

Calculated risk-taking by predators as a factor in Batesian mimicry

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A simulation model is constructed from a set of disc equations (Holling 1959b) incorporating a probability term which represents calculated risk-taking by the predator, and determines the proportion of encountered models and their perfect Batesian mimics which are sampled by the predator. The risk-taking parameter (R) is assumed to be a function of both model:mimic ratio (the higher the ratio, the lower R) and availability of alternate prey (the greater the availability, the lower R).

The model was tested with an artificial predator-prey system in the laboratory, and was able to predict mimic mortality under most conditions. Computer simulation experiments were then conducted to explore a variety of relationships, including the functional response to mimic density, the effect of alternate prey density on mimic mortality, and the effect of proportion of models on the effectiveness of mimicry as an anti-predator strategy. Despite its simplicity the model makes predictions qualitatively similar to those of more complex models, and to the results of various empirical studies of mimicry. The importance of considering the alternate prey to be an integral component of any mimetic system is discussed.

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Un modèle mathématique est développé à partir d'un système de "disc equations" (Holling 1959b) comportant un terme probabilistique qui représente le risque calculé pris par le prédateur et détermine la proportion capturée parmi les modèles et de leurs copies Batésiennes parfaites rencontrés. Le paramètre affecté au risque pris par le prédateur (R) est présumé être fonction à la fois du rapport numérique modèles/copies (plus ce rapport est élevé, plus R est petit) et de la disponibilité de proies concurrentes (plus la disponibilité est grande, plus R est petit).

Lorsque mis à l'épreuve en laboratoire à l'aide d'un système prédateur-proie artificiel, le modèle a permis de prédire la mortalité des copies sous la plupart des conditions examinées. Des expériences de simulation à l'aide de l'ordinateur ont ensuite permis d'explorer diverses relations pertinentes, entre autres, la réponse fonctionnelle à la densité des copies, l'influence de la densité des proies concurrentes sur la mortalité des copies et l'effet de la proportion des modèles sur l'efficacité du mimétisme en tant que stratégie anti-prédation. Malgré sa simplicité, le modèle permet de faire des prédictions qualitativement équivalentes à celles de modèles plus élaborés et conformes aux résultats de plusieurs études empiriques portant sur le mimétisme. L'auteur discute l'importance de considérer la proie concurrente en tant que composante essentielle de tout système prédateur-proie impliquant le mimétisme.

Introduction

The ecological literature contains numerous mathematical models of Batesian mimicry, each with a somewhat different conceptual basis, and each concerned with a different subset of the set of all possible variables playing a role in any Batesian mimicry system. Most of these models, however, share a common feature: a mechanism whereby the predator periodically resamples the model-mimic complex. The predator is variously assumed to "forget" his

experience with the model as time elapses (e.g. Holling 1965), to ignore models and mimics for only a finite interval after each exposure to a model (e.g. Huheey 1964; Estabrook and Jespersen 1974; Brower *et al.* 1970), or simply to make occasional errors. This paper considers another possibility, a stochastic process whereby the predator samples models and their mimics with a probability determined by the availability of alternate prey, and by the probability that the sampled individual will be a noxious model (i.e. by the model:mimic ratio). The predator is therefore assumed to take a "calculated risk" that the encountered prey is an unpalatable model, and his willingness to take such a risk

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depends upon the ease with which he can satisfy his hunger with alternate prey alone. A simple mathematical model embodying this hypothesis was constructed and subsequently tested in an artificial predator-prey system (a blindfolded human subject searching for sandpaper discs). Computer simulation experiments were then conducted to determine the ecological consequences of the proposed mechanism.

The Model

The model was constructed by solving simultaneously the following set of equations.

$$[1] \quad N_1 = aRX_1 (T_T - T_{H1}N_1 - T_{H2}N_2 - T_{H3}N_3)$$

$$[2] \quad N_2 = aRX_2 (T_T - T_{H1}N_1 - T_{H2}N_2 - T_{H3}N_3)$$

$$[3] \quad N_3 = aX_3 (T_T - T_{H1}N_1 - T_{H2}N_2 - T_{H3}N_3),$$

where X_1 , X_2 , X_3 = densities of mimics, models and alternate prey, respectively; N_1 , N_2 , N_3 = number of mimics, models, and alternate prey captured; T_{H1} , T_{H2} , T_{H3} = handling times for the three prey types; a = the searching rate; R = the probability that the predator will sample (i.e. taste) an encountered prey; and T_T = total hunting time available. Parameter R represents the willingness of the predator to take a calculated risk, and is assumed to be a function of model:mimic ratio (X_2/X_1) and availability of alternate prey (X_3). Note that alternate prey are assumed to be readily distinguished from both models and mimics, and the predator eats every alternate prey encountered. Equations 1 to 3 are basically disc equations (Holling 1959b), modified by inclusion of parameter R , and expansion of the handling time component to include time utilized handling other types of prey. (No time is assumed to be used rejecting models or mimics.)

It is further assumed that the model and mimic are distinguishable to the predator (perfect mimicry). Thus,

$$N_1/N_2 = X_1/X_2$$

$$[4] \text{ or } N_2 = N_1 X_2/X_1.$$

This additional equation allows simultaneous solving of the disc equations to determine N_1

through N_3 . The equation for mimics, for example, becomes

$$[5] \quad N_1 = aRX_1 T_T / (1 + aRT_{H1}X_1 + aRT_{H2}X_2 + aT_{H3}X_3).$$

The model assumes that the instantaneous searching rate and the three handling times are constant. An artificial predator-prey system was devised to test these assumptions, to obtain estimates of the parameter values, to determine empirically the effect of model:mimic ratio on R , and to test the resulting model.

The Predator-Prey System

The artificial system chosen to test the model was a modified version of that devised by Holling (1959b) to test the original formulation of the disc equation. A blindfolded human subject (the predator) searched for paper discs (3.8 cm diameter) scattered over the surface of a table (9 square ft). Two types of discs were used: sandpaper, representing models and mimics, and plain cardboard, representing alternate prey. Discs representing the three types of prey were distributed randomly and independently of one another, except that discs were not allowed to overlap. They were not tacked to the table. The subject searched by tapping a single finger across the table, recognizing the "prey" both by their sound and feel. If an encountered disc was to be "eaten" the predator removed it from the table, setting it to one side before resuming search. Each experiment lasted 2 min (T_T).

Mimics and alternate prey could be eaten without penalty. However, any attempt to eat a model resulted in the subject being given 1.0 ml of vinegar via a tygon tube held in the mouth. This stimulus, administered by an experimenter with a syringe, was intended to represent the noxious taste of a model, and caused the "predator" to put the prey down.

A signal was also required to inform the predator of his hunger state, in order that he not ignore the model-mimic complex entirely. A device termed "the hunger simulator" was built for this purpose. It consisted of an audio-frequency generator (Heathkit 1G-82), an amplifier, a speaker, and a special circuit to control sound amplitude. This circuitry caused the amplitude to increase slowly with time, and to be decremented instantaneously, at the push

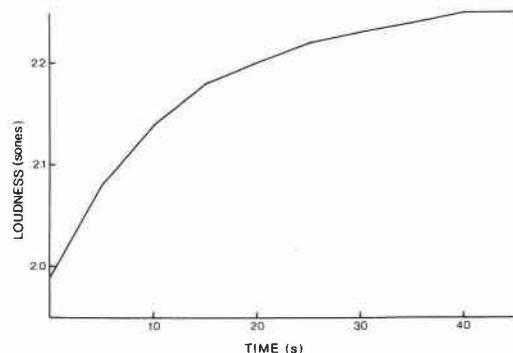


FIG. 1. An example of the way in which the loudness of the hunger simulator's signal increases with time between captures. See text for details.

of a button, whenever a prey (mimic or alternate) was eaten. Following a decrement, the amplitude slowly increased again. The perceived loudness of the sound represented the hunger signal to the predator, its slow buildup the increase of hunger between captures (due to digestion and consequent emptying of the stomach), and its instantaneous decrement the ingestion of a prey and consequent decrease in hunger. Schematics for the hunger simulator will be provided by the author on request.

The amplitude of the sound produced was measured at intervals with a soundmeter (Brüel-Kjaer No. 2205) and these measurements (ranging from 54 to 82 dB at 1000 cycles per second (cps) 1 ft from the speaker) were converted into perceived loudness (sones) according to the equation (Stevens 1955)

$$[6] \quad \text{Loudness} = 0.06 (\text{dB})^{0.3}.$$

An example of the results of these measurements and transformations (Fig. 1) demonstrates that the acceleration of the curve decreases with time, loudness eventually reaching an asymptotic level. The relationship therefore closely resembles that between hunger and time, determined for invertebrate predators by Holling (1966).

Unfortunately, the decremental aspect of the hunger simulator was not as realistic since a constant voltage drop produces a variable decrease in loudness (hunger): a prey capture has less effect on a hungry predator (i.e. the prey appears to weigh less to him) than on a predator near satiation. It was not feasible to design this feature out of the apparatus, but its

effect on the results is felt to be minor, being averaged over a number of prey captures at various hunger levels.

In experiment I, conducted only to obtain parameter estimates, alternate prey density (X_3) was held constant at 50 per table. Model and mimic density totalled 100 per table in each experiment, but model:mimic ratio was varied: six trials each (in random order) were conducted at ratios of 9:1, 7:3, 5:5, 3:7, and 1:9. The "predator" was allowed to use his own discretion with respect to when to pick up prey, but was told that the object of the exercise was to keep sound amplitude as low as possible (amplitude was maximal at the beginning of each experiment) without receiving too many aversive stimuli. He was cautioned to be as consistent as possible between trials, and 10 preliminary trials preceded the actual experiment, which was conducted over 2 days. These preliminary trials were also used to select a maximum sound amplitude, one which would be obnoxious but not painful.

Handling times were measured (using a Lafayette Mini Event Recorder) for each prey item "eaten," as the time between picking up the prey and resuming search. The number of models and mimics touched during searching was also recorded. The proportion of these picked up was taken as the best estimate of R . Searching rate was estimated from the equation

$$[7] \quad a(\text{ft}^2/\text{s}) = \frac{(\text{models and mimics touched})}{(120 - \sum t_{Hi})} \times \frac{9 \text{ ft}^2}{100 \text{ prey}}.$$

In experiment II, conducted as a test of the model, alternate prey density (X_3) and model density (X_2) were both held constant at 50 per table. Mimic density (X_1) varied, six runs each being conducted (in random order) with 10, 30, 50, 100, and 150 mimics per table, providing model:mimic ratios of 5:1, 5:3, 1:1, 1:2, and 1:3 respectively. The experiment was conducted over 2 days, with only the number of captures of each prey type being recorded.

Prey were not replaced in either experiment. To a certain extent, therefore, prey densities were not constant during a trial, although, strictly speaking, this is required for application of the disc equation (Royama 1971). However, the percentage of mimics captured never

TABLE 1

Mean values for model parameters, determined empirically in experiment I

Model:mimic ratio	T_H (s)			a (ft ² /s)	R
	Mimic	Model	Alternate		
9:1	1.94	0.61	1.97	0.038	0.15
7:3	2.23	0.62	2.16	0.035	0.19
5:5	2.20	0.62	2.08	0.034	0.22
3:7	2.22	0.66	2.18	0.028	0.46
1:9	2.20	0.82	2.36	0.032	0.57
Best estimate	2.22	0.63	2.14	0.033	—

exceeded 20% and was usually less than 10% (21/30 trials in experiment I; 23/30 in II). The total percentages of all types of prey captured were only 13 and 12% in the two experiments respectively.

A computer program was written for the model and simulations run on an IBM 370/155 computer using a variety of densities for each prey type.

Results and Discussion

Experiment I

The average values for the parameters measured are shown in Table 1 for each model:mimic ratio. Parameter "a" appears quite constant over the range of model:mimic ratios but handling times appear to depart from constancy either when the proportion of models is high (mimic-handling time), low (model-handling time), or both (alternate prey-handling time). The best estimates of these parameters were taken to be the means of the values measured at the three intermediate ratios. When mimics were scarce the predator appeared to handle prey more rapidly (i.e. "wolf down" his food) than when they were more abundant. However, deviations from constancy were slight and were not considered to be significant.

A plot of R versus (X_1/X_2) was curvilinear, suggesting a square-root transformation of the independent variable. A regression on the transformed data produced the equation $R = 0.1017 + 0.166 (X_1/X_2)^{0.5}$, significant at $p < .001$. Since alternate prey density was constant in this experiment the effect of X_3 on R was assumed, for the simulation experiments, as

$$[8] \quad R' = R/(X_3/5.555)$$

where 5.555 is the density (number per ft²) of

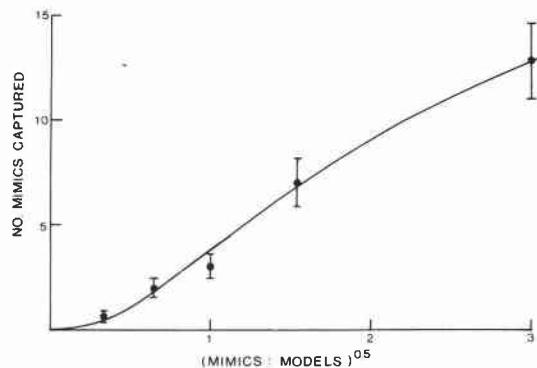


FIG. 2. The effect of mimics:models ratio on the number of mimics captured in experiment I. Observed data shown as means ± 1 SE. Curve is number of captures "predicted" by the model. Densities: $(X_1 + X_2) = 11.111$; $X_3 = 5.555$.

alternate prey used in this experiment. In other words, doubling the density of alternate prey halves the probability that an encountered mimic will be eaten. Additionally, R' was constrained in the simulation to be ≤ 1.0 , so that more prey cannot be eaten than are encountered.

There was a close correspondence (Fig. 2) between the observed number of mimics captured and the number predicted by Eq. 5, using the parameter estimates and functions described above. The correspondence is not, of course, unexpected, but it does suggest that the use of constant handling time estimates leads to an adequate description of the data.

Experiment II

The predicted and observed results for this experiment, in which only mimic density varied, are shown (Fig. 3) for the four lowest mimic: model ratios. Again, the correspondence is excellent, suggesting that Eq. 5 has predictive

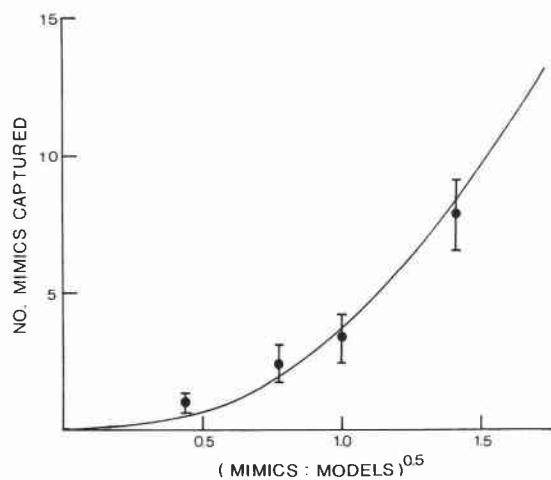


FIG. 3. The effect of mimic: model ratio on the number of mimics captured in experiment II. Curve is predicted number of captures, using the estimates of α , T_{HI} , and R derived in experiment I. Observed data shown as means ± 1 SE. Densities: X_1 variable; $X_2 = 5.555$; $X_3 = 5.555$.

powers in addition to the descriptive powers noted above. However, the model's usefulness was much less at the highest mimic: model ratio (3:1), where the observed value was 40% less than predicted. This was also true for alternate prey and models, and the "predator" reported that the large number of prey on the table (250) had a "confusion effect" on him. For this reason the aberrant result is considered to be an artifact of the testing situation rather than a failure of the model. A confusion effect may in fact operate in nature, and has been suggested as one way in which prey aggregation behaviors (such as schooling) serve an anti-predator function, reducing the predator's hunting efficiency (Hobson 1968; Neill and Cullen 1974).

Simulation Experiments

(1) Functional Response to Mimic Density

The relationship between number of mimics captured and mimic density (Fig. 4), with constant model and alternate prey densities, is a typical Holling (1959a) type 2 functional response. Holling's (1965) model of Batesian mimicry predicts a sigmoid (type 3) functional response, owing to the inclusion of predator learning as a model component.

(2) Effect of Mimic: Model Ratio on Mimic Mortality

As the proportion of mimics increases (with both the sum of model and mimic densities,

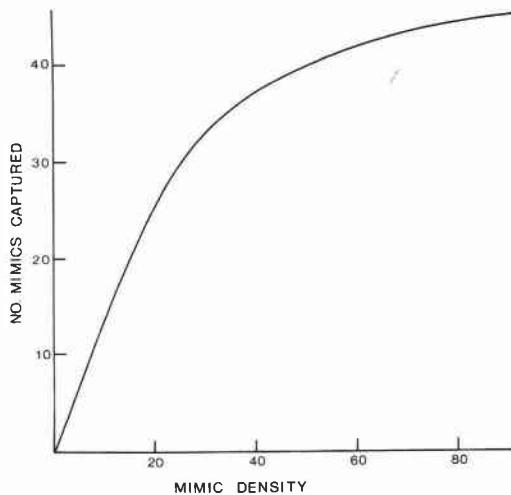


FIG. 4. Simulated functional response of predator to mimic density. Densities of other prey were constant: $X_2 = 1.111$; $X_3 = 5.555$.

and alternate prey density kept constant) the number of mimics captured increases at a decreasing rate, becoming asymptotic to an upper limit set by handling time (Fig. 5).

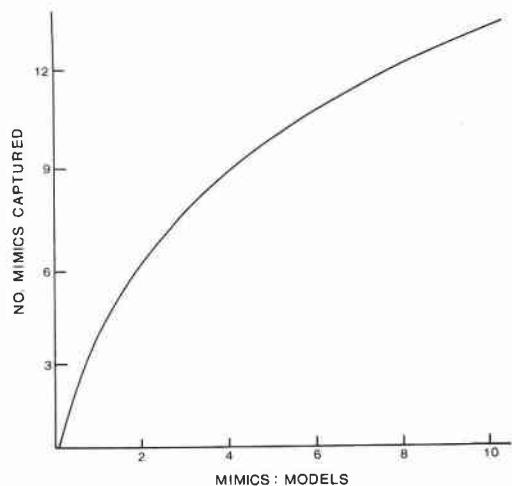


FIG. 5. Simulated effect of mimic: model ratio on mimic mortality. Densities: $(X_1 + X_2) = 11.111$; $X_3 = 5.555$.

(3) Effect of Mimic: Model Ratio on Model Mortality

Under the same conditions as the previous simulation, model mortality initially increases and then declines (Fig. 6). Model mortality is maximal when $X_1/X_2 = .25$, i.e., when models

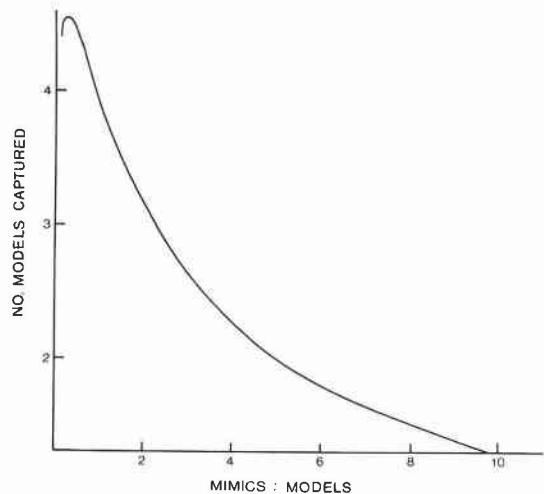


FIG. 6. Simulated effect of mimic:model ratio on model mortality. Densities as in Fig. 5.

outnumber mimics by 4 to 1. The domed form of the curve apparently results from the interaction of two consequences of increasing mimic:model ratio: (i) a rapid initial increase of predator sampling rate; and (ii) a slower decrease in the proportion of models, resulting in decreasing model mortality despite further increases of sampling rate.

(4) Effect of Mimic: Model Ratio on Alternate Prey Mortality

Under conditions identical to those of the two previous simulations, the number of alternate prey captured declines as the probability

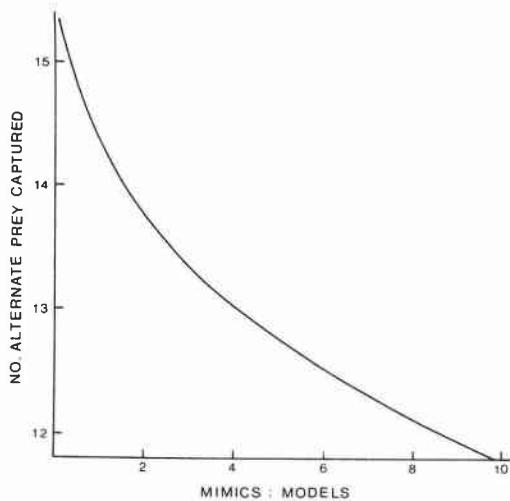


FIG. 7. Simulated effect of mimic:model ratio on alternate prey mortality. Densities as in Fig. 5.

increases that encountered members of the mimicry complex are edible (Fig. 7). The mimics fulfill more and more of the nutritional requirements of the predator, who consequently exerts less pressure on alternate food sources.

(5) Effect of Alternate Prey Density on Mimic Mortality

This simulation was conducted with constant model and mimic densities, and the assumption that $R = f(1/X_3)$ as described above. Under these conditions, increasing the availability of alternate prey decreases the mortality suffered by the mimic population (Fig. 8). It should be stressed that the relationship between R and X_3 was not determined empirically. However, it seems reasonable to hypothesize some relationship of this sort, such that the predator reduces his sampling of the model:mimic complex as his ability to fulfill his nutritional requirements in other ways increases.

The value of this simulation result is to focus attention on the alternate prey species as integral parts of any mimicry situation. Many authors, both modellers and empiricists, have failed to consider their import. Reiskind (1965), for example, states, "Studies of Batesian mimicry must always take into account the characteristics of the three basic units—the model, the mimic and the selective agent (predator)." The alternate prey are ignored. Yet the present simulations suggest that these prey both influence and are influenced by (simulation 4) the Batesian mimicry complexes around them.

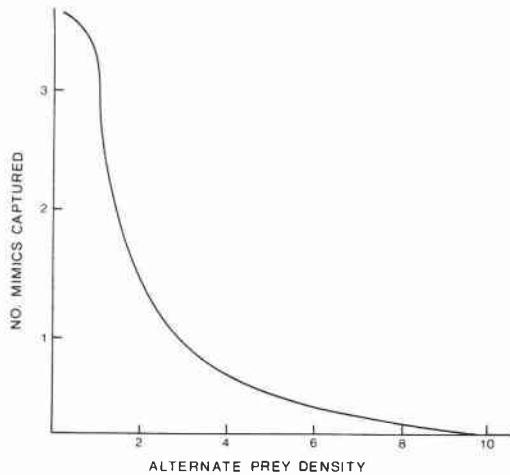


FIG. 8. Simulated effect of alternate prey density on mimic mortality. Densities: $X_1 = 1.111$; $X_2 = 5.555$.

These suggestions are supported by some data in the literature. Sexton (1960), for example, found that *Tenebrio* disguised as unpalatable fireflies (*Photinus pyralis*) suffered less mortality when presented to lizards in conjunction with alternate prey than when presented with models. Sexton suggested that the predator's "image" of the model is less exacting when the model is not present, i.e. the lizards can only distinguish mimic from model when the two are presented simultaneously. An alternative explanation is that the lizards were less hungry when alternate prey were present, and consequently less willing to "test" the mimic. Brower (1971) reports that the rate of sampling of butterflies (models and mimics) by birds depends upon the availability of alternate prey. Holling (1965) has also drawn attention to the influence of alternate prey, concluding that they "should be included as an essential feature of mimicry theory," though in his model their effect comes about in an entirely different fashion (via hunger effects on reactive distances and learning rates).

(6) Effectiveness of Mimicry as an Anti-predator Strategy

The percentage effectiveness of mimicry was calculated as

$$[9] \quad \% = [(N_4 - N_1)/N_1] 100$$

where N_4 represents the number of mimics captured when only mimics and alternate prey are available (i.e. Eqs. 1 through 3 solved for N_1 , with $R = 1$ and $X_2 = 0$). Effectiveness is shown in Fig. 9 as a function of the percentage of models in the mimicry complex. As mimics become relatively more abundant the effectiveness of mimicry declines, but the strategy remains beneficial to the mimic, in this particular example, even when it comprises 96% of the model:mimic complex. Thus models need not outnumber mimics for mimicry to be an effective anti-predator strategy, a prediction made by other simulation models (Huheey 1964; Holling 1965; Emlen 1968; Brower *et al.* 1970; Estabrook and Jespersen 1974). As the structural details of these models vary considerably, the conclusion may be considered a highly robust one. The prediction has also received empirical support (e.g. Brower 1960). The present simulation further suggests that the percentage effectiveness of mimicry may be more affected by the proportion of models when these are very abundant

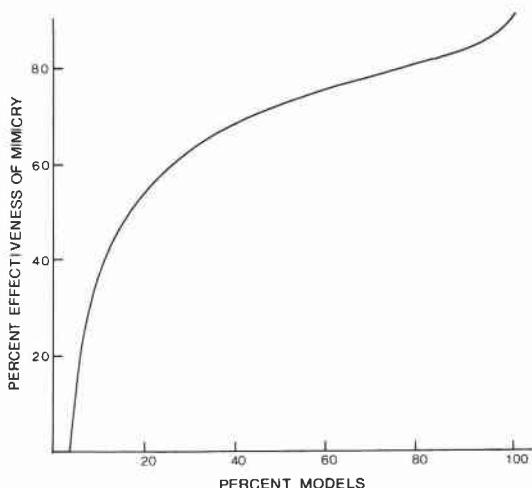


FIG. 9. Effect of model frequency on the percentage effectiveness of mimicry in the simulation model. Densities: $X_1 = 1.111$; $X_3 = 5.555$.

(>90% of the population) than when they are less abundant (40–90%). This also appears to be the case in some data for starlings feeding on artificial mimics (Brower 1960, Fig. 2).

General Discussion

The present model differs from other models of mimicry in that predators sample encountered prey with a probability dependent upon the probability of the prey being edible (shown experimentally in an artificial predator-prey system), and the probability of finding an alternate type of prey. Only one other model, that of Holling (1965), includes the effect of alternate prey density on mimic mortality, but in a tactical rather than a strategic fashion. The present "risk-taking" model makes very similar predictions, but is much less complex (and less realistic).

Estabrook and Jespersen (1974) have also taken a strategic approach to the problem of mimicry. In their model the parameter " b " represents "the benefit to the predator from eating a mimic, divided into the loss ... from eating a model." These authors conclude, however, that when models and mimics are randomly and independently distributed the predator's best strategy is either to eat everything or eat nothing, depending on the value of b . Doubtless this result is due to a failure to include alternate prey density in their model.

The risk-taking model, of course, neglects a number of factors known to be important in real-world mimicry systems. These include distribution of model and mimic (Brower *et al.* 1970; Estabrook and Jespersen 1974); degree of resemblance between them (Sexton 1960; Duncan and Sheppard 1965; Emlen 1968; Pilecki and O'Donald 1971); noxiousness of model (Duncan and Sheppard 1965; O'Donald and Pilecki 1970; Brower *et al.* 1970; Estabrook and Jespersen 1974), and palatability of alternate prey (Holling 1965). It would be difficult to modify the disc equation approach to take all of these factors into consideration without making it extremely complex. The price paid for simplicity, however, is the certain knowledge that the model is only a crude approximation of the real world.

Acknowledgments

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