EXPERIMENTAL STUDIES OF MIMICRY IN SOME NORTH AMERICAN BUTTERFLIES

PART I. THE MONARCH, *DANAUS PLEXIPPUS*, AND VICEROY, *LIMENITIS ARCHIPPUS ARCHIPPUS*[1]

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INTRODUCTION

When the vast literature on mimicry is considered, the striking lack of experimental evidence for its existence is remarkable. Morgan (1896, 1900), while studying learning in chicks, designed mimicry experiments which showed that they can associate an unpleasant feeding experience with a particular color and pattern. Thereafter, the chicks would also reject modifications ("mimics") of the same color pattern. More recently, Mühlmann (1934) used dyed and treated mealworms as "models," and partially dyed ones as "mimics" in experiments with several species of passerine birds in an attempt to show how similar a model and mimic must be to deceive the birds. The work of Mostler (1935) on wasp-mimicry showed that birds could learn to reject wasps, and then also would mistake like-colored insects for wasps and reject them. Working on the problem of beetle mimicry, Darlington (1938) carried out experiments with captive *Anolis* lizards, which showed that they rejected the model beetle, and also mimic beetles. The laborious efforts of Finn (1895, 1896, 1897a, 1897b), Marshall (1902), Pocock (1911), Swynnerton (1919), Carpenter (1921, 1942), and Jones (1932) are paramount among the many attempts to determine the relative edibility of mimetic butterflies to various vertebrate predators. Both Marshall and Swynnerton reported some evidence for the existence of mimicry in the complex African butterfly fauna, on the basis of feeding experiments with captive Baboons and captive Rollers (*Coracias garrulus* Linné) respectively, but the major parts of both works were devoted to the more general problem of cryptic *versus* warning coloration in butterflies.

As Poulton (1909) pointed out, in North America there are three relatively simple examples of supposed mimicry in butterflies. The purpose of the present study is to describe an experimental investigation of mimicry in these North American butterflies, and it will be presented as three papers which deal separately with each of these three mimicry complexes. The same methods were employed for each complex, and the three parts were carried out as a continuous investigation over a period of 60 days. The first series of experiments was carried out with *Danaus plexippus* (Linné) and *Limenitis archippus archippus* (Cramer), presumed model and mimic, respectively. *D. Plexippus* is known respectively as the Monarch and *L. a. archippus* is known as the Viceroy; they will hereafter be referred to by their common names. The second series of experiments was a study of the model, *Battus philenor* Linné, and its mimics, *Papilio troilus* Linné, *P. polyxenes* (Fabricius), and the black female form of *P. glaucus* Linné. The third series was a study of the model, *Danaus gilippus berenice* (Cramer), and its mimic, *Limenitis archippus floridensis* (Strecker). The

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experiments were designed to investigate the following relationships between models and mimics and a selected bird species, to be used as a caged predator:

1—the reaction to models by individually caged experimental birds;
2—the reaction to mimics by the same experimental birds, after they had had initial laboratory experience with the models;
3—the reaction to mimics by individually caged control birds, which had had no prior laboratory experience with the models.

An experimental study demonstrating these three points could be expected to show the effectiveness of mimicry, within the limitations of the experimental conditions.

Materials and Methods

The technical difficulties inherent in these experiments were minimized by the choice of an especially favorable situation in which to undertake the investigation. The Archbold Biological Station, near Lake Placid, Florida, provided excellent laboratory facilities, without which the work would have been impossible. In addition the required butterflies are relatively abundant in this area of Florida.

The Florida Scrub Jay, *Cyanocitta coerulescens coerulescens* (Bosc), was selected as the predator in the mimicry experiments. It is non-migratory and is found in areas in which Sand Pine (*Pinus clausa* (Engelm.) Vasey), scrubby oaks (*Quercus myrtifolia* Willd., *Q. geminata* Small, and *Q. catesbaei* Michx.), Saw Palmetto (*Serenoa repens* (Bartr.) Small), and Dwarf Wax Myrtle (*Myrica pumila* Michx.) predominate (Bent, 1946, and Amadon, 1944). The diet of the Scrub Jay is said to be about 60% animal matter, on the basis of analyses of stomach contents of sixteen birds (Bent, 1946), and includes beetles, butterflies, moths, caterpillars, and grasshoppers. Sprunt (1954) stated that the animal matter is 50% and did not note the presence of Lepidoptera in the stomach contents. Amadon (1944) observed Scrub Jays feeding in nature at the Archbold Biological Station, primarily on acorns and insects. The male and female Scrub Jays have similar plumage and size, though the males may be slightly brighter in color and larger than the females. Amadon also observed that in his experience a hiccup sound is peculiar to the female Scrub Jay. These birds are particularly easy to trap, and readily adapt to life in a cage (Amadon, 1944, and Bent, 1946).

Eight Florida Scrub Jays were trapped on the Archbold Biological Station property between 14 April and 17 April 1956. Since the young are known to hatch in early to mid April, it may be assumed that these Scrub Jays were all at least one year old. As noted above, the sex of these jays is difficult to determine from plumage, and even from size. However, in an attempt to ascertain the sex of the nine individuals used in the experiments, all but one were weighed prior to release. The following weights were recorded on 17 June 1956:

No. of bird	Weight in gms.	Tentative sex determination
C-1	84.0	male
C-2	66.5	female
C-3	83.0	male
C-4	77.0	female (hiccup)
E-1	88.0	male
E-2	74.0	female (hiccup)
E-3	71.0	female
E-4	—	mate of E-3
E-4A	77.5	female

From a generalization based on weight alone, C–2, E–3, and E–4A (a replacement for E–4, captured 1 June 1956) seemed to be females. E–4, the probable wild mate of E–3, was not weighed prior to release. On the basis of the hiccup sound mentioned by Amadon (1944), C–4 and E–2 could be considered females. C–1, C–3, and E–1 could have been males.

Each bird was confined in a cubic cage thirty inches on a side, with sides and top covered with aluminum-painted wire of

one-half inch square mesh. The cages were arranged in the laboratory in two racks of four each, within two adjacent enclosures 6′ wide × 13′ 5″ deep × 7′ 8″ high. Each enclosure had a door (3′ 6″ wide × 7′ high) at one end, and both the door and the top of each enclosure were made of one-half inch square mesh. The eight bird cages were identical in every possible respect, as were the two enclosures. The individual bird cages were separated from one another by opaque cardboard, so that at no time could one bird see another. In each enclosure there was a pair of white porcelanized reflectors, each with a 100 watt incandescent bulb, fastened on the wall opposite the rack bearing the cages. These lights were on during all the experiments, and off when experiments were not in progress. Daylight entered the laboratory through a large skylight of northern exposure. The aluminum-painted steel tray floor of each of the eight bird cages was covered with sifted white sand obtained from the area where the birds were caught. Two perches at heights of 8″ and 16″ were provided in each cage, and each had a water bottle accessible at all times.

The eight birds were given a regular feeding at 5:30 P.M. daily. The standard laboratory diet consisted of approximately: 5 cc scratch (cracked corn and wheat), 1 cc pebbles, 2 cc Purina chow (for hens), 2 pecan meats, 1 peanut, 2 sunflower seeds, and 4 Scarabaeid beetles (*Phyllophaga prununculina* Burmeister). Occasionally, one or more additional items were given simultaneously to all birds. These included hard boiled egg, egg shell, lettuce, chopped meat, bread, and insects of various orders.

Experimental Insects

Insects of the orders Coleoptera, Hemiptera, Orthoptera, and Lepidoptera were attracted by a 15 watt G-E black light stationed on an outside platform of the laboratory. These were collected each night and stored in a cold room (about 3° C.) for use in the feeding experiments with the Scrub Jays. It is of interest that wild birds, including the Florida Scrub Jay, fed regularly at dawn on the remaining insects that had been attracted to the light the night before. The butterflies used in the experiments were obtained by collecting in the field, or by rearing the adults from eggs laid by confined female butterflies, or from larvae found in the field and reared in the laboratory. Supplies of butterflies were also stored in glassine envelopes in the cold room for use as needed. The particular source of each species will be noted as the experiments are described. No effort was devoted at this time to a study of the proportions of models and mimics in given localities.

Preliminary Experiments

To determine whether or not any erratic behavior existed among the eight Scrub Jays, all of the birds were given identical preliminary tests with several orders of insects. All birds responded similarly to representative Coleoptera (e.g., *Phyllophaga prununculina* and *Dyscinetus morator* Fabricius, Scarabaeidae, *Epicauta tenuis* (Leconte), Meloidae); Orthoptera (e.g., Acrididae, and *Gryllotalpa hexadactyla* Perty, Gryllidae); Hemiptera (e.g., *Lethocerus uhleri* (Montandon), Belostomatidae); and Lepidoptera (e.g., *Pholus fasciatus* (Sulzer) and *Xylophanes tersa* (Linné), Sphingidae; *Phoebis sennae eubule* (Linné), Pieridae; *Papilio glaucus* Linné (yellow female and male), *P. palamedes* (Drury), and *P. marcellus* (Cramer), Papilionidae). In each trial for each bird, a stopwatch was used to record the time in seconds for the bird to seize an insect, and if the bird then ate the insect, this time was also recorded. Similarity among all the birds in their reaction times in seizing the insects, and also in their responses to the insects after seizure, indicated that they were a reasonably uni-

form group with which to conduct experiments on mimicry. The set of mean reaction times, based on twelve trials for each of the eight birds, gave an observed standard deviation of 1.34 seconds, with a mean value of 3.31 seconds and a range of from 1.5 to 5.0. A table in David, Hartley, and Pearson (1954) showed that for eight observations the ratio of range to standard deviation must be 3.399 at the 5% significance level; the ratio of range to standard deviation here is 2.61 so that there is no significant difference among the eight observations, i.e., the birds' mean reaction times in seizing insects.

During the preliminary trials, two readily available butterflies, *Papilio glaucus* (yellow female and male) and *P. palamedes* which are not known to be involved in mimicry either as models or as mimics, were eaten in every case by all eight birds. It was therefore decided that these two species, obtained as living adults by local field collecting, would be used as the edible control butterflies throughout the course of the experiments. Hereafter they will be referred to as "non-mimetic butterflies." In all of the experiments the butterflies were immobilized by pinching the thorax before they were placed with a pair of forceps on the floor of a bird cage. For uniformity and stability all butterflies were presented lying on their sides, with wings together dorsally. Therefore in the experiments with models and mimics only mimicry in the characters of the underside of the wings was being tested. The immobilization of the butterflies and their sideways placement in the cages were arbitrarily decided upon to eliminate the following variables: (1) a mobile butterfly might be more or less difficult for a bird to catch depending on its amount of activity and its location in a cage; (2) mimicry might be more or less effective depending on whether a bird saw the upper or lower wing surfaces of a temporarily resting butterfly, or both surfaces of a flapping butterfly. The role of behavior of models and mimics in increasing or diminishing the effectiveness of mimicry would be interesting in itself (e.g., it is known that two forms of the African butterfly, *Hypolimnas dubius* de Beauvais, which mimick two closely allied *Amauris* models, differ from one another in behavior as well as color and pattern, as discussed by Ford, 1953), but the present experiments do not attempt to investigate this aspect of the problem. Every bird was allowed two minutes to react to each butterfly presented. At two minutes an uneaten butterfly was removed. Whenever possible, living butterflies were used, but the data indicated that the reaction to any given species of butterfly was the same whether live or dead specimens were presented to the birds. In a few trials, dead and rather dried specimens, of non-mimetic butterflies only, had to be used, and rarely a slightly moldy non-mimetic butterfly was used in the absence of fresh material. Even these butterflies were quite acceptable as food to the jays. If a living model or mimic remained untouched throughout a trial, it was used again in successive trials. If a model or mimic was in any way torn or injured by a bird, however, it was not used again.

The Mimicry Experiments

Of the eight Scrub Jays, four were randomly selected as experimental birds; the other four were control birds. The mimicry experiments were designed so that each trial consisted of giving a bird a pair of butterflies in succession, one non-mimetic butterfly and one model or one mimic. In each trial, the order of presentation of the non-mimetic butterfly and the model or mimic was determined by a random number table, with the use of consecutive digits in a different vertical column for each bird. If a digit read 0–4, a non-mimetic butterfly was given first, followed by a model (or mimic), but if a digit read 5–9, a model (or mimic) was given first, followed by a non-mimetic butterfly. By this method

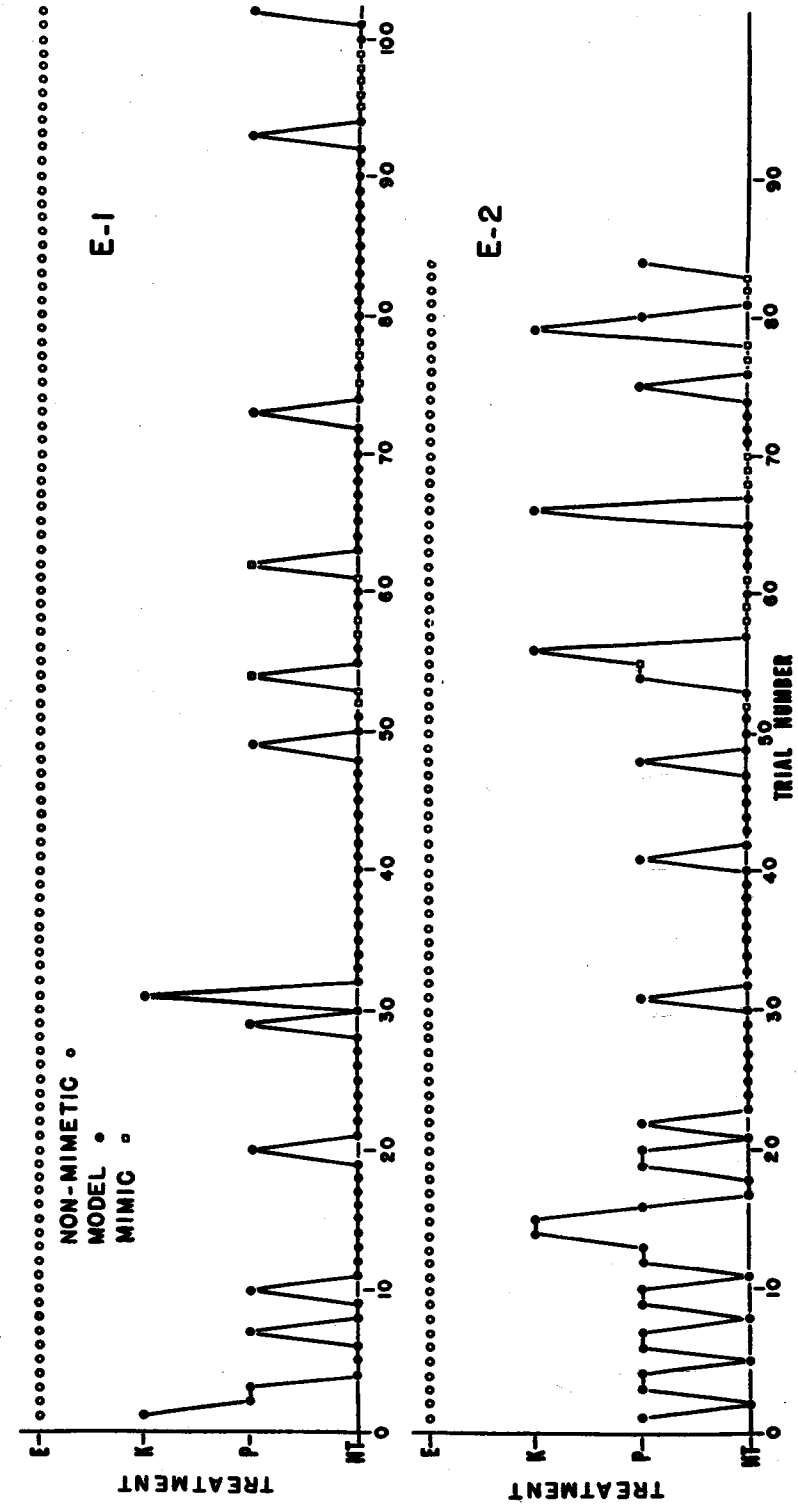

FIG. 1A. Diagrams for experiments with the Monarch and the Viceroy. Experimental birds E-1 and E-2.

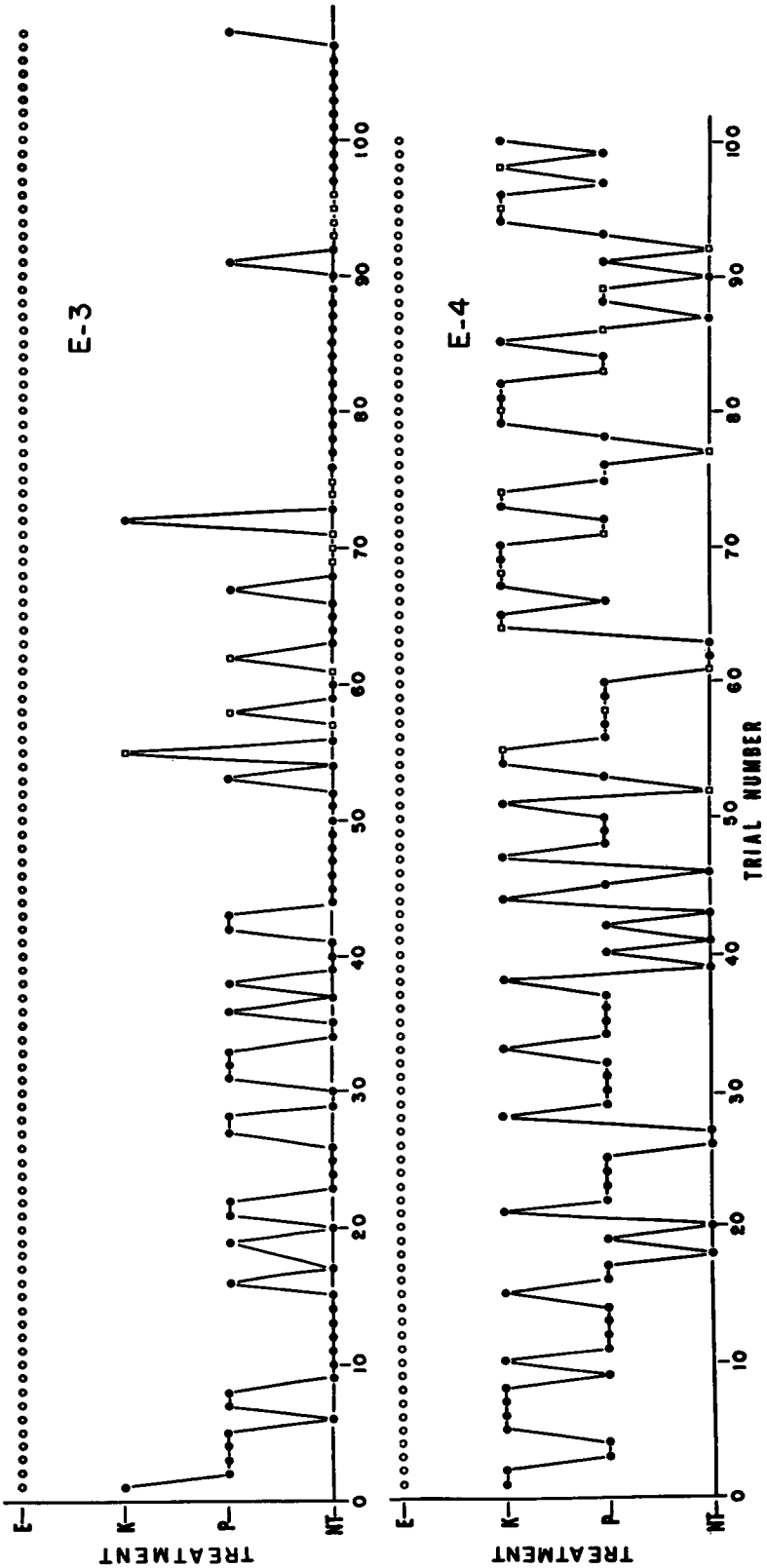

FIG. 1B. Experimental birds E–3 and E–4.

runs of more than two of each kind of butterfly were eliminated, and the following consecutive trials were possible (model or mimic = M; non-mimetic butterfly = N): (1a) M,N; (1b) M,N. (2a) N,M; (2b) N,M. (3a) M,N; (3b) N,M. (4a) N,M; (4b) M,N. Use of these randomized pairs avoided subjective repetition of any sequence in the presentation of the butterflies to the birds, and prevented the birds from reacting to the butterflies on the basis of an expected order of sequences. After each bird was given the first butterfly in a trial, it did not receive the second until each of the other birds had received its first butterfly. Thus for each bird the time interval between trial 1a and 1b was about the same as it was between trial 1b and 2a. The design of the experiments did not eliminate the possibility that the birds might predict the second butterfly given in each trial on the basis of the first one given, but the data suggested that this was not the case.

The experimental birds were given models and non-mimetic butterflies, randomly in pairs as described, until the birds had developed a relatively reliable pattern of behavior toward the model species. At this time, the mimic was substituted for the model in one trial. Subsequent substitutions of the mimic for the model depended on the particular pattern of behavior of the individual bird, and will be discussed when the data are considered.

The control birds were given mimics and non-mimetic butterflies randomly in pairs, by the same procedure used for the experimental birds. The difference between the two sets of birds was that only the experimental birds were given experience with models.

Experiments with the Monarch and Viceroy

The classic example of mimicry among North American butterflies is the Monarch-Viceroy situation, cited by Walsh and Riley (1869). In spite of a small amount of evidence to the contrary, the Monarch generally has been considered relatively unpalatable to vertebrate predators. Poulton (1909) commented upon the relative edibility of the Viceroy. He was of the opinion that the Viceroy is a Müllerian mimic, unpalatable like its model, basing his views on the supposed origin of the Viceroy from a warningly colored ancestor, like *Limenitis arthemis* (Drury), and on the assumption that warningly colored butterflies are unpalatable to predators. Walsh and Riley (1869) assumed that the Viceroy is a Batesian mimic, edible to vertebrate predators. It seemed fitting to begin the mimicry experiments with this long-debated problem of the Monarch and the Viceroy.

Geographic Distribution and Sources of Butterflies

The range of the Monarch covers North America, northeastward to central Ontario (Klots, 1951). The Viceroy is more limited in its distribution, ranging from central Canada south to South Carolina, Georgia, and Louisiana. The species possibly forms a north-south cline with *Limenitis archippus floridensis,* the mimic of the southern danaid, *Danaus gilippus berenice.* The latter mimic and model both occur in Florida. The Viceroy (*L. archippus archippus*) does not reach central Florida, which makes it certain that the Florida Scrub Jays used in these experiments had never had experience with the Viceroy in nature. However, the birds may have attempted to eat Monarchs, which are present at the Station in winter and spring.

The source of Viceroys for the feeding experiments was over-wintering hibernacula collected in Litchfield Co., Conn., in February 1956. The larvae from these were reared to the adult stage at the Archbold Biological Station. The Monarchs were obtained locally in Florida by collecting living adults and by rearing

adults from eggs obtained from females in outdoor insect cages, and also from larvae collected in the field. Both male and female butterflies were used in the experiments, but because female Viceroys resembled Monarchs more closely in size, females of this species were used in most trials. It should be noted that the relative size of models and mimics in nature is probably of little significance compared to their similarities of color and pattern, and that the effect of size on mimicry could assume a disproportionate importance under experimental conditions. The sex of a butterfly *per se* did not affect the reaction of any bird. A total of approximately 1,000 butterflies was used.

Results

The basic data for the feeding experiments with Monarchs and Viceroys are presented in figures 1A. and 1B., diagrams E–1, E–2, E–3, and E–4, and in figure 2, diagrams C–1, C–2, C–3, and C–4. The four categories of reaction to the butterflies by the birds were selected on the basis of observed behavior of the birds. "NT" means that the butterfly was not touched by the bird during the two minute test period. The NT category sometimes was accompanied by characteristic behavior on the part of a bird which will be discussed below. The "P" category means that the bird pecked the butterfly but not to the point of any injury which in nature would impair the insect's ability to reproduce. Pecking could imply tasting, but the contact of the beak of the bird with the external surface of the butterfly is what is meant here. The "K" (killed) category is used when a bird had torn the body of the butterfly so that in the wild it would have died, or could not have reproduced, but the bird left the torn specimen uneaten. "E" refers to the fact that the bird had eaten the butterfly, leaving only the wings and legs, which were picked off and discarded.

From an examination of the diagrams of the experiments (see figs. 1A and 1B;

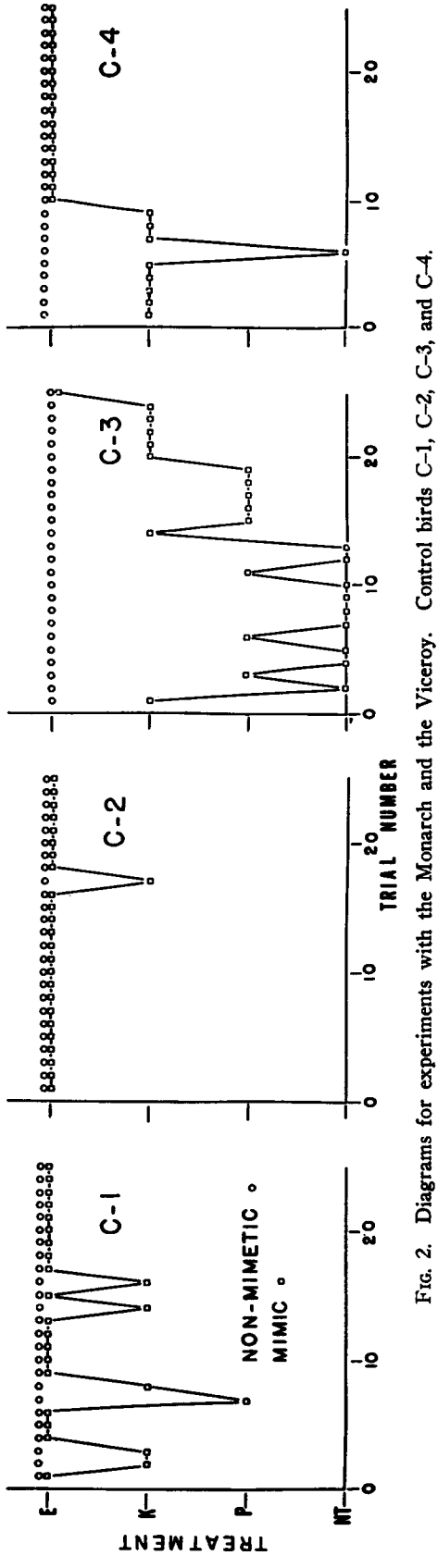

Fig. 2. Diagrams for experiments with the Monarch and the Viceroy. Control birds C–1, C–2, C–3, and C–4.

fig. 2), it will be evident that in all trials for both experimental and control birds, the non-mimetic butterfly (white circle) of each pair of butterflies in any given trial was eaten. In only four trials in this entire investigation, a bird was reluctant to eat a non-mimetic butterfly. When such hesitation occurred, the trials were stopped for a few minutes, and were not continued again until the bird readily accepted and ate the non-mimetic butterfly. Therefore every recorded trial indicates that a non-mimetic butterfly was eaten by a bird. The model, the Monarch, (black circle) was given in couplet with a non-mimetic butterfly to the four experimental birds for at least 51 trials prior to the substitution of the mimic, Viceroy, (white square) for the Monarch. The Monarch was not eaten by the four experimental birds in any trial. The diagrams for E–1, E–2, and E–3 show that during the initial trials, the Monarchs were pecked, killed, and not touched, and that the "not touched" category became more frequent as the birds learned that the Monarch was not palatable. All four birds reacted in their initial trial with the Monarch by killing or pecking the butterfly. This suggests either that the four experimental birds had not had experience with Monarchs in the field prior to capture, or, if they had experienced Monarchs in the wild, they had not remembered the unpalatability of Monarchs on sight alone under the cage conditions. That the lesson of unpalatability was never finally learned in the course of the experiments is seen in the repeated lapses of E–1, E–2, and E–3 into pecking or killing a Monarch after several trials during which the Monarch was not touched. On the basis of sight alone, E–4 was outstanding in its failure to remember for more than two successive trials that the Monarch was unpalatable.

The question of when to substitute Viceroys for Monarchs was complicated by the fact that the birds showed these periodic lapses when a model was again pecked or killed. In order to minimize the chance that a Viceroy would fall on the observed "error" pattern, i.e., the killing or pecking of the model, the presentation of each mimic was determined by the individual error pattern of each bird. A Viceroy was substituted for a Monarch soon after a bird had made an error on a Monarch. This meant that a bird had just been exposed to the unpleasant qualities of a Monarch before being offered a Viceroy. Because experience with each bird was the only guide, the technique of substitution of the mimic necessarily improved with time. For E–1, from trial 63 on, for E–2, from trial 57 on, and for E–3, from trial 63 on, no Viceroy was given unless it followed (1) a trial in which a Monarch was pecked or killed, and (2) a trial in which a Monarch was not touched, in that order. With the design of the experiments adjusted so that any pattern of natural pecking and/or killing lapses would be likely to fall on the model, as can be seen on the diagrams, the mimic was not touched.

Although E–4 did not learn to refuse the Monarch on sight, its treatment of the Viceroy shows no discrimination of the latter from the Monarch. The Viceroy was not eaten by any of the four experimental birds, and was not even killed by E–1 and E–2.

The four control birds, C–1, C–2, C–3, and C–4, were given trials with the Viceroy (mimic) and non-mimetic butterflies. Because the number of Viceroys available was limited, each control bird could be offered only 25. After these 25 Viceroys had been used, each control bird was given only the non-mimetic butterfly in each trial for the total number of trials shown in the "no. seize" column for each control bird on table 2. Each of the control birds ate every non-mimetic butterfly offered, although only the 25 which correspond to the Viceroy trials are shown in fig. 2, diagrams C–1, C–2, C–3, and C–4. The reaction to the Viceroy by C–1 indicates that it was palatable to that

TABLE 1. *Reactions of the experimental and control birds to Viceroys*

A. Comparison of no. "not touched" *vs.* no. "pecked—killed—eaten"

	Control birds				Experimental birds			
	C-1	C-2	C-3	C-4	E-1	E-2	E-3	E-4
NT	0	0	9	1	14	12	12	4
P—K—E	25	25	16	24	2	1	3	12

B. Comparison of no. "not touched—pecked—killed" *vs.* no. "eaten"

	Control birds				Experimental birds			
	C-1	C-2	C-3	C-4	E-1	E-2	E-3	E-4
NT—P—K	6	1	24	9	16	13	15	16
E	19	24	1	16	0	0	0	0

bird in most of the trials (diagram for C–1). C–2 ate the Viceroy in all but one trial as the diagram shows. In the case of C–3, most of the Viceroys were not touched, or were pecked or killed, and in only one trial, the last, was a Viceroy eaten. In the first nine trials, C–4 killed Viceroys, and once did not touch a Viceroy, but from trial 10 on, it ate all Viceroys.

STATISTICAL ANALYSIS OF THE DATA

Table 1,A shows a comparison of the treatment of the Viceroy for the category "NT" compared with the lumped categories "P-K-E" for all eight birds. On the hypothesis that the experimental birds and the control birds reacted to the Viceroy in the same way, a chi-squared test gave a value of 80.81, d.f. = 7, with the Yates correction factor, which was used in all chi-squared tests (table 1,A). The probability of obtaining these results, or worse ones, given this hypothesis, is less than .001. It may therefore be said that the two groups of birds did not react to the Viceroy in the same way, and that the control birds pecked, killed, and ate Viceroys significantly more than the experimental birds did. Similarly, when the data were analyzed to compare the categories "NT-P-K" with "E," the chi-squared value was 116.81, d.f. =7, P less than .001 (table 1,B). The control birds ate significantly more Viceroys than the experimental birds did; in fact, no Viceroys were eaten by the latter group.

In addition to an analysis of the response to the Viceroys by the experimental and control bird groups, con-

TABLE 2. *Reaction times of jays in seizing butterflies (in seconds to the nearest whole second)*

	Monarch					Viceroy					Non-mimetic butterflies				
Birds	Mean time seize	Min. time	Max. time	No. seize	No. NT	Mean time seize	Min. time	Max. time	No. seize	No. NT	Mean time seize	Min. time	Max. time	No. seize	No. NT
C-1	—	—	—	—	—	8	1	100	25	0	3	1	14	92	0
C-2	—	—	—	—	—	5	2	11	25	0	5	2	25	95	0
C-3	—	—	—	—	—	10	1	36	16	9	1	1	3	101	0
C-4	—	—	—	—	—	11	2	46	24	1	6	1	76	94	0
E-1	9	1	31	12	76	14	6	22	2	14	1	1	3	102	0
E-2	27	1	102	25	48	20	20	20	1	12	1	1	2	84	0
E-3	36	1	119	24	69	22	4	41	3	12	2	1	16	108	0
E-4	12	1	88	72	12	30	2	112	12	4	3	1	10	100	0

sideration was also given to the reaction times of the birds in seizing the butterflies. The measure of time which has particular application for mimicry is the interval between the time a bird first saw a butterfly placed in its cage to the time when the bird first pecked or seized the butterfly. The mean time in seconds that each bird took to seize the Monarch, the Viceroy, and the non-mimetic butterflies used in the present experiments was calculated, and is shown on table 2. To indicate the range of seconds for each bird in seizing the butterflies of each group, the minimum and maximum times in seconds are also given. Since the experimental birds did not touch many Monarchs and Viceroys, the number of butterflies seized (from which the means were calculated) and also the number that were not touched are given in separate columns.

As table 2 shows, the time which the experimental birds took to seize Monarchs and Viceroys was considerably greater than that for non-mimetic butterflies, which suggests that the birds did not discriminate the Viceroy from the Monarch. If a similar hesitation in seizing a Monarch and its mimic were shown by an experienced bird in nature, escape of the butterfly from predation would be likely because of the time factor alone.

These data also suggest a correlation with the relative palatability of the various butterflies. The mean-times-seize of all the birds for the palatable non-mimetic butterflies are less than those of the control birds for the Viceroy.

Behavior of the Scrub Jays

In the description of the categories of reaction to the butterflies by the birds, it was noted that the "NT" category was sometimes accompanied by characteristic behavior on the part of a bird. This consisted of the bird ruffling its feathers and shaking its body, and/or by what I termed a "hop routine." The hop routine was a repetition of a series of hop movements by a bird, from perch, to side of cage, to floor, to perch, which often persisted for the full two minutes of a test, if an unpalatable model or its mimic had been presented.

A detailed examination of the occurrence of the feather-ruffling reaction in the individual birds shows a definite correlation between the reaction and the unacceptability of a given butterfly species to a bird. For the experimental birds, the feather-ruffling often occurred when either a Monarch or a Viceroy was presented. Thus E–1 gave this reaction in 77 out of 88 trials (88%) with the Monarch, and in 13 out of 16 trials (81%) with the Viceroy. The reaction was given by E–2 in 43 out of 73 trials (59%) with the Monarch, and in 9 out of 13 trials (69%) with the Viceroy. E–3 gave the reaction in 42 out of 94 trials (45%) with the Monarch, and in 5 out of 15 trials (33%) with the Viceroy. E–4 showed this reaction in 6 out of 84 trials (7%) with the Monarch, and in 2 out of 16 trials (13%) with the Viceroy. The reaction was never given by any of the birds when a non-mimetic butterfly (palatable) was presented.

The control birds also gave this same reaction when the Viceroy was presented, although on the whole less frequently than the experimental birds did. C–1 gave the reaction for 3 out of 25 Viceroys (12%); C–2 for 0 out of 25 Viceroys (0%); C–3 for 19 out of 25 Viceroys (76%); C–4 for 3 out of 25 Viceroys (12%). As might have been expected on the basis of the experimental birds, C–3, the bird that reacted to the Viceroy as an unpalatable butterfly during all but the last trial, also gave a high proportion of feather-ruffling reactions to the Viceroy.

Learning and Memory in the Scrub Jays

Although a study of learning in the Florida Scrub Jays was not the primary purpose of this inquiry, a few words

should be devoted to this aspect of the experiments. De Ruiter (1952) described, in his work with Jays (*Garrulus glandarius* Linné) and Chaffinches (*Fringilla coelebs* Linné), how the birds became used to the inedibility of small sticks, and refused to peck at them. After experience with the twigs, the birds also refused to peck at caterpillars bearing close similarity to the twigs. Only if a caterpillar were pecked by accident would the birds, thus rewarded, continue to hunt for caterpillars. If they found only sticks again, they soon ceased pecking. This behavior has been termed an example of habituation by Thorpe (1956). In so far as the Scrub Jays found the Monarch butterfly inedible in a series of 50 trials, one might have expected habituation to develop in the course of the experiments. Indeed, the theory of mimicry suggested by Müller (1879, 1881) assumes that young birds learn by experience which butterflies are inedible and remember what they have learned. However, the repeated lapses of the Scrub Jays into pecking the Monarch show a persistent trial-and-error learning pattern. Swynnerton (1915) in referring to the mistaken attacks of his caged birds on unpalatable insects noted: ". . . no bird could be too old or too experienced to make continual mistakes of this kind." Similar "forgetfulness" is reported by Sadovnikova (1923). She found that in maze learning in passerine birds, individual birds would occasionally show periods of "forgetting" when they entered blind alleys which they had previously learned to avoid. The pattern of apparent forgetfulness shown by the Scrub Jays thus may be of a general nature, or may be associated with cage experiments. The experimental behavior can not be extended to imply that such short-term forgetfulness (day to day) exists among Scrub Jays in the wild; this is not known.

In spite of the short-term lapses of memory seen in the Scrub Jays, the data did show that the birds could remember to reject a Monarch and a Viceroy on sight alone after a period of about two weeks. E–1 rejected a Monarch and a Viceroy after 16 days of 82 trials with unrelated butterflies of the *Battus* mimicry complex; E–2, after 19 days of 84 such interim trials; E–3, after 15 days of 82 such interim trials. Tests of memory in the Scrub Jays after longer periods had elapsed were not possible in these experiments.

Discussion

The first point to be considered is that of the reaction to the model, the Monarch, by the four experimental birds. As the data showed, the Monarch was unacceptable on sight alone at some time to all the experimental birds. The theory that models are unpalatable, and that their color pattern is a sign of unpalatability, is thus supported. Following a period of learning during which the experimental birds were given the Monarch, these birds did not even touch the Viceroy in many trials, and in no case did the birds eat a Viceroy. That the Viceroy is not as inherently unpalatable as the Monarch was shown by the control birds, and this will be discussed below. The highly significant difference in the treatment of the Viceroy by the two sets of birds is attributed to the experience of the experimental birds with the unpalatable Monarch, and to the subsequent association by these birds of the color pattern of the Viceroy with that of the Monarch. Under the conditions of the experiment, it has been shown that mimicry in the case of the Monarch and Viceroy is effective.

The status of the edibility of the Viceroy demands further consideration. According to Bates's idea (1862), the mimic was presumed to be a butterfly edible to vertebrate predators, especially to birds. Müller (1879), in dealing with a particular complex of closely related species of mimetic butterflies in South America (Heliconiidae) which had puzzled Bates, resolved the problem by suggesting that

the entire complex of "models" and "mimics" was unpalatable to predators. The pooling of their numbers thus reduced the number of losses per species to the learning of inexperienced birds. In the present experiments, the status of the Viceroy as a Batesian or Müllerian mimic is not entirely evident, and it brings to mind Swynnerton's repeated emphasis on the range of edibility of butterflies to birds (1919). That the experimental birds in no instance regarded the Viceroys as edible is clear. The reaction to the Viceroy by E–1 and E–2 (fig. 1A) shows that those birds never killed that butterfly, although E–2 killed three Monarchs after the commencement of Viceroy trials. E–1 and E–2 were not discriminating the Viceroy from the Monarch as something different and edible. E–3 (fig. 1B) in trial 55 apparently did discriminate between its first Viceroy and Monarchs. Subsequent trials indicate either that the bird failed to maintain its discriminative ability, perhaps in part due to the design of the trials plus the adjustment for natural error, or that the bird found the Viceroy unpalatable, and established a general reaction to both Monarch and Viceroy as inedible. The fluctuating responses of E–4 (fig. 1B) to the Monarch and Viceroy show that the bird failed to remember on sight alone that the Monarch was inedible. The treatment of the Monarch and Viceroy was so consistent that it seems likely that this bird was not discriminating between the two, and perhaps found them both unpalatable. At any rate the Viceroy was not eaten in preference to the Monarch by E–4.

All four experimental birds showed identical, characteristic behavior, discussed above, to both the Monarch and Viceroy, which supports the idea that there was no discrimination of one from another. However, although the Monarch and Viceroy were treated in this generalized manner, a trial can be cited in which a bird clearly distinguished one Viceroy from Monarchs on the basis of a slight difference in color. For E–3, trial 62, there is reason to believe that the pecking of this Viceroy was due to its coloration which was somewhat more brown than previous or succeeding ones. The butterfly had been presented inadvertently, and the instant curiosity and pecking reaction of the bird to the slight color discrepancy was noted. The problem of discrimination *vs.* generalization of models and mimics by the Scrub Jays will be discussed in more detail in Part III of this series of papers. For the present, it can be said that although the data for the experimental birds show that the Viceroy was rejected by them, they do not clearly show why. For E–1 and E–2, the rejection of the Viceroy seems to be based on the fact that the birds learned that the Monarch was unpalatable, and could not discriminate the Viceroy from the Monarch. The data for E–3 and E–4 could be interpreted in the same way as for E–1 and E–2, or alternatively, that the Monarch and Viceroy were both found by experience to be unpalatable and were recognized as one or as separate color patterns, but in either case rejected.

The control birds gave further indication of the inherent edibility of the Viceroy. As the diagrams showed (fig. 2), the Viceroy was not as edible as the non-mimetic butterflies for C–3, and in part this was true for C–1 and C–4. C–2 regarded the Viceroy as an edible species. C–4 appears to have learned to eat the Viceroy. The reaction of C–3 to the Viceroy is comparable to the initial learning pattern of E–1 for the Monarch, but the Viceroy was more acceptable to C–3 toward the end of the experiment. It is possible that the control birds, particularly C–3, had some pre-capture experience with the Monarch, and associated the Viceroy with the Monarch, although no bird refused to peck its first Viceroy. The geographic distribution of the Viceroy precludes any experience with that exact color pattern in nature by these jays.

The learning patterns of E–3 and E–4 and of C–1, C–3, and C–4 could be interpreted to lend support to the hypothesis that the Viceroy is a classical Müllerian mimic. Additional evidence for this view is suggested by the reaction times of the control birds in seizing Viceroys, which were longer than those for seizing non-mimetic butterflies. However, rather than try to place the Viceroy in a rigid, all-or-none category which implies more than the data show, the Viceroy is here considered more edible than its model, the Monarch, but initially less edible (except to C–2) than the non-mimetic butterflies used in these experiments.

Summary

1) This paper is the first in a series of three which present experimental studies of mimicry in some North American butterflies.

2) The experiments were designed to study the effectiveness of mimicry in these butterflies with the use of eight Florida Scrub Jays (*Cyanocitta coerulescens coerulescens*) as caged predators. The butterflies were immobilized and their wings were folded together dorsally, so that only mimicry in the characters of the underside of the wings was being tested in these experiments.

3) The present experiments tested mimicry in the classic example of the Monarch (*Danaus plexippus*) and Viceroy (*Limenitis archippus archippus*).

4) The results of these experiments show that the non-mimetic butterflies, used in couplet with each model or mimic, were eaten in every trial by all birds.

5) The four experimental birds were given numerous trials with the model, the Monarch. The Monarch was not eaten by these birds in any trial, and in many trials was not touched, after initial learning had taken place.

6) After the experimental birds had been given more than 50 trials with the Monarch, the Viceroy was substituted for the Monarch at intervals. The Viceroy was never eaten by the four experimental birds, and in many trials was not even touched.

7) Characteristic behavior shown by the four experimental birds after the presentation of both Monarchs and Viceroys indicated no discrimination between the two species of butterflies.

8) The four control birds had no prior laboratory experience with the Monarch, and these birds ate the Viceroy in many trials.

9) A statistical analysis of the reaction to the Viceroy by the experimental and control birds indicated that the two groups did not react to the Viceroy in the same way. The difference in response is attributed to the prior laboratory experience of the experimental birds with the Monarch. The color pattern of the Viceroy was apparently associated with the complete inedibility and similar color pattern of the Monarch. Under the conditions of the experiment, mimicry has been shown to be effective.

10) The data indicate that the Viceroy is more edible than the Monarch, but less edible than the non-mimetic butterflies used in the experiments. In addition, the control birds took longer to seize Viceroys, on the average, than they took to seize the non-mimetic butterflies. Therefore the Viceroy is not termed either a Batesian or a Müllerian mimic in the classical sense.

11) Learning behavior and memory in the Scrub Jays were considered briefly. The records showed that three of the four experimental birds remembered to reject a Monarch and a Viceroy on sight alone, after a period of over two weeks had elapsed since their last experience with these butterflies.

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