

Feeding Experiments Using the Red Avadavat, *Amandava amandava*, with Reference to the Effectiveness of Batesian Mimicry

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Abstract. Four series of feeding experiments, each simulating a different type of Batesian mimicry, were carried out using captive red avadavats (Aves: Estrildidae) as predators. When presented with non-mimic alternative prey together with model and mimic prey, most birds rejected only models first, but gradually became unwilling to eat mimics spending a long time. It was therefore suggested that there may be some mental process involved in avian feeding behavior. In the absence of non-mimics, most birds took the poorest mimic, showing that the presence of alternative prey had an important influence on the survival of a Batesian mimic.

Throughout the experiments, a striking individual variation in the response of birds toward the prey was observed and the significance of such variation is discussed.

Introduction

Ever since its inception, the theory of mimicry proposed by Bates (1862) has drawn great interest from evolutionary biologists, ecologists and ethologists. Following Brower's (1958 a, b, c) laboratory demonstration of the actual effect of such Batesian mimicry using butterflies as prey and scrub jays as predators, many experimental studies concerning Batesian mimicry have been performed both under laboratory and natural situations.

Among these studies, the main subjects were the protective advantage of an "incipient mimic" which only slightly resembles its unpalatable "model" species and the evolution of mimicry as a process of "perfection" of similarity in the mimic. The main experimental method used was a simulation of a Batesian mimicry situation, using various types of artificial models and mimics as prey, and captive or wild insectivorous vertebrates, such as birds and lizards, as predators. Experiments have been carried out both in the laboratory (Schmidt, 1958, 1960; Sexton, 1960; Duncan and Sheppard, 1965; Reiskind, 1965; Alcock, 1970a, b; Brower et al., 1971; Shideler, 1973; Schuler, 1974; Terhune, 1977) and in a suburban environment (Morrell and Turner, 1970; Ford, 1971; Pilecki and O'Donald, 1971; Ikin and Turner, 1972; Lea and Turner, 1972; Boyden, 1976) and have been well reviewed by Wickler (1968) and Edmunds (1974).

Almost all such studies reached the same conclusion: that even an imperfect mimic had a protective advantage against predation by birds and lizards, and that the more closely the mimic resembled its model, the more effectively it was avoided by predators. Both Morrell and Turner (1970) and Lea and Turner (1972) explained these results using psychological terms that predators (wild birds in these cases) "generalized" the imperfect mimic

with the model, but also could "discriminate" the poor mimic or non-mimic (control) from the good mimic.

However, in spite of so many detailed studies some problems remain. First, the expression "simultaneous generalization and discrimination" is difficult to understand. Since the term *generalization* is somewhat vague, an alternative definitive expression should be introduced. Second, the importance of alternative prey has tended to be ignored, although recently Schuler (1974, 1980) has investigated this aspect in detail from the viewpoint of Holling's (1965) theory. Third, temporal, intraspecific and interspecific variations of response in predators were often ignored due to data obtained during the whole experimental period being summed up for statistical analysis. Especially for birds, supposedly the most important diurnal predators of insects, such variations seem to be striking when compared with those of lizards (Johki and Hidaka, 1979) and probably other insectivorous predators. It is therefore likely that these variations have an influence on the establishment and evolution of Batesian mimicry in insects.

In this study we carried out four series of feeding experiments simulating Batesian mimicry using wild-caught birds, red avadavats (*Amandava amandava*), as predators. Here we laid emphasis on the response of the *individual* bird and its temporal aspects. The mental (or psychological) process in the feeding behavior of birds was also studied.

Materials

The experimental birds, red avadavats, *Amandava amandava*, were captured with mist nets near Lake Biwa, in October, 1978. All twelve birds captured were from the same flock and were judged to be young birds under one-year old.

All birds were kept together in a large laboratory aviary (1.0 m × 1.5 m × 1.2 m) and fed commercial seed mixture and vegetables. Prior to the experiments, each bird was transferred from the aviary to individual small cages (40 × 30 × 40 cm) in another experimental room. Four birds were transferred to individual cages at one time for an experiment, the other birds being left in the aviary during the four birds' experimental period. When the experiment for the first four birds finished, they were returned to the aviary and another four birds were subjected to experiment.

The four individual cages were arranged near the window of the experimental room, and artificially illuminated between 7:00 A.M. – 9:00 P.M., although the day-length exceeded this period due to the incursion of natural daylight from the window. Birds were given seed mixture and water until the experiment started.

The "prey" used in all experiments were millet grains placed in a small glass cup (4 cm in diameter and 1.5 cm in depth), the side of which was colored by wrapping with vinyl tape (the color of the tape used will be mentioned in the procedure of each experiment). Due to technical difficulty we did not color the millet grain itself. Such an experimental design is not inappropriate since birds have been shown to utilize the color pattern of a card on which a bait was placed as a cue for judging prey palatability (Morrell and Turner, 1970).

Millet grains were dipped in either a 3% solution of quinine hydrochloride (unpalatable food) or in distilled water (palatable food) and then dried. The quinine-soaked grains tasted considerably bitter to humans.

Experiments and Results

The experiments in this study consisted of four series, each simulating a different type of Batesian mimicry. Quinine-soaked unpalatable grains placed in a cup were used as “models” and palatable ones as “Batesian mimics” or non-mimic controls. A set of two to four cups, each containing 5.0 g of palatable or unpalatable grains, placed on the white-colored floor of each bird cage and the bird was allowed to take food freely, although it would not eat during the period of non-illumination.

Except for one series (Experiment IV), 24 hr trial was conducted, beginning at 10:00 A.M. when, daily, grains remaining in each cup were removed, weighed immediately and replaced by a fresh 5.0 g of grains. The decrease in the weight of grains from 5.0 g was recorded as the amount of food eaten during the previous 24 hr’s trial.

The procedure of each experiment and its results was as follows:

1. EXPERIMENT I

Procedure

This experiment was a “preliminary test” and was the simplest one. Twelve birds were used and each bird was offered two “prey” cups, one colored red (carmine red) (R) and the other green (deep green) (G). During the five or six days, which we called the “preliminary period”, both red and green cups contained palatable grains, but for the next five days one of them served as an unpalatable “model”, containing quinine-soaked grains (R for birds No. 1, 2, 7, 8, 11 and 12; G for birds No. 3, 4, 5, 6, 9 and 10). During the last period of the experiment, the “retention period”, birds were offered only palatable prey in both cups again. The cup of the same color for the unpalatable “model” in the quinine-conditioning period was regarded as a perfect Batesian mimic, and the cup containing palatable grains throughout the experimental period as a non-mimic control.

In this experiment the model and mimic did not appear simultaneously, but the mimic followed the model. For birds No. 1–4, we inadvertently omitted trials of the preliminary period, and the length of the retention period was shorter than that for other birds.

Results

The total amount of grains taken per day by each bird during the preliminary, quinine-

Table 1. Total amount of grains (g) taken per day by each bird in Experiment I.

Bird No.	Preliminary period	Quinine-conditioning period	Retention period
1	—	2.692±0.143	2.807±0.344
2	—	3.226±0.060	3.266±0.547
3	—	2.984±0.176	2.967±0.490
4	—	3.720±0.341	3.372±0.557
5	3.155±0.293	3.154±0.191	2.875±0.392
6	3.392±0.262	3.394±0.236	2.921±0.427
7	2.844±0.183	3.013±0.155	2.751±0.379
8	3.047±0.435	3.062±0.182	2.801±0.381
9	2.857±0.266	2.925±0.290	2.674±0.387
10	2.978±0.358	2.960±0.226	2.759±0.525
11	2.975±0.417	3.081±0.212	2.642±0.260
12	3.237±0.560	3.193±0.415	2.814±0.288

Mean±SD (g)

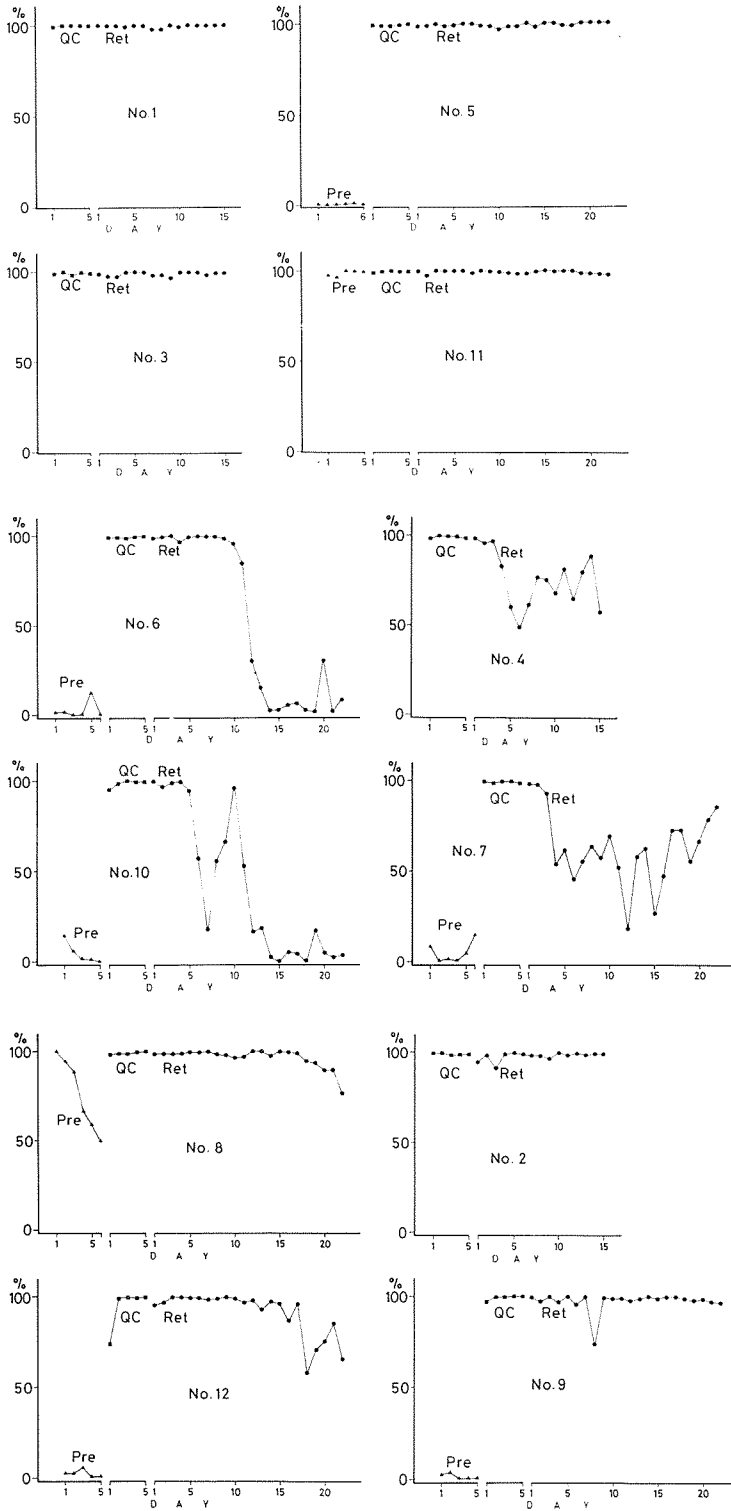


Fig. 1. Daily change in the feeding rate of each bird from a non-mimic (control) cup in Experiment I. *Pre*: preliminary period, *QC*: quinine-conditioning period, *Ret*: retention period.

conditioning and retention periods are shown in Table 1. Although marked differences among individual birds were evident, no change in the amount of food intake was seen among the three different experimental periods for each bird (by t-test). This shows that birds took almost the same amount of food throughout the experiment whether or not an unpalatable prey occurred in the cage. Therefore, we will hereafter represent the daily change in the amount of food intake from each cup as a percentage of the total intake.

Fig. 1 shows the daily change in the feeding response of the birds as a percentage of the food intake from a non-mimic cup. During the preliminary period almost all birds observed took food not from both cups but ate exclusively from one. This may represent a result of a "search image" in a broad sense, as a positive feedback in the birds' feeding behavior (Tinbergen, 1960), or a "conservatism" of this species to their food as pointed out by Alcock (1971). It should also be noted that there are remarkable individual variations of the response during the last period (retention period), during which Batesian mimic and non-mimic cup were presented. These variations can be classified into four types: First, like Nos. 1, 3, 5 and 11, the type which continued to take food solely from a non-mimic cup and never tried to eat mimics; second, like Nos. 6 and 10, the type which first ate non-mimics but soon began to eat mimics solely; third, like Nos. 4, 7, 12 and probably No. 8, the type which came to take food from both mimic and non-mimic cups at a roughly constant rate after it changed from eating solely from non-mimics; and last, like Nos. 2 and 9, the type similar to the first type but differing in the point that it *sometimes* ate considerable amount of mimics.

Considering that the behavior of birds during the retention period was influenced by the memory of an unpleasant experience with unpalatable models in the quinine-conditioning period, the birds of the third and last types are interesting because they were presumably in trouble and thus took a middle way of feeding. From a viewpoint of a mimetic advantage to the prey, this type of Batesian mimic has a protective effect against all birds except those of the second type classified above.

2. EXPERIMENT II

Procedure

The response of birds to the "imperfect mimic" was examined. Since birds Nos. 1, 3 and 11 died after Experiment I and bird No. 6 was unhealthy, eight birds were used. Each bird was offered three types of prey cup: red (R), green (G) and a third "mimic" cup of either orange (Or) or yellow-green (YG). Eight birds were divided randomly into two experimental groups: Nos. 2, 4, 9 and 12 were offered the red model, green non-mimic and orange mimic, while Nos. 5, 7, 8 and 10 were offered the green model, red non-mimic and yellow-green mimic. Cup position was randomly changed every day and the experiment continued for 14 days.

Unlike the design of Experiment I, the model and mimic were presented simultaneously and the bird could compare the color among model, mimic and non-mimic.

Results

The response of each bird to the model, non-mimic and imperfect mimic cups is shown in Fig. 2 as the daily change in the rate of food intake from each cup. In most cases, it took two or three days for a bird to establish a stable feeding pattern, and we therefore ignored the data for days 1 and 2 when calculating the average amount eaten per day from each cup (Table 2). Except for the case of two birds, Nos. 5 and 10, the imperfect mimic was protected from bird predation, being eaten significantly less than non-mimics ($P < 0.001$,

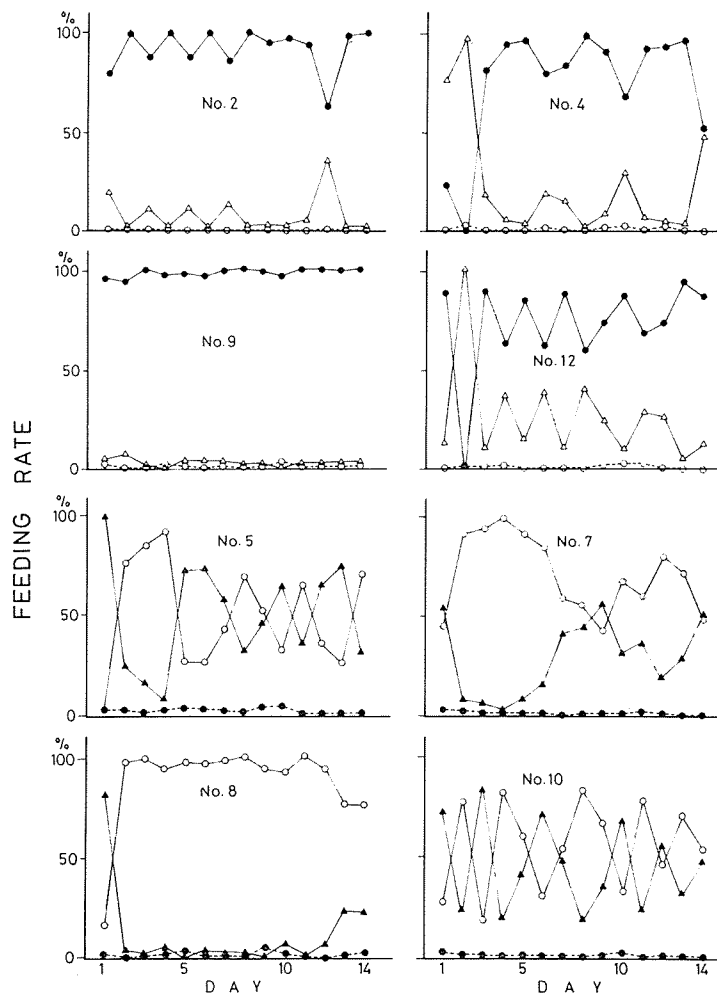


Fig. 2. Daily change in the feeding rate of each bird from model, mimic and non-mimic cups in Experiment II. ●: green (G), ○: red (R), ▲: yellow-green (YG), △: orange (Or). The unpalatable model is R for the birds No. 2, 4, 9, 12 and G for Nos. 5, 7, 8, 10, each being shown by the broken line.

by t-test). There is, however, also a significant difference between the amounts of the model and mimic eaten by birds No. 2, 4, 7 and 12 (Table 2). Such a difference seems to be important in considering the effects and evolution of Batesian mimicry and will be argued in the discussion.

3. EXPERIMENT III

Procedure

This experiment simulated Batesian mimicry in a situation where there were several kinds of mimics resembling their model to various extents, and no non-mimic present. The same eight individual birds as in Experiment II were used, and each was offered four cups of prey, one a model of deep-green (G_1 , same as "G" in Experiments I and II) and three mimics of it: perfect being deep-green (G_1), the imperfect being spectrum-green (G_2) and the poorest, yellow-green (YG).

Table 2. Average amount of grains (g) eaten per day by each bird from each cup in Experiment II. The data of days 3–14 were used (see text).

Bird No.	G (NM)	Or (Mi)	R (Mo)	Model-Mimic	Mimic-Control (NM)
2	3.001±0.365	0.255±0.368	0.016±0.015	*	**
4	2.920±0.362	0.457±0.394	0.031±0.033	**	**
9	2.887±0.192	0.017±0.025	0.018±0.023	—	**
12	2.311±0.565	0.529±0.307	0.029±0.029	**	**

Bird No.	G (Mo)	YG (Mi)	R (NM)	Model-Mimic	Mimic-Control (NM)
5	0.038±0.041	1.414±0.733	1.490±0.653	**	—
7	0.020±0.022	0.844±0.528	2.204±0.694	**	**
8	0.038±0.034	0.152±0.211	2.325±0.289	—	**
10	0.008±0.014	1.340±0.766	1.742±0.676	**	—

Mean±SD (g)

{	Mo : model	— P>0.05	} by t-test
{	Mi : mimic	* P<0.05	
{	NM: non-mimic (control)	** P<0.01	

Color code

G : deep green
R : carmine red
YG: yellow-green
Or : orange

The experiment was somewhat similar in its situation to that of Duncan and Sheppard (1965) and one might predict that most birds would take food mainly from the poorest yellow-green mimic cup in the absence of a palatable non-mimic. The position of four cups was changed daily.

Results

Fig. 3 shows the daily change in the rate of food intake from the model cup and its three kinds of mimics. Since a longer time than in Experiment II was needed for most birds to establish a stable feeding pattern, the data for days 1–7 were excluded from the calculation of the average amount eaten per day (Table 3). Five birds out of seven (Nos. 4, 7, 8, 9 and 10) behaved as predicted above, by avoiding the perfect mimic (G_1) and mainly eating the poorest mimic (YG). However, even for these birds, no significant difference was detected between the amounts taken from cups G_1 and G_2 . Bird No. 12 took food irrespective of cup color, probably selecting on the basis of a certain cup position. The feeding response of bird No. 2 was quite exceptional. It completely avoided the poorest mimic (YG) and mainly ate the second mimic (G_2).

4. EXPERIMENT IV

Procedure

The last series of experiment was carried out in order to improve the fault of the former three experiments that the prey did not “move” for one day. In this series the unit period of a feeding trial was shortened from 24 hr to one hour. The position of the cups was changed after every one-hour trial, and five successive trials were made daily, 10:00 A.M. – 3:00 P.M. In this experiment, bird No. 6 was substituted for No. 5 which died in the course of Experiment III. The other seven birds were the same as used in Experiments II and III. Four prey cups were offered to each bird: blue (B), light-blue (LB),

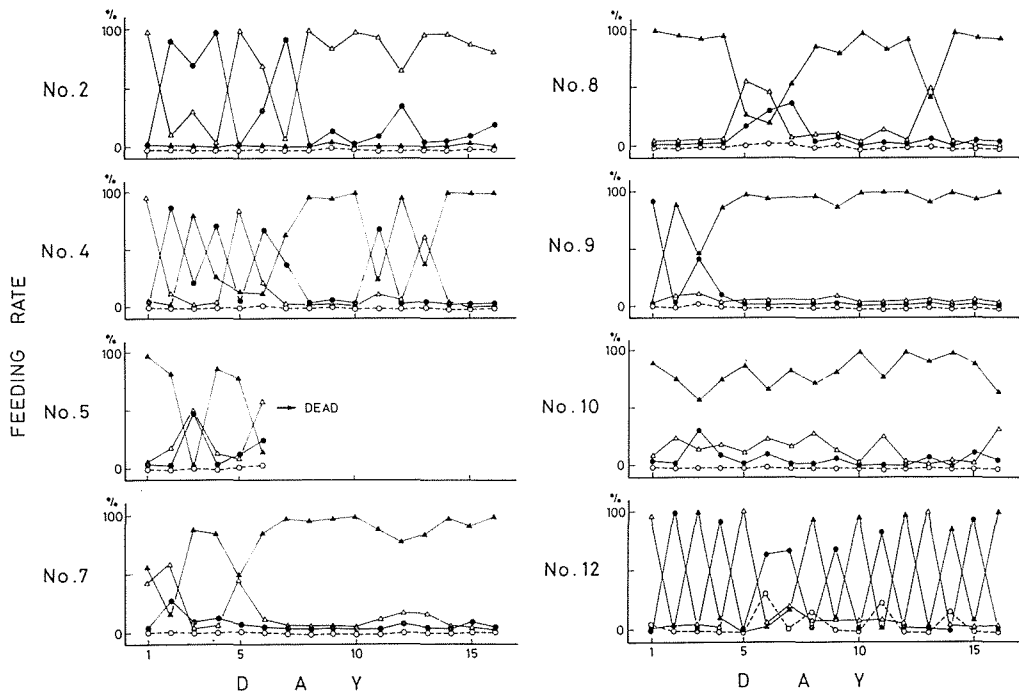


Fig. 3. Daily change in the feeding rate of each bird from model (same as G_1) and its three kinds of mimic (G_1 , G_2 , YG) cups in Experiment III. \circ : model (broken line), \bullet : G_1 , \triangle : G_2 , \blacktriangle : YG.

Table 3. Average amount of grains (g) eaten per day by each bird from each cup in Experiment III. The data of days 8–16 were used (see text).

Bird No.	$G(Q)$	G_1	G_2	YG
2	0.009 ± 0.008	0.301 ± 0.314	2.515 ± 0.298	0.034 ± 0.030
4	0.008 ± 0.008	0.273 ± 0.632	0.268 ± 0.582	$2.571 \pm 0.587^*$
5	—	—	—	—
7	0.006 ± 0.009	0.053 ± 0.071	0.143 ± 0.164	$2.221 \pm 0.134^*$
8	0.029 ± 0.027	0.067 ± 0.052	0.182 ± 0.302	$1.650 \pm 0.311^*$
9	0.017 ± 0.031	0.021 ± 0.022	0.034 ± 0.043	$1.969 \pm 0.218^*$
10	0.005 ± 0.012	0.082 ± 0.092	0.272 ± 0.320	$2.267 \pm 0.418^*$
12	0.113 ± 0.160	0.550 ± 0.783	0.294 ± 0.630	1.208 ± 1.043

$G(Q)$: model; G_1 , G_2 , YG: mimics

Mean \pm SD (g)

* : YG was eaten significantly more than G_1 and G_2 ($P < 0.01$, by t-test).

Color code

$\{G(Q)\}$: deep green

G_2 : spectrum green

YG : yellow-green

orange (Or) and yellow-orange (YO). Unpalatable grains were placed in either the blue or orange cups which served as models (B, for birds No. 2, 4, 6 and 7; Or, for Nos. 8, 9, 10 and 12). There were thus two pairs of cups: the model-mimic pair and two non-mimics.

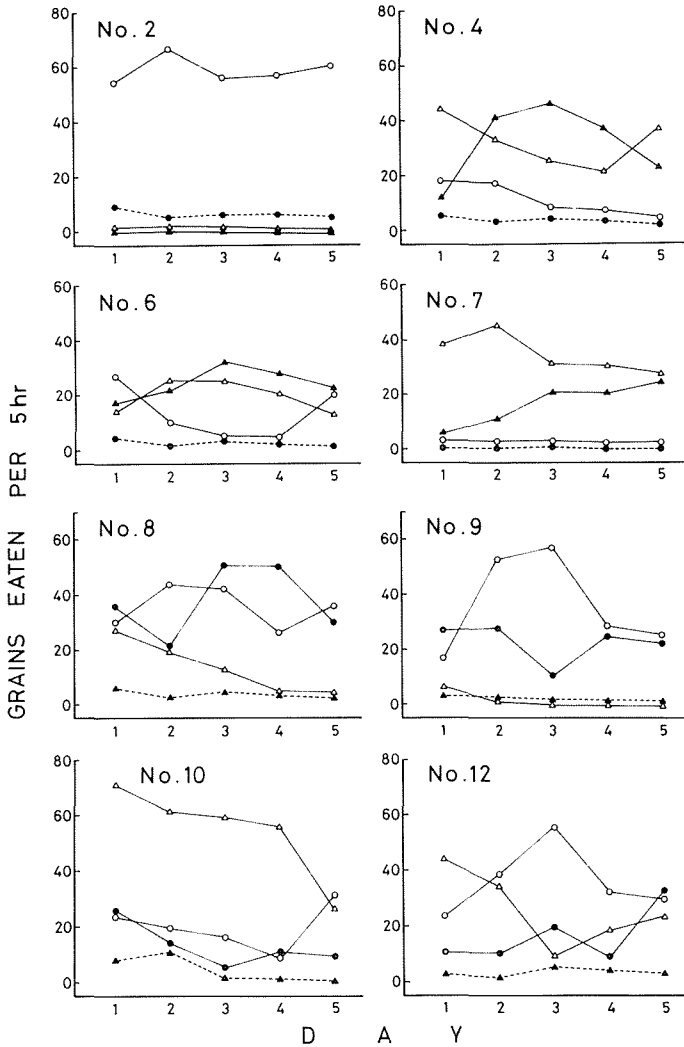


Fig. 4. Daily change in the number of grains eaten by each bird from four kinds of cups in Experiment IV. ●: blue (B), ○: light-blue (LB), ▲: orange (Or), △: yellow-orange (YO). The model cup is B for the birds No. 2, 4, 6, 7 and Or for Nos. 8, 9, 10, 12, each being shown by the broken line.

Results

The daily amounts of grain eaten from each cup in five trials were totaled and are shown in Fig. 4 as the daily change for each bird. In the case of birds No. 4, 7, 8 and 9, the imperfect mimic was protected, but it took two or three days (10–15 repeated trials) before the bird avoided a mimic to a similar extent to the model and came to eat randomly from two non-mimic cups. More than five days' trial would be necessary for birds No. 6 and 10 to come to avoid an imperfect mimic. Birds No. 2 and 12 behaved in the same fashion as in Experiment III: No. 2 completely avoided the two non-mimics and took food from the imperfect mimic cup or even from the model cup, while No. 12 ate grains irrespective of the color of the cup, if they were palatable.

Discussion

Advantage of Batesian Mimicry

In all series of experiments of this study, we could demonstrate the protective advantage of a Batesian mimic even if it poorly resembled its model. From this viewpoint, we only confirmed conclusions of many experimental studies simulating Batesian mimicry (cf. Edmunds, 1974). However, comparing the behavior and the process of learning of each bird, and considering the temporal aspects of response in individuals, there are some points which need consideration.

The first point is about mechanisms by which a mimic escapes predation by birds, even if the mimic poorly resembles its model. Bates (1862) considered that predators would be "deceived" by a mimic into believing that it was the same species as an unpalatable "model" insect. This may currently be reasonably explained using the psychological terms that predators make a "generalization" between a model and a mimic (Morrell and Turner, 1970; Lea and Turner, 1972). However, the term "generalization" is ambiguous in that it is unclear whether or not predators are aware of differences between models and mimics and discriminate between them, although Morrell and Turner (1970) state that predators (wild birds in this case) make both discrimination and generalization "to some extent". Our results are not inconsistent with these theories, but, if possible, the true character of such a "generalization" must be definitely explained through an external (behavioral) and internal (psychological) process.

From the result of Experiment I (Fig. 1), we classified the response of birds to the perfect mimic into four types, each reflecting the mental state of individual birds. Of these four types, the behavior of the third (Nos. 4, 7, 8 and 12) and the last (Nos. 2 and 9) groups is important because the birds belonging to these types were apparently under the state of trouble: they were obviously aware of palatability of the mimic but could not eat entirely from a single cup as before, due to some mental cause. It might be a kind of unrest or fear and it is difficult to explain the results for these birds in terms of the discrimination/generalization concept. The situation of Experiment I, in which there was a time delay between the appearances of model and mimic, has also been observed in nature (Rothschild, 1963; Waldbauer and Sheldon, 1971) and it is therefore probable that predators respond to such models and mimics in almost the same way as seen in Experiment I.

It is also notable that there seems to be a high frequency of mentally-sensitive birds in the natural population (in our result, six birds out of twelve were mentally sensitive). Birds of this type presumably play an important role in the regulation of prey populations and in the production of a differential advantage in the various mimetic and non-mimetic insects. Although the mental process in a predators' behavior is difficult to analyze experimentally and is usually treated out of an object of statistical analysis, we think it the most important aspect in studying predatory behavior.

Experiments II and III provide further evidence for the existence of the predators' mental process in recognizing a Batesian mimic (Figs. 2 and 3). Even for birds which came to avoid an imperfect mimic as well as a model, it took a considerable time to establish a stable feeding pattern as compared with the rapid avoidance reaction toward a model. In other words, those birds gradually became *unwilling* to eat a mimic spending a long time. Furthermore, most birds apparently discriminated between a mimic, model and non-mimic respectively, completely avoiding a model and eating only a small amount of mimic. However, the situation seen in our design of Experiments II and III may be un-

common in nature because wild birds will have few opportunities to simultaneously compare a model and mimic, but will randomly encounter them and other non-mimics individually. If the visual recognition of prey by a predator includes two process, one sensory and the other mental, then only the mental process might be necessary for birds in Experiments II and III because they could easily detect the difference between model and mimic.

The second point in the discussion about the effectiveness of Batesian mimicry is the importance of alternative prey. The importance of alternative prey has already been noted by several authors (Brower *et al.*, 1971; Schuler, 1974, 1980), and Holling (1965) regarded the presence or absence of alternative prey as one of the most important factors influencing the effectiveness of Batesian mimicry and took it into account when formulating a theoretical model.

The result of Experiment III (Fig. 3, Table 3) directly shows the importance of a non-mimic alternative prey. In this experiment, non-mimic prey was absent (three palatable preys were all mimics), and the poorest mimic (YG) was mainly "attacked", being regarded as the most acceptable prey by most birds except for Nos. 2 and 12. Especially for birds No. 7 and 8, the mimic YG was treated quite differently between Experiments II (Fig. 2) and III (Fig. 3): in the presence of alternative prey (non-mimetic R) YG was effectively avoided, while in its absence YG was the most frequently attacked. Although the conditions of these two experiments strikingly contrast each other, and such situations may be rare in nature, these facts suggest the marked influence of alternative prey on the survival of a mimic.

It is likely that the degree of effectiveness of the Batesian mimic depends on the presence or absence of alternative prey. Schuler (1974) experimentally showed that the appearance and relative palatability of alternative prey as well as their presence or absence strongly influenced the effectiveness of Batesian mimics, although in our studies such stimuli were kept constant.

Individual Variation in Birds

Throughout Experiments I-IV, a striking individual variation in the response of birds toward the prey was observed, some responses functioning in favor of the protection of mimics, and others not. Individual variation in avian feeding behavior has often been reported (Brower, 1958 a, b, c; Holmes *et al.*, 1978; Schmidt, 1960; Alcock, 1971; Schuler, 1982; Shirota, 1980) and its importance and possible role in the evolution of Batesian mimicry in prey insects noted. Alcock (1971) listed three kinds of differential response in predators which could probably have caused the mimicry to evolve: a temporal change in the response of the same predator, variation among conspecific individuals, and interspecific differences in predatory behavior. Here we will discuss about the individual variation in birds' feeding behavior and its temporal change through all series of our experiments.

Table 4 summarizes the feeding response of the birds used in this study (except for Nos. 1, 3 and 11 which were tested only in Experiment I), being categorized as to whether or not the mimic prey was effectively avoided in each experiment. In spite of the fact that the interval between subsequent experiments exceeded two months, it seems that most birds had an inflexible response from the viewpoint of whether or not to behave in favor of the Batesian mimics. However, birds No. 2 and 12 changed their modes of behavior in Experiment III and maintained this tendency to Experiment IV. It is therefore con-

Table 4. Summary of the feeding response of nine birds in Experiments I–IV (see Discussion).

Bird No.	Experiment No.			
	I	II	III	IV
2	O	O	X	X
4	O	O	O	O
5	O	X	(died)	
6	X	—	—	O
7	O	O	O	O
8	O	O	O	O
9	O	O	O	O
10	X	X	X	X
12	O	O	X	X

The mimic was:

O: avoided effectively ($P < 0.05$, by *t*-test)

X: treated similarly to the non-mimic ($P > 0.05$)

—: not tested

cluded that the feeding pattern of individual birds is not always inflexible but sometimes undergoes fundamental changes. Yet we may say that it does not change kaleidoscopically so as to counteract the importance of individual variation, even after it changed fundamentally.

Let us consider the influence of individual variation on the establishment and perfection of Batesian mimicry. Accepting the idea that predators avoid a Batesian mimic even if it resembles its model imperfectly, two kinds of mechanism are proposed: One is a “threshold model”, in which predators attack mimics only when they are below the threshold of mimetic degree, although the threshold is individually specific and may be changed according to the predators’ hunger level and the presence or absence of alternative prey. The second model is a “probability-gradient model”, in which there is no threshold for a predators’ attack, but where the more perfectly a mimic resembles its model, the higher a probability that predators will avoid it. In the former model individual variation will apparently play an important role, and even in the latter case it will be important if the shape of attack probability curves is individual-dependent. It is unknown which type of mimic-avoiding mechanism our birds, red avadavats, belong to, but a “probability-gradient model” is likely to be more applicable because the mental process discussed above, greatly influencing the feeding behavior in this species, seems to be inappropriate for the incontinuous “threshold model”. Moreover, in other animals such as invertebrate predators, in which a mental process and learning have a minor role in feeding behavior, a “threshold model” may well be applicable.

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