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FORAGING IN A DYNAMIC MIMICRY COMPLEX

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Foragers confront numerous problems in finding and capturing suitable food items. Prey species have a wide variety of defense mechanisms, including Batesian mimicry. Briefly explained, a Batesian mimicry complex consists of a model species that is in some way repellent or less valuable to a predator attempting to eat it, and a mimic or mimics that are more desirable but in some way resemble the noxious models. The predator benefits from learning quickly to avoid the models, but also from distinguishing mimics and retaining them in its diet. If, however, the model and mimic are not always physically distinguishable, then predators occasionally may have to attack a model if they are to exploit the mimics. Various factors could then determine whether a predator will risk including a mimicry complex in its diet. In this study I examine whether the following four variables affect the behavior of a predator encountering a model-mimic system.

The ratio of models to mimics may be very important in deterring predation. As the number of models encountered increases, predators may be less willing to attack a mimicry complex. J. Brower (1960) looked at the relationship between the relative abundance of mimics and the efficacy of the complex in discouraging predators. She found that, if as few as 30% of the prey were models, a significant amount of protection from predation would occur.

Second, can the distribution of models and mimics in space be a useful cue to predators? Arnold (1978) used a Markov encounter process to predict that predators would behave differently when encountering nonrandom, clumped distributions of models and mimics rather than random ones. Using similar methods, Luedeman et al. (1981) added alternative prey items as a way of allowing models and mimics to adopt heterogeneous distributions. They also hypothesized that nonrandom distributions could modify predator behavior.

Obviously, if high-quality, abundant alternative prey items are readily available, the predator may be less inclined to risk attacking a mimicry complex. Although the need to consider alternative food sources is mentioned often, the actual effect of alternatives has rarely been tested. Dill (1975) found that the presence of alternative prey reduced predation on a simulated mimicry complex.

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He explained that the effect of alternatives is to reduce the predators' willingness to risk the mistake of attacking a model. Getty (1985) presented a theoretical model in which the availability of nonmimetic prey items was a key predictor of whether predators would attack a mimicry complex.

Finally, can the success of mimicry complexes be influenced by the time of first appearance of the models, relative to that of the mimics? Bobisud (1978) and Huheey (1980*a*) hypothesized that temporal separation or allochrony between the model and mimic species is advantageous. If mimics delay emergence until after the model species have appeared and "educated" the predators, all members of the mimicry complex should benefit (Huheey 1980*a*). The reaction of foragers to noxious models and edible mimics that are separated in time has not, to my knowledge, been examined experimentally.

THE MIMICRY COMPLEX

The foragers studied were long-eared chipmunks, *Eutamias quadrimaculatus* (27 females and 13 males), trapped in El Dorado County, California, between June 6 and September 11, 1980. Each animal was kept in an individual cage at 22.2° C and 16 h of light per day for the length of the experiment and fed Purina laboratory rat chow.

The food items used as the mimicry complex were dough balls. They were a yellowish mixture of white flour, egg yolk, and milk, rolled into balls with a diameter of 0.3 cm and allowed to dry to hardness. The mimics (*X*) were left unaltered, but the models (*M*) had a few grains of quinine hydrobromide placed in their center. I inserted small pieces of either copper or steel wire into the center of all the dough balls so that I could tell models from mimics by using a magnet. Which type of dough ball held the copper wire was alternated throughout the experiments. I used six chipmunks in a series of preliminary tests. When given a choice, they preferred mimic dough balls to rat chow; they ate 2.68 times more (by weight) of the dough-ball mixture. They exhibited aversive reactions after sampling quinine-laced dough balls. No statistical criterion was used, but in preliminary trials, mimics did not appear to be differentially selected by the chipmunks. Therefore, it was assumed that the animals could not distinguish between models and mimics without biting them. The discriminatory abilities of the animals were examined in more detail after the experiments were completed. The animals used in the preliminary testing were the last to be used for the formal experimentation, which took place after a period of several months during which the animals apparently had "forgotten" these experiences. Their responses were within the range exhibited by the others and no consistent trend of over- or undersampling was observed. No statistical test was deemed necessary.

EXPERIMENT A

Methods

The foraging apparatus was a wire-enclosed arena 91.5 cm × 91.5 cm × 25.5 cm. Ninety cups were attached to the floor of the arena in six rows of 15 cups

each. The rows were 10.2 cm apart and each cup contained a single dough ball, either a model or mimic. Five possible ratios of models to mimics were used: 9:1, 7:3, 5:5, 3:7, and 1:9. In a 5:5 ratio, for example, 45 mimics and 45 models were placed in the arena.

Prey were distributed either randomly or nonrandomly. In a random distribution, whether a given cup contained either a model or a mimic was determined from a random-number table. All five ratios of models to mimics were used with the random distribution. In a nonrandom distribution, the 90 cups were divided into 10 groups of 3 cups by 3 cups. All 9 cups within a group would contain either models or mimics. In a 5:5 ratio this would result in 5 groups of all models. Which of the 10 groups contained models or mimics was also determined from a random-number table. Only model-mimic ratios of 7:3, 5:5, and 3:7 were used in the nonrandom distribution. Thus, there were eight different combinations of model-mimic ratios and distributions. For all groups, new random distributions were generated for every new trial.

In both types of distribution, the dough balls were placed in a spatially uniform arrangement since the distance between individual dough balls was constant. There were no physical cues for the chipmunks that would signal a boundary between groups in a nonrandom distribution. Thus, in overall appearance, there was no difference between random and nonrandom distributions.

The importance of this type of nonrandom distribution is that it controls for spatial effects. In the design used, dough-ball density is equal at any given point in both random and nonrandom arenas. Any difference between the two treatments can be attributed solely to distribution. An alternative method such as placing dough balls in defined piles or clumps would make the results more difficult to interpret. Such factors as changes in searching and encounter rates and whether piles of food items are especially attractive or repellent would have to be considered.

The 40 animals were assigned randomly among the eight groups. Each group of five animals then experienced only that one combination of ratio and distribution in this experiment. For brevity and convenience, the groups will be referred to by the type of distribution of the dough balls, random (N) or nonrandom (NR), and by the percentage of mimics (10, 30, 50, 70, or 90).

All animals were handled extensively before the beginning of formal experimentation. Handling included placement in the arena with food so that they could become habituated to the experimental procedures. During the experiment, the chipmunks were allowed to forage in the arena for half an hour. Afterward, the number of empty cups and their positions were counted to determine the total number of models and mimics removed by an animal. These totals were divided into two categories. First, dough balls that were removed but did not have obvious bite marks were listed as not sampled (NS). This total was subtracted from the number removed to determine the number of models and mimics sampled (S). A distinction is made between the two categories because many dough balls could be displaced from their cups by an active but nonforaging chipmunk. Therefore, I could not assume that an intact, removed dough ball had been picked up and then dropped by a chipmunk. Only dough balls with obvious toothmarks could be related with certainty to a foraging event. Therefore, all my analyses of foraging

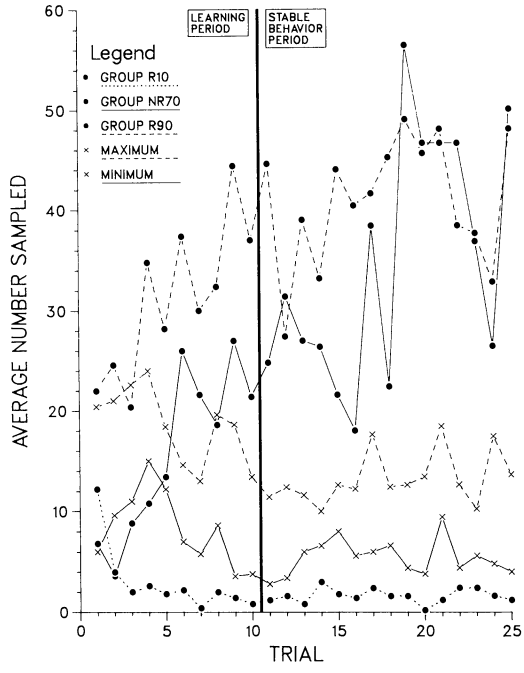

FIG. 1.—Average number of dough balls sampled for the five animals in each group per trial. Groups NR70 and R90 foraged extensively. Groups R30, R50, R70, NR30, and NR50 showed some level of sampling throughout the experiment. These groups are represented as a range by two curves; where maximum and minimum are plots of the highest and lowest average number sampled values among the five groups for each trial. Only in group R10 do the chipmunks almost totally ignore the complex (R = random, NR = nonrandom; numbers 10 through 90 refer to percentage of mimics).

behavior are based on the S dough balls. The NS dough balls were only examined for evidence of discriminatory behavior.

Dough balls that were completely consumed and those that were only bitten were scored as equally sampled without using gradations in amount. If the amount eaten per dough ball sampled were measured, there would be significant differences between mimics and models. I was only interested in the number of attacks initiated, however. Obviously, more of an attacked edible item will be eaten than of an attacked noxious item.

Each animal had a total of 25 trials with no more than 1 trial per day. All animals were deprived of food for 8–16 h before a trial and provided an excess of rat chow immediately afterward, regardless of performance. This ensured that animals could get sufficient nutrition without sampling the mimicry complex. The amount of rat chow eaten was not measured.

Results

I divided the data into two periods: the first 10 trials, which were a learning period, and the last 15, in which behavior was assumed to be stable (fig. 1). In the

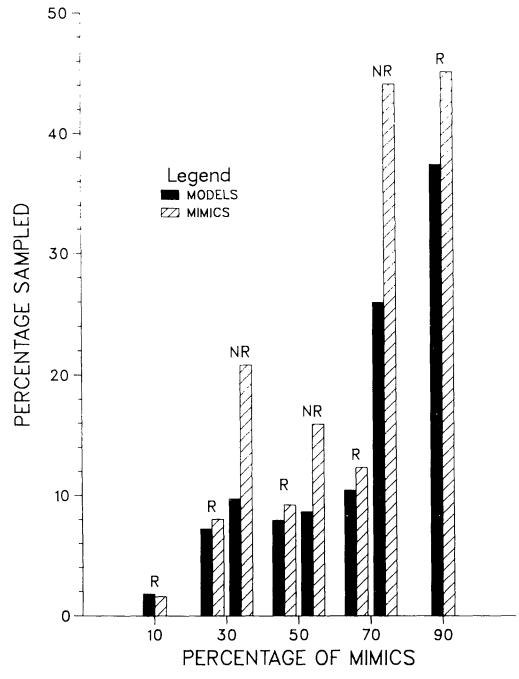

FIG. 2.—Percentages of different types of dough balls sampled from those available by percentage of mimics in the population. Notice how much more the percentage of mimics sampled exceeds the percentage of models sampled in the nonrandom than in the random groups.

learning period, the numbers of dough balls sampled on the first trial were not substantially different from group to group. In the subsequent nine trials, the groups diverged with some groups sampling more than others. Trial 10 was arbitrarily designated as the end of the learning period. From trial 11 to trial 25, the number of dough balls sampled per group remained relatively constant with the exception of the group NR70, which showed a slow increase (fig. 1).

From the data, it is apparent that the assumption from the preliminary testing that models and mimics are indistinguishable except by sampling was, to a degree, incorrect. In theory, the chipmunks encountering the random distribution should do no better than random chance at selecting mimics, because there are no reference cues. Therefore, the percentage of mimics sampled should roughly reflect the percentage present. Four of the five random-distribution groups, however, sampled more mimics than models as a percentage of the total available (fig. 2). In total, of the chipmunks in these groups that sampled more than 20 dough balls during the length of the experiment, 17 of 19 did better than predicted by pure chance alone. A sign test indicates that this result is significant ($P < 0.001$).

Nevertheless, the deviations from the expected were small. Only one animal did more than 10% better. The average animal sampled only about 2.7% more mimic

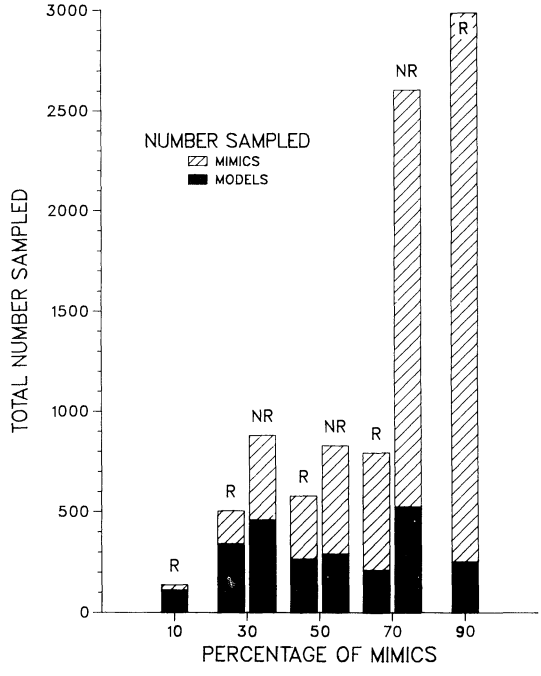

FIG. 3.—Total number of dough balls sampled from mimicry complexes with different distributions and percentages of mimics. Increase in the number of dough balls sampled is the result of more mimics, not more models, being attacked.

dough balls than could be expected by chance. By the same criterion, animals in nonrandom treatments did much better. Each of the 15 chipmunks sampled more mimics than predicted by random search, with the average animal choosing 14.3% more mimics than expected. (Compare the difference between percentage of mimics sampled across distributions in fig. 2.) Therefore, it seems that although there is discrimination, its effects are small in comparison to the other factors and do not seriously confound the other results.

The possibility exists that the chipmunks could distinguish models from mimics before biting them. If this were true, the NS dough balls should be biased in favor of the models. This was not the case; indeed, the bias was toward mimics overall. For the random-distribution groups, on the average, the bias per animal in favor of mimics was 2.6% greater in the NS total than in the S total. Of the 25 animals in this distribution, 16 showed more discriminatory ability in removed mimics (NS) than in sampled mimics (S). Although these results are not significant, the trend in the direction opposite to the expected recalls a phenomenon previously noticed in animals reacting to an attacked mimic as if it were noxious (J. Brower 1960). This trend is not found in the nonrandom groups because of the much larger bias toward mimics in the number sampled. Therefore, the dough balls left in the cups are rather weighted toward models, which will tend to be removed accidentally. This confounds the relationship between dough balls removed and dough balls

TABLE 1

NUMBER OF MODELS (*M*) AND MIMICS (*X*) SAMPLED BY EACH ANIMAL FROM TRIAL 11 THROUGH TRIAL 25

	RANDOM DISTRIBUTION (GROUP *M:X*)									
	R10		R30		R50		R70		R90	
ANIMAL NO.	9 : 1		7 : 3		5 : 5		3 : 7		1 : 9	
1–5	7	1	99	45	71	69	97	274	49	506
6–10	3	0	55	32	41	50	33	96	44	509
11–15	8	0	5	4	62	68	14	37	33	335
16–20	77	8	178	81	46	73	34	95	33	452
21–25	17	2	4	1	46	52	33	80	93	929
Total	112	11	341	163	266	312	211	582	252	2731
Average/ Trial/ Animal	1.49	0.15	4.55	2.17	3.55	4.16	2.81	7.76	3.36	36.41

	NONRANDOM DISTRIBUTION (GROUP *M:X*)					
	NR30		NR50		NR70	
	7 : 3		5 : 5		3 : 7	
26–28	165	129	97	199	79	390
29–31	108	118	23	68	69	480
32–34	100	66	73	102	123	440
35–37	60	87	57	87	121	370
38–40	25	21	41	81	132	398
Total	458	421	291	537	524	2078
Average/ Trial/ Animal	6.11	5.61	3.88	7.16	6.99	27.71

sampled. In fact, every animal in the NR groups had higher percentages of models in the NS category.

The experiment produced a steplike difference in the animals' sampling behavior in the last 15 trials. It can be seen from figures 2 and 3 that if frequency of mimics is greater than some critical point, a large response in total numbers sampled is triggered. In random-distribution groups, this extensive sampling occurs only when mimics make up 90% of the population, but with nonrandom distributions, extensive sampling occurs with a population of 70% mimics. In the remaining six groups, the number sampled was much less (table 1).

The data from the last 15 trials (in which behavior was relatively stable) were analyzed by a three-factor analysis of variance with mixed design and arcsine transformation (Bruning and Kintz 1977). The factors in analyzing the total number sampled per animal (from table 1) were the ratio of *M* to *X*, the type of distribution, and whether models or mimics were sampled. All main effects were significant and can be explained as follows. The significance of *M:X* ratio ($F = 18.39$, df = 4,30, $P < 0.001$) indicates that as the frequency of edible mimics increased, so did the number of dough balls sampled. Distribution had a significant effect in that more dough balls were sampled in nonrandom distributions ($F =$

12.23, df = 1,30, $P < 0.005$). Finally, in the total experiment, significantly more mimics were sampled than models ($F = 83.23$, df = 1,30, $P < 0.001$), primarily because animals exposed to higher frequencies of mimics foraged more extensively. The two-way interaction between $M:X$ ratio and distribution was significant ($F = 20.08$, df = 4,30, $P < 0.001$) because extensive sampling occurred at lower frequencies of mimics in nonrandom (70%) than in random (90%) distributions. Finally, as the percentage of models in the population changed, the number of models sampled remained constant. The number of mimics sampled increased, however, as they made up an increasingly larger proportion of the population (fig. 3). This gives a significant interaction between $M:X$ ratio and the number of models or mimics sampled ($F = 55.54$, df = 4,30, $P < 0.001$).

EXPERIMENT B

Methods

After finishing the 25 trials of the initial experiment, all animals experienced a further manipulation which depended on the groups' previous performances. An alternative food source was provided to the two groups of chipmunks that had sampled extensively (R90 and NR70). The addition of this palatable, readily available alternative food tested the willingness of the chipmunks to continue exploiting the mimicry complex. The alternatives were dough balls composed of the same ingredients as the mimics with a tasteless food coloring to make them green.

Fifteen cups to hold the alternatives were added to the experimental arena. They were placed midway between the original six rows of 15 cups so as to be 5.1 cm from each row. The alternate cup positions were between the cups of the second, eighth, and fourteenth columns. Each cup held one alternative. All other conditions and procedures remained unchanged and each animal ran five trials with the alternatives present.

In the other six groups the addition of alternatives would have had a minimal effect on the mimicry complex because sampling was already limited. For the manipulation in these groups, all 90 cups contained only mimics; thus, all the animals were presented with 100% edible dough balls. The intent was to simulate temporal separation because the chipmunks had been conditioned by excess models to largely avoid the mimicry complex. Each animal ran five trials under this new condition.

Results

The chipmunks in the two groups with alternative food items (NR70 and R90) preferentially selected nonmimetic dough balls, and the number sampled from the mimicry complex declined during the course of the experiment. The data are summarized in table 2 and were analyzed by an ANOVA with factors of group, trial number, and sampling choice (models, mimics, or alternatives).

Preference for the alternatives is clear (table 2, fig. 4) because, in total, 59.6% of the alternatives and only 32.6% of the models and mimics were sampled in the five

TABLE 2

DATA FOR THE FIVE TRIALS WITH ALTERNATIVE FOOD ITEMS

	GROUP NR70				GROUP R90			
TRIAL	No. MX	%MX	No. A	%A	No. MX	%MX	No. A	%A
Average	34.7	38.5	—	—	39.8	44.2	—	—
1	50.0	55.6	8.8	58.7	37.4	41.6	7.6	50.7
2	27.4	30.4	8.6	57.3	26.0	28.9	7.6	50.7
3	30.2	33.6	9.2	61.3	35.6	39.6	6.8	45.3
4	20.6	22.9	11.8	78.7	19.0	21.1	9.8	65.3
5	30.4	33.8	10.2	68.0	17.2	19.1	9.0	60.0

NOTE.—For groups NR70 and R90, No. MX and No. A refer to the average number of dough balls sampled from the mimicry complex (both models and mimics) and alternatives, respectively. %MX and %A refer to the percentage sampled from a total of 90 for the mimicry complex and 15 alternative dough balls. Average refers to the 15 trials prior to addition of the alternatives.

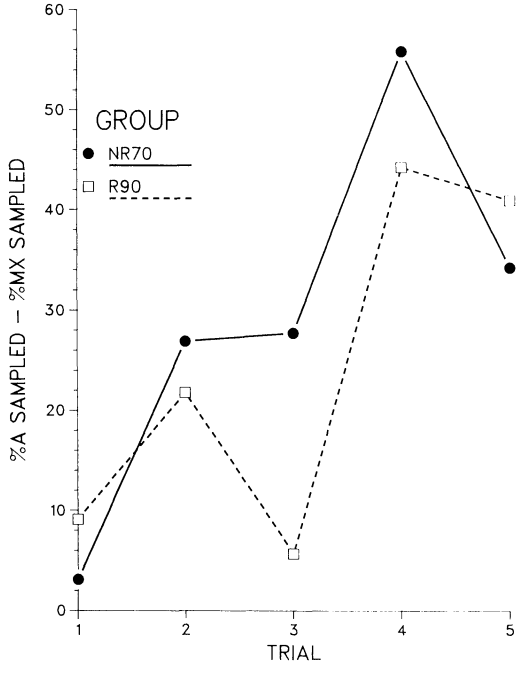

FIG. 4.—Difference between the percentage of dough balls sampled from the population of alternatives (%A) and the percentage sampled from the mimicry-complex population (%MX) per trial.

TABLE 3

AVERAGE NUMBER OF DOUGH BALLS SAMPLED PER GROUP IN THE CHANGING-RATIO EXPERIMENT

	GROUP								
TRIAL	NR70	R10	R50	R30	R70	NR30	NR50	R90	MEAN
1	6.8	3.2	7.0	10.6	15.6	15.6	21.8	22.0	12.75
2	3.6	6.2	16.2	10.2	11.4	20.2	21.6	24.6	14.25
3	8.8	11.8	15.2	13.0	20.2	21.4	23.6	20.4	16.80
4	10.8	9.4	13.0	22.2	24.2	20.0	30.8	34.8	20.65
5	13.4	14.2	17.6	23.8	17.6	28.4	23.2	28.2	20.80
Mean	8.7	9.0	13.8	16.0	17.8	21.1	24.2	26.0	
Groupings									

NOTE.—Data for groups R90 and NR70 are from the first five trials of experiment A and show the reaction of naive animals to the initial presentation of favorable model-mimic ratios. Data for the other six groups are from the five trials with 100% mimics and show the reaction of animals conditioned by unfavorable model-mimic ratios. The groupings indicate groups whose means per trial were not significantly different from one another when compared by multiple pairwise t-tests ($P < 0.05$, df = 4, one-tailed test).

trials ($F = 12.14$, df = 2,16, $P < 0.001$). The decline in the number sampled was from an average of 51.9 dough balls of all types in the first trial, to 33.4 by the fifth ($F = 11.24$, df = 4,32, $P < 0.001$). This was a decline in the number sampled from the mimicry complex, not in the number of alternatives sampled. Thus, the emphasis in sampling shifted from the model-mimic complex to the alternatives. As the percentage of alternatives sampled increased with subsequent trials, the percentages of models and mimics sampled declined (table 2, fig. 4), resulting in a significant two-way interaction between trials and the type of dough ball sampled ($F = 2.77$, df = 8,64, $P < 0.025$).

During the five trials with alternatives, the animals sampled less from the model-mimic population than they had before the alternatives were added. The significance of the decline is shown by a matched-pair t-test of animals before and after the addition of the alternatives ($t = 2.290$, df = 9, $P < 0.025$).

The data from the five trials of the six groups provided with 100% mimics were analyzed along with the first five trials of groups R90 and NR70 when these animals were naive (experiment A). As shown previously (figs. 1, 3), these two groups sampled extensively. If temporal separation is to be an effective mimic strategy, predators that have encountered unfavorable model-mimic ratios should respond more slowly than naive predators to a favorable situation.

A two-factor ANOVA showed that all groups of animals significantly increased the number sampled during the five trials ($F = 8.72$, df = 4,128, $P < 0.001$). The increase was from an average of 12.75 in the first trial to 20.80 in the fifth (table 3). The eight groups differed significantly ($F = 2.33$, df = 7,32, $P < 0.05$), but the interaction between groups and trials was nonsignificant ($F = 0.93$, df = 4,28). Since there was no significant interaction between the factors, I compared the means of the groups per trial, using multiple pairwise t-tests to determine among

which groups significant differences occurred in the number of dough balls sampled (table 3). The groups seem to fall into three categories based on how rapidly they increased their sampling: slow (NR70 and R10), moderate (R30, R50, and R70), and fast (NR30, NR50, and R90).

DISCUSSION

The Effect of Distribution and Ratio

In a random distribution of prey items, a distribution of 30% models prevented extensive sampling by the chipmunks. This result agrees with earlier research (J. Brower 1960; L. Brower et al. 1960; J. Brower and Brower 1962; Huheey 1980*b*) and suggests that models need not outnumber mimics for a complex to be adaptive, even when the models are not extremely distasteful or emetic. As noxiousness increases, the frequency of models may be decreased even further with the mimicry complex still remaining effective (Getty 1985). When distribution is nonrandom, however, the effectiveness of the complex is diminished for the mimics. A higher frequency of models is needed to substantially inhibit foraging.

In the nonrandom distributions, the animals increased their success rate in finding mimics, indicating that they were not searching the environment in a strictly random manner. A simple behavior pattern such as continued sampling in an area where a mimic was found would greatly increase success rate. In such a way, the effect of the distributional factor may be to increase the predictability of the environment. Once a single mimic is found, the frequency of mimics in that area is known to be higher than the frequency in the general population.

Therefore, it is better for the mimic to be distributed randomly. Any factor that makes a mimic easier to find and identify as edible would be deleterious for individuals of that species. The situation would seem to be reversed for models because they should benefit from increased predictability and correct identification by the predator. At equal model-mimic ratios in this experiment, however, more of both models and mimics were sampled in nonrandom than random distributions (fig. 3), suggesting that the model species also benefits from a random distribution.

It is likely, however, that clumps are more apparent in nature than in this experiment. The distance between two models in a group was the same as the distance between a model and a mimic on the outside of adjacent groups. If clumps are further apart, then a model grouping may be remembered and avoided more efficiently. This in turn would reduce the number of models taken and make it advantageous for models to clump.

Furthermore, although a nonrandom distribution was deleterious for both models and mimics, it was more so for mimics. When the dough balls were randomly distributed, the ratio of models to mimics at the end of a trial was roughly equal to the initial ratio. In nonrandom distributions, the difference between the number of mimics and models sampled was much greater because of the distributional cue which aided the chipmunks in finding the mimics (fig. 2). The effect of distribution on predation over the long term was not measured because the original ratio was

restored after every trial. It is conceivable that a nonrandom distribution could be adaptive for a model species if predation has a cumulative effect; the mimic population could drop so low that further foraging would not be beneficial to the predators. Once this point is reached, the remaining models may be almost totally free from predation. Therefore, although more models are sampled in the short term in nonrandom distributions, survivorship may increase over the long run.

As mentioned in the results, there was a slight but consistent effect of animals sampling more mimics than would be predicted by chance in the random-distribution groups. This effect indicates that the initial assumption of a perfect mimicry complex was not entirely correct and may affect predators' reactions to a mimicry complex. Previous studies have shown that the amount of protection from predation that a mimic gains can be strongly influenced by the degree to which it resembles the model (Sexton 1960; Duncan and Sheppard 1965; Morrell and Turner 1970; Pilecki and O'Donald 1971). In these experiments, however, the influence was probably minimal relative to the effect of distribution, as revealed in figure 2 by a comparison of the percentages of dough-ball type sampled between distributions. Further experiments that systematically measure and vary the level of discrimination may produce valuable insights. Getty (1985) hypothesized that imperfect mimicry may be responsible for partial prey preferences in predators and for the stability of model-mimic-predator populations.

Finally, it is of interest to note how slowly the naive animals in the 70% mimic, nonrandom distribution group (NR70) increased exploitation of the mimicry complex. This group was the only one to show a continuous increase during trials 11 to 25. Also, although this group eventually was sampling as many dough balls as group R90 (fig. 3), its initial increase was slower (fig. 1, table 3). This lag may be because of the time needed to learn the distributional cue to efficiently exploit this condition. Therefore, in nature the deleterious effect to the mimicry complex of a nonrandom distribution may not be constant, but may increase in severity during the season.

This study suggests that in the wild, species involved in mimicry complexes may try to use distribution to their advantage. Communal roosting among distasteful butterflies is a known phenomenon, and gregarious behavior has been positively correlated with increasing unpalatability (for a review, see Benson 1971). Further research on how models and mimics distribute themselves in relation to each other could be quite interesting and valuable.

The Response to Changing Ratios

Estabrook and Jespersen (1974), Bobisud and Potratz (1976), and Arnold (1978) examined mimicry as a Markov encounter process. Their consensus is that when models and mimics are randomly distributed (not clumped), the optimal predator strategy should be either to attack every individual of a mimicry complex or to attack none of them. If models and mimics have constant costs and benefits, then the all-or-none response is determined by the ratio of models to mimics. The limitation of these models is that they assume overall constant model-mimic ratios and unchanging environments. In nature, however, model-mimic ratios can fluc-

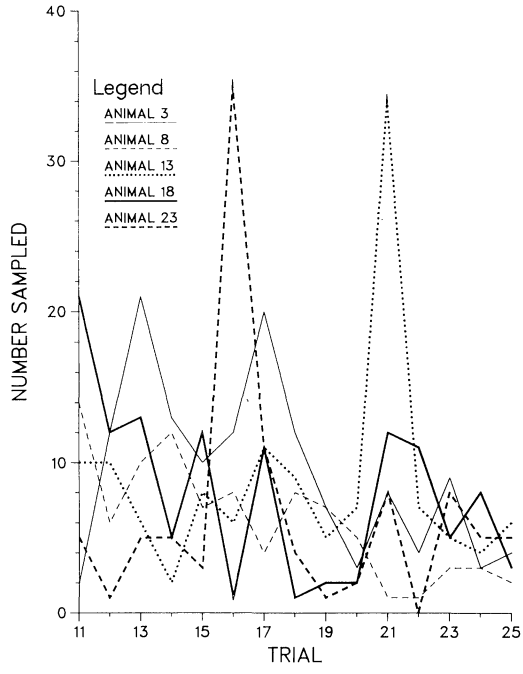

FIG. 5.—Number of dough balls sampled per trial for the five individuals in group R50. Each animal continues to sample the mimicry complex throughout the 15 trials of this experiment.

tuate greatly (L. Brower and Brower 1962; Brodie 1981). If this assumption is relaxed, the all-or-none prediction may no longer hold.

A predator's foraging behavior has a bearing on whether allochrony as proposed by Bobisud (1978) and Huheey (1980*a*) could be an effective strategy. An animal that never sampled after initial bad experiences would be unable to detect a favorable increase in mimic frequency. My results show that foragers can detect the increase in the numbers of mimics: few of the animals actually stopped sampling the complex. As a representative example, figure 5 shows the data for each animal in group R50: the animals continued to challenge the mimicry complex from trial 11 through trial 25. These results suggest that existing encounter models (Estabrook and Jespersen 1974; Bobisud and Potratz 1976; Arnold 1978) should be increased in sophistication to include the need to sample for changing ratios.

The groups in table 3 might be put into three classifications: slow, moderate, and fast responses. Groups NR70 and R10 show a significantly slower increase in numbers sampled. Groups R30, R50, and R70 show a moderate increase and NR30, NR50, and R90 show a fast increase (R70 and NR30 might actually be considered as moderately fast). The sudden increase in mimics as hypothesized in allochrony would seem to be favorable to the mimics when they are initially rare

(10% or less of the population). This result supports Huheey's suggestion (1980*a*) that for allochrony to work well for mimics, the models must appear first and essentially alone, so that predators could for a time sample nothing but models. If mimics were present and occasionally sampled, this would give the predator a mixed signal and could keep them sampling.

A random distribution of only 10% mimics is effective because it discourages almost all sampling (fig. 1). The reason for the slow increase in NR70 was discussed in the previous section. If some level of sampling remains (groups R30, R50, R70, NR30, and NR50 in fig. 1), the effectiveness of allochrony is lessened. In fact, the two nonrandom groups (NR30 and NR50) show a response that is as rapid as that of naive animals encountering 90% mimics (table 3). The data thus seem to indicate that allochrony is less effective when models and mimics are clumped and the animals have had enough time to learn this. The low efficacy of allochrony may be related to the fact that the chipmunks, on the average, sampled more (table 1) and found disproportionately more mimics in nonrandom distributions at equivalent model-mimic ratios (figs. 2, 3). Also, the animals in nonrandom distributions were conditioned to finding mimics in groups. A 100% mimic presentation is just another (albeit larger) group.

In summary, the data suggest that for mimic species using allochrony, it is most advantageous to be rare and unpredictably distributed before the rapid rise in frequency.

The Effect of Alternative Prey Items

Holling (1965), Dill (1975), Luedeman et al. (1981), and Getty (1985) have suggested that the effectiveness of mimicry depends on the quality to the predator of the alternative to attacking the complex. Readily available, high-quality, nonmimetic prey items should always be added to the predator's diet with the result that perhaps the mimicry complex is attacked less often. For the greater part of this study, the animals had two broad choices: adding the mimicry complex to their diet, or avoiding the complex and eating only rat chow. One of the drawbacks to the rat chow was that it was not readily available. The chipmunks could get it only after the trial. Availability of rat chow during the trial might have increased the quality of the alternative option and thereby reduced sampling of the mimicry complex. Conversely, if the animals had not been given rat chow to satiation after every trial, their hunger levels would have been higher and they probably would have increased their sampling of the dough balls. Instead of manipulating the rat chow, I enhanced the attractiveness of the alternative option by simulating the appearance of a new, highly palatable prey item (i.e., green dough balls). The improved alternative option had a significant effect in that the number of models and mimics sampled declined in groups R90 and NR70 (fig. 4). This is clear evidence that the presence of desirable alternative food sources can decrease the amount of predation experienced by a mimicry complex. Because only 15 alternatives were available, satiation was not possible and sampling of the model-mimic complex still occurred. If enough alternatives had been presented, the chipmunks might have been induced to avoid the mimicry complex altogether.

This result reinforces the need to think of mimicry complexes as part of entire

communities. It is not enough to demonstrate that an animal can benefit by preying on a mimicry complex, but this benefit must be greater than the average benefit gained from eating only alternative prey. In this experiment, for groups R90 and NR70, the benefit from sampling the mimicry system exceeded the benefit of eating only rat chow, but probably did not exceed the benefit of eating nonmimetic dough balls. Interestingly, this may mean that models need not have a cost associated with them (i.e., be either noxious or poisonous), but simply must provide less benefit than the average alternative prey item. As long as the frequency of mimics is small enough, the average benefit of including a mimicry complex will not exceed the benefit of using only alternative prey.

Ideas along this line of reasoning have been presented before. Lindroth (1971) suggested that some models may be difficult to catch rather than distasteful. He proposed that several genera of flea-beetles with effective escape mechanisms (Alticinae and Chrysomelidae) are models for ground beetles (genus *Lebia*). Thompson (1973) suggested a similar mechanism for maintaining color polymorphisms in a spittlebug (*Philaenus spumarius*), as well. Gibson (1974) showed experimentally that finches (*Bathilda sulficauda*) became hesitant in attacking a mimicry complex based on models that were able to escape. Thus, it is possible in all these cases that a predator including such mimicry complexes in its diet would receive a net benefit, but less than if it ignored the complex altogether and concentrated only on alternative prey.

Finally, my results suggest that for strategies such as allochrony to be successful, the mimic might have to delay its appearance until there are many alternative prey available as well.

SUMMARY

Chipmunks encountering a simulated Batesian mimicry complex with the models and mimics randomly distributed only foraged extensively when mimics were 90% of the population. If the models and mimics were nonrandomly distributed, however, extensive foraging occurred when mimics were 70% of the complex. The groups that did not forage extensively were tested to see how rapidly they could detect a favorable change in the frequency of mimics. I found that success in escaping detection for the mimics was closely linked to how well sampling behavior was eliminated in the prior treatment. Animals which experienced nonrandom distributions seemed particularly adept at detecting a favorable change. The groups that did forage extensively were presented with a new, readily available alternative food source. The results demonstrate that the effectiveness of Batesian mimicry can be increased in environments when alternative prey are available.

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