Hawks Select Odd Prey

Abstract. *Hawks were offered one color of mouse for ten consecutive captures and then a choice between that and another color. The birds usually selected the odd, or unusual, color. This behavior is probably adaptive because odd prey in nature would be unfit.*

I have shown that, when hawks are presented with an aggregation of gray and white mice, there is a strong tendency for the birds to select prey of the color to which they have been accustomed (*1*), a phenomenon which Tinbergen (*2*) has termed the specific searching image (SSI). I also found that there was a slight tendency to select uncommon, or odd, mice. The conspicuousness of prey had little influence on selection in these experiments. I present here data on the influence of these factors on a predator that encounters prey animals one at a time, instead of in aggregations.

Six tamed American kestrels (*Falco sparverius*) were allowed to prey upon albino laboratory mice, some of which had been dyed gray with food coloring. Experiments were conducted in a well-illuminated room, 6.8 by 4 by 3.7 m with occluded windows. Mice were presented individually on pedestals about 10 cm square and 15 cm high, and the hawk was placed on a perch approximately 2 m away. The substrate on which the mice were presented was painted gray. Each hawk was first presented with a single white mouse for ten consecutive captures (Table 1, part A). On the 11th trial the hawk was given a choice: one white and one gray mouse were presented. This experimental sequence was repeated daily. Three of the six hawks tested chose white mice on the 11th trial for three or more days, and two birds took gray mice on the first choice (Table 1, column 1). Once the first gray mouse was taken, the experiments were continued for 15 more days, presenting one white mouse for ten consecutive trials and then a choice between one gray and one white mouse on the 11th trial. The number of gray mice chosen in these 16 days is presented in column 2 of Table 1. One bird, Walda, never chose a gray mouse even after 16 days of experiments. The entire series of experiments was then repeated, each hawk being offered one gray mouse (instead of a white mouse) for ten captures and then a choice between a gray mouse and a white mouse (Table 1, part B). If the SSI influences prey selection, the birds would be expected to choose white mice in part A and gray mice in part B. If oddity is a determinant of prey selection, we would expect the birds to choose gray mice in part A and white mice in part B. Selection for conspicuousness would result in the taking of white mice in both parts A and B.

All birds except Walda selected a significantly higher proportion of odd mice in the last 16 experiments of both parts A and B. For five of my six birds (Walda omitted), the selectivity index (*3*) is 7 ± 2.09 for part A, 25.6 ± 1.12 for part B, and 11.3 ± 1.09 for both parts combined. The ± indicates the 95 percent confidence limits of the index. If there were no selection, or random selection, the selectivity index would be 1. The observed results clearly differ from random and indicate a strong preference for odd or novel mice.

The two birds that took gray mice on the first choice in part A (Gandalf and Belle) took at least several gray mice in part B before switching to white mice (Table 1). These two birds also chose a higher percentage of odd (gray) mice in part A than they did in part B where the odd mice were white. This suggests that Gandalf and Belle had an overall preference for gray mice. Similarly, Thorin, Varda, and Bree chose several white (common) mice before switching to gray odd mice in part A, Walda did not switch at all. All four of these birds switched rapidly in part B, where odd mice were white and took a greater proportion of odd mice in part B than in part A. This suggests an overall preference for white mice in these four birds. I have previously interpreted such an overall preference as a long-term SSI, one which cannot be switched easily by experience with other kinds of prey (*1*). There appears to be no consistent rationale for the establishment of a long-term SSI in these or previous experiments. Birds often switch their long-term SSI during a lengthy experiment. In two previous experiments, Gandalf had shown a strong preference for white mice and then shifted to a weak preference for gray, a preference maintained in the experiment reported here. Varda had shown a strong preference for white mice in one previous experiment and maintained this preference in the present experiment. The other four birds were hand-reared and had experience only with white mice prior to the experiments, yet one of the four (Belle) showed a preference for gray mice.

Since the substrate was gray in all experiments it is possible to interpret the preference for white mice in four of the birds (and, in particular, Varda) as a selection for conspicuous mice. This is unlikely since two birds preferred gray mice and also because conspicuousness has not been an important factor in my previous experiments which utilized the same experimental apparatus.

In my previous work (*1*) uncommon or odd mice were presented simultaneously with common mice in all experiments, a situation involving what I call simultaneous oddity, and the results showed strong evidence for a long-term SSI and some evidence for the selection of odd mice. My experiments here involve sequential oddity, and the results indicate that oddity is more important than the SSI in determining prey selection, opposite to what was found in experiments involving simultaneous oddity.

Theoretically, one might expect a predator to show a greater tendency to select the odd animal out of an aggregation (simultaneous oddity) than to choose the animal which is odd in terms of prior experience in a situation involving only two prey individuals (sequential oddity). An odd animal in an aggregation might catch and hold the predator's attention more readily than the common animal. The lack of strong selection for simultaneous oddity in my experiments may be an artifact of the experimental design. A moving mouse attracts a hawk's attention more than a stationary mouse, a mouse with its back to the hawk is more likely to be attacked than one fac-

Table 1. Results of sequential oddity experiments.

Bird	Part A: ten white mice, then choice		Part B: ten gray mice, then choice	
	No. white chosen before first gray	No. gray taken last 16 experiments	No. gray chosen before first white	No. white taken last 16 experiments
Gandalf	0	16	2	15
Belle	0	16	9	14
Thorin	7	13	0	16
Varda	7	12	1	16
Bree	3	13	0	16
Mean	3.4	14	2.4	15.4
Walda	16	0	0	12

ing the hawk, and other randomly occurring variables may influence a hawk's selection of prey as well. (I was unable to monitor, let alone control, these extraneous variables.) In experiments involving simultaneous oddity, a common mouse is more likely to be exhibiting attractive, randomly occurring behavior than the odd mouse. For example, if mice of two colors are presented in a ratio of 9 : 1, the common mouse is nine times as likely to show a given attractive behavior at any given moment. In my experiments involving sequential oddity, common and odd mice each have equal probability of showing a given behavior. Thus the influence of oddity may have been obscured by random, irrelevant variables in my previous experiments involving aggregations of prey.

It is possible that reinforcement plays a role in determining the results of present and previous experiments, but I doubt it. The possibility exists because birds were not fed until after the last experiment of the day, and the color of the last mouse taken thus might act as positive reinforcement for a preference of that color. However, in all experiments the birds were fed regardless of the color of the last mouse and thus there is no reason why two birds in part A, and three birds in part B, shifted preferences. Further, a detailed analysis of previous experiments (*1*) in which mice of both colors were always available showed no correlation between the color of the mouse last taken on one day and the first mouse taken the next, when the influence of the long-term SSI was taken into account. Last, to test the possible role of reinforcement, Belle was run for ten additional days beyond those listed in part B of Table 1. In these 10 days, the mouse selected in the choice situation (11th trial) was invariably white. The bird was not allowed to feed but was then presented with a single gray mouse which it captured and the bird was then fed. In spite of the reinforcement for gray, the bird continued to choose white mice for the 10 days.

Since the birds were not permitted to feed on the first ten mice on each day, lack of reinforcement acting against the selection of that color may have been influencing the results. This also seems unlikely because the birds continued to prey upon mice in a situation where choice was not possible, in spite of the fact that they were not reinforced. Further evidence against the hypothesis can be seen in the length of runs of captures of a given color of mouse, without reinforcement, in my previous experiments, in which the birds always had a choice between gray and white. In these experiments the birds showed runs of captures of a given color of mouse greater than ten on 34 percent of the possible occasions, in spite of the fact that this often meant that the birds were continually selecting the odd or uncommon color of mice. In the 5440 individual trials, mice were presented in a ratio of 9 : 1 for 55 percent of the time, 8 : 2 for an additional 18 percent, and 7 : 3 for yet another 13 percent. Lengthy runs, particularly of the odd or uncommon color, are unlikely because of the various random influences on selection discussed above. The relatively high incidence of lengthy runs, in spite of the variety of factors which militate against them, suggests that negative reinforcement is not important in determining prey selection in my experiments.

The data thus seem to indicate a preference for odd mice in five out of six birds tested. In the remaining bird (Walda), a long-term SSI appeared to be the most important factor determining prey selection, a factor which also influenced the results from the other five birds.

Many observations and experimental results fit into the generalization that predators select odd prey (*4*), but unequivocal data are lacking. Goshawks (*Accipiter gentilis*) have been shown to select the uncommon color morph out of flocks of domestic pigeons (*Columba livia*), but odd colored pigeons can be considered to be conspicuous relative to the flock in which they fly (*5*). Other evidence for the selection of odd prey is essentially anecdotal. My results suggest that oddity is an important factor in prey selection. Odd animals are almost invariably unfit animals and a prudent predator would select unfit animals out of a prey population (*6*). Selection of unfit animals would benefit both predator and prey and tend to drive the predator-prey system to optimal yield.

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References and Notes

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7. Supported by NSF grant GB-8771. I thank J. J. Bakker, C. H. Black, C. C. Horton, L. J. Moseley, and H. F. Sears for technical assistance and J. A. Feduccia and R. H. Wiley for comments on the manuscript.

12 November 1974; revised 20 January 1975

Learning: Rapid Aversive Conditioning in the Gastropod Mollusk *Pleurobranchaea*

Abstract. *Untrained* Pleurobranchaea *feed voraciously when presented food and withdraw from electrical shocks. We trained experimental animals in ten trials spaced 1 hour apart to withdraw from food alone by electrically shocking them if they fed or were indifferent to food. The greatest increase in the number of learned withdrawal responses occurred within 12 hours after conditioning, and was accompanied by long-lasting increases in the threshold and latency of feeding responses. Control animals, which received food and shock alternately (unpaired) every half hour, showed considerably weaker changes than experimentals. These control responses quickly returned to initial levels after conditioning.*

Invertebrates offer attractive experimental material for investigations aimed at the cellular basis of associative learning inasmuch as they show simple, controllable behaviors and possess correspondingly simple nervous systems (*1*). Among these animals the mollusk *Pleurobranchaea* is uniquely suited for study because it exhibits strong associative learning as shown by classical and avoidance conditioning of its feeding behavior, and because it is the only animal in which evidence of learning can be detected in completely isolated nervous systems (*2*). The behavioral changes produced to date in *Pleurobranchaea*, however, require many days of conditioning to become firmly established. Such long periods of time present serious technical difficulties for experiments aimed at pinpointing the quality, time of consolidation, and locus of the cellular and physiological events that underlie learning. For this reason, we have sought and now report on long-lasting behavioral changes, attributable to associative learning, which can be produced in only 1 day. The effectiveness of the present conditioning paradigm, together with the suitability of the behaviors of *Pleurobranchaea* for physiological analysis (*3, 4*), provides a new and useful experimental system for studying learning.

Specimens of *Pleurobranchaea californica* (MacFarland) of about equal size and having a mean weight of 175 g were obtained off the coast of southern California. The animals were maintained individually in transparent plastic trays (6.5 liters in volume) so that they could be viewed from