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Theoretical Investigations of Automimicry, I. Single Trial Learning*

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Abstract. The theory of automimicry is explored mathematically on the assumption that predators can learn to avoid noxious prey by sight for some finite period after a single noxious experience. Automimetic advantage is an inevitable consequence of the evolution of an unpalatability dimorphism. An established automimetic situation is analogous to an established perfect Batesian mimicry situation, although the evolutionary bases of the two phenomena are different. In both situations, the mimetic advantage depends upon the proportion of unpalatable prey, the memory span of the predators, and the abundance of the prey relative to the predators. Automimetic advantage is maximal when the prey are neither too common nor too rare. Remarkably low proportions of unpalatable prey can confer very substantial immunity to the population. A surprising prediction of the model is that the evolution of unpalatability will not occur in rare prey species unless they first become Batesian mimics. This in turn could lead to the evolution of mimicry complexes containing many species forming a whole spectrum of unpalatability.

Recent discoveries in the field of ecological chemistry indicate that the palatability of certain prey to their predators varies according to the particular kind of food ingested by the prey during their development. In the most thoroughly studied case—that of the monarch butterfly (*Danaus plexippus* L.)—adults that lay their eggs upon cardiac glycoside-containing milkweed plants (Asclepiadaceae) produce offspring which are severely emetic when ingested by birds, whereas larvae feeding on nonpoisonous milkweeds become highly palatable butterflies.[1]

While it was historically held that wild monarch populations are homogeneous with respect to palatability, the fact is that populations from Florida, Massachusetts, Trinidad, W.I., and Costa Rica exhibit a palatability dimorphism with anywhere from 10 to 90% of the adult butterflies being emetic.[2] Predicting that this would be the natural situation, Brower, Brower, and Corvino[1] originated the idea of automimicry which states that because predators will be unable to discriminate visually between palatable and unpalatable individuals of the same species, a noxious experience with an unpalatable morph will effect conditioned visual avoidance resulting in the subsequent rejection of both forms, i.e. an automimetic advantage for the population. Clearly, automimicry itself does not evolve in the same way that Batesian mimicry does, because an individual automimic can have no selective advantage over an individual automodel. Automimetic advantage is, in fact, an inevitable consequence of the evolution of unpalatability dimorphisms and the evidence for such dimorphisms is now indisputable. Mathematically the advantage derived by a population through automimicry will be analogous to that gained by a population of palatable Batesian mimics which have evolved a resemblance so perfect in every detail to their model that the predator is incapable of discriminating between the two species on sight alone. Moreover, in both situations the mimetic advantage must be frequency-dependent, i.e. the unpalatable prey (automodels or models) must not become too rare or else the palatable prey (automimics or Batesian mimics) will be encountered so often that the advantage of the mimicry will be lost. Huheey[3] has presented a formal development of certain of the assumptions of frequency dependence in a valuable advance of this subject.

In this paper we explore the theoretical automimetic advantage of an established palatability dimorphism, as well as the analogous case of an established perfect Batesian mimicry situation, by formulating a new mathematical model based on facts previously established as representing an actual natural situation. The results of this investigation shed new light on unpalatability, mimicry, and predation theory in general.

Mathematical Model. The first assumption of our mathematical model is that alternative palatable prey are available in the natural environment of the predator. Secondly, we assume that a single encounter with an unpalatable prey kills the prey and will condition a predator to reject subsequent individuals of the same species on sight alone, irrespective of palatability. Such single trial learning, or at least single periodic reinforcements after the initial learning, has been experimentally established for a variety of vertebrate predators and noxious insects[4] and is particularly striking in our experiments with blue jays (*Cyanocitta cristata bromia* Oberholser) and emetic monarch butterflies in which some individual birds not only learned to reject numerous monarchs but actually retched at the sight of them when offered more monarchs on days after the initial emetic experience.

The first variable we consider is n. The average duration of time over which predators remember to reject prey after a single noxious experience will result in a finite number of induced prey rejections equal to $n-1$. This number, in addition to the single emetic experience is n. If a predator did not encounter a noxious prey, it would eat n individuals in a comparable unit of time. This definition of n is similar to Huheey's.[3] There are many factors which affect n in nature, including: the abundance of alternative palatable prey,[5] the memory span of the predators, and the degree of noxiousness of the model, for example the number of emetic units carried by a butterfly.[6] For our analysis we have chosen values of n ranging from 1 to 100. In the light of recent evidence[7] on emetic butterflies, we consider Huheey's[3] low values of n to be much too restrictive.

The second variable we consider is m, the number of prey available per predator in the natural population. We have varied this value from 0.05 to 10,000 to represent a wide range from the prey being very rare in relation to the predators to the opposite extreme in which they are exceedingly abundant. The m

variable is to be envisaged in relation to n as follows: when $n = m$, the number of prey available equals the number of prey that each bird could eat were it not to encounter an unpalatable one. For example, if $n = m = 25$, there are 25 prey per predator and each predator could eat 25. If $n > m$ then there are too few prey to satiate the predators, whereas if $n < m$ there are more prey available than can be eaten.

There is a possibility that the searching image phenomenon may lead to nonlinear changes in predation with changing values of m. Moreover, m may also be affected by sex-related differences in the behavior of the prey. In many insects, for instance, males tend to aggregate in particular areas, whereas females are usually dispersed. Thus, predators near areas of male aggregation will experience high m values while those in other areas will not.

To simplify plotting the calculated values, we have expressed n and m as n/m varying from 0.01 to 100. This parameter can be regarded as the predation potential: when $n/m > 1$ the predation potential is high and in the absence of unpalatability survival would be 0. When $n/m < 1$ there is a surplus of prey and some would survive regardless of palatability.

To some extent m and n will not be independent variables. This follows from memory decay which has a temporal component. Thus when m is small, encounters will be rare and n will also tend to be small. Similarly, when m is large, n will tend to be large too because of secondary reinforcement of the predators' learned rejection which is produced by the frequent sight of the unpalatable prey. It has been suggested[8] that when vertebrate predators have learned to avoid a warning pattern, simply seeing other prey which bear the pattern without attacking them leads to a further reduction in the number of attacks they make. By using n/m in our graphs we have at least partially circumvented this interdependence problem because the ratio n/m will be relatively unaffected by simultaneous increase or decreases in both n and m.

The final variable is the frequency of unpalatable prey in the predators' sample of the population which we designate as k'. This value may or may not be the same as the actual frequency of unpalatable prey in the population as a whole, which we shall call k. For example, unpalatable individuals might behave in a more conspicuous manner than palatables so that k' could be larger than k. As we have noted, k varies widely in the natural environment, at least in monarch butterfly populations.

If all individuals in a prey population are palatable, the fraction surviving predation can be expressed as

$$j_0 = 1 - n/m. \qquad (1)$$

This formula only describes situations in which $n/m < 1$. When the predators can consume all the prey individuals ($n/m = 1$) there will be no survival and $j_0 = 0$. When $n/m > 1$, j_0 is a negative number and since negative survival has no relevant biological meaning, we have adopted the convention of letting $j_0 = 0$ in this case. This accounts for the abrupt break in the curves at $n/m = 1$.

If some of the prey individuals are palatable and others unpalatable (i.e. if automimicry exists) the situation is more complicated. Each predator eats at

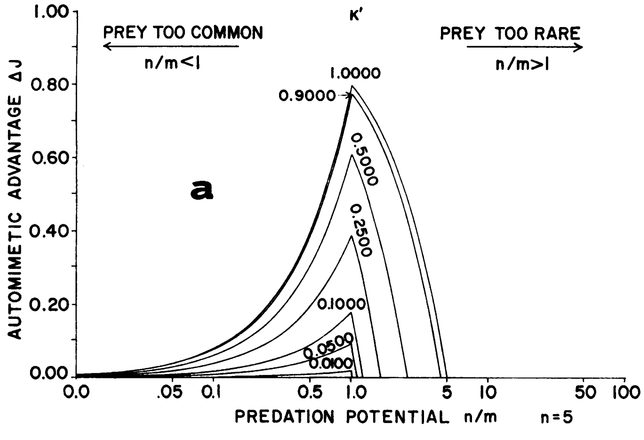

FIG. 1.—(a) Effect of prey abundance (m) and frequency of unpalatable prey (k') on the automimetic advantage (Δj). n, the induced prey rejection memory span, is low ($n = 5$).

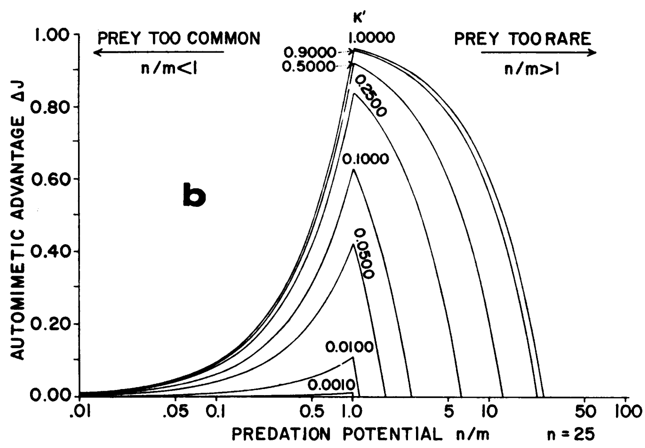

FIG. 1.—(b) Same as Fig. 1a, except n = 25.

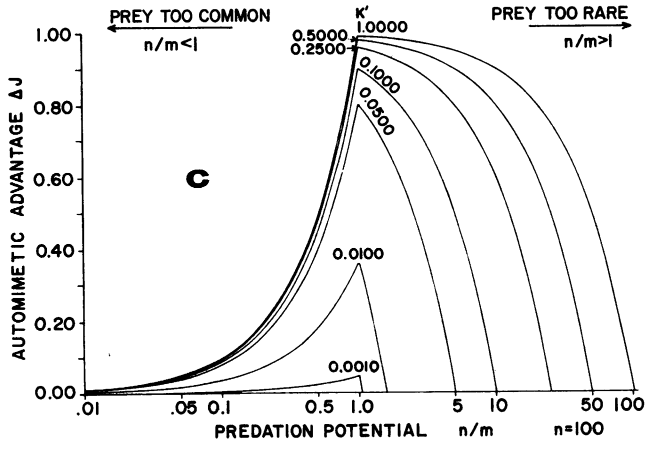

FIG. 1.—(c) Same as Figs. 1a and 1b, except n = 100.

least one prey and the fraction $(1 - k')$ that encounter palatable ones will go on to eat a second while those that encounter unpalatable ones will stop. The fraction $(1 - k')^2$ that do not encounter an unpalatable in the first two prey eat a third, and so on. The average number of prey eaten by one predator is given by the geometric series

$$1 + (1 - k') + (1 - k')^2 + \ldots . + (1 - k')^{n-1} = \frac{1 - (1 - k')^n}{k'}.$$

The fraction of the prey population eaten is $(1 - (1 - k')^n)/mk'$ and the fraction surviving is

$$j_{k'} = 1 - \left(\frac{1 - (1 - k')^n}{mk'}\right). \qquad (2)$$

The advantage of automimicry, Δj, is found by subtracting Eq. (1) from Eq. (2)

$$\Delta j = j_{k'} - j_0. \qquad (3)$$

This value represents the average increased probability of survival of an individual prey organism in a population which results from the occurrence of automimicry.

Eq. (2) breaks down when $k' = 0$, since the fraction on the right side becomes indeterminate. However, when $k' = 0$, it is clear that $j_{k'} = j_0$, so the desired result is given by Eq. (1). This can be verified by applying a simple limiting process to Eq. (2): when k' approaches 0 it is found that the limiting value of $j_{k'}$ equals the value of j_0 given by Eq. (1).

The mathematical model was initially explored with a Wang 370/362E electronic calculator system and then programmed on an IBM model 2C 1130 digital computer linked to a 1627 plotter. Each curve is based on several hundred points.

Results. The automimetic advantage (Δj) is greatest when $n/m = 1$, that is, when predators could eat every prey animal in the population (Figs. 1*a*, *b*, *c*). The magnitude of the automimetic advantage increases as both k' and n increase. Above some critical value of k', the rate of increase of automimetic advantage declines (Fig. 2). For example, when $n = 20$, the increase in population survival obtained by increasing k' from 0.25 to 1.0 is only 15%. To put it another way, an 80% automimetic advantage is afforded by a k' value of 0.25 when $n = 20$, by a k' of 0.10 when $n = 50$, and by a k' of 0.05 when $n = 100$.

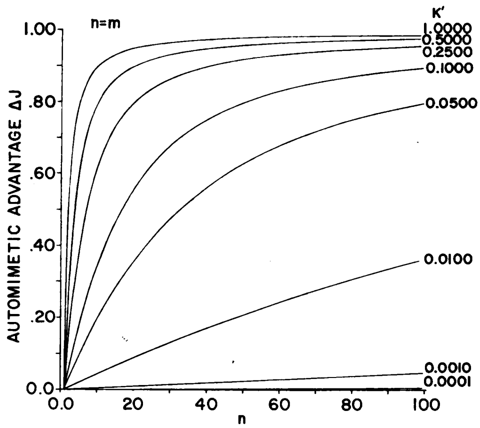

Fig. 2.—Effect of the number of induced prey rejections (n) and the frequency of unpalatable prey (k') on the automimetic advantage under optimal conditions ($n/m = 1$).

There are critical points in both n (about 20) and k' (about 0.25). Increasing either parameter above these values confers little increased protection; the species is already protected to almost the same degree as it would be were it entirely unpalatable.

When n/m is not equal to 1, the automimetic advantage is reduced. Nonetheless, high values of n and k' can increase survival even when the n/m ratio departs substantially from 1 in either direction (Figs. 1*a*, *b*, *c*).

At low k' values the rate of loss of automimetic advantage with changing predation potential is less when the prey are too common than when they are too rare. Under these circumstances (*i.e.* when $n/m < 1$) even very low k' values confer a significant selective advantage (Fig. 1*a*, *b*, *c*).

Discussion. Assumptions: The model described in this paper considers mortality resulting solely from vertebrate predation on a prey population. In the instance of the monarch butterfly—the only example so far studied in detail—there are no data which indicate, nor any reason to suspect, that the innate viability or fecundity of individuals are affected physiologically by their palatability status. Thus, the effect of automimicry would be largely independent of other causes of mortality and can be considered separately from them.

Values for the parameters n and k' were chosen to include experimentally determined values and are therefore representative of natural situations. We have no data on the third parameter, m, the number of prey per predator. However, in the monarch butterfly this value oscillates annually with a large amplitude as a result of the phenomenal migratory ecology of the species. In most of North America m is small during the northward migration in the spring. By late summer successive generations have increased the size of the butterfly populations all over northern North America and m is large. Aggregation of butterflies leads to larger m values during the autumnal migration and perhaps to still larger ones in the wintering areas, such as on the Monterey Peninsula in California and on the west coast of Florida.

The model assumes that the number of prey a predator eats depends only on the predator's appetite and experience with the prey's palatability. It might be argued that when m is small (i.e. the prey is rare) predators will have such difficulty finding prey that this assumption is not fulfilled. In the case of insects, however, many phytophagous species have patchy distributions associated with similar distributions of their food plant.[9] The result of such a distributional pattern is that m is small in most areas, but large for those predators near concentrations of prey. Thus, the type of distribution a prey species shows must be considered in calculating m, and a species with a low overall m may still have populations locally abundant enough to benefit from automimicry.

Implications. The decrease in automimetic advantage (Δj) as the predation potential (n/m) departs from 1 is intuitively obvious. When the predation potential is less than 1, there is a surplus of prey and some will survive regardless of the frequency of unpalatables (k) in the population. Conversely, when the predation potential is more than 1 there are always some predators that have not yet had the opportunity to learn that the prey is distasteful and these individuals will be ready to snap up the first prey they encounter.

The increase in survival resulting from a large n is also intuitively obvious. For any level of unpalatables, k', the probability of eating an unpalatable at the ith position in a series of n samplings is the same for any value of $n \geq i$. Since one unpalatable causes the predator to stop eating the prey, a larger value of n results in more prey being rejected than a small one.

A remarkable feature of our model is the effectiveness of low frequencies of unpalatables in conferring high automimetic advantages. A population in which 25% of the individuals are unpalatable receives nearly as much protection as one with 100% unpalatable as long as n is 20 or more (Fig. 2). For a prey species in which palatability is determined by the food plants which are themselves chemically heterogeneous, this phenomenon will allow an increase in prey population size with little loss of the advantage of uniform unpalatability. The low proportion of models necessary for protection is also applicable to Batesian mimicry, and once again points to the fallacy of the classical argument that the palatable mimic must be very rare relative to its model. In fact, laboratory experiments and computer simulation by earlier authors have already shown this idea to be incorrect.[10]

Even very low k values confer some protection when n is large. For example, under optimal conditions, a k' of 0.0001 produces a 0.5% increase in survival when $n = 100$. Thus we can conclude that gene mutations which confer unpalatability on a species will under such conditions have a high chance of being preserved by selection.

The actual selective process leading to the fixation of genes for unpalatability in natural populations is complex and will be presented in a later paper.

At low k' values the rate of loss of automimetic advantage with changing predation potential is less when the prey are too common than when they are too rare. The relevance of this is that mutations conferring unpalatability will tend to have a higher initial selective value in common or gregarious species than in rare, dispersed ones. This leads directly to the conclusion that very rare species probably will not be able to evolve unpalatability without first evolving Batesian mimicry of an already established model (or Müllerian mimicry complex). Incidentally, this finding lends support to Huheey's[11] speculations about the evolution of unpalatability which were based on other premises.

Once a rare species evolved Batesian mimicry, its predation potential would in effect be moved towards the optimum. However, if enough palatable species enter a complex in this manner, the k value of that complex would be reduced. This is turn would provide a milieu in which gene mutations for unpalatability would gain a selective advantage, thus pushing the k value back towards a more optimal level. It is easy to envisage this process leading to a large group of mimetic species centering around a single color pattern with species in all stages of palatability.

The degree of unpalatability of a prey species affects the protection it receives in two ways. In the first place, a predator will remember for a longer time a prey species that makes it violently ill or is particularly noxious in other respects than one with less pronounced unpleasant effects. This leads to a larger n value for the more unpalatable species. Secondly, a mildly distasteful prey may have to be sampled twice, or even twice in a row, before a predator stops eating it. We have devised equations to describe these two additional situations and have analyzed them for the same values of n, m, and k' described in this paper. We will discuss the results of these calculations in detail in a subsequent publication. Briefly, the shape of the curves is the same as in the present situation, but the Δj values are smaller. Nevertheless, even under the most restrictive conditions, two distasteful prey in a row, automimicry confers a marked increase in survival.

These calculations suggest that it should be possible to analyze the average protection afforded the large tropical mimicry complexes which include many species of different taxonomic groups. These have heretofore been considered as Müllerian assemblages. However, if our predictions are correct, they should consist of species exhibiting a whole spectrum of palatabilities. We now propose to return to the field to test the predictions generated by this mathematical model.

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