend its acceptance:

J. C. Howell
Royal E. Shanks
Gordon E. Hunt
Arthur W. Jones

Accepted for the Council:

Hilton A. Smith
Dean of the Graduate School

THE POSSIBILITY OF THE EXISTENCE OF MIMICRY BETWEEN TWO SPECIES
OF SOUTHERN APPALACHIAN SALAMANDERS

A Dissertation
Presented to
The Graduate Council of
The University of Tennessee

In Partial Fulfillment
of the Requirements for the Degree
Doctor of Philosophy

by
Lowell Preston Orr
March 1962

33

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I. INTRODUCTION

Investigators familiar with the amphibia of the Great Smoky Mountains have long been puzzled by the amazing resemblance between the red, orange, or yellow-cheeked variants of the Desmognathus ochrophaeus carolinensis Dunn population (Fig. 1) and the red-cheeked salamander, Plethodon jordani jordani Blatchley (Fig. 2). In this study, these two species will be referred to by their sub-specific names, carolinensis and jordani. The problem is especially intriguing in that the frequency of the red-cheeked variant in carolinensis is highest where this polymorphic species is sympatric with jordani in the Smokies. Outside the range of jordani the incidence of the red cheek coloration among normally patterned carolinensis (Fig. 3) is quite low.

Numerous individuals have suggested that the similarity can be best explained in terms of mimicry. According to the theory of mimicry, the two distantly related species are protected by having similar color patterns which "advertise" to predators an undesirable characteristic found in one or both of the species sharing the color pattern. Two basic types of mimicry have been proposed. In Batesian mimicry, the red cheek patch of jordani could be considered warning or aposematic coloration which would "advertise" to predators some distasteful or undesirable quality found in jordani (the model). The red-cheeked variant of carolinensis (the mimic), which exhibited pseudaposematic or false warning coloration, would thus gain survival value from its close

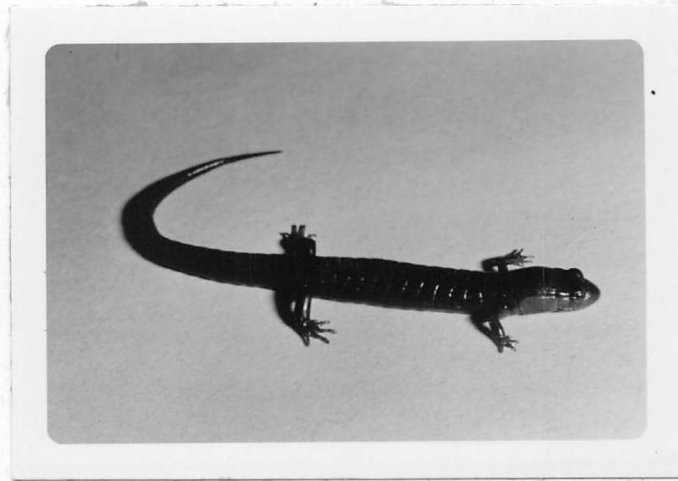


FIGURE 1

RED-CHEEKED PHASE OF DESMOGNATHUS OCHROPHAEUS
CAROLINENSIS DUNN

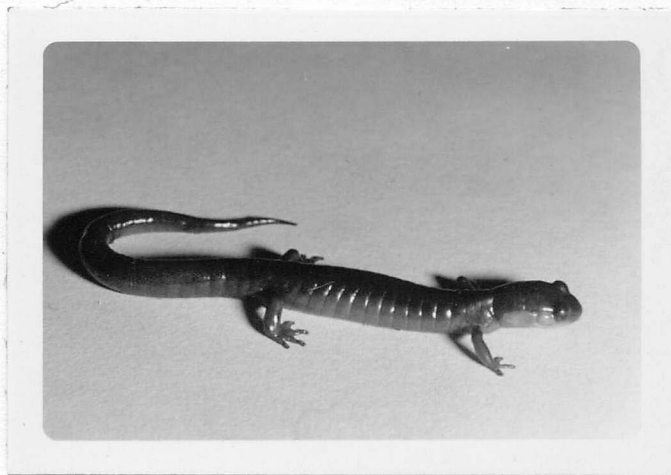


FIGURE 2

PLETHODON JORDANI JORDANI BLATCHLEY

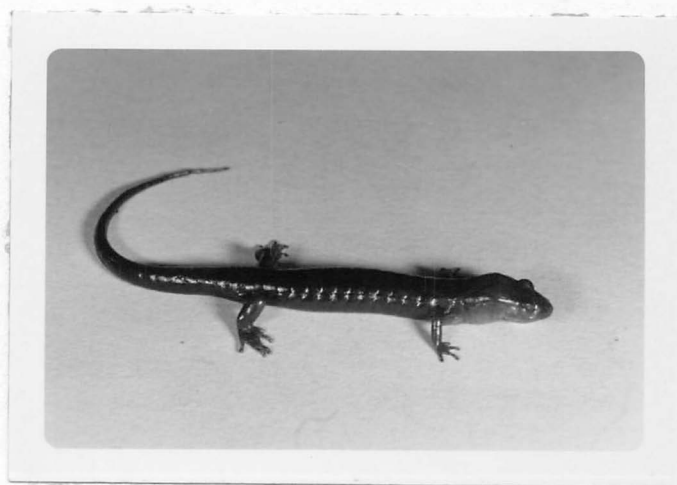


FIGURE 3

NORMAL COLOR PATTERN OF DESMOGNATHUS
OCHROPHAEUS CAROLINENSIS DUNN

resemblance to the model even though it possessed none of the undesirable qualities. In Müllerian mimicry, both jordani and the red-cheeked carolinensis would possess undesirable qualities and thus the model and the mimic are both protected by undesirable characteristics.

Although this problem has been recognized for over thirty-five years, no field research has been conducted to actually test the hypothesis of mimicry between jordani and carolinensis. The purpose of this research project is to investigate the possibility that mimicry exists between these two species by both field and laboratory approaches.

Dunn (1927) first described the yellow-cheeked variety of Desmognathus as a new mountain race and referred to it as Desmognathus fuscus imitator. Later (1928) Pope concluded from his studies that it was merely an unstable color variety of Desmognathus fuscus carolinensis. Bishop (1947), however, regarded it as a subspecies of Desmognathus ochrophaeus and assigned it its present status of Desmognathus ochrophaeus carolinensis.

Attempts to account for this color variation have been made by several investigators. Dunn (1927) concluded that his specimens exhibited "a clear case of mimicry," and that "coincidence scarcely avails to explain the resemblance in color of the one form to another."

Noble (1931), however, questioned the plausibility of the mimicry theory by noting that the presence of red cheeks seemed to have no survival value and therefore the characteristic could not have been evolved by natural selection. Instead he suggested that "it is possible that parallel modifications in unrelated genera are linked with physiological mutations having such a value."

Bishop (1947) later added supporting evidence to the mimicry theory in his description of red-legged individuals of carolinensis from Tusquitee Bald, $7\frac{1}{4}$ miles southeast of Andrews, North Carolina. This area is within the range of the red-legged salamander, Plethodon jordani shermani. He observed that "the discovery of another population of the same subspecies of Desmognathus which has taken on the color characteristics of a second member of the genus Plethodon would strengthen Dunn's contention." This red-legged variety of carolinensis was first described by Brimley (1928).

Additional evidence which tends to support the mimicry theory was submitted by King (1939). He found that of 285 individuals of carolinensis collected in the Great Smoky Mountains National Park, twenty per cent displayed yellow, orange, or red cheek patches. An altitudinal breakdown of this series showed that only five to six per cent of the individuals collected below 3,000 feet had cheek coloration, while twenty-four per cent of those collected above 5,000 feet had the characteristic. If mimicry does exist between these two species, one would expect a higher frequency of mimics in the upper elevations where jordani is common since predators would have experienced the unpalatable characteristics of jordani at these elevations and thus would not prey upon the similarly colored red-cheeked carolinensis.

Huheey (1960) has approached the problem experimentally by conducting feeding experiments using a garter snake, Thamnophis sirtalis, a sparrow hawk, Falco sparverius, and two migrant shrikes, Lanius ludovicianus, as predators upon normal carolinensis and jordani. In his studies he found that the snake readily ate two jordani and concluded

that "it appears that there is no undesirable factor in jordani as far as the garter snake is concerned." Preliminary feeding experiments with the hawk in which the hawk rejected twenty-eight per cent of the jordani and none of the carolinensis indicated that the bird possibly could discriminate between the two species. In his more extensive and controlled feeding experiments with the migrant shrikes, he found that the jordani had a significantly higher survival rate when presented to the predators as compared to the carolinensis.

In attempting to solve this problem, it would seem that the best approach would be to test certain established characteristics or rules of mimicry (Wallace, 1867; Shull, 1936; Cott, 1940) which must be met in all valid cases of mimicry. The failure of investigators to employ these generally accepted criteria has been the basis of criticism presented against claims of mimicry (Shull, 1936).

The first of these rules is that the mimic must have a distinctively different color pattern from the non-mimetic individuals. Obviously this must be so, since a close similarity in appearance would indicate only similar phylogenies (Shull, 1936).

Furthermore, the resembling forms (model and mimic) must occupy the same area if the mimetic relationship is to be effective. In the case of Batesian mimicry, the presence of the palatable mimics without sympatric unpalatable models would have no effect in "educating" or deceiving predators.

In the same sense, the model must be much more numerous than the mimic for effective deception of predators. It has been stated (Cott,

1940; Sheppard, 1959) that success in Batesian mimicry is dependent upon the comparative rarity of the mimic, otherwise "the results of experimental testing would encourage an enemy to renewed attacks." In Müllerian mimicry this scarcity of the mimic would not be a necessary factor since both species display the aposematic signal.

Furthermore, there should be a direct relationship between the frequency of mimics and the frequency of models in a given area (Sheppard, 1959). In other words, an area supporting a very dense population of jordani should also produce a higher number of mimics in the carolinensis population. This should be true since the frequency of mimics in a population must be established by the selection pressure exerted by predators. Again this situation would hold true only in Batesian mimicry.

A final characteristic of mimicry which should be found in all mimetic complexes is a distinct difference in the liability of attack between the model and the non-mimetic members of the complex. In both Batesian and Müllerian types of mimicry this would be essential to prove the existence of undesirable qualities in the aposematic models. In Batesian mimicry, it would also be necessary to observe that the predators were sufficiently deceived by the pseudaposematic signal of the mimic. Each of these proposed criteria was applied in this study to determine the possibility of mimicry existing between carolinensis and jordani.

II. REVIEW OF THE LITERATURE

The Theory of Mimicry

The theory of mimicry has long been a controversial subject. Shortly after Darwin proposed his theory of natural selection, Bates (1862) formulated a theory of mimicry in which it is assumed that a palatable species derives survival value from mimicking an unpalatable or undesirable species, which normally is conspicuously colored. Müller (1879) later proposed a theory of mimicry in which it is assumed that both resembling species are distasteful, and thus the number of individuals sacrificed to predators before the predators are "educated" is divided between two species.

In addition to these two theories of mimicry, Darwin's original theory of natural selection resulted in a great many descriptions of supposed examples of mimicry and other forms of adaptive coloration. Most of these descriptions concerned the Lepidoptera, and undoubtedly many proposed accounts of adaptive coloration were the products of over-enthusiastic naturalists who naively assigned warning coloration to practically all brilliant color patterns and mimicry to almost every non-related pair of resembling species (Dodson, 1952). It would be expected then that since this time the concept might have had numerous critics (Shull, 1936; McAtee, 1932; Heikertinger, 1944; Urquhart, 1957).

McAtee's investigation (1932), in which he studied the number of protectively and non-protectively colored insects in 80,000 bird stomachs, did much to question the effectiveness or even existence of adaptive

coloration. In this study he concluded that birds seemed to eat protectively and non-protectively colored insects in proportion to the density of the insect populations. This study has been vigorously attacked, however, by such adherents of adaptive coloration as Huxley (1932), Cott (1932), Poulton (1932), Dunn (1935), and others. Their general consensus was that the data in the study were presented in a misleading manner in that McAtee tabulated only the number of stomachs containing adaptively and non-adaptively colored insects, instead of making a determination of the actual numbers of these insects.

Shull (1936) also has questioned the existence of adaptive coloration with the bulk of his criticism directed at mimicry. Since his criticisms are fairly representative of most of the criticisms leveled at the theory, they will be considered in some detail below.

In many instances of recognized mimetic complexes it is often not known that one of the species actually has undesirable qualities. For years this point has been one of contention in the classic Monarch-Viceroy butterfly complex. It has been questioned by some (Urquhart, 1957) whether the Monarch actually has undesirable qualities. Brower (1958), however, seems to have resolved this problem in her very thorough feeding experiments in which she found that Florida jays, Aphelocoma coerulescens, did discriminate between the Monarch (model) and other non-mimetic butterflies after a few trials. Darlington (1938) also produced convincing evidence that lizards of the genus Anolis learned to discriminate between unpalatable beetles (models) and non-mimetic beetles. The reliability of feeding experiments under laboratory conditions has been questioned

by some (Manders, 1911; McAtee, 1932), but undoubtedly these experiments can be important sources of evidence if carefully conducted.

Another major objection to mimicry is that the similarities between model and mimic may not be sufficient to deceive. It has been suggested by several that what may appear to the human as closely similar forms may not appear similar to predators (Beddard, 1892; Lutz, 1933). Anthropomorphic interpretations could be misleading if the color vision of predators differs from human color vision. Training experiments with various predators indicate that the spectral ranges used by these animals vary considerably (Cott, 1940) so that the above objection could be valid.

The effectiveness of mimicry has also been questioned in the case of predators which lack color vision entirely. Undoubtedly many mammals and reptiles lack color vision. Cott (1940) refutes this objection to the mimicry theory on the grounds that similarities in color will produce similar perceptions of tone in colorblind animals and this effectively is adaptive coloration.

A final difficulty regarding the deception of predators is the problem of deceiving nocturnal predators. This problem has been considered by numerous individuals (Hecht and Marien, 1956; Cott, 1940; Huheey, 1960; Mertens, 1956). Walls (1942) contends that owls lack color vision. Rochon-Duvigneaud (1943), however, has submitted evidence that owls can perceive red in light intensities lower than that in which man is capable of distinguishing the color. Huheey suggests that the discerning abilities of nocturnal predators under low light intensities

may not be an important factor since the nocturnal prey could be exposed during the day by diurnal predators.

A third major objection to many supposed cases of mimicry is that often the chief predators of the mimicking individuals are not known. The defense of this objection by advocates of mimicry seems to be more difficult than the defense of other criticisms since very few field observations have been made of predators actually attacking individuals of the mimetic complex. Birds have long been suspect as the chief predators of butterflies, but accounts of bird predation on butterflies in the field have been rare (Carpenter, 1935; Urquhart, 1957). However, predators which prey only occasionally upon a species could be responsible for the evolution of a mimetic pattern in this species. An extremely important concept in the theory of natural selection is that very small coefficients of selection will suffice to guide evolution in a certain direction (Dobzhansky, 1951). Thus differential predation of very low intensities could be enough to alter gene frequencies in the population of the prey. In the same sense, mimicry need not be completely effective for the evolution of a mimetic pattern since it need only be effective enough to give mimicking species a slight advantage over non-mimetics.

A final major objection to mimicry is that warning coloration itself is not believed to be effective in preventing predation. If warning coloration is not effective, then mimicry cannot be effective, since it is dependent upon the cloak of warning coloration. Undoubtedly much criticism concerning the effectiveness of warning coloration has emerged from McAtee's study mentioned earlier. A convincing study by

Jones (1932) does much to defend the theory of warning coloration. He found that of 5,000 freshly killed insects presented to birds at the edge of a woods, the least accepted were those conspicuously marked with red, orange, or yellow color patterns. The studies of Brower (1958, a, b, c), Carpenter (1937), and Darlington (1938) can be cited as evidence that warning coloration in most cases is effective in relaxing predation pressure.

The theory of mimicry has withstood the attacks of critics in most instances. However, critics have undoubtedly contributed much to the stature of the theory by demanding better research techniques including the moving of many students of adaptive coloration from the confines of a museum to the field.

The Ecology and Speciation of *D. o. carolinensis* and *P. j. jordani*

The range of *D. o. carolinensis* extends from southwest Virginia to northern Georgia (Conant, 1958). This species is found throughout the Great Smoky Mountains National Park from an elevation of 1,400 feet to the highest elevation in the Park, 6,643 feet (King, 1939).

This mountain subspecies of *D. ochrophaeus* is an extremely variable salamander not only with respect to its color pattern but also with respect to its habitat. Hairston (1949) has found that at higher elevations (above 4,500 feet) this polymorphic species is indiscriminate in its choice of habitat and may be found at considerable distances from water. Thus it is commonly found under fallen bark, logs, and rocks on the forest floor as well as in seepage areas at these higher elevations. During this study it was found to be particularly abundant under rocks

and debris in gullies which carried little or no water. At lower elevations, however, it seems to be restricted to more aquatic environments along or in streams (Hairston, 1949; Dunn, (1926). Hairston (1949) has suggested that differences in temperature and humidity between high and low elevations are responsible for this shift in habitat with the change in elevation.

The variability of the color pattern of this species has been discussed by numerous investigators (Conant, 1958; King, 1939; Hairston, 1949; Bishop, 1947). Many individuals have a light dorsal stripe with irregular edges, with the stripe color various shades of gray, tan, yellow, or red. Older individuals normally lack the stripe, are bluish-black in color, and often have brownish heads. Juveniles have light colored dorsal spots arranged in a zig-zag pattern along the dorsum. These spots, like the stripes, vary widely in color. It has been noted that a correlation seems to exist between elevation and the intensity of coloration in this species, with the darkest individuals found at the highest elevations (King, 1939; Hairston, 1949).

In comparing the time of activity of carolinensis to other species of Desmognathus, Hairston (1949) has found that carolinensis is ninety-nine per cent nocturnal as compared to other species of Desmognathus, which may be as low as ninety per cent nocturnal. D. o. carolinensis also tends to be slightly arboreal during its active time.

P. j. jordani (the supposed model) is unique in its restriction to the Great Smoky Mountains. Here it seems to be associated primarily with the spruce-fir forests above 4,500 feet but has been taken as low

as 2,750 feet. This red-cheeked, bluish-black salamander may be found in abundance in or under rotten logs, or under flat rocks on the forest floor at the upper elevations. Although the species is considered more terrestrial than carolinensis, the two often are found together either in a habitat normally preferred by carolinensis or in the more terrestrial habitat of jordani. The coloration of jordani varies to a much less extent than carolinensis. The coloration of the cheek patch varies from a light pink to red and in some individuals may be lacking entirely. However, the complete absence of cheek coloration is uncommon (Bishop, 1947; King, 1939). Of 234 jordani observed for color pattern variations in this study, four lacked the cheek coloration entirely, while in twelve the coloration was reduced to a narrow band on the dorsal part of the cheek. Other variations included one individual with red on the forelegs, one with flecks of red on the dorsum, and one juvenile with six paired orange spots on the dorsum.

P. j. jordani is similar to several other members of the genus Plethodon in that it exudes an extremely slimy mucus from the tail, and to a lesser extent, from the body. The secretion of this slime seems to be stimulated by pressure exerted upon the animal in handling and can easily be noted when the tail is squeezed.

The Plethodontidae, the family to which these species belong, undoubtedly had as its point of origin the Appalachian Mountains of the eastern United States (Dunn, 1926). It is believed that the early forms of this lungless group probably were linked to the highly oxygenated waters of the mountain streams.

Three major lines of descent from the ancestral Plethodon stock have been recognized (Piatt, 1935). These are the Desmognathus, the Stereochilus-Gyrinophilus, and the Plethodon-Oepidus lines and are shown in Figure 4. Of these, the primitive stream-inhabiting forms remain in the region of their Appalachian origin, while many of the others, which early attained terrestrial specialization, have dispersed as widely as the Pacific Coast, Europe, and South America.

Dunn (1926) considers Desmognathus quadra-maculatus, an inhabitant of the mountain streams, as the most primitive member of Desmognathus. Desmognathus monticola also is an aquatic species and probably has evolved from the primitive quadra-maculatus. The first evidence of terrestriality is found in Desmognathus fuscus which emerged from a split of monticola. Since D. fuscus occupies a more terrestrial niche than monticola, it avoids competition with the latter. A montane form of fuscus then gave rise to an even more terrestrial form, carolinensis, which entered the colder, more humid niche of the upper elevations. This then leaves only the evolution of wrighti, the most terrestrial of all Desmognathus to be explained. Hairston (1949) suggests that it has diverged from D. ochrophaeus and is able to coexist with D. o. carolinensis by virtue of its small size and complete terrestriality. Hairston adds further:

The evolution of the terrestrial series of Desmognathus has been viewed as depending for its first step upon a physiological change involving the ability to withstand an increased amount of desiccation The physiological change has in each case been followed by morphological ones—more rounded and elongate tail, smaller size, loss of vomerine teeth in the male, etc.

He also makes the interesting observation that as species become more terrestrial, they also become more nocturnal and arboreal.

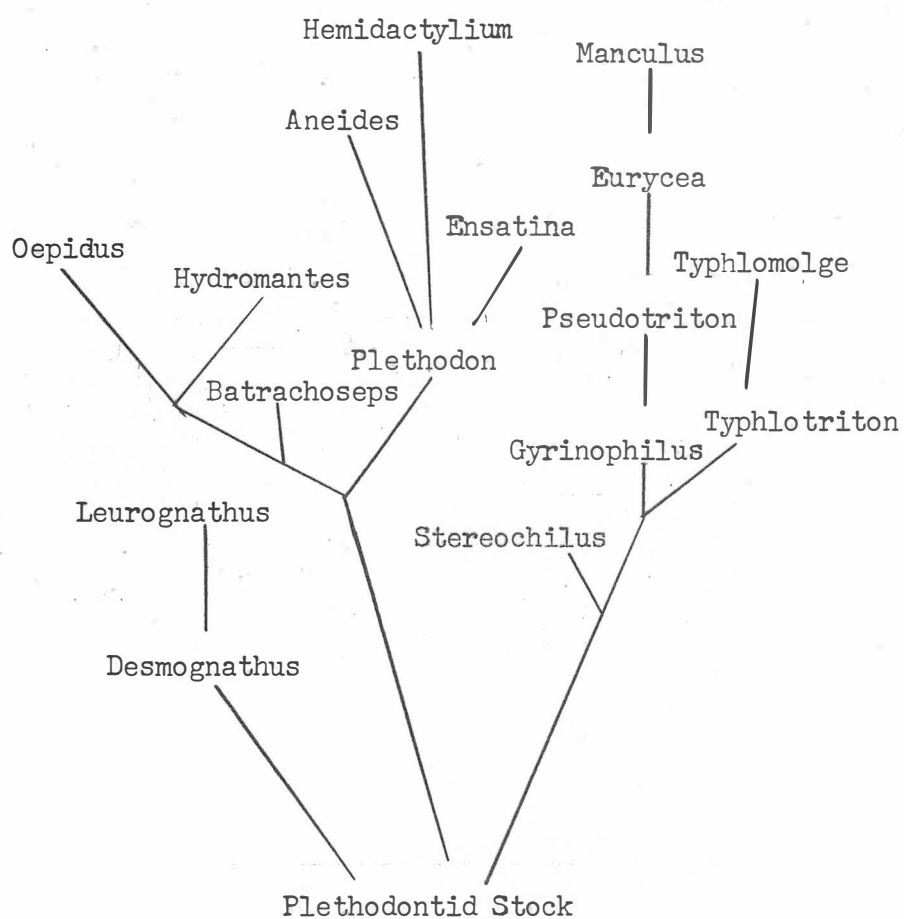


FIGURE 4

PHYLOGENY OF THE FAMILY PLETHODONTIDAE
(FROM PIATT, 1935)

The common ancestor of the Desmognathus and Plethodon-Oedipus lines is not known. Hairston and Pope (1948) have reviewed the speciation of the Plethodon group and consider yonahlossee as the most primitive of the group. From it evolved the ancestor of the jordani group which subsequently diverged to produce metcalfi and jordani. Members of the genus Plethodon are believed to have been among the earliest to become specialized for a terrestrial existence.

III. THE REGION OF THE STUDY

The field research for this study was conducted in the Great Smoky Mountains National Park during the summers of 1960 and 1961.

Many geological, climatic, and biological factors interact within the Great Smokies to produce an unusually diverse environment. Undoubtedly the complexity of these factors accounts in part for the large number of salamander species found within the Park. These factors will not be discussed in detail here since they have been described in excellent accounts by many investigators.

The vegetation of the Great Smokies, which has received particular attention because of its complexity, has been described by Cain (1935, 1943, 1945), Oosting and Billings (1951), and Whittaker (1956).

Willis King's studies (1939, 1944) provide the best survey of the herpetology of the Park, while Hairston's work (1949, 1950) adds additional information on the Plethodontids. Studies of birds have been made by Tanner (1955) and Wetmore (1939), while mammals have been studied by Komarek and Komarek (1938).

The geology of the area has been treated by Philip King, et al. (1958) and Neuman (1947), and climates have been discussed by Shanks (1954).

IV. THE COLOR PATTERN OF D. O. CAROLINENSIS

It was stated earlier that one important characteristic of all valid mimetic complexes is that the mimics must have a distinctively different color pattern from the non-mimetic individuals.

To test this rule, observations were made on 587 carolinensis collected within the park, and descriptions were recorded of the color patterns of each. Of the 587 individuals recorded, 151 (26 per cent) displayed cheek coloration. Orange to red patches were present in 139 (92 per cent) of the total number of colored-cheeked individuals, ten were yellow (7 per cent), and two were light gray to white (1 per cent). Six carolinensis were observed which had reduced cheek patches with only a slight amount of color showing. Mutational changes in red animal pigments to yellow and eventually to white seem to be common (Goldschmidt, 1940).

The contrast between the red-cheeked carolinensis and what might be considered a normal adult carolinensis has been illustrated in Figures 1 and 3. It is obvious from these photographs that there is a distinct difference between the two forms shown. Although not all red-cheeked carolinensis deviate as widely from the normal carolinensis as the salamander pictured in Figure 1, it is apparent from the data above, that relatively few have the cheek coloration reduced to such a point that the red-cheeked individuals would be difficult to differentiate from the normal carolinensis.

The contention that there is a distinct difference between the red-cheeked variants and normal carolinensis has received further support

from the confusion which existed among early taxonomists as to the proper classification of the red-cheeked variants. As has been mentioned earlier, Dunn (1927) first considered these variants a new race before Pope (1928) described them accurately as a color variety of carolinensis.

The term "normal" is a disturbing term to one familiar with this highly variable species. As can be seen in Figures 5 through 13, the species varies widely with respect to color and to pattern.

Not only do some of the variants closely resemble jordani, but others tend to resemble species of other genera such as Plethodon cinereus, Plethodon dorsalis, and to a limited extent, Eurycea bislineata. Noble (1931) also has made this observation and has suggested that "the integument of Amphibia is limited in the number of possible patterns which it is able to assume and hence the repetition of various patterns during evolution." Other variants closely resemble other members of Desmognathus such as ochrophaeus, monticola, and fuscus.

A complete tabulation of all the variations in the color pattern of carolinensis would be a monumental task. However, a few of the more conspicuous variations observed during this study are listed below. Although red is mentioned in most cases, other colors such as orange, yellow, gray, tan, brown, and rust were often found in the patterns given here.

1. Red on proximal portion of forelegs..
2. Red on proximal portion of all legs.
3. Red snout.
4. Red eye lids.
5. A single large red splotch in middle of dorsum.
6. Red or yellow post ocular stripe.
7. Uniform coloration except for dorsal stripe along tail.

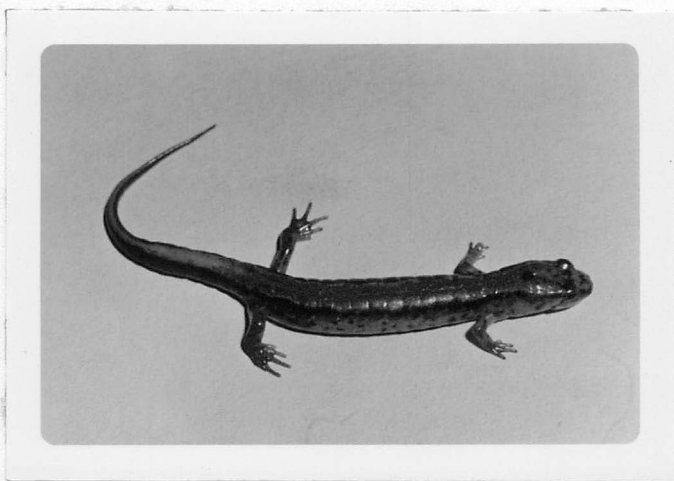


FIGURE 5

A COLOR VARIANT OF D. O. CAROLINENSIS

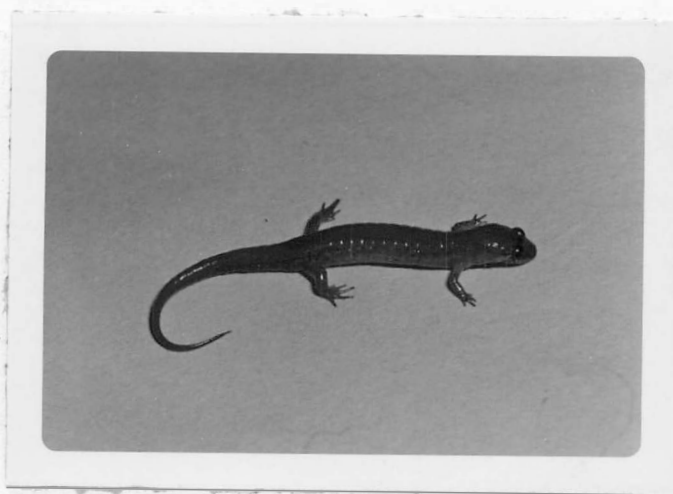


FIGURE 6

A COLOR VARIANT OF D. O. CAROLINENSIS

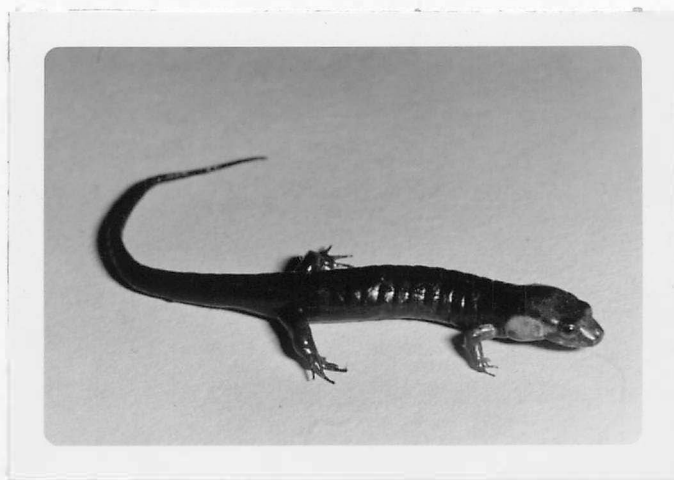


FIGURE 7

A COLOR VARIANT OF D. O. CAROLINENSIS

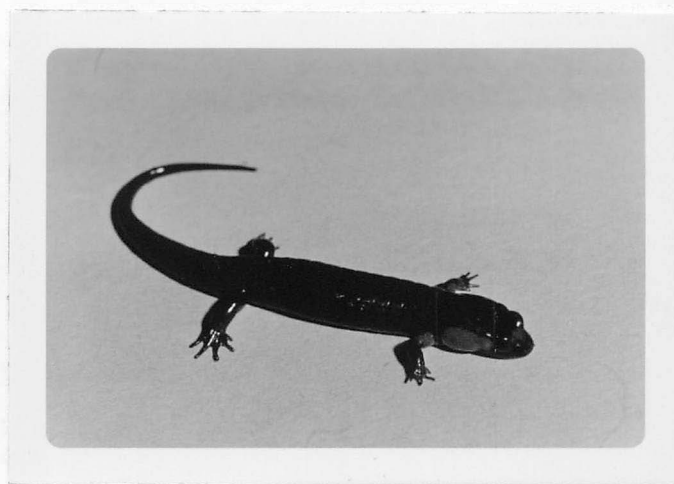


FIGURE 8

A COLOR VARIANT OF D. O. CAROLINENSIS



FIGURE 9

A COLOR VARIANT OF D. O. CAROLINENSIS

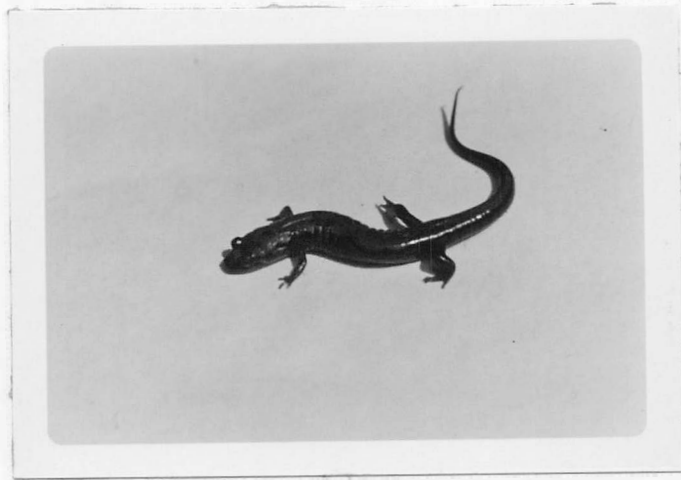


FIGURE 10

A COLOR VARIANT OF D. O. CAROLINENSIS



FIGURE 11

A COLOR VARIANT OF D. O. CAROLINENSIS

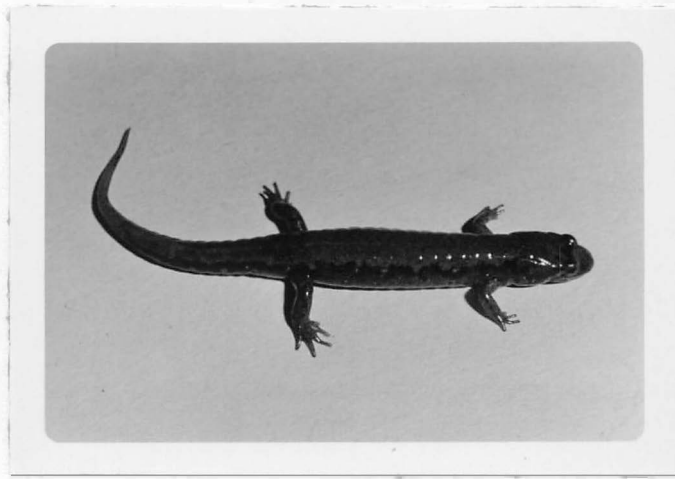


FIGURE 12

A COLOR VARIANT OF D. O. CAROLINENSIS

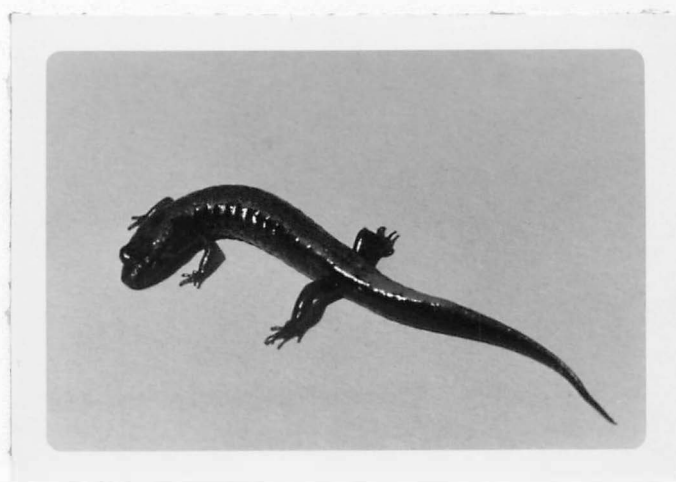


FIGURE 13

A COLOR VARIANT OF D. O. CAROLINENSIS

8. Broad, red, straight-edged stripe on dorsum.
9. Two straight lines down dorsum.
10. Black spots on chin and belly.
11. Scalloped band along dorsum.
12. Entire animal light orange in color.
13. Silver or brassy flecks along sides.
14. Mottled dorsum of various colors.

V. THE RANGES OF P. J. JORDANI AND D. O. CAROLINENSIS

Methods

A characteristic of all valid mimetic complexes is that the mimic occurs only where the range of its species overlaps the range of the model. Mimics should not appear in areas where sympatry does not exist since predators would have no experience with the undesirable characteristics of the models and thus would not be deceived by forms mimicking these models.

This rule of mimicry was tested first by making collections at approximately equal intervals along the east-west axis of the Park in an attempt to delimit the range of jordani within the Park. Observations were made from Davenport Gap and Mt. Sterling Gap at the eastern border of the Park to Gregory Bald, which is close to the western border. Elevations, color patterns, snout-vent lengths, and habitats were also recorded in this phase of the study. The populations of carolinensis were also studied with particular reference to their color pattern and the frequencies of forms resembling jordani were recorded. This phase of the research was supplemented by records of the ranges of the two species kept in the National Park museum.

Red-cheeked carolinensis have been reported by numerous investigators to occur outside the Park. These records in the literature, in addition to data supplied by correspondence with other investigators, have provided evidence for the occurrence and approximate frequency of red-cheeked carolinensis outside the Park.

Results

The areas investigated in this study are indicated in Figure 14, while the results of these investigations are summarized in Table I.

P. j. jordani was found to range from Mt. Sterling Gap westward to Gregory Bald. This is an extension of the range of jordani westward since Park records had previously reported it only to Spence Field. The limits of its altitudinal range remain from 2,750 feet to 6,643 feet. Except in the Chimneys-Indian Gay region, jordani was found to be uncommon below 4,000 feet. The unusual occurrence of this species at 2,750 feet will be discussed later.

Both jordani and carolinensis were found together in seven general areas. In four of these areas, red-cheeked carolinensis were also found with their supposed models which is what one would expect if this is a case of mimicry. The region of Blanket Mt. (4,609 feet), however, is particularly interesting since the red-cheeked carolinensis were found here but not jordani. Since this situation was unique, the mountain was approached first from the Elkmont (northeast) side and later from the Tremont (southwest) side by way of Jakes Gap. Thorough searching on both sides of the mountain yielded only a small sample of carolinensis, but the frequency of red-cheeked carolinensis in this sample was relatively high (25 per cent). P. glutinosus was common in this area and seemed to occupy the niches normally held by jordani at these elevations. Also, the specimens of carolinensis found on the Tremont side of the mountain were unusual in that they were found primarily under leaf litter or under logs in drier habitats than they normally occupy. D. fuscus, which seemed to be more

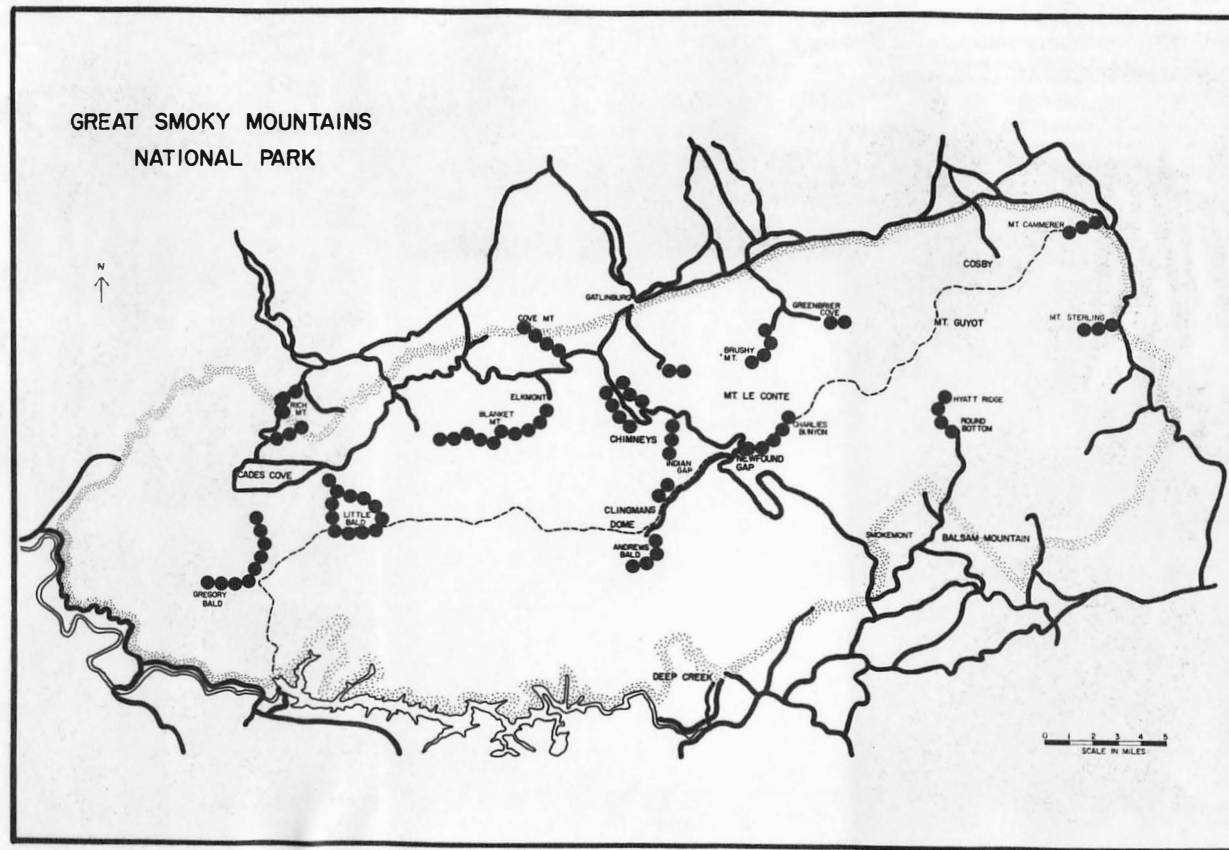


FIGURE 14

AREAS SAMPLED FOR *P. J. JORDANI* AND
D. O. CAROLINENSIS IN THE
 GREAT SMOKY MOUNTAINS

TABLE I

THE PRESENCE OR ABSENCE OF P. J. JORDANI AND D. O. CAROLINENSIS
IN FOURTEEN AREAS OF THE GREAT SMOKY MOUNTAINS NATIONAL PARK

Locality	Elevation	Number of <u>jordani</u>	Number of <u>carolinensis</u>	Number of red-cheeked <u>carolinensis</u>
Mt. Sterling Gap to Fire Tower	3,800 to 5,700	5	10	1
Davenport Gap toward Mt. Cammerer	2,000 to 4,700	0	9	0
Round Bottom to Hyatt's Ridge	3,160 to 5,000	5	45	0
Hiking Club Cabin toward Brushy Mt.	2,100 to 4,050	3	7	4
Newfound Gap to Charlies Bunion	5,200 to 5,900	8	22	5
Chimneys Overlook toward Indian Gap	3,750 to 4,250	3	38	8
Forney Parking Lot to Andrew's Bald	6,300 to 5,850	6	13	0
Fighting Creek Gap to Cove Mt.	2,300 to 4,000	0	0	0
Elkmont to Blanket Mt.	2,500 to 4,150	0	6	1
Tremont to Jake's Gap	1,800 to 4,000	0	6	2
Cades Cove to Spence Field	2,300 to 4,800	9	2	0
Cades Cove to Little Bald	2,300 to 4,800	1	0	0
Road to Rich Mt. Fire Tower	2,300 to 3,500	0	0	0
Cades Cove to Gregory Bald	2,300 to 4,750	1	0	0

common than carolinensis at all elevations, was found in the seepage areas at higher elevations normally associated with carolinensis.

Another interesting finding in this phase of the field study was the absence of red-cheeked carolinensis in the Hyatt's Ridge area. This region has been described by Hairston (1950) as a zone of intergradation between P. j. jordani and P. j. metcalfi. The Plethodons found in this area did present a confusing array of characteristics which included those of jordani and metcalfi. However, five red-cheeked Plethodons were found which could be positively identified as the subspecies jordani and had no characteristics of metcalfi. D. o. carolinensis were abundant in the area, but none of the forty-five individuals observed had red cheeks.

The presence of red-cheeked carolinensis outside the range of jordani has been reported by several investigators. The red-cheeked variants have been reported from the areas given in Table II.

If this is a case of mimicry, the frequent occurrence of red-cheeked carolinensis outside the range of jordani is inexplicable except by chance. As was noted above, the situation occurred within the Park at Blanket Mountain, where three red-cheeked individuals were found in a small sample of twelve carolinensis, also on Wayah Bald in North Carolina, where four of eleven carolinensis (36 per cent) collected were red-cheeked. The samples are too small, however, to provide an accurate estimate of the frequency of the red-cheeked variants in these areas.

The presence of "mimics" in low frequencies outside the range of jordani does not seem to conflict with the hypothesis of mimicry

TABLE II
RECORDS OF RED-CHEEKED CAROLINENSIS OCCURRING
OUTSIDE THE RANGE OF P. J. JORDANI

Location	Reported by	Elevation	Frequency of "Mimics"
Wayah Bald, North Carolina	Brimley (1928)	5,200	2 of ?
Wayah Bald, North Carolina	Pope (1928)	5,200	2 of 7
Wayah Bald, North Carolina	Huheey (1961) and Brandon	5,150	2 of 4
Highlands, North Carolina	Brimley (1928)	3,800	?
Highlands and Vicinity, North Carolina	Gordon		Probably less than 1%
Highlands and Vicinity, North Carolina	Hairston (1949)	3,800	3 of 63
Nellie, North Carolina (Haywood County)	Brimley (1928)	?	?
Black Mountains, North Carolina	Hairston (1949)		2 of 300
Warwoman Dell, Georgia	Huheey (1961) and Brandon	?	?

(Huheey, 1960). One would expect the mutant gene or genes for the red-cheeked condition to be passed to populations outside the range of jordani if the populations of carolinensis are continuous or were continuous during the time the mimetic pattern was being evolved. However, the frequency of the mimetic pattern could not be high since predation pressure upon the mimics would be as great as that upon non-mimetics.

The frequency of red-cheeked carolinensis in the region of Highlands, North Carolina, reported by Gordon and Hairston, seems to be of the magnitude one would expect if the manifestation of this characteristic resulted from gene flow from the Smokies. However, the elevation of these collecting sites reported in Table II may be important factors in the frequency of the "misplaced mimics." This point will be considered in greater detail later.

Earlier it was mentioned that some investigators feel that carolinensis not only mimics jordani in the Great Smokies but also mimics the red-legged salamander, P. j. shermani, of the Nantahala Mountains in North Carolina. Since Wayah Bald is located within the restricted range of shermani, it seems unusual that no red-legged carolinensis have been reported from this area although three different investigators have found red-cheeked carolinensis in the region. Bishop (1947) mentioned that he received a series of red-legged carolinensis collected from Tusquitee Bald, which is within the range of shermani. However, no mention was made of the frequency of this variant in the region. Brimley (1928) originally described this red-legged variation in carolinensis from an individual collected in Haywood County, North Carolina. This is outside the range of shermani.

Of the 587 carolinensis recorded as to color pattern in this study, twelve were found to have red legs. All of these observations were made within the Great Smokies. Eleven of these had only red forelegs, while one had splotches of red on the proximal portion of all legs. This low frequency (2 per cent) is what one would expect for mimics outside the range of their models. However, if it can be shown that the frequency of red-legged carolinensis is also low within the range of shermani, while the frequency of red-cheeked carolinensis is high at upper elevations outside the range of jordani, then mimicry seems to be a poor hypothesis for this resemblance between unrelated species.

In testing the second established rule of mimicry that resembling forms must occupy the same area, it has been found that exceptions to this rule exist in the supposed carolinensis-jordani mimetic complex. These exceptions exist both within the Park and outside the Park. Gene flow could account for a low frequency of mimics outside the range of the models. However, the data indicate here that in some instances the red-cheeked carolinensis may be in higher frequencies outside the range of jordani than one would expect from such a diffusion of genes. This would indicate then that some factor other than mimicry is involved in the evolution of the cheek coloration in carolinensis.

VI. DETERMINATION OF THE RELATIVE ABUNDANCE OF THE SUPPOSED MIMICS AND MODELS

Methods

It has been suggested that the slime exuded by jordani may be the unpalatable characteristic which reduces the predation pressure upon this supposed model (Huheey, 1960). Since carolinensis does not possess this characteristic or any other perceivable undesirable feature, it seems that, if this is mimicry, it would be Batesian mimicry.

In order for mimicry to be effective in presumed Batesian mimetic complexes, the mimic must be rare as compared to the model. Also, if mimicry does exist among resembling forms, a high population density of models should support relatively high frequencies of mimics within the mimicking species. It should be possible then to find a correlation between the frequency of red-cheeked carolinensis in the total carolinensis population and the density of the jordani population in a given area.

These two requisites of the mimicry hypothesis were tested in this study by sampling the carolinensis and jordani populations at various elevations. Eight belt transects were used in this sampling and were placed at elevations ranging from 2,950 feet to 5,350 feet. It was found that it was impossible to space these transects at equal altitudinal intervals since suitable sites could not always be found at the desired elevation.

The transects were usually placed along dry gullies and varied in length depending upon the suitability of the area. In all transects, twelve quadrats were picked at random for sampling. Each quadrat was

twenty-five feet by twenty-five feet and was placed in the gully in such a manner that the gully was included in the quadrat with the remainder of the quadrat extending onto the forest floor. Where the gullies were deep, the width of the gully and only one side of the gully were included in the quadrats. It might seem that this method would favor the collection of large numbers of carolinensis while few jordani would be sampled. Since the gullies averaged approximately nine feet in width, the remainder of the quadrat extended far enough onto the forest floor to insure adequate sampling of jordani. This method also seems justified since jordani were often found in the gullies.

The limits of the square quadrats were set by a heavy cord. The cord was marked off in feet so that the salamanders could be recorded in respect to their distances from the gully.

All of the transects were placed in the general area between Indian Gap and the Chimneys Campground. Data recorded in this study included elevations, species collected, color patterns, snout-vent lengths, habitat descriptions, distances from the gully, and general descriptions of the areas within the quadrat. An aneroid altimeter was used in determining elevations.

Description of the Transects

Transect number one was located at Indian Gap, the type locality of P. j. jordani. The vegetation type of the area is spruce-fir. The transect followed an eroded gully which varied in width but averaged approximately seven feet in width. Flat rocks, a few boulders, and fallen trees were found throughout the length of the gully, while the

remainder of the transect extended onto the moss-covered forest floor. Although the gully was primarily dry when sampled, a few springs fed it in places. The transect had a southwest exposure and was located at an elevation of 5,200 feet.

The second transect sampled was also located at Indian Gap and paralleled the first. It also ran the length of a dry gully and extended from the Appalachian Trail to the Indian Gap-Chimneys trail. The description of the first transect also applies to this transect except that the gully was approximately three feet wide in the second transect. The carolinensis sampled in these two transects were found primarily under rocks in the gullies, but some were found under bark and logs on the forest floor which is typical of the jordani habitat.

Transect number three was the least productive of the eight transects sampled. It followed the Indian Gap-Chimneys trail at an elevation of 4,350 feet and had a northwest exposure. Rhododendron thickets and dry conditions along the trail seemed to be the causes for the small number of salamanders collected from this transect.

The fourth transect sampled was at 3,800 feet and followed a gully which had flowing water at the time the sampling was conducted. The slopes of this northwest facing transect were characterized by many seepage areas. D. f. fuscus and D. quadra-maculatus were abundant in these wet habitats, while the specimens of carolinensis collected were found away from the gully in drier habitats. Rhododendron maximum and Leucothoe editorum interfered with optimum habitat conditions for jordani in some areas. The gully varied in width from five feet at

the upper portion of the transect to fifteen feet at the base of the transect. The tree stratum of this area consisted primarily of Betula alleghaniensis and Tilia heterophylla.

Transect number five, located at 3,900 feet, was more uniform throughout its length than the previous transect and seemed to offer nearly optimum habitat conditions for jordani and carolinensis at this elevation. The transect was similar to others in that it followed a spring-fed gully on a sheltered slope. The forest type could best be described as cove-hardwood with Aesculus octandra and Betula alleghaniensis predominating. The presence of fuscus and quadra-maculatus in the wet gully of this transect undoubtedly accounts in part for carolinensis being restricted to the terrestrial habitat normally associated with jordani. The transect had a northeastern exposure.

Transect number six extended from the Indian Gap-Chimneys trail near the West Prong of the Little Pigeon River and followed another eroded gully. The gully carried only run-off water and was dry throughout its length at the time of sampling. This transect was located at an elevation of 3,600 feet and had a western exposure. Tsuga canadensis, Tilia heterophylla, and Aesculus octandra dominated the tree stratum. Rhododendron maximum also was common along the rocky slopes of the gully. The gully varied in width from four feet to eight feet.

Transects seven and eight were located in the vicinity of the Chimneys Campground and were parallel to each other. Since they were similar, they will be considered together. Both were located at an elevation of approximately 3,000 feet in rock-strewn gullies. The

gullies were deeply cut and were generally wider than the others sampled. Both transects were nearly ideal habitat areas for the two species of salamanders. The slopes of the gullies were covered with rocks twelve to eighteen inches in diameter, and the forest floor had a thick leaf litter on top of two to three inches of soil. Fallen trees and tree branches were common in the area sampled. The forest type could again be classified as cove-hardwood with Tsuga, Aesculus, and Tilia predominating.

These two transects were unique in that they yielded the greatest number of jordani of all transects sampled. This is unusual since the elevation is at the lower altitudinal limit of jordani. The entire cove seemed atypical of this elevation. Desmognathus wrighti, a salamander normally restricted to higher elevations, was found in these transects, while fuscus, a species common at lower elevations, was not found. The carolinensis sampled here were more melanistic than those in other areas. This is a characteristic of the species at upper elevations. The vegetation of this area was not sampled, but it is suspected that it too would include species found primarily in northern hardwood or spruce-fir forest types.

The findings from this area, then, strongly support the contention that generalizations regarding the fauna and flora at various elevations may be misleading and that factors such as cold air drainage or exposure may offset other factors correlated with altitudinal differences.

Results

The data obtained from sampling the eight transects are summarized in Table III.

TABLE III

RELATIVE ABUNDANCE OF JORDANI, NON-MIMETIC CAROLINENSIS,
AND MIMETIC CAROLINENSIS IN EIGHT TRANSECTS

Transect Number	Locality	Elevation	Numbers of salamanders			Per cent of <u>jordani</u> in Transect	Per cent of "mimics" in <u>D. o. c.</u> population
			<u>P. j. j.</u> Models	<u>D. o. c.</u> Mimics	Non-mimetics		
1	Indian Gap	5,200	21	9	41	29.6	18.0
2	Indian Gap	5,200	21	9	36	31.8	20.0
3	Indian Gap to Chimneys trail	4,350	6	5	19	20.0	20.8
5	Indian Gap to Chimneys trail	3,925	15	20	77	13.4	20.6
4	Indian Gap to Chimneys trail	3,825	8	12	43	12.7	21.8
6	Indian Gap to Chimneys trail	3,600	27	9	24	45.0	27.3
7	Chimneys Campground	3,000	62	22	39	50.0	36.1
8	Chimneys Campground	2,950	56	42	50	37.8	46.7

The data concerning the relative numbers of jordani and red-cheeked carolinensis are graphically illustrated in Figure 15. In six of the eight transects the number of red-cheeked carolinensis was less than the number of models. It should be remembered that if Batesian mimicry is to be effective, the mimics should be rare as compared to the models. Transects three, four, five, and eight undoubtedly do not meet this basic rule of mimicry. The others would be questionable depending upon one's interpretation of the term "rare." If the numbers of mimics in the questionable transects are expressed as percentages of the total jordani-red-cheeked carolinensis population, these values for transects one, two, six, and seven are 30 per cent, 30 per cent, 25 per cent, and 26 per cent, respectively. It seems unlikely that a mimic which is one-third as plentiful as its model could be considered rare in the population.

Before drawing definite conclusions concerning the validity of the mimicry hypothesis as it relates to this rule, an important point should be considered. In general, it may be stated that the number of mimics in any Batesian mimetic complex should be low to have an effective mimetic relationship. However, it must be borne in mind that the effectiveness of mimicry does not have to be 100 per cent in order to give the mimetic individuals a selective advantage over non-mimetics and that the effectiveness of mimicry will tend to vary inversely with the mimic-model ratio (Huheey, 1960). The number of mimics which can be effectively supported by models in a mimetic complex seems to depend upon two important factors (Brower, 1960). First, the distastefulness of the model is important in educating predators. If the undesirable quality is extremely

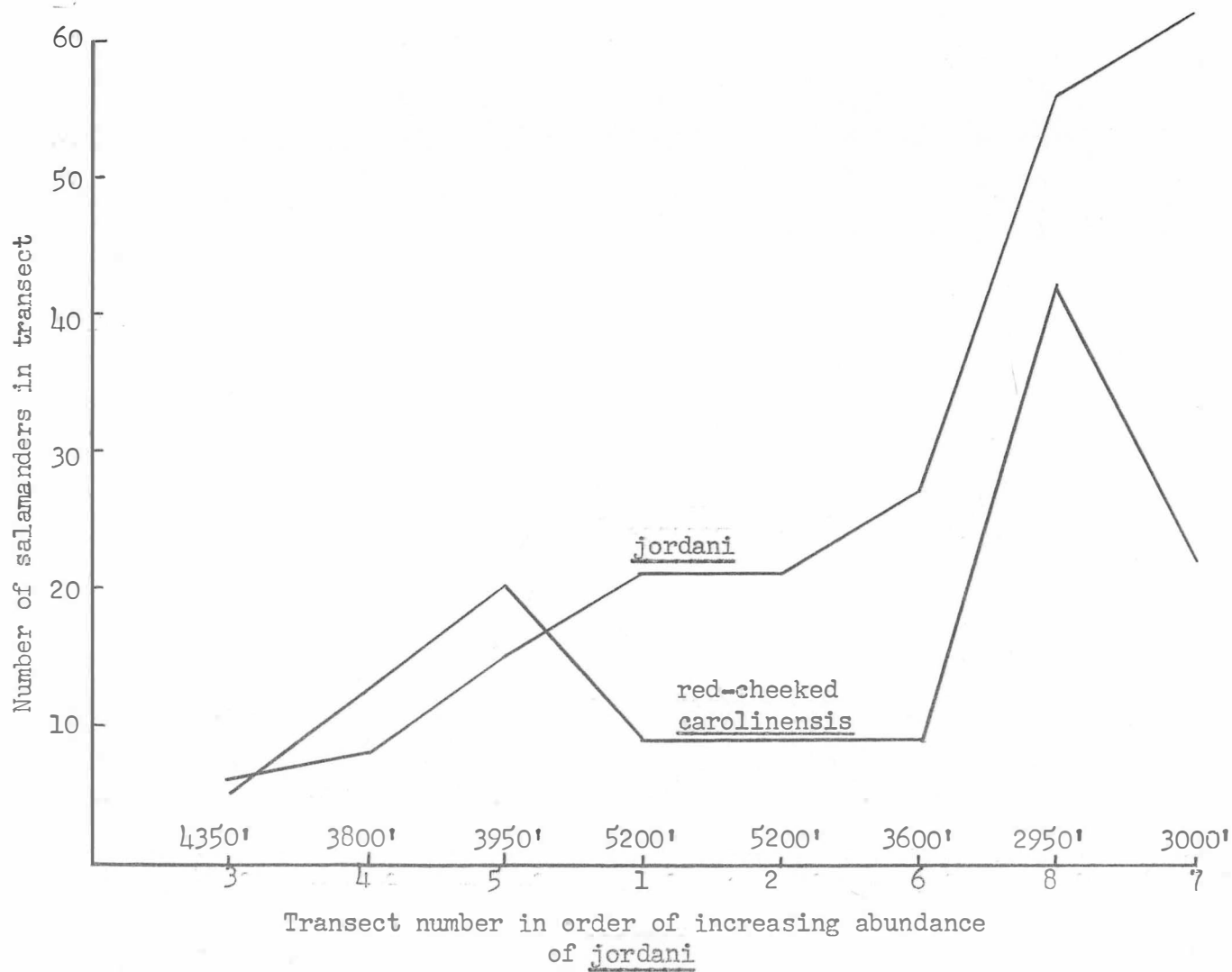


FIGURE 15

RELATIVE ABUNDANCE OF JORDANI AND
RED-CHEEKED CAROLINENSIS

obnoxious, predators would be discouraged from experimenting with the mimetic individuals and a high proportion of mimics could exist in a complex and still gain survival value. Also, the degree of resemblance between mimic and model would determine the frequency of predator deception. If the resemblance were poor, most predators would not be deceived and the mortality rate among mimics would be high.

Brower (1960) has experimentally tested the problem of mimic proportions as they relate to the effectiveness of mimicry and has found that in near perfect mimetic complexes, where the model is extremely distasteful and the resemblance between model and mimic is perfect, the complex can actually support more mimics than models and still be effective.

Therefore, before one can conclude with certainty whether the number of red-cheeked carolinensis found in this study are in reasonable proportions to the number of jordani, to satisfy the hypothesis of relative rareness, it seems essential to know: (1) the degree of unpalatability possessed by jordani, (2) the effectiveness of the mimetic pattern in deceiving the predator, (3) the proven natural predator which can be used in testing (1) and (2).

It was mentioned earlier that, if mimicry is operating between carolinensis and jordani, there should be a direct correlation between the density of jordani in an area and the frequency of red-cheeked individuals in the carolinensis population in the same area. To test this, the number of jordani found in each transect was plotted against the per cent of carolinensis having the mimetic pattern. The regression

line fitted to these data indicates a positive correlation as is shown in Figure 16.

Since the samples in this study were of unequal sizes, tests of significance based upon percentages were not valid. To avoid this, a chi-square test was employed in which the absolute numbers of red-cheeked carolinensis and normal carolinensis were used. The null hypothesis in this analysis was that the proportion of red-cheeked individuals in the carolinensis population was independent of the frequency of jordani and of any other factor. The probability that the frequency of red-cheeked carolinensis is independent of the proportion of jordani in the transects or of any other factor was found to be less than 0.005 ($\chi^2 = 26.15$, d.f. = 7).

This indicates, then, that some factor or factors is responsible for a positive correlation between these two sets of values. This factor could be mimicry, but other factors in the environment could not be discounted as possibly influencing the frequency of jordani and red-cheeked carolinensis in the same area.

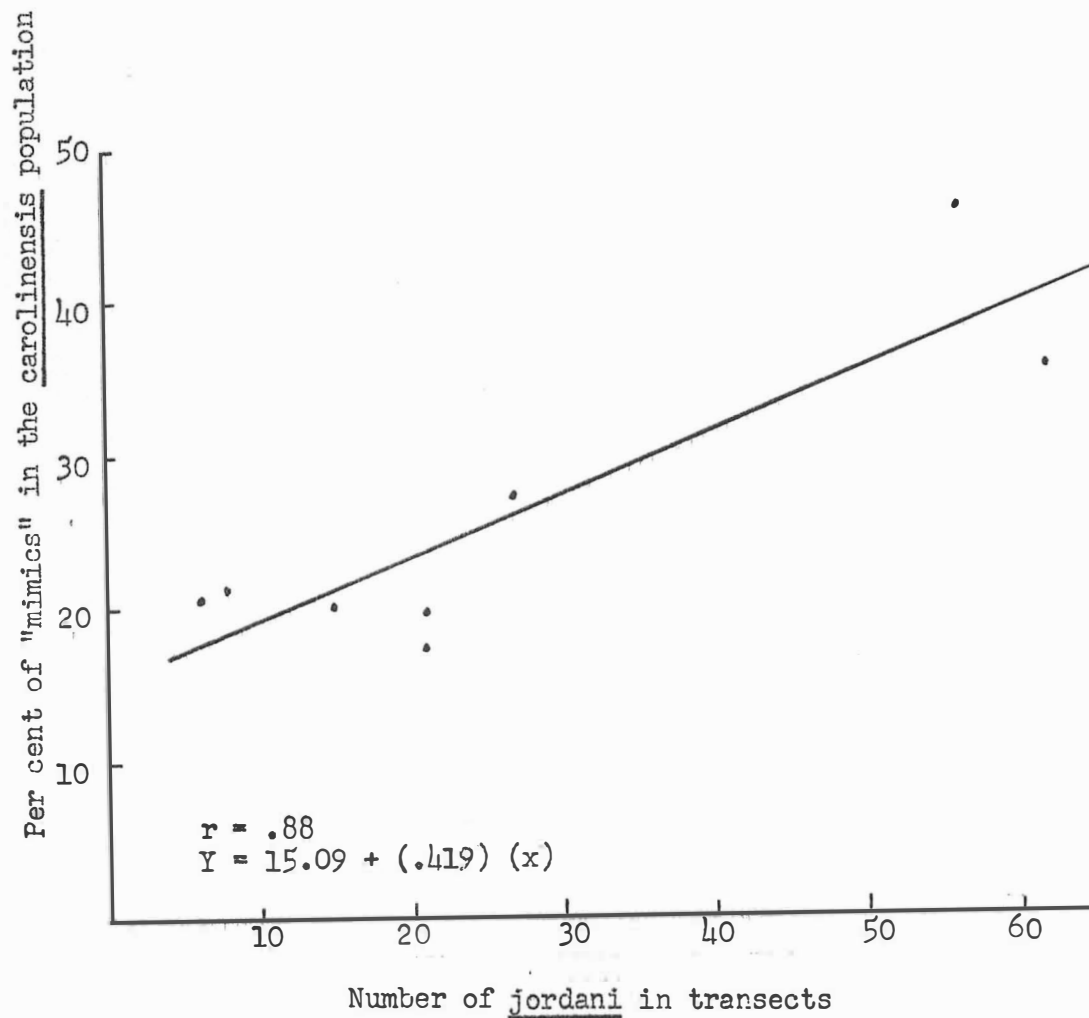


FIGURE 16

CORRELATION BETWEEN THE NUMBER OF JORDANI IN TRANSECTS
AND THE PER CENT OF RED-CHEEKED CAROLINENSIS
IN THE TOTAL CAROLINENSIS POPULATION

VII. FEEDING EXPERIMENTS

In the study of any suspected mimicry complex, the determination of a natural predator which discriminates between the supposed mimics and non-mimetics is of utmost importance. Many other criteria of valid mimetic complexes have their exceptions which make a conclusive decision difficult or impossible. However, if one could ascertain the natural predators of the models and mimics by field observation or stomach analyses and then prove the discriminating behavior of this predator, he then could greatly strengthen any decision concerning the supposed mimetic complex. Such an approach was attempted in this study.

Hairston (1949) has stated that "salamanders are fed upon by almost any carnivorous species that is able to catch them." Furthermore, the salamanders themselves seem to feed upon any organism that is within a reasonable size range. This implies that many predators could be considered potential predators upon carolinensis and jordani. However, in considering the altitudinal ranges, activity time, stomach analyses, and field observations of the predators, the list of logical predators was narrowed down to Thamnophis sirtalis sirtalis, Blarina brevicauda, Gyrinophilus danielsi, and Desmognathus quadra-maculatus. These predators were used in feeding experiments to determine their ability to discriminate between jordani and red-cheeked and normal carolinensis.

Thamnophis sirtalis sirtalis

Thamnophis sirtalis sirtalis, the eastern garter snake, has been reported by King (1939) to range from 1,000 feet to 6,000 feet in the

Great Smokies. This garter snake was observed during this study at elevations as high as 5,200 feet. In personal correspondence, R. E. Gordon has related two accounts of garter snakes disgorging P. j. melaventris. This salamander is sufficiently similar to P. j. jordani for one to conclude that Thamnophis undoubtedly is a natural predator upon jordani.

Preliminary feeding experiments were first attempted with Thamnophis to determine their feeding behavior toward jordani and carolinensis. Five snakes were used in this phase of the experimentation. The snakes were kept in glass laboratory cages until the time of feeding. At that time a snake was isolated from the others and presented a normal carolinensis. After the snake exhibited some feeding response to this salamander, a jordani was then presented. Following this, a jordani and normal carolinensis were presented simultaneously at equal distances from the snake to determine a possible preference in the feeding behavior of the snake. In the first feeding trials, all snakes ate all salamanders introduced and showed no preference between species. When the two species of salamanders were presented simultaneously to the snake, the snake invariably attacked and ate the first salamander which moved. The size of the salamanders did not seem to be a factor in these experiments. The second feeding trial was conducted six days later. In this trial, three snakes exhibited the same feeding responses to the salamanders as were recorded during the first trial. Two of the snakes, however, failed to eat any of the salamanders introduced. Within a week these two snakes had died. Two weeks from the last trial, a third snake

died. At the time it was not known whether these snakes died as a result of deleterious qualities possessed by the salamanders or whether some other factor was responsible for their deaths.

The death of a predator from eating an undesirable prey would in no way add to or detract from the effectiveness of the mimetic complex and thus would not have an important bearing upon determining the effectiveness of mimicry with that predator. However, if certain deleterious characteristics of prey could be demonstrated, it would be possible that other predators with better sensory perception would be aware of the undesirable factor and thus would avoid the prey. For this reason, a second experiment was designed to demonstrate possible deleterious qualities of either jordani or carolinensis.

In this second feeding experiment, twelve snakes were divided into two groups with six snakes being fed only carolinensis and six only jordani. The snakes were fed two salamanders at each feeding and were fed once a week for five weeks. During this time two snakes died. One died from unknown causes while the other was destroyed after it developed a fungus infection on the upper jaw and could not eat. Both of these snakes were in the group which fed only on carolinensis. It seems unlikely that the death of a single snake could be attributed to its prey. It is possible that the snakes in the first feeding experiments may have died from excessive heat since the room in which they were kept became quite hot during the afternoons.

A final series of feeding experiments was conducted with Thamnophis as the predator. The experimental design of these experiments was

patterned after that of Brower (1958; a, b, c). Eight snakes were used in these experiments; four were used as controls and four were used as experimentals. The experimental animals differed from the control animals in that the former were given jordani and normal carolinensis, while the controls were given red-cheeked carolinensis and normal carolinensis.

Each snake was fed two salamanders at each trial. A random number table was used to determine the order of presentation of salamanders. An odd number drawn at random meant that a jordani was to be fed first and was to be followed by a normal carolinensis. An even number chosen at random indicated that a normal carolinensis was to be introduced first. The same method was used in feeding the controls except that red-cheeked carolinensis replaced the jordani. Thus a single salamander was presented to the garter snake at a time and was followed by a second after the snake had had ample time to exhibit some pattern of behavior toward the first salamander.

The four patterns of behavior used in these feeding experiments included: eaten, (E); killed or seriously injured, (K); bitten but not seriously injured, (B); and not touched, (NT). By "not seriously injured," it is meant that the animal would probably be able to survive and reproduce under natural conditions.

In Brower's studies of the Monarch-Viceroy butterfly complex, models (Monarchs) and non-mimetics (Papilio glaucus and P. palamedes) were fed to an experimental group of four Florida jays, while non-mimetics and mimics (Viceroy) were fed in couplets to a control group of four birds. After the experimental birds had established a reliable

pattern of behavior of rejecting the models, mimics were then presented to them. The results of this study showed that the experimental birds did not eat any of the models presented to them. When the mimics were substituted for the models at intervals, they also were not eaten. The non-mimetics, when fed in couplets with either the models or the mimics, were eaten in every trial. The behavior of the predators in these experiments thus indicated that the mimetic complex was effective when exposed to predation by Florida jays under laboratory conditions.

The results of this series of feeding experiments with Thamnophis are given in Figures 17 and 18. It can be seen that the predators were relatively consistent in eating all salamanders presented to them. Snakes C-10, C-12, E-2, and E-6 all failed to attack the salamanders at some time during the trials. It seems, however, that there were factors involved in this failure to eat other than any distasteful quality of a particular salamander. Snake C-10 was blind (shedding its skin) during the sixth trial. Snake C-12 stopped eating at the third trial and was replaced by another snake (C-1) after the sixth trial. If this failure to eat denoted a reaction to unpalatable food and if the snakes could discriminate between the salamanders, one would expect a snake to eat the normal carolinensis and reject the jordani in a single trial. As can be seen from Figure 18, this did not happen. Both salamanders were always rejected when the snakes did not eat. In trials seven and eight, red-cheeked carolinensis were substituted for models in the experimental group. Although no pattern of behavior warranted this switch, it was done merely as an attempt to note any change in behavior of the predators

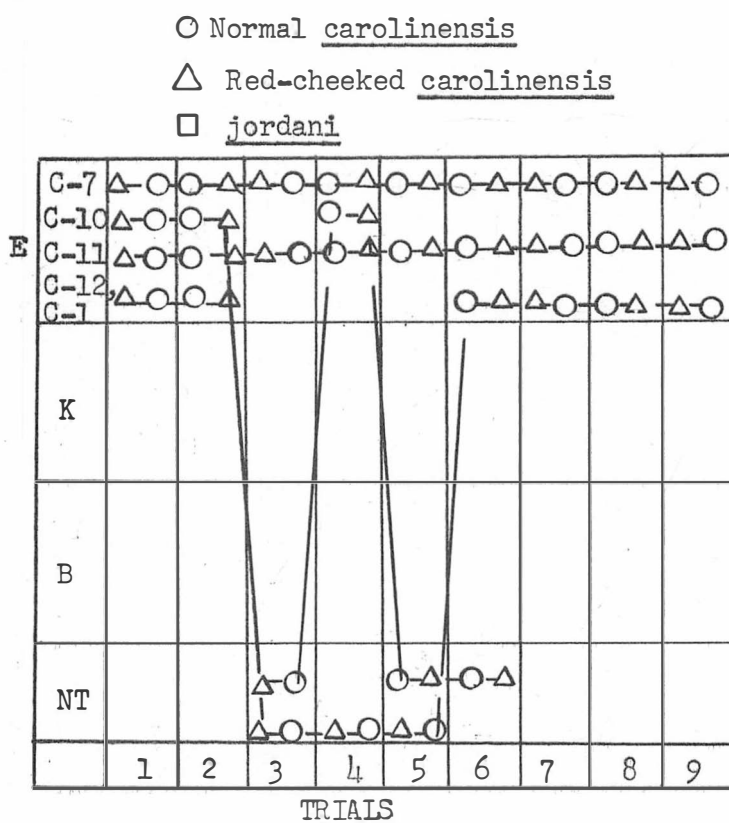


FIGURE 17

FEEDING EXPERIMENT RESULTS OF THE CONTROL
 GROUP OF THAMNOPHIS SIRTALIS

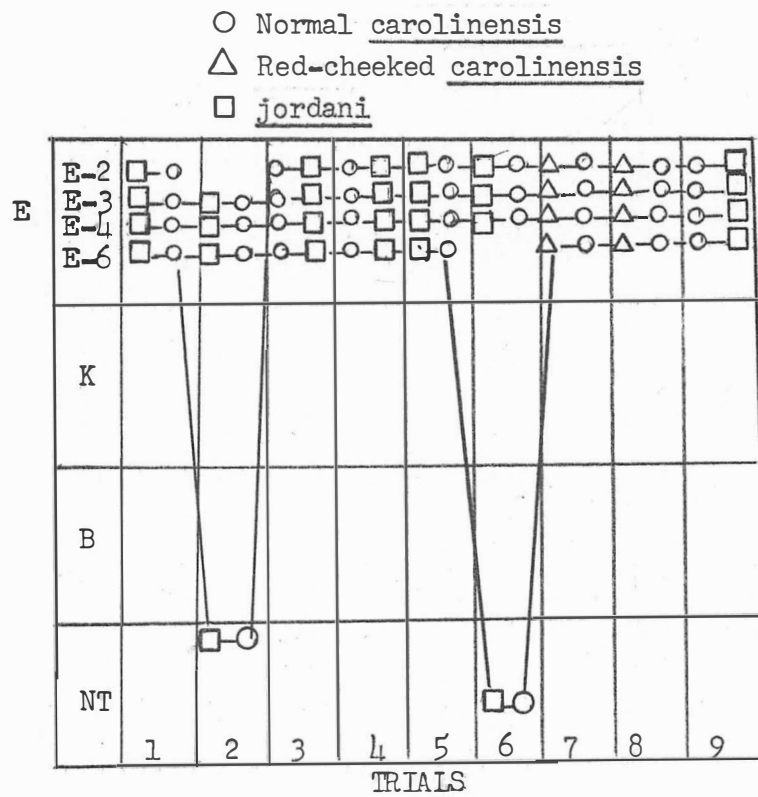


FIGURE 18

FEEDING EXPERIMENT RESULTS OF THE EXPERIMENTAL
 GROUP OF THAMNOPHIS SIRTALIS

not expected under the rules of mimicry. The red-cheeked carolinensis were eaten as readily as the other salamanders.

In these studies with garter snakes, the two species of salamanders exhibited conspicuously different defense mechanisms. The carolinensis were much more aggressive than jordani and often bit the upper jaw of the snakes. This same aggressive behavior was often noted when collecting the salamanders. The tails of carolinensis also broke off much more readily when attacked than did those of jordani. However, none of these mechanisms seemed to be effective in preventing predation under laboratory conditions.

In summarizing these feeding experiments, it seems that 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 the salamanders are preyed upon by Thamnophis sirtalis sirtalis in captivity.

Blarina brevicauda

It is known that shrews feed at least in part upon salamanders. Blarina brevicauda, the large short-tailed shrew, would seem to be the most logical species to test as a predator since it is the largest of shrews and also is abundant in the ranges of jordani and carolinensis (Komarek and Komarek, 1938).

Aluminum Sherman live traps were used to trap Blarina in the Great Smoky Mountains at Indian Gap (5,300 feet), Greenbrier Cove (2,400 feet), and in a cove near the West Fork of the Little Pigeon

River (3,200 feet). Shrews were caught in the latter two areas.

The first shrew captured was used in preliminary feeding experiments to determine whether it could be considered a predator upon salamanders and to determine a suitable feeding program from its behavior. In these experiments, the shrew was placed in a glass aquarium ($9\frac{1}{2}$ " x $9\frac{1}{2}$ " x $17\frac{1}{2}$ ") which had been divided into two compartments. A nest of leaf litter was prepared in one compartment. The other compartment served as a feeding chamber and had no leaf litter in it. One jordani and one normal carolinensis of approximately equal size were secured by three inch strings to a board at the far end of the feeding chamber. Strings of this length were used to enable the salamanders to display possible defense mechanisms. It was necessary to secure the salamanders since the shrew would drag the salamanders back to its nest and eat them unnoticed. The shrew reached the feeding chamber through an opening in the partition equidistant between the two salamanders. The position of the salamanders (right or left side) was picked at random for each trial.

Nineteen feeding trials were conducted with this shrew. Of seventeen observed trials, carolinensis was attacked and killed first nine times, and jordani was attacked and killed first eight times. Twice the shrew attacked and killed the salamanders unnoticed. During these trials the shrew exhibited no ability to discriminate between the two species of salamanders and seemed to attack the first salamander it came upon. If the shrew attacked the tail of jordani, it was obviously disturbed by the slime which exuded from the tail. Its usual behavior

pattern after such an encounter was to withdraw, shake its head, and rub its snout with its forelegs. However, invariably the shrew returned to the head of the jordani and began eating at this point. At no time did the shrew fail to kill and partially eat the jordani. During four trials the shrew ate all of the jordani except the tail. During the other trials, both salamanders were eaten in entirety.

The shrew exhibited other behavior patterns which are of interest. Shortly after its capture, the shrew was fed recently killed Peromyscus, earthworms, and various types of insects. It normally ate one Peromyscus per day. After feeding experiments were initiated, however, the shrew seemed to prefer the salamanders and rejected the mice.

The shrew seemed to have very poor vision and to rely almost entirely upon olfactory perception of the prey. Immediately after a salamander was placed in the cage, the shrew became excited, actively sniffed the cage, and ran around the cage until it found the salamander. Upon finding the salamander, the shrew would bite it, withdraw, and then attack again. This was repeated several times until the salamander was killed.

After preliminary feeding experiments had been concluded, more elaborate experiments with six Blarina were conducted following Brower's experimental design. The shrews were caged in two large glass aquaria. Again, each shrew had access to two compartments, one a nesting compartment and the other a feeding chamber. A small amount of wood shavings was used as nest material so the shrews could not conceal themselves.

It was soon found that collecting enough natural food for six

shrews for feeding between trials was a prodigious task. Because of this, the shrews were gradually shifted to a diet consisting of one part raw hamburger and one part oatmeal. The shrews would eat this mixture but seemed to prefer natural foods. This hamburger mixture was kept in the cages of the shrews at all times.

The same feeding procedure was followed with Blarina as was used with Thamnophis. Three shrews were used as controls and three served as experimentals. The salamanders used in this series of experiments, however, were not tied but instead were merely dropped into the feeding chamber. The results of these feeding experiments are given in Figures 19 and 20.

Shrews of the control group (Figure 19) performed as one would expect. Since these animals had had no experience with jordani, one would not expect them to reject the red-cheeked carolinensis. In the experimental group, however, none of the shrews failed to kill the jordani at any trial. If these animals were aware of some undesirable characteristic in the jordani and if they could distinguish jordani from the normal carolinensis, one would expect the shrews to reject the supposed models after the first few trials. In Brower's studies, the predators established a consistent pattern of behavior of rejecting the model. After such a behavior pattern was established, the mimics were then introduced. They too were rejected.

In this study, red-cheeked carolinensis were introduced to the experimentals in place of jordani in trials nine, ten, thirteen, and sixteen to determine possible discrimination between jordani and

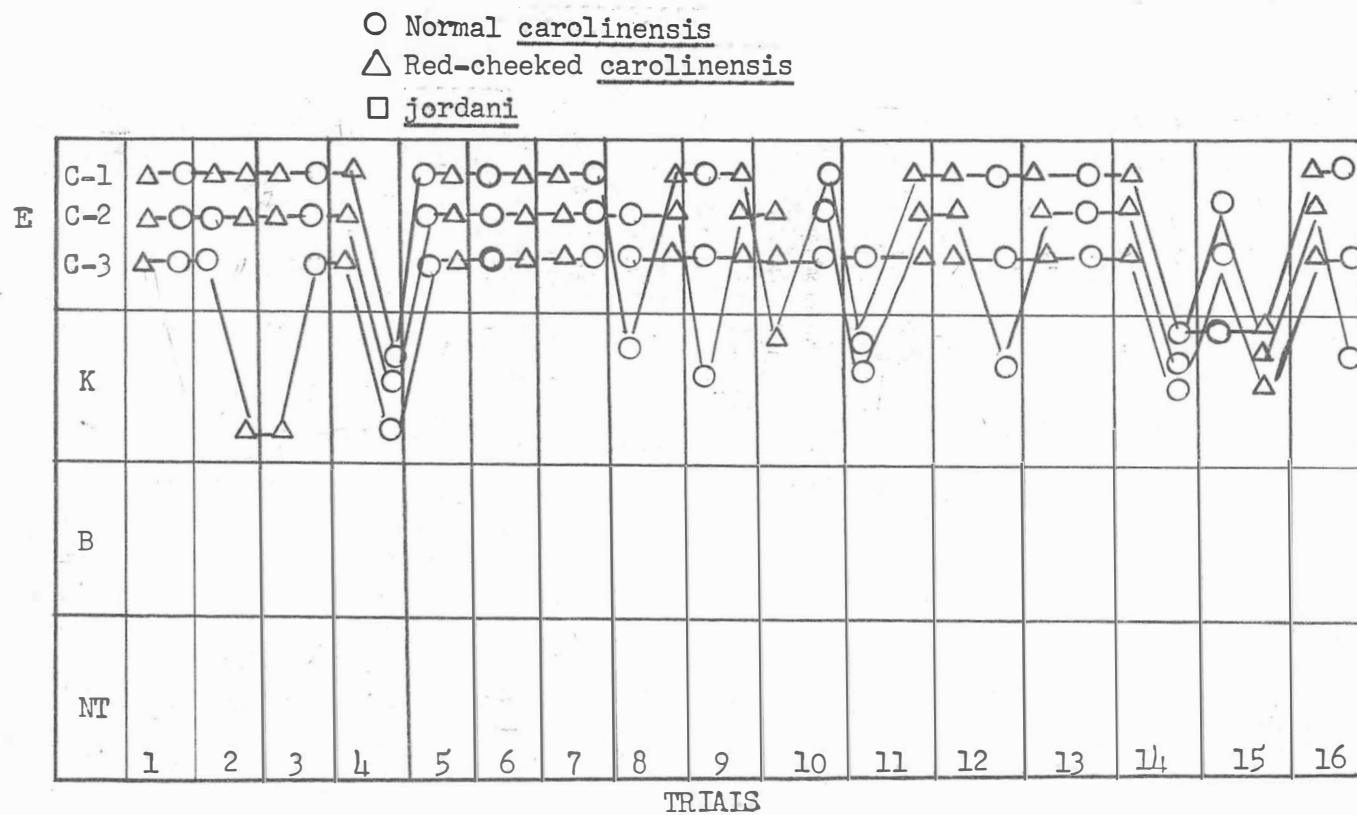


FIGURE 19

FEEDING EXPERIMENT RESULTS OF THE CONTROL
 GROUP OF BLARINA BREVICAUDA

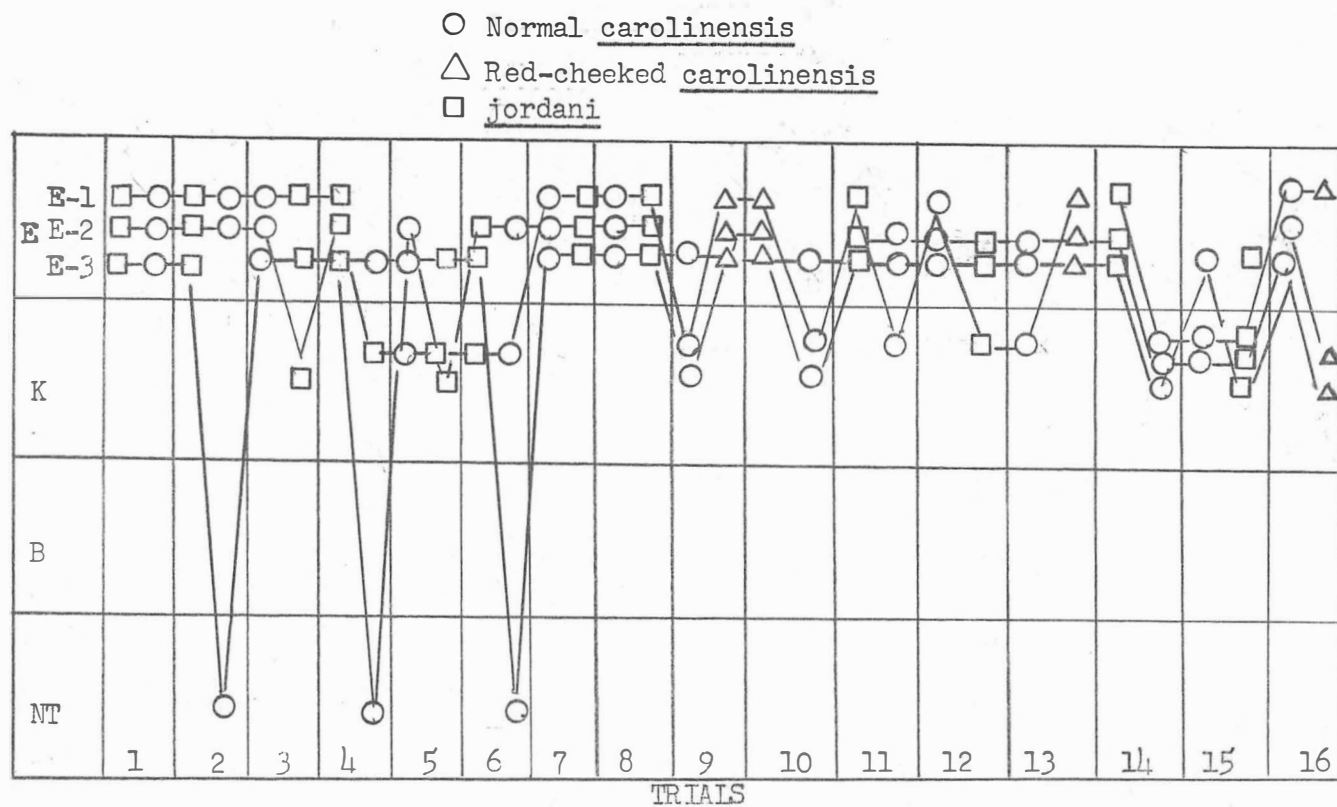


FIGURE 20

FEEDING EXPERIMENT RESULTS OF THE EXPERIMENTAL
 GROUP OF BLARINA BREVICAUDA

red-cheeked carolinensis by the shrews. As was noted with Thamnophis, the red cheeked carolinensis were eaten as readily as the jordani.

It is obvious that Blarina does not discriminate between jordani and either the red-cheeked or normal carolinensis. It has been demonstrated that the slime of jordani in some instances does disturb Blarina, but the undesirability of this characteristic is not great enough to prevent predation under laboratory conditions. Even if Blarina did reject jordani because of the slime, it is extremely doubtful that the red-cheeked carolinensis would be rejected also because the apparently poor vision of the predator would probably prevent it from recognizing the similarities between the supposed model and the supposed mimic.

Gyrinophilus danielsi danielsi and Desmognathus quadra-maculatus

Several investigators have reported that the two primitive salamanders, G. danielsi and D. quadra-maculatus, prey upon jordani. Huheey (1961) has reported an observation of quadra-maculatus disgorging a jordani. J. T. Wood has made observations (personal correspondence) of danielsi disgorging jordani. During this study it was noted that both quadra-maculatus and danielsi often fed upon carolinensis and jordani when kept for a time with these species in collecting containers.

Feeding experiments were conducted with danielsi and quadra-maculatus to test their discriminating ability between jordani and normal carolinensis. These two predators were placed with carolinensis and jordani in screen cages which had sloping tin strips along the tops of the cages to prevent the escape of salamanders. Each cage measured 18" x 18" x 24" and was placed on the forest floor at Indian Gap in the

Great Smokies. The bottoms of the cages were covered with moss. Ten quadra-maculatus were placed in one cage with six jordani and six carolinensis. The same number of jordani and normal carolinensis were placed in the other cage with ten danielsi. All carolinensis and jordani were of approximately equal size.

These cages were observed at intervals of approximately five days to determine the number of salamanders eaten and to add more salamanders to replace those eaten. From August 4 to August 27, quadra-maculatus ate eight jordani and six carolinensis. During this interval of time, danielsi ate fourteen jordani and twelve carolinensis.

It was interesting to note that those jordani and carolinensis which remained in the cages at the end of the five-day period usually had no tails. Evidently autotomy is a more effective defense mechanism against large salamanders than with other predators.

These data indicate that danielsi and quadra-maculatus are undoubtedly natural predators upon jordani and carolinensis. However, it appears that these predators are similar to the other predators tested in that they display no discrimination between jordani and carolinensis.

Preliminary Feeding Experiments with Other Predators

Numerous small mammals were live-trapped while efforts were being made to capture Blarina. These mammals included Peromyscus leucopus, Peromyscus nuttalli, Peromyscus gossypinus, Peromyscus maniculatus, and Clethrionomys gapperi. Of these, maniculatus and gapperi seemed to be most common within the range of jordani. Both of these species are

primarily herbivorous, but it was decided to test these animals in preliminary feeding experiments to determine the possibility of their being natural predators upon jordani and carolinensis.

Six maniculatus were placed in a laboratory cage and were presented both species of salamanders. Eleven feeding trials were conducted and in only two of these trials did the mice feed upon the salamanders. In the sixth trial, after being starved for twenty-four hours, the maniculatus ate one jordani but not the carolinensis. In the ninth trial, the mice ate another jordani and the tail of carolinensis. In the other trials, the characteristic behavior of the mice was to ignore the salamanders after they had been briefly examined. When other food was placed in the cage with the mice, they began feeding immediately. Additional feeding trials were not conducted, since the mice did not seem to be natural predators.

The feeding behavior of four C. gapperi tested was much like that of maniculatus, although gapperi seemed to be much more secretive and seldom would leave their nests when salamanders were presented. They seemed to feed only in darkness. Eleven trials were also conducted with these red-backed mice. In the seventh trial, after twenty-four hours of starvation, the mice ate the tail, hind legs, and part of the abdomen of a jordani and all parts of a carolinensis except the abdomen. In the eighth trial, the tail of a jordani was eaten. This feeding occurred unnoticed during the night. In all other trials the salamanders were not touched. It was concluded from these trials that gapperi was not an important natural predator.

During this study an attempt was also made to detect possible bird predation upon salamanders under natural conditions. Robert E. Gordon has reported (personal correspondence) a field observation of a brown thrasher (Toxostoma rufum rufum) which attacked and carried off a P. j. melaventris at Highlands, North Carolina. Between attacks upon the salamander by the bird, Dr. Gordon was able to identify the salamander and reported that the melaventris had received three wounds which "would have led to its ultimate death"

A screen cage (4' x 4' x 1') was constructed which was similar in design to those used in the danielsi and quadramaculatus feeding experiments. The cage was placed at Indian Gap. Moss, small rocks, and about one inch of soil were placed in the cage to approximate natural conditions. On July 28, twelve jordani, nine normal carolinensis, and three red-cheeked carolinensis were placed in the cage. This ratio of carolinensis to jordani was the same ratio found in the populations when the area was sampled earlier. When checked on July 31, no salamanders had been removed. On that date more salamanders were added to bring the total to thirty-six. On August 21, all moss and soil were removed from the cage to expose the salamanders directly to predation. Still no decline in numbers was observed when the final check was made on August 27. Observations at dawn and dusk in this general area also failed to reveal bird predation upon salamanders.

However, the results of this phase of the study could not be interpreted as meaning that bird predation upon salamanders necessarily does not exist since the study was of rather short duration. Since this

study was conducted during a time of abundant food supply for birds, it is possible that the birds were not attracted to the feeding station. Also it is possible that such a feeding station as this should remain in place for an extended length of time to permit birds to become accustomed to it. However, this approach to the detection of predation under natural conditions seems to have certain advantages over feeding experiments conducted under laboratory conditions.

Since most diurnal birds undoubtedly have color vision, it seems that they possibly could discriminate between models and non-mimetic individuals. However, there are a number of conflicts in the assumption that birds can and do discriminate between jordani and carolinensis and thus are responsible for the evolution of the mimetic pattern in carolinensis.

An obvious difficulty in this assumption is that birds having color vision are largely diurnal while the salamanders in question are primarily nocturnal. Of the many jordani observed during this study, only one was found on top of leaf litter during the day. Nocturnal birds undoubtedly do feed upon salamanders. Stupka (unpublished report) has found salamander remains in one stomach of thirty-nine screech owl stomachs examined. The salamanders consisted of four Plethodon cinereus individuals. It is questioned, however, whether nocturnal birds have color vision. As was mentioned earlier, Walls contends that owls cannot discern color. Even if one assumed that nocturnal birds do have color vision, it would still seem unlikely that colors in prey could be perceived under low light intensities.

Huheey's suggestion that the nocturnal prey may be uncovered by foraging diurnal predators seems plausible. Gordon's account of the brown thrasher attacking melaventris at dusk adds support to this theory. The frequency of this type of predation under natural conditions would seem to be rather low, however.

Another unresolved problem is whether the slime of jordani is objectionable enough to natural bird predators to cause a relaxation of predation pressure. Furthermore, if such obnoxious qualities do exist, do the birds associate the red cheek with this quality and thus attack and kill non-mimetic carolinensis in greater frequencies than mimetic carolinensis and jordani? The first problem was tested by Huheey (1960). He concluded that "jordani has a certain amount of protection of this nature, the effectiveness of which depends somewhat upon the nature, condition, and behavior of the predator." Unfortunately, he has no red-cheeked carolinensis to test the birds' ability to associate the red-cheeked condition with the slime of jordani.

If birds prey infrequently upon salamanders and if the effectiveness of the warning coloration of jordani is slight, one would question the effectiveness or even existence of mimicry in this case. Brower's studies have shown that birds forget the significance of the aposematic signal of the prey. It seems, then, that in nature, the birds would have to have frequent experiences with the aposematic models to retain their ability to associate the warning coloration with undesirable characteristics of the model. It seems doubtful that frequent predation upon salamanders by birds occurs.

VIII. DISCUSSION

Earlier it was stated that it was not possible to determine the reasonable proportion of red-cheeked carolinensis in the supposed jordani-carolinensis complex until more was known concerning the degree of unpalatability possessed by jordani and the degree to which natural predators are deceived by the mimetic resemblance. Feeding experiments with the most probable predators on these salamanders indicated that no undesirable quality exists in jordani which is intense enough to prevent consistent predation under laboratory conditions. In some instances, the slime of jordani seemed to be a disturbing factor to Blarina, but this sliminess did not add to the survival rate of jordani in these experiments. Since the supposed aposematism of jordani was not effective, any imitation of this color pattern should be likewise ineffective. This was found to be true when the red-cheeked carolinensis were exposed to predators under laboratory conditions.

Since these data do not support the theory of mimicry with these predators, at least, it is obvious that on the basis of these data no proportion of supposed mimics in the carolinensis population could be maintained by predation. It must be emphasized that these conclusions can be drawn only for the predators tested in this study. The list of potential predators not tested is immense, and the possibility that a predator exists which does discriminate between the two species is not discounted.

The possibility of predation upon salamanders by birds has been discussed previously. Huheey's work (1960) has been briefly described

in which he found that jordani had a significantly higher survival rate than did normal carolinensis when these two species were preyed upon by two migrant shrikes (Lanius ludovicianus). Since this is the only study conducted in which birds have been used as predators upon salamanders, the study should be examined more closely.

In Huheey's study, the jordani and carolinensis were each divided into two groups: those under seventy millimeters in length, and those over seventy millimeters in length. He found that the combined numbers of large and small jordani surviving the predation were significantly higher than the combined numbers of large and small carolinensis surviving predation ($x^2 = 9.2$; d.f. = 1; $P \Rightarrow 0.001$). However, if these same data are treated in a different manner in which a test of significant difference is made between the two size classes, irrespective of species, it is found that the large salamanders have a significantly higher rate of survival than do the small salamanders ($x^2 = 7.91$; d.f. = 1; $P = < 0.01$). In other words, the interpretation of this last test would be that some factor other than chance seems to be operating to give the large salamanders a higher survival rate than the smaller salamanders. Since the species were not separated in this last test between size classes, it seems that the only logical factor which could account for this difference is size.

In attempting to determine whether size or some unpalatable characteristic of jordani is involved in Huheey's feeding experiments, the data can be tested by other approaches. If a test for significant difference is made between the small carolinensis and the small jordani,

it is found that there is no significant difference between the survival rates of these two species ($x^2 = 3.64$; d.f. = 1; $P = < 0.10$). However, when the numbers of large jordani surviving the predation are compared with the numbers of large carolinensis surviving the predation, the survival rates of jordani are found to be significantly higher than those of the large carolinensis ($x^2 = 4.17$; d.f. = 1; $P = < 0.05$). This would suggest that the jordani in the large group were possibly larger than the carolinensis in the group over seventy millimeters. Since individuals of jordani are in general larger than carolinensis, this seems plausible.

This discussion is not meant to discredit Huheey's study. It is meant only to show that the size of salamanders--in addition to possible undesirable qualities in some species--could be a factor in determining the survival rates of salamanders when exposed to bird predation.

The findings of this study have indicated that mimicry does not seem to be a good explanation for the resemblance between red-cheeked carolinensis and jordani. Although this study is limited to the mimicry hypothesis, other possible explanations will be reviewed.

1. Hybridization. According to this hypothesis, the red-cheeked carolinensis are hybrids between jordani and normally colored carolinensis. Hybrids between different genera have been reported among amphibians (Noble, 1931). However, as Noble has mentioned, these hybrids seldom grow to maturity. False hybrids also have been known in which the sperm of one species may do nothing more than activate the parthenogenetic development of the egg, but there is no combination of nuclear material.

It seems that hybridization can be discounted in the case of the red-cheeked carolinensis since these color variants have no morphological characteristics of jordani other than the cheek patch and are identical to other forms of carolinensis in all respects except color.

2. Genetic drift. If the carolinensis populations were small, if non-random mating occurred, and if the small populations were relatively isolated from other such populations, genetic drift could account for the retention and increase in frequency of some non-adaptive characteristic in the populations. However, the fact that carolinensis occupies so many habitat types indicates that there are few barriers which would isolate small breeding populations of this species. Also, this theory would fail to explain the widespread frequency of the red-cheeked condition.

3. Red cheek coloration attracts prey. Huheey (1960) mentioned (and rejected) the possibility that the red-cheek patch may attract insects and thus give survival value to the salamanders in respect to their prey. This hypothesis does not seem valid for several reasons, the most important being that it does not explain why the red-cheeked condition is found in highest frequencies where jordani is most abundant and not found in high frequencies elsewhere. Furthermore, since most insects are insensitive to the red range of the spectrum (Wigglesworth, 1950), they would not be attracted to the red cheek patch of salamanders.

4. The cheek coloration is a pleiotropic characteristic which is linked to a physiological mutation which has selective value. This hypothesis has been proposed by Noble (1931) but rejected by others

(Huheey, 1960) on the basis that it does not explain the occurrence of red-cheeked carolinensis where these color variants are sympatric with jordani and the occurrence of the red-legged variants where these forms are sympatric with shermani.

It has been stated that no other hypothesis explains the resemblance between color variations of carolinensis and the two sub-species of Plethodon jordani as well as that of mimicry. Since the hypothesis of mimicry is not supported by the findings of this study, an alternate explanation must be selected.

Of the four hypotheses proposed above, the fourth seems to be the most reasonable explanation of this phenomenon. It, like that of mimicry, also has certain inadequacies which must be tested in further studies. However, this hypothesis also has certain attributes which should be considered.

Edaphic, climatic, and biotic factors of high elevations unquestionably differ from those of lower elevations. Various species of salamanders such as P. j. jordani, P. j. shermani, and D. wrighti are well adapted to these environments and seldom are found beyond the influences of their montane environments. If one assumes that the mutation or mutations which are responsible for the manifestation of the red cheek patch in carolinensis also are responsible for certain physiological changes which have selective value at high elevations, it would then follow that the frequency of this red-cheeked condition would be greatest where jordani is abundant. As was mentioned earlier, this situation was found to exist within the Great Smokies.

However, this correlation would also support the hypothesis of mimicry, unless it could be shown furthermore that red-cheeked carolinensis are common at high elevations outside the range of jordani. To support the hypothesis of a physiological adaptation, it would be necessary for these areas outside the range of jordani to have environmental influences similar to those within its range where the red-cheeked carolinensis are common. This would be a difficult point to prove.

Nevertheless, there are some data available which may support the above premise. In considering the ranges of jordani and the red-cheeked carolinensis, it was found that red-cheeked variants were found on Blanket Mountain (to 4,609 feet), but no jordani were found. The theory of physiological adaptation still would not explain the absence of jordani but would account for relatively high frequencies of red-cheeked carolinensis. According to the mimicry hypothesis, high frequencies of the mimics could not exist without the model.

It was also mentioned earlier that a relatively high frequency of red-cheeked carolinensis seems to exist on Wayah Bald (5,100 feet) in the Nantahala Mountains of North Carolina. This would be expected if the red-cheeked condition were linked to a physiological advantage. It must be emphasized again, however, that these data are based upon very small samples of carolinensis, and more thorough investigations of both areas would be necessary before conclusive decisions could be drawn.

. Sufficient data are available concerning the frequency of red-cheeked carolinensis in the vicinity of Highlands, North Carolina,

(3,800 feet) and the Black Mountains (all elevations) to indicate that the frequency of the red-cheeked condition in these areas is very low (3 of 63 and 2 of 300, respectively). This seems to conflict with the theory of physiological adaptation. However, it is questioned whether one would expect high frequencies at Highlands because of its relatively low elevation. The low frequencies in the Black Mountains would be more difficult to explain, however, since Mt. Mitchell of the Black Mountains reaches an elevation of 6,682 feet.

The validity of the physiological adaptation hypothesis can be determined in part by the presence or absence of red-legged carolinensis in high frequencies where these forms are supposedly sympatric with shermani. If these forms are in high frequencies as the red-cheeked form is in the Smokies, then the physiological adaptation theory cannot stand and mimicry would seem to be the only explanation. However, as mentioned before, there is no evidence to support the assumption that red-legged carolinensis are in any higher frequencies within the range of shermani than they are anywhere else.

King (1939) and Hairston (1949) have reported that carolinensis seems to be more melanistic at higher elevations than at low elevations. This observation was also made in this study. It seems that the altitudinal variation in coloration must be reflective of environmental factors which vary quantitatively from low to high elevations. In the same sense, it seems possible that environmental factors may also have been instrumental in the evolution of cheek coloration in carolinensis.

IX. SUMMARY

A study was conducted in the Great Smoky Mountains National Park to determine the validity of the mimicry hypothesis which has been proposed to explain the resemblance between red-cheeked color variants of Desmognathus ochrophaeus carolinensis and Plethodon jordani jordani, the red-cheeked salamander. Five basic rules of mimicry were tested in both field and laboratory approaches to the problem.

The color patterns of carolinensis were recorded in 587 individuals observed. Of this number, 25.7 per cent displayed some cheek coloration which included color variations of red to orange, yellow, and white. Red to orange cheek colors were found in 92 per cent of all carolinensis having cheek coloration. These supposed mimics of jordani differed markedly in appearance from the normal carolinensis.

An attempt was made to delimit the range of jordani within the Park. Observations were also made of the presence or absence of red-cheeked carolinensis within and outside this range of jordani. D. o. carolinensis was found with jordani in seven general areas investigated. Red-cheeked carolinensis were found in the vicinity of Blanket Mountain, but no jordani were found in this general area. The presence of mimics outside the range of models is not what one would expect if mimicry exists between the two species. Also, no red-cheeked carolinensis were found within a large sample of carolinensis collected on Hyatt's Ridge, even though jordani was present in the area. Records of red-cheeked carolinensis occurring outside the Park were cited from the literature. The frequency of mimics at Wayah Bald, North Carolina, may be higher

than one would expect under the rules of mimicry. No evidence was available to indicate that the frequency of red-legged carolinensis was any higher within the range of P. j. shermani than in any other area.

Eight transects were placed at elevations ranging from 2,925 feet to 5,390 feet within the Great Smokies to determine the relative abundance of jordani and red-cheeked carolinensis. It was found that a positive correlation seemed to exist between the number of jordani and the frequency of red-cheeked carolinensis in the areas sampled. The percentage of supposed mimics in the total jordani-red-cheeked carolinensis population varied in the areas sampled from 25 per cent to 60 per cent. It is questionable whether the supposed mimicry is effective enough to support this high frequency of mimics.

P. j. jordani and red-cheeked and normal carolinensis were exposed to four different types of predators in an attempt to detect differences in the survival rates between the two species of salamanders. The predators used in these laboratory feeding experiments included the eastern garter snake (Thamnophis sirtalis sirtalis), the large short-tailed shrew (Blarina brevicauda), the mountain spring salamander (Gyrinophilus danielsi danielsi), and the black-bellied salamander (Desmognathus quadra-maculatus).

All of these predators readily fed upon all salamanders presented to them. No differences were noted between the survival rates of carolinensis and jordani when exposed to these predators under laboratory conditions. Preliminary feeding experiments were also conducted with the long-tailed deer mouse (Peromyscus maniculatus) and the red-backed

mouse (Clethrionomys gapperi), but additional feeding experiments were not conducted with these mice since they did not seem to be natural predators. An attempt was also made to detect bird predation upon salamanders under natural conditions. No predation was found to exist under the conditions of the feeding experiment.

No evidence supporting either Batesian or Müllerian mimicry could be found under the methods and conditions of this study. Alternate hypotheses for the explanation of the resemblance between red-cheeked carolinensis and jordani were discussed. These alternate hypotheses include the following: (1) hybridization has taken place or is occurring, (2) genetic drift has occurred, (3) the red cheek coloration attracts prey, and (4) the cheek coloration is a pleiotropic characteristic which is linked to a physiological mutation which has selective value. Of these four possible explanations, the fourth was considered to be the most plausible explanation of the resemblance between red-cheeked carolinensis and jordani.

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