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Stevan J. Arnold

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THE EVOLUTION OF A SPECIAL CLASS OF  
MODIFIABLE BEHAVIORS IN RELATION TO  
ENVIRONMENTAL PATTERN

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Interest in the evolution of learning has usually focused on taxonomic comparison on a grand scale (Harlow 1958; Thorpe 1963). The origins of different kinds of learning phenomena (habituation, conditioning, insight learning, imprinting, etc.) have been sought by comparing the learning capacities of higher taxonomic categories such as phyla, classes, and orders (Bitterman 1965). The adaptive significance of learning phenomena is not so well understood, but it is commonly supposed that learning is either always advantageous or favored in “unpredictable” environments. Some recent studies suggest that the capacity to form associations between some aspects of the environment and the inability to form associations between other aspects of the environment is related to the ecology of particular species (Garcia and Ervin 1968; Garcia et al. 1973). The implication of these studies is that variables characterizing the learning process have responded to natural selection. If we consider the problem of how learning might evolve in small steps and adjust to local differences in environment, we find surprisingly little theoretical work.

The model discussed here was designed to explore the microevolution of a particular kind of learning, avoidance conditioning. The model applies to only a special kind of avoidance conditioning, namely, situations in which two states of the environment cannot be distinguished by simple inspection. Estabrook and Jespersen (1974) and Bobisud and Potratz (1976) discussed the consequences of the model for Batesian mimics confronted with predators that show avoidance conditioning. Bobisud and Potratz also extended the model to consider multitrial learning and clarified the conditions under which avoidance conditioning will evolve. The purpose of the present report is to examine the microevolution of avoidance conditioning in relation to environmental pattern.

Suppose that an organism is faced with the problem of trying to avoid some deleterious state of the environment while exploiting some other advantageous state of the environment. The environment is ambiguous in the sense that the two states of the environment are indistinguishable to the organism. In the model the dispersion pattern of the two environmental states is specified by two variables. The organism’s modifiable avoidance behavior is characterized by a single variable representing the time required to forget a deleterious experience.

A fourth variable specifies the relative disadvantage of exploiting the deleterious environmental state. From the standpoints of familiarity and nomenclature, it is easiest to think about the model in terms of a predator exploiting a system of noxious models and indistinguishable Batesian mimics. In this case the problem becomes, How will the modifiable avoidance behavior of the predator evolve in relation to the dispersion pattern of the model and mimics and the relative badness of models? While the theoretical model will be presented in terms of this special problem, it also applies to the somewhat more general problem of how one kind of avoidance conditioning might evolve in relation to environmental pattern.

#### THE MODEL

I will briefly review the model discussed by Estabrook and Jespersen (1974) and provide some amplifications.

*The environment of models and mimics.*—The environmental pattern of models ( $M$ ) and mimics ( $X$ ) is completely specified by two conditional probabilities. Let  $p(M|M)$  be the conditional probability that the predator encounters a model given that a model was just encountered, and let  $p(X|X)$  be the conditional probability that the predator encounters a mimic given that the predator has just encountered a mimic. Then  $p(X|M) = 1 - p(M|M)$  is the conditional probability that the predator encounters a mimic given that a model was just encountered; and, similarly,  $p(M|X) = 1 - p(X|X)$  is the conditional probability that the predator encounters a model given that a mimic was just encountered. Estabrook and Jespersen designate  $p(M|X)$  with the symbol  $p$  and  $p(X|M)$  with the symbol  $q$ .

The sequence of model and mimic encounters is then a regular Markov process. Consequently, we can solve for the unconditional or stationary probability of encountering a mimic,  $f = p(X|M)/[p(X|M) + p(M|X)]$ .

This relationship is shown graphically in fig. 1. The unconditional probability of encountering a model is  $1 - f$ . The model assumes that the environment of models and mimics,  $[p(X|X), p(M|M), f]$ , is unaffected by the foraging behavior of the predator.

The dispersion pattern of models and mimics is a function of the two conditional probabilities  $p(M|M)$  and  $p(X|X)$  (fig. 1). Models and mimics are clumped when  $p(M|M) > 1 - f$  and  $p(X|X) > f$ , and they are dispersed when  $p(M|M) < 1 - f$  and  $p(X|X) < f$ . Models and mimics are independently segregated when  $p(M|M) = 1 - f$  and  $p(X|X) = f$ . Estabrook and Jespersen imply that mimics can be dispersed when models are clumped. This is not the case. Under the conditions of the model,  $p(M|M) = 1 - f$  whenever  $p(X|X) = f$ , and so models will be clumped whenever mimics are clumped and dispersed whenever mimics are dispersed.

The expected clump size of models may be expressed as the mean run length of models,  $E(L_M)$ , and is a simple increasing function of the conditional probability of model-to-model transitions:

$$E(L_M) = 1/[1 - p(M|M)]. \quad (1)$$

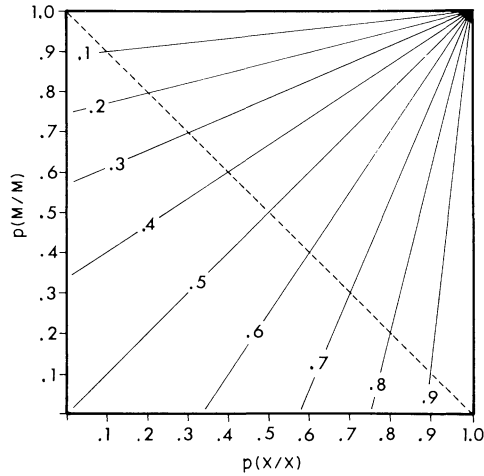


FIG. 1.—The frequency of mimics and the dispersion pattern of models and mimics as a function of the conditional probability of encountering a mimic given that a mimic was just encountered,  $p(X|X)$ , and the conditional probability of encountering a model given that a model was just encountered,  $p(M|M)$ . The frequency of mimics,  $f$ , is shown with solid lines. Environments in which models and mimics are randomly dispersed are indicated with a dashed line. Above the dashed line both models and mimics are clumped, and below the dashed line both models and mimics are dispersed.

Similarly, the expected run length of mimics,  $E(L_X)$ , is a simple increasing function of the conditional probability of mimic-to-mimic transitions:  $E(L_X) = 1/[1 - p(X|X)]$  (Pielou 1969).

The uncertainty of the environment, given the identity of the environmental state just encountered, is a function of the dispersion pattern of models and mimics. Suppose that we represent this conditional uncertainty,  $H_c$ , as the

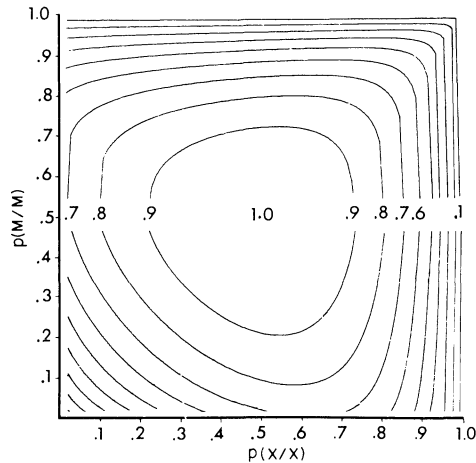


FIG. 2.—The conditional uncertainty of the environment,  $H_c$ , as a function of the conditional probabilities  $p(X|X)$  and  $p(M|M)$ .

average number of yes-no questions required to determine the identity of the next environmental state, given the identity of the current state. Then

$$H_c = -\{f[p(X|X) \log_2 p(X|X) + p(M|X) \log_2 p(M|X)] \\ + (1-f)[p(M|M) \log_2 p(M|M) + p(X|M) \log_2 p(X|M)]\}$$

(Garner 1962).

The environment is most uncertain when models and mimics are equiprobable and randomly dispersed (fig. 2). Notice that when models and mimics are clumped (upper right, figs. 1-2) the environment is relatively predictable.

*The success of the predator in the environment.*—We can imagine a large class of predators that are subject to two constraints. First, only two behavioral responses can be given to either models or mimics, eat (*E*) and ignore (*I*). Second, from the standpoint of the predator, the models and mimics are completely indistinguishable. At each encounter the models and mimics remain indistinguishable unless the predator eats.

Thus only four compound events are possible: eat a model (*EM*), eat a mimic (*EX*), ignore a model (*IM*), and ignore a mimic (*IX*). Let  $w(EM)$ ,  $w(EX)$ ,  $w(IM)$ , and  $w(IX)$  represent the relative gain to the predator from each of these compound events. We also specify that when the predator eats a model the change in the economy of the predator is  $-b$  times the gain experienced when a mimic is eaten:  $w(EM) = -b$  and  $w(EX) = 1$ . Thus  $b$  represents the relative badness of models. When the predator ignores a model or mimic, there is no change in the predator's economy:  $w(IM) = 0$  and  $w(IX) = 0$ . The expected gain to the predator is then

$$S = p(EM)w(EM) + p(EX)w(EX) + p(IM)w(IM) + p(IX)w(IX), \\ = p(EX) - bp(EM), \quad (2)$$

where  $p(EX)$ ,  $p(EM)$ ,  $p(IX)$ , and  $p(IM)$  represent, respectively, the unconditional probabilities of eating a mimic, eating a model, ignoring a mimic, and ignoring a model. The model assumes that alternative food sources are available to the predator. Thus  $S$  is the expected gain with respect to the model-mimic resource, and the problem is to evolve behavior such that  $S$  is maximized.

*Nonmodifiable predators.*—We may now compare the expected gains of predators employing various behavioral strategies. First, consider the expected gain to a predator which always eats,  $S_0$ . Since the predator will eat models and mimics in relation to their relative proportions,

$$S_0 = f - b(1 - f). \quad (3)$$

For predators that always ignore,  $S = 0$ . The expected gain of predators that always eat is greater than zero only when  $[f - b(1 - f)] > 0$ . Consequently, predators that always eat will be superior to predators that always ignore only when the badness of models is less than the ratio of mimics to models,  $b < f/(1 - f)$ .

For a predator with randomly varying behavior such that it eats in  $r$  proportion of all encounters irrespective of past experience, the expected gain is  $S_r = r[f - b(1 - f)]$ . Since by definition  $r$  is always less than 1, a predator with

such random behavior will always be inferior to either a predator that always eats (when  $S_r > 0$ ) or a predator that always ignores (when  $S_r < 0$ ).

*Modifiable predators.*—Consider the class of modifiable predators that behave in the following way. The predator eats only as long as it encounters mimics. Once a model is encountered and eaten, the predator ignores the next  $N$  states (models and mimics) and then resumes eating. The variable  $N$  may be taken as a variable of forgetting or waiting time with time measured in units of models and mimics. Estabrook and Jespersen (1974) showed that for such a predator  $p(EX) = f(1 - Z^{N+1})/[f(1 - Z^{N+1}) + p(M|X)(N + 1)]$  and

$$p(EM) = p(M|X)/[f(1 - Z^{N+1}) + p(M|X)(N + 1)],$$

where  $Z = 1 - p(M|X) - p(X|M)$ . Consequently, the expected gain to a predator with waiting time  $N$  is

$$S_N = \frac{f(1 - Z^{N+1}) - bp(M|X)}{f(1 - Z^{N+1}) + p(M|X)(N + 1)}. \quad (4)$$

An alternative derivation shows that

$$p(EX) = \frac{(1 - f)p_{X,M}^{N+1}}{p(M|X) \sum_{s=0}^N p_{M,M}^s} \quad (5)$$

and

$$p(EM) = \frac{(1 - f)}{\sum_{s=0}^N p_{M,M}^s}, \quad (6)$$

where  $p_{M,M}^s$  is the probability of encountering a model in exactly  $s$  steps given that a model was just encountered, and  $p_{X,M}^s$  is the probability of encountering a mimic in exactly  $s$  steps given that a model was just encountered.

As Estabrook and Jespersen (1974) showed, a predator that always eats is a special case of the more general class of modifiable predators just described. When  $N = 0$ , equation 4 reduces to equation 3.

#### THE PROBLEM

With this model we would like to determine the conditions under which modifiable predators of the type just described are superior to nonmodifiable predators that always eat or always ignore. We will also examine the relationship between the optimal waiting time of modifiable predators, optimal  $N$ , and the variables which characterize the environment.

#### RESULTS

The general form of equation 4 as a function of  $N$  is shown in figure 3. The expected gain of the predator,  $S_N$ , is a unimodal function of waiting time,  $N$ .

*Conditions for the evolution of modifiable behavior.*—Bobisud and Potratz (1976) found that predators with modifiable behavior ( $N > 0$ ) are superior to predators that always eat and to predators that always ignore only when

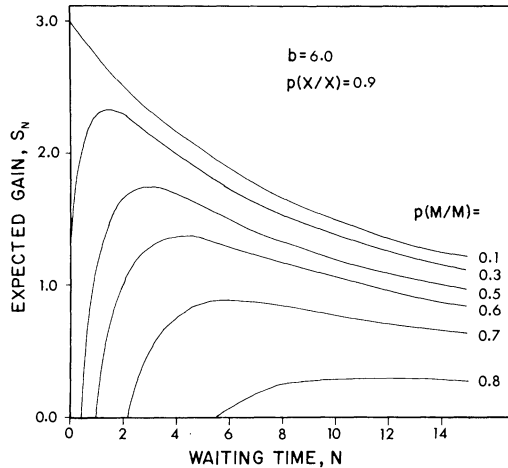


FIG. 3.—The expected gain of a predator with modifiable behavior,  $S_N$ , as a function of waiting time,  $N$ .

$bp(p + q) < q < b/(b + 1)$ . Careful consideration of this inequality reveals that it is true only when  $p + q < 1$ , that is, when models and mimics are clumped. Thus modifiable behavior will evolve only when models and mimics are clumped. This condition corresponds to one class of relatively predictable environments (figs. 1–2).

This necessary condition for the evolution of modifiable behavior can also be seen in the results of some computer runs (figs. 4–7). An alternative form of equation 4, derived by substituting equations 5 and 6 into equation 2, was solved for many values of  $p(X|X)$ ,  $p(M|M)$ ,  $b$ , and  $N$ . This alternative form is no more manageable than equation 4 but gives identical numerical results. It was used simply because Estabrook and Jespersen's (1974) derivation was not yet available at the time of the computer runs. Calculations for other figures were done using equation 4.

*The relationship between optimal waiting time and the environment.*—The most interesting result of the present study is that optimal waiting time,  $N$ , should evolve in relation to environmental pattern. The optimal  $N$  is an increasing function of the conditional probability of model-to-model transitions,  $p(M|M)$  (cf. within columns in figs. 4–7). Thus optimal waiting time is an increasing function of the expected clump size of models. The optimal  $N$  is also a decreasing function of the conditional probability of mimic-to-mimic transitions,  $p(X|X)$  (cf. within rows in figs. 4–7).

These two trends may be related in the following way. When  $p(X|X)$  is small, the conditional probability of mimic-to-model transitions,  $p(M|X)$ , is large, since  $p(X|X) + p(M|X) = 1$ . As  $p(M|X)$  becomes large or, alternatively, as mimics become rare, the predator will tend to encounter runs of models separated by only a few mimics. Consequently, as  $p(M|X)$  becomes large, the effective clump size of models becomes large even though the expected run length of models may remain constant. Thus the optimal  $N$  seems to be an increasing function of the effective clump size of models. The optimal



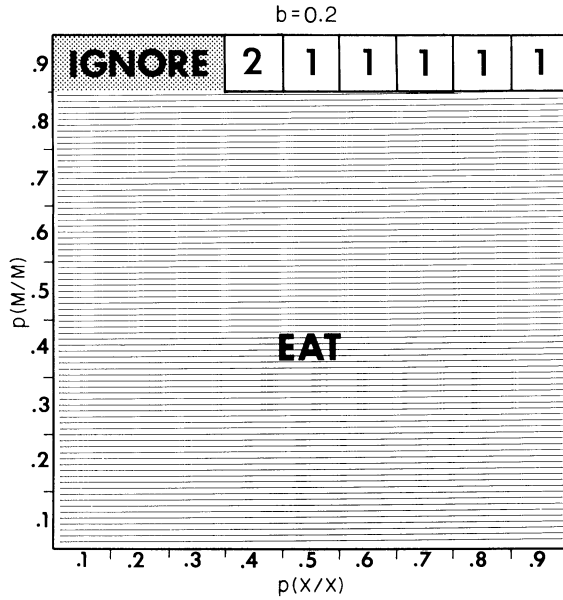


FIG. 4.—Optimal foraging behavior as a function of the conditional probabilities  $p(X | X)$  and  $p(M | M)$  when the loss to the predator from eating a model equals one-fifth of the gain from eating a mimic,  $b = 0.2$ . In environments overlaid with horizontal lines, the optimal strategy is always to eat. In environments overlaid with stippling, the optimal strategy is always to ignore. Open cells indicate environments in which predators with modifiable behavior will be favored. Numbers indicate the optimal  $N$ , or waiting time, for particular environments.

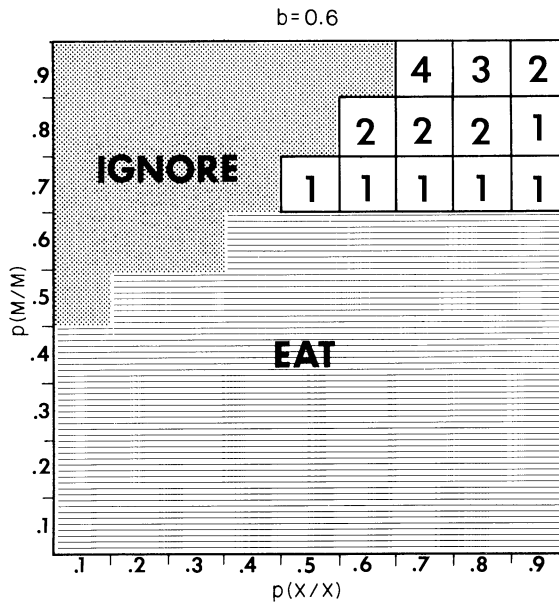


FIG. 5.—Optimal foraging behavior as a function of the conditional probabilities  $p(X | X)$  and  $p(M | M)$  when the loss to the predator from eating model equals 0.6 of the gain from eating a mimic,  $b = 0.6$ . Conventions as in fig. 4.

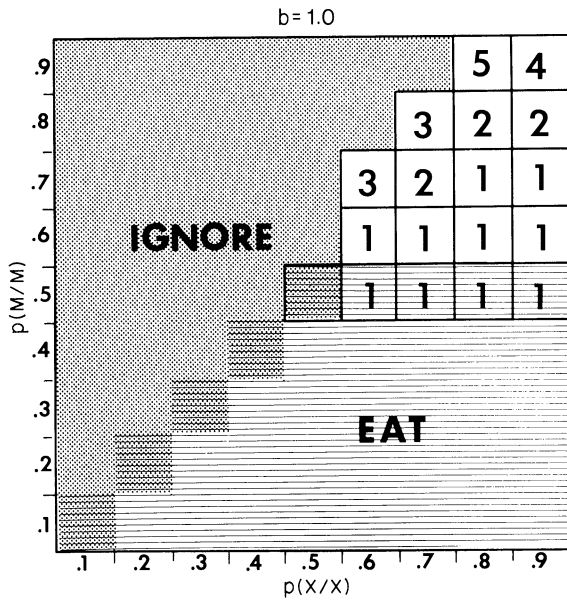


FIG. 6.—Optimal foraging behavior as a function of the conditional probabilities  $p(X|X)$  and  $p(M|M)$  when the loss to the predator from eating a model equals the gain from eating a mimic,  $b = 1.0$ . Overlapping markings indicate environments in which two or more strategies are equally profitable. Conventions as in fig. 4.

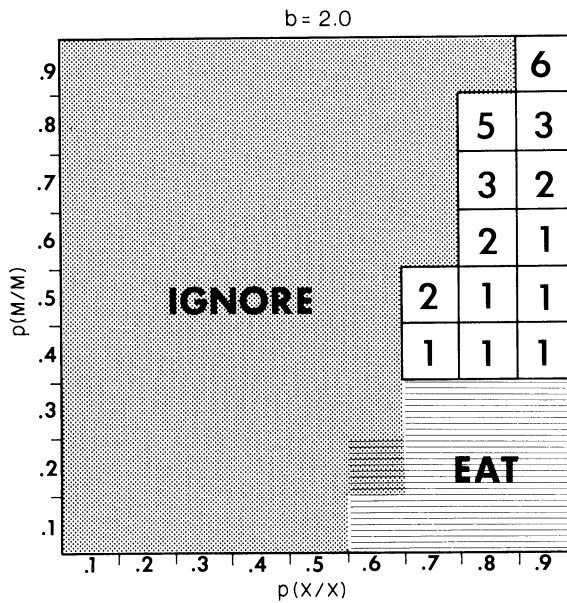


FIG. 7.—Optimal foraging behavior as a function of the conditional probabilities  $p(X|X)$  and  $p(M|M)$  when the loss to the predator from eating a model equals twice the gain from eating a mimic,  $b = 2.0$ . Conventions as in figs. 4 and 6.

$N$  also increases with  $b$ , the badness of models (cf. corresponding cells in figs. 4-7).

In evolutionary time we can expect selection to adjust the waiting time,  $N$ , of the modifiable predator to the effective clump size of models and to the relative badness of models. We can expect an optimal  $N$  to evolve such that the predator tends to skip clumps of models, once the first model in the clump is sampled, and exploit the intervening clumps of mimics. Predators will skip further, that is, wait longer, if models are more debilitating.

Behavioral strategies with  $N$  large will be optimal in some environments. The conditions are less restrictive than Estabrook and Jespersen (1974) imply if we consider the range of conceivable environments in terms of the expected clump size, or run length, of models and mimics rather than in terms of transition probabilities. In general, modifiable behavior is superior to non-modifiable behavior when badness of models,  $b$ , is compensated by large clump sizes of models and mimics. From equation 1 we can see that the clump size of models will be greater than 10 only when the conditional probability of model-to-model transitions,  $p(M|M)$ , is greater than 0.9. Models and mimics equiprobable and  $b = 1$  is a particularly informative special case, since under these conditions the expected gains of predators that always eat or always ignore both equal zero. The expected gains of some modifiable predators under these conditions are shown in figure 8. Notice that a waiting time as large as 100 is very superior to nonmodifiable behavior if the clump size of models and mimics is very large. This figure also illustrates the tendency of optimal  $N$  to increase with clump size.

A predator able to distinguish models and mimics will have an expected gain,  $S$ , of 0.5 if models and mimics are equiprobable and  $b = 1$ . A predator that cannot distinguish models and mimics before eating will do nearly as well

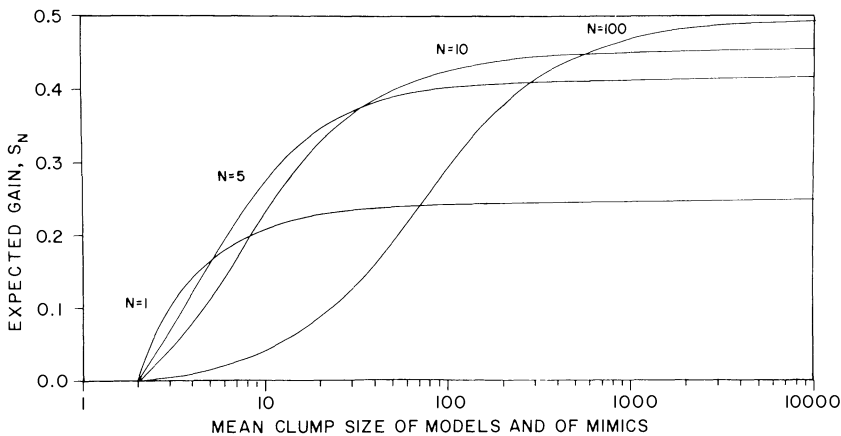


FIG. 8.—The expected gain of a predator with modifiable behavior as a function of the mean clump size of models and mimics. Models and mimics are equiprobable. Under this condition predators that always eat or always ignore will both have an expected gain of zero.

under these conditions if models and mimics are highly clumped and  $N$  is very large (fig. 8).

Modifiable behavior with  $N$  larger than 100 will be optimal in some environments. For example, if  $b = 100$  and the mean clump size of models and mimics is 1,000,  $p(M|M) = p(X|X) = 0.999$ , then a waiting time of 509 is the optimal strategy. The expected gain,  $S_N$ , of a predator with  $N = 509$  in this environment is 0.265, compared with 0 for a predator that always ignores and  $-49.5$  for a predator that always eats.

#### DISCUSSION

In the preceding section we imagined selection working on alternative phenotypes in which  $N$  was fixed during each phenotype's lifetime. Consider more sophisticated phenotypes that modify  $N$  as a function of experience. In this case the optimal values of  $N$  shown in figures 3–8 indicate the waiting time which, once achieved through a process mediated by experience, will maximize gain in the environment. A sophisticated predator of this kind will generally be inferior to a predator with  $N$  fixed and optimal for the environment. However, sophisticated predators might be favored if the variables specifying the environment,  $p(M|M)$ ,  $p(X|X)$ , and  $b$ , change during the phenotype's lifetime or between generations.

Will a modifiable strategy with  $N$  fixed and very large, near infinity, ever be optimal? The expected gain of such a predator approaches 0 as  $N$  goes to infinity. If  $N$  is near infinity, the predator will ignore for the rest of its lifetime once a model is eaten; the predator makes an essentially irreversible switch in behavior. A predator of this kind may be optimal if the environment is exceedingly coarse-grained, in the sense of Levins (1968). Suppose that during the lifetime of the phenotype the environment consists either of models only or mimics only, but the state of the environment (models only or mimics only) is unpredictable from one generation to the next or to a female broadcasting sedentary offspring. Predators with an irreversible switch will always eat, and consequently show the optimal strategy, in environments with mimics only. They will approach the optimal strategy in environments with only models. If predators with an irreversible switch are ever optimal, it will be in environments that are exceedingly coarse-grained.

All the modifiable predators discussed so far share the characteristic of one-trial learning. The predator ignores  $N$  models or mimics as soon as one model is eaten. Consider a predator characterized by a simple learning variable,  $K$ , as well as by the forgetting variable,  $N$ . The predator eats until  $K$  models are eaten in succession. Once this occurs the predator ignores the next  $N$  models or mimics and resumes eating. The modifiable predators discussed previously correspond to predators with  $K = 1$ . Predators with  $K = 1$  will probably always be superior to predators with  $K > 1$  if the environment of models and mimics is a first-order Markov process specified by stationary transition probabilities. If these conditions are met, the predator cannot improve its prediction about future environmental states by sampling more than one model. If the environment is a higher-order Markov process or if the

transition probabilities are not stationary, then models might exist both in clumps and as strays surrounded by mimics. In such environments, a predator with delayed learning,  $K > 1$ , might be optimal since the predator could distinguish between models in clumps and stray models before changing its behavior.

Bobisud and Potratz (1976) have considered a predator in which the decision to ignore is a function of the number of mimics just eaten in succession and the ingestion of two successive models. They found that such predators were always inferior to predators with instantaneous learning,  $K = 1$ , when the environment of models and mimics is a first-order Markov process.

The simple model,  $N$  variable and  $K = 1$ , can be applied to a wide variety of environmental problems in addition to classical model-mimicry systems. Two key characteristics are that the states in the environment must be indistinguishable and have differing effects on the economy of the organism. The other formal assumptions of the model must also be satisfied. In particular, we always suppose that the sequence of encounters with the two states of the environment is a first-order Markov process. Two fanciful examples will indicate the variety of applications.

Suppose an aquatic, tube-dwelling worm is faced with a stimulus ambiguity with regard to shadows. A shadow sometimes represents a predatory fish and sometimes represents a nonpredatory fish or seaweed. The worm can give two responses to a shadow; it can remain extended and continue to filter feed, or it can withdraw into its tube and so interrupt feeding. If the worm remains extended when the shadow is nonpredatory, it gains 1 unit. If the worm remains extended when the shadow represents a predator, the resulting attack results in a loss of  $b$  units. There is no change in the worm's economy if it withdraws when the shadow is predatory or nonpredatory. Suppose that the worm remains in the tube until  $N$  shadows have passed every time a predatory attack follows the stimulus shadow. This modifiable behavior will sometimes be superior to the nonmodifiable behaviors of always remaining extended or always withdrawing when shadows pass over. A necessary condition is that encounters with predatory shadows be clumped in time and that encounters with nonpredatory shadows be clumped in time. If modifiable behavior is a viable strategy, then the optimal  $N$  or waiting time in the tube will be an increasing function of the clumping of predatory encounters in time and the severity of the attacks.

Now consider a bird foraging for hidden prey in a seemingly uniform environment such as a mud flat. Suppose that the bird cannot tell when a prey lies under a particular small area until the bird pokes with its beak. The bird gains 1 unit if it pokes and captures prey. The bird loses  $b$  units if it pokes and no prey is present. Suppose that there is no change in the bird's economy if it ignores—fails to poke at—the small area, regardless of whether a prey is hidden there. Consider a bird with modifiable behavior such that the bird continues to poke in adjacent areas as long as it captures prey with each poke. Once the bird fails to capture prey, it walks and so skips over the next  $N$  small areas and then resumes poking. If this behavior is profitable, the optimal  $N$ , walking distance, will be an increasing function of the expected distance between clumps of prey.

Baker (1974) studied the foraging behavior of black-bellied plovers on mud flats. He found that birds walked further after an unsuccessful poke than after a successful poke. Baker suggests that clumping of prey may have favored the evolution of this behavior. The model described here adds some plausibility to this proposal.

#### SUMMARY

A simple model is used to compute the selective advantage of one kind of avoidance conditioning. The model is developed in terms of a predator exploiting a stochastic environment of models and indistinguishable Batesian mimics. Nonmodifiable predators that either always eat or always ignore are compared with modifiable predators that ignore for some time,  $N$ , once a debilitating model is eaten. Modifiable behavior is superior to nonmodifiable behavior only when models and mimics are clumped. This condition corresponds to one class of relatively predictable environments. Optimal waiting time, optimal  $N$ , is an increasing function of the mean clump size of models and the relative badness of models. Thus the model predicts that selection will adjust the waiting time of modifiable predators such that the predator will tend to skip over clumps of debilitating models and exploit the intervening clumps of mimics. Predators should skip further, wait longer, as models become more debilitating. Very long waiting times,  $N > 100$  models and mimics, will sometimes be optimal if the clump size of models is very large.

The implications of the model for the evolution of delayed learning, irreversible switches ( $N$  near infinity), and predators that modify  $N$  with experience are discussed.

The model is briefly applied to the evolution of predator avoidance by tube-dwelling worms and to the foraging behavior of predators searching for hidden prey in order to indicate the range of possible applications.

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#### LITERATURE CITED

- Baker, M. C. 1974. Foraging behavior of black-bellied plovers (*Pluvialis squatarola*). *Ecology* 55:162-167.
- Bitterman, M. E. 1965. Phyletic differences in learning. *Amer. Psychol.* 20:396-410.
- Bobisud, L. E., and C. J. Potratz. 1976. One-trial versus multi-trial learning for a predator encountering a model-mimic system. *Amer. Natur.* 110:121-128.

- Estabrook, G. F., and D. C. Jaspersen. 1974. Strategy for a predator encountering a model-mimic system. *Amer. Natur.* 108:443-457.
- Garcia, J., J. C. Clarke, and W. G. Hankins. 1973. Natural responses to scheduled rewards. Pages 1-41 in P. P. G. Bateson and P. H. Klopfer, eds. *Perspectives in ethology*. Plenum, New York.
- Garcia, J., and F. R. Ervin. 1968. Gustatory-visceral and telereceptor-cutaneous conditioning—adaptation in internal and external milieus. *Comm. Behav. Biol.* 1:389-413.
- Garner, W. R. 1962. *Uncertainty and structure as psychological concepts*. Wiley, New York.
- Harlow, H. F. 1958. The evolution of learning. Pages 269-290 in A. Roe and G. G. Simpson, eds. *Behavior and evolution*. Yale University Press, New Haven, Conn.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Monogr. Pop. Biol.
- Pielou, E. C. 1969. *An introduction to mathematical ecology*. Wiley-Interscience, New York.
- Thorpe, W. H. 1963. *Learning and instinct in animals*. Harvard University Press, Cambridge, Mass.