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THE ROLE OF LEARNING IN THE FEEDING BEHAVIOR OF BLACK-CHINNED HUMMINGBIRDS

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Investigations of learning behavior in animals below humans have been carried on for the past fifty years, beginning with the concept of trial-and-error learning as employed by Lloyd Morgan (1894). A review of the literature, however, reveals that learning behavior in wild birds has received only scant attention. Watson and Lashley's studies of orientation in Noddy and Sooty terns are perhaps the most notable of early experiments with wild birds, although they were more interested in searching for the mechanism of orientation which guides birds in migratory flight than in investigating the learning process itself. As far as captive and domestic birds are concerned, Thorndike's (1898) work with chicks and Whitman's (1919) work with pigeons are outstanding, the former for introducing the concept of associative learning and the latter for showing the effects of conditioning on delayed sexual instincts.

This paper is a study of the learning behavior of the Black-chinned Hummingbird (*Archilochus alexandri*), based on observations and experiments conducted over the past five years in Phoenix, Arizona. During the spring and summer months of 1939 and 1940, and the spring of 1941, I spent an average of four hours daily in observation or experimentation. Less intensive work was done in 1938, 1942, and 1943. Of the two dozen or so individuals observed, eight served as subjects in feeding experiments.

In this paper the term learning refers to that process whereby the bird modifies original or instinctive ways of behaving. The product of learning may be an acquired or perfected skill, a conditioned response, a habit, or a behavior pattern. In testing the learning product three criteria are applied: (1) the learning activity must show repetition of trials; (2) change in behavior must result from this repetition; (2) this change in behavior must be constant enough to leave no doubt that learning has taken place.

It is not always possible to distinguish instinctive behavior from learned behavior, but we can with reasonable reliability recognize a product of learning in an experimental situation by applying the above criteria. In applying these criteria to an experimentally devised learning situation, we might be troubled by the supposed necessity of identifying the behavior pattern that is being modified. Is it a pure instinct or something that has already been learned? If it is an instinct, the criteria apply; if it is an act already acquired but undergoing further change, the criteria still apply. It is not the purpose of this paper to mark off succeeding stages in the modification of an original reflex or other behavior pattern. If the definition for learning given above includes modification of any subsequent stage, then any behavior that is modified in the light of the criteria set forth legitimately falls within the scope of this study.

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FEEDING ADAPTATIONS

A general description of the feeding adaptations of hummingbirds at this point will indicate the possible directions learning takes. Observation of a hummingbird engaged in feeding discloses a versatility of motor skills—hovering about plants as though suspended from its wings, pirouetting in mid-air, flying backward, forward, upward, downward, from side to side like a pendulum—all performed with the greatest precision and ease. A hummingbird is indeed peculiarly adapted for rapid, intricate maneuvering about flowers and for extracting the nutriment within them.

As pointed out by Ridgway (1892:292), the hummingbird's aerial proficiency is made possible by such anatomical features as (1) short upper arm and long hand bones which gain for the bird a rapid wing stroke, (2) long, recurved processes of the bones supporting the tail which make possible well-developed caudal muscles that help the bird balance itself while hovering and assist the wings in backward flight, and (3) large pectoral muscles essential to rapid, prolonged flight.

The bill and tongue are highly specialized for extracting nectar and minute insects from the innermost recesses of most flowers visited by hummingbirds. The bills of North American species are quite uniform in shape and differ from each other chiefly in size. The bills of the small species occurring in the United States average about three-fourths of an inch in length while those of the Blue-throat (*Lampornis clemenciae*) and Rivoli (*Eugenes fulgens*) hummingbirds measure about one and one-fourth inches.

The tongue is tubular for part of its length and the tip fimbriated (Lucas, 1891). There remains some doubt as to the precise manner in which liquid foods and tiny insects are taken from flowers. According to Lucas, there can be no sucking action since the posterior section of the tongue is so constructed as to prohibit the creation of a vacuum or even partial vacuum. Gosse (in Ridgway, 1892:289) suggests capillary action as the mode of drawing up liquids, and this is quite possible.

The viscous saliva secreted by a hummingbird and the fimbriated tip of its tongue make possible the capture of minute insects in flowers. As my observations reveal, a hummingbird has voluntary control of the forked tip of its tongue, but whether the bird searches out the hidden insects with its tongue or finds them haphazardly is not clear. Exposed insects obviously are perceived visually. The tactile and visual senses seem to predominate in insect-feeding and the bird appears to respond largely to the size, color, form and movement of insects and spiders.

The perceptual mechanism involved in the selection and recognition of aerial insects and spiders is not as freely open to experimentation as is the mechanism involved in the selection and recognition of flowers, but if the hummingbird utilizes experience in perfecting its flower-feeding technique, there is no reason why it should not perfect its insect-feeding technique in a comparable manner.

The food of hummingbirds includes hymenopterans, hemipterans, dipterans and spiders. These include a multitude of bug-like, fly-like and spider-like species. Taken as a whole, those chosen by hummingbirds are noted for their small size and dark color. The source of these insect foods is varied. Inside the flower corollas minute thrips abound, whereas outside the corollas and on the surfaces of the plant parts predominant insects are black- and green-backed beetles; vines, shrubs and trees are visited for certain spiders which suspend themselves by their silk; and at dusk the air teems with gnats which constitute a large portion of hummingbird diet. The insects which hummingbirds consume, therefore, either move about in full view of the hummer or are concealed and must be sought out.

It is clear that the tongue is adapted for procuring both insects and nectar. The

tubes are intended solely for drawing up liquid foods since they are too small to permit the passage of even the smallest beetles found in flowers. Capillarity alone is insufficient to draw liquid into the crop. When the liquid fills the tubular tongue, the tongue must be emptied. This is done by the contraction and dilation of the tongue muscles which force the liquid out of the tube through the posterior end into the crop. Extending the tongue narrows the tube, thus increasing capillary action, whereas retracting the tongue not only draws the tongue back toward the oesophagus but also widens the tube so that emptying of it is facilitated. When exposed to the air for a few minutes, the tongue dries and the bird loses control of it. Wetting the tongue with water restores action almost instantly.

BEHAVIOR OF IMMATURE BLACK-CHINS

This part of the study deals with two pairs of nestling Black-chins. Data for the first pair are available for fourteen days of their nest life, from April 20 to May 4, 1939. The nestlings succumbed on May 4, after the parent bird either deserted them or was killed. Data for the second pair were collected during their entire nest life and during a fortnight after they left the nest, altogether from April 24 to May 29, 1943.

Food responses of nestlings.—During the first few days after hatching the nestlings lay so deep in the nest that their food response could not be observed directly. But the behavior of the parent bird on the nest as she fed the young, together with the nature of the feeding-brooding routine, at least indicated the nestlings' response to the parent bird. Later, by experimental means, it was possible to observe the actual food response of the nestlings.

During the first two or three hours after the first bird hatched, the parent visited the nest frequently, but instead of perching on the rim of the nest and waiting for the food response of her young, she poked her bill deep into the nest and jabbed, then dropped on the nest to brood. This action is unlike the feeding action that followed later in the day when the bird paused on the nest, then at the appropriate moment regurgitated food as she pointed her bill down into the nest. Once the adult bird waited fully a half minutes on the rim of the nest before delivering her food.

Over a period of five hours, the adult bird visited the nest and poked her bill down into it on an average of 2.8 times per hour. The next day, when the second bird hatched, the number of trips dropped to 2.1 per hour. When the nestlings were three and four days old, the rate was 2.1 trips per hour. In a similar study (Bené, 1940:209), the rate of feeding two- and three-day-old nestlings was 2.3 times per hour as compared with 2.1 reported in this study.

Once the feeding routine is established, it appears that the parent bird does not feed the young until the food response is given. On those occasions when the parent flew to the nest and immediately poked her bill down into it, she might have been attempting to feed the young or she might have been arranging shell fragments or nest material. This seems to be borne out by the following data. When the feeding routine is well established, the number of trips to the nest to feed the young increases from day to day. Referring to the nestlings observed in 1939 (Bené, 1940:209), the number of trips per hour to feed young increased as follows: April 20, 2.3; April 23, 2.4; April 27, 2.5; April 29, 3.0; and May 1, 3.1. From these figures it would seem that 2.8 trips per hour recorded for the first day in the study in 1943 is much too high, particularly in view of the fact that only one nestling, not two, was being fed.

Though a form of reflex action, the food response is subject to modification; it becomes more efficient as the nestling gains experience. At first, when the nestlings are blind, the food response is given indiscriminately to a variety of tactile and auditory

stimuli, but gradually responses to those stimuli which bring no food are inhibited and responses to stimuli which bring food are facilitated. When a medicine dropper filled with honey was tapped against the bill of a nestling, the food response was immediately given and the honey was dropped into its gaping mouth; but after repeated tappings of the mandibles without delivery of honey, the food response of the nestlings was inhibited.

Tactile stimuli are the most effective in eliciting the food response, whether they be the touch of the female's bill, the touch of one's finger, or the tap of a medicine dropper. Even when the nestlings are able to see, they respond to tactile stimuli of a foreign nature so long as food accompanies them. This response is shown in the advanced stages of nest life, as late as two days before leaving the nest.

Tactile stimuli alone do not constitute the entire food-response pattern. As the feeding routine becomes established, the nestlings learn to associate such factors with the presence of food as the *purr* of the parent's wings as she approaches the nest, the fixed station on the rim of the nest from which she feeds them, and the sight of their parent. Regardless of the conditioning agents in the pattern, whether or not the food response is facilitated or inhibited will depend on the presence or absence of food in the associational pattern.

Probing response.—One of the nestlings which left the nest on May 15 spent most of its time perched in the vicinity of the nest, usually on a twig of a bird-of-paradise shrub. The other, which left the nest a day later, chose the sheltered twig of an ash tree. Neither made any attempt to probe the flowers within full view of their perches. They seldom changed perches, preferring to wait for the parent bird who visited them at frequent intervals. Approaching her young, the adult bird would delay the feeding act, intermittently flying up to the young, then retreating, as though prodding them to leave their perches. But the young birds did not move. At this stage the older fledgling was 22 days old. The only acts that bore any semblance to feeding behavior were the extension and retraction of the tongue, stropping the bill, and probing twigs and leaves with the bill.

As each day brought additional strength to the young, the parent bird prodded them more frequently. She was still feeding them on the thirteenth day after they had left the nest. By this time the young grew bolder in their flight from twig to twig and tree to tree, even hovering among the leaves for seconds at a time and probing the leaves on wing. But the bird-of-paradise, scabiosa, honeysuckle, and larkspur blooms visited by adult birds were ignored by the young. Once an adult male Black-chin flew to the blooms of a bird-of-paradise shrub, and probed within a few feet of one of the fledglings. The young bird watched the intruder feed. When he left, the fledgling still made no attempt to search the flowers.

Twelve days after this incident, on May 30, one of the young approached a bird-of-paradise bloom and probed it. Then it flew to the ash tree and hovered among the leaves as though searching for insects. At this date the young were rarely seen on the premises (fig. 2) and the parent bird scarcely visited them. After May 31, sixteen days after the older bird had left the nest, the fledglings were no longer seen. Not until June 6 were immature Black-chins seen again, when what seemed like one of the young appeared, probing the large fiery red blooms of a canna. It fed awkwardly and attempted to gain a foothold on the bloom it probed. During the latter part of June both young were feeding from syrup glasses in the yard, though how the birds discovered them escaped observation.

The original response of the young to flowers also escaped my observation, but of

significance is the fact that the young probed twigs and leaves as soon as they had left their nest. I failed to see any insects on these twigs and leaves.

As the immature bird acquired strength of flight the probing response underwent further development to include hovering. The probing-hovering response resembles the technique of the adult bird when it searches the leaves of trees for insects. At this stage the immature bird still lacked the perfected motor coordination aerial feeding demands. Even when it had extended its search for food to flowers, it still lacked the smooth, rapid maneuverability characteristic of the adult bird.

The probing response of hummingbirds is comparable to the pecking response of domestic chicks, but since neither the feeding mechanisms nor the diets of fowls and hummers are identical, a reliable comparison of the rate of learning is hardly possible. Breed (1911) found that at first chicks rarely succeed in getting the food pellet swallowed, missing it forty-five times out of fifty trials. After fifty trials a day for five days, they are successful eighty per cent of the time.

Whether the young hummingbirds recognize flowers as a source of food while still dependent on the adult bird for food was not conclusively evident in their behavior. With hummingbirds there can hardly be an association of the taste of liquid foods with the appearance of the source of food until actual contact with the food in the flower is made. And this association can be effected only through exploration or trial and error. The nestling hummingbirds in this study had experienced only the taste of sweets regurgitated into their mouths by their parent and the taste of syrup I artificially fed them. An observation of significance is the fact that while the fledgling birds were still dependent on the parent for food, they nevertheless did some independent exploring, hovering about the leaves of trees and probing them.

PERCEPTION OF FOOD SOURCES AND MODIFICATION OF RESPONSES

The hummingbird, mature or immature, does not conduct its search for food from one spot or center but attempts to respond to as much of the environment as it can. Any one observing a hummingbird can not fail to note the scope and intensity of its search for prospective sources of food. Should the probing response yield an insect, a direct association of the insect with the thing probed results. If perchance a flower instead of a leaf yielded the insect, a similar association would be effected. Exploration is the keynote to learning, as the results of experiments to follow will make clear.

Response to color.—It has been held that specific color preferences are shown by hummingbirds, but according to my own studies (Bené, 1941:237), the hummingbird does not inherit a preference for any particular color. Rather color preference may be conditioned by experience and training. Or, to put the matter in other words, a hummingbird may be trained to select a source of food regardless of its color.

It is generally agreed that for the light-adapted eye the maximal sensitivity lies in the yellow-green region, between wave lengths 580-530 $m\mu$ (Woodworth, 1938:539-550). If color sensitivity influences choice, then the color preferred would be yellow to green, not red as is commonly believed. Since hummingbirds visit flowers of all colors, there is no reason to believe that any single color or combination of colors is especially attractive.

Response to scent of flowers.—There is no evidence of a special olfactory sense that guides hummingbirds to flowers. If receptacles of strongly scented honey, such as orange honey fortified with fresh orange blossoms, are hidden in a flower bed, the untrained Black-chin ignores them, darting past the spot of the hidden honey without

stopping to investigate. Even hummingbirds trained to feed from glasses containing catclaw or orange honey failed to locate the concealed glasses. Of the flowers visited by hummingbirds only a small proportion are strongly scented. This, however, does not preclude the possibility that once a flower is accepted its scent enters into the total associational pattern of recognition.

The scent of a flower does not appear to warn the hummingbird of its toxic nature. Young hummingbirds exploring various flowers indiscriminately visit such obnoxious plants as the oleander (*Nerium*) only to leave them instantly upon contacting the corollas. My records show not a single instance of an adult bird probing the oleander, yet in Phoenix hummingbirds commonly build their nests on the twigs of this shrub.

Taste discrimination.—My experiments show that the Black-chinned Hummingbird can discriminate differences in the concentration of sweets like syrup and diluted honey. The reaction of an adult female to syrup and honey solutions of varying concentration is shown in table 1. Starting with a honey solution containing 5 drops of honey in one ounce of water, the experimenter gradually increased the concentration by 5 or 10 drops. The bird's rejection of the solution is indicated when she takes only two or three quick sips, and acceptance when she takes a short or long drink. Between 60 to 70 drops of honey in one ounce of water is the minimum threshold of acceptance, whereas for syrup the minimum threshold is $1\frac{1}{2}$ teaspoonfuls of sugar per ounce of water. Undiluted commercial honey is also rejected since it is too viscous for the bird's tongue. Incidentally, at the minimum thresholds of 60 drops of honey and $1\frac{1}{2}$ teaspoonfuls of sugar, the viscosities of honey and syrup solutions are about equal.

Table 1
Taste discrimination of an adult Black-chinned Hummingbird, showing minimum threshold of acceptance of syrup and honey solutions

Trip	Drops of honey per ounce of water	Reaction
1	5	2 quick sips
2	10	2 quick sips
3	15	2 quick sips
4	20	2 quick sips
5	25	2 quick sips
6	30	3 quick sips
7	35	2 quick sips
8	40	2 quick sips
9	50	2 quick sips
10	60	short drink
11	70	long drink
	Teaspoonfuls of sugar per ounce of water	
1	2	long drink
2	$1\frac{1}{2}$	long drink
3	1	2 quick sips

The kinds of sweets preferred by hummingbirds are matters of individual differences in taste. Most birds prefer syrup made with white sugar. Brown sugar syrup is least preferred. Commercial honey ranks next to white sugar syrup in preference. Some of the birds have even accepted syrup flavored with fruit juices and one bird I had nursed for a broken lower mandible accepted various combinations of syrup, honey, egg yolk, milk, limewater, and B₁ complex mixed in various proportions.

The associative process.—That hummingbirds associate the superficial features of a flower with the nutriment it holds may be shown experimentally. The experiment to be described is typical of several conducted with adults as subjects. The subject of

this experiment was an adult male Black-chin who was conditioned to feed from syrup feeders. Prior to the experiment he had been feeding from lilac-colored buddleia and pink, red, yellow, and orange nasturtiums.

In a preliminary experiment several nasturtium blooms with some of the spurs clipped were placed over the mouths of small vials and one-ounce wine glasses filled with honey or brown sugar syrup. These were hidden in the nasturtium beds so that the flower decoys could not be distinguished from genuine nasturtium blooms. Mistaking these decoys for real flowers, the bird probed them, discovered that they held an abundance of sweets, and thereafter looked for them in the nasturtium beds. From March 20 to 23 the bird discovered all the decoys, but his reaction to them varied, owing to conditions beyond the control of the experimenter. At times the flower decoys withered and clogged the vials. Bees that found the vials would keep the bird away from the decoys.



Fig. 1. Adult male Black-chinned Hummingbird drinking white sugar syrup; used as subject in experiment relating to associative process.

On March 24 a red nasturtium was placed over the mouth of a wine glass filled with honey and the decoy placed on a pedestal in a secluded spot on the porch (fig. 2) away from the bees but in contact with a nasturtium plant that trailed up a trellis. While probing some nasturtium blooms on the trellis, the bird stuck his bill into the decoy and took a long drink. He returned several times and drank unhesitatingly, although after each trip parts of the decoy were removed until only two petals, five sepals, and the stamens and pistils remained. At this last stage of deformity, the mutilated decoy began to move about in the honey as the bird touched it. On the sixth trip to the feeder, when most of the glass was exposed and only two petals remained, the bird refused to touch the flower, preferring instead others feeders with whole flowers in them.

Next day I repeated the experiment, beginning with a whole decoy. From 10:27 until 11:12 the bird responded favorably, but as soon as the mutilated decoy moved about in the honey the bird quickly withdrew his bill.

Up to this point the vials and glasses were filled with honey or brown sugar, but upon finding that the bird was partial to white sugar syrup I eliminated the first two foods and began the experiment anew. The time was 11:12. A summary of the bird's reactions after 11:12 is given in table 2.

Prior to the experiment the bird responded to the whole decoy. Whether the bird sensed anything unnatural about it was not indicated by his behavior. Later, response to the form of the whole flower was modified by the quantity of sweets it held. Preference for the ordinary supply of sweets in the natural flowers was transferred to the increased supply in the decoys, indicating that the bird is quick to perceive differences in the quantity of nutriment in sources of food.

The association of abundance of nutriment with the form of the food source proceeded to the point where the decoy no longer remained stationary. Not accustomed to

Table 2

Responses of a male Black-chinned Hummingbird to a decoyed artificial feeder

Time of trip	Condition of flower decoy	Bird's reaction
11:35	Whole yellow nasturtium	Accepts
11:40	5 sepals removed	Accepts
11:53	Middle front petal removed	Accepts
12:05	1 rear petal removed	Accepts
12:20	Remaining rear petal removed (Observation interrupted)	Accepts
2:05	No change in decoy	Accepts
2:42	1 front petal removed	Accepts
2:53	Remaining front petal removed	Accepts, departs, returns, and feeds
3:01	Stamens removed	Accepts, departs, returns, and feeds
3:16	Spur now $\frac{3}{8}$ " by $\frac{1}{8}$ "	Feeds hesitatingly
3:25	Spur removed from glass	Refuses to feed; flies to another feeder with whole flower in it
	(Spur restored to glass)	
3:35	Spur same size as at 3:16	Accepts; drinks even as bill pushes spur around glass
3:40	Spur now $\frac{1}{4}$ " square	Accepts, pushing spur around as he feeds
3:51	Spur $\frac{1}{8}$ " square	Accepts; bird tries to keep bill on moving spur
4:01	Spur $\frac{1}{16}$ " square	Accepts, but bill misses moving spur
4:18	Spur removed from glass	Accepts, aiming bill at speck of pollen on side of glass
4:28	Pollen removed	Accepts, drinking directly from glass

feeding from a flower that moved as it did in the experiment, the bird was forced to make another set of adjustments—from a stationary source of food to a moving one; from a whole decoy to a speck of pollen on the side of the glass, as though all the syrup came from that speck; and finally, from the changing form of the decoy to the fixed form of the glass feeder itself.

Other birds subjected to similar experimental study transferred the association from decoy to glass without the intermediate steps indicated in table 2. When the decoy was summarily removed, they would pause before the undisguised glass, at first a little bewildered at the sudden change; then they would become excited and probe other flowers aimlessly; finally they would plunge their bills into the glass feeders. After that they would drink unhesitatingly.

Some individuals sampled the feeders without the benefit of a disguise, as did four immature Black-chins three to five months old. But in these cases the birds were apparently searching for water, not food. They mistook the sweet liquid for water. I have seen young hummingbirds try various sources for water: the nozzle of a hose, a leaking faucet, the lid of a typewriter ribbon box. More often undisguised feeders are left unsampled, so that those who sampled them were evidently induced to do so by thirst.

Whatever may be the original response to flowers, the fact remains that response to different forms may be conditioned. At first the bird responds positively to the whole flower and is indifferent to the undisguised feeder, the latter providing an unfamiliar set of stimuli. Following contact with the sweets in the feeder and after a number of trials (though usually only one trial is necessary) the bird associates taste of sweets with the form of the feeder so that afterwards the sight of the feeder alone elicits the feeding response. The conditioned response to form of feeder has transfer value; that is, after acquisition of this response, the bird does not hesitate to sample all sorts of objects that

resemble in shape the feeder, such as an empty flower vase, a milk bottle, or even my empty pipe bowl.

Hummingbirds recognize food sources long after their discovery. Thus, after feeding repeatedly from receptacles of honey or syrup over a period of months, presumably the same individuals would recognize them upon returning to the yard six to nine months later. It is conceivable that hummingbirds are not only capable of recognizing flowers from which they had been feeding from year to year but also capable of adding new forms to their list through learning.

Association of taste with position of food source.—The experiment to be described not only shows the mode by which taste is associated with position of food source but also the rapidity with which the association is effected. The subject was an adult female Black-chinned Hummingbird who had been feeding regularly from syrup and honey glasses. At the time of this experiment no other hummingbird was visiting the premises. The experiment was conducted on the front porch of a house with the experimenter seated behind the window of a room adjoining the porch.

The subject was given a choice of three glasses placed on stands of various heights so as to facilitate the association of the contents of each glass with the height and position of the stand. The stand occupied by the glass containing plain water was 37 inches high; the middle stand occupied by the glass containing weak syrup was 33 inches high; and the stand occupied by the glass containing strong syrup was 30 inches high. The weak syrup contained $\frac{1}{2}$ teaspoonful of sugar in one ounce of solution, not acceptable to the bird, and the strong syrup 2 teaspoonfuls of sugar in one ounce of water, acceptable to the bird. Learning was regarded as having taken place when the bird persistently visited the strong syrup to the exclusion of the other two. The bird's reaction and rate of learning is shown in table 3.

Table 3

Progress made by female adult Black-chin in learning to associate position of feeder with concentration of syrup

Trip	Time	Bird's reaction
1	4:07	Visits strong syrup and accepts
2	4:35	Visits weak syrup first and rejects; plain water second and rejects; strong syrup third and accepts
3	5:09	Visits strong syrup and accepts
4	6:05	Visits weak syrup first and rejects; strong syrup second and accepts
5	6:30	Visits plain water first and rejects; strong syrup second and accepts (Experiment resumed the following day)
6	8:15	Visits strong syrup first and accepts; plain water second and rejects
7	8:38	Visits strong syrup and accepts.
8	9:00	Same
9	9:21	Same
10	9:41	Same
11	10:01	Same
12	10:27	Visits strong syrup first and accepts; momentarily stops at weak syrup but does not sample it

The first two trips were largely of an exploratory nature. The bird discovered what the feeders held. Apparently, the bird's curiosity still persisted for the next four trips, for she continued to make random samplings. After the sixth trip learning registered and for the next five trips the association of the strong syrup with its position in the battery was definitely fixed. It is interesting to note that on the twelfth trip the bird

paused momentarily before the weak syrup, but aware of its weakness, flew off without sampling it. This is a genuine test of learning, for the bird inhibits its food response without actually contacting the unsatisfactory food. Of significance is the fact that though some fourteen hours had elapsed between the fifth and sixth trips, only one error was made.

The rate of learning can be hastened by introducing a distasteful substance. Table 4 shows the behavior when salt water is substituted for plain water. To disrupt the association formed in the previous experiment, the salt water was placed on the lowest stand, previously occupied by the strong syrup, and the strong syrup placed on the highest stand, previously occupied by plain water.

Table 4

Reactions of female adult Black-chin to substituted salt solution		
Trip	Time	Bird's reaction
1	10:58	Visits salt water first and rejects vigorously; visits strong syrup and accepts
2	11:26	Visits strong syrup and accepts
3	11:44	Pauses momentarily before salt solution upon arrival; visits strong syrup and accepts
4	12:17	Visits strong syrup and accepts
5	12:55	Same
6	1:21	Same
7	1:50	Same
8	2:31	Visits salt solution first and takes a short sip but rejects vigorously; visits strong syrup and accepts
9	3:10	Visits strong syrup and accepts
10	3:51	Same
11	4:34	Same
12	5:09	Same
13	5:52	Same
14	6:17	Visits strong syrup first and accepts but upon leaving, momentarily pauses a foot away from salt solution

As compared with the previous experiment, learning registered after the first trip to the salt water. The only mistake made was on the eighth trip.

This pleasure-pain aspect of learning is universal among animals and the rate at which obnoxious or painful stimuli are avoided after contact is made does not vary greatly among different classes of vertebrates. The frog, according to Schaeffer (1911), when offered hairy caterpillars leaves them alone after ejecting the obnoxious insects four to seven times. Fish can master a similar lesson in short time, as Reighard's (1909) investigation of warning coloration demonstrates: When small fish of the genus *Atherina*, stained red and some made unpalatable with the tentacles of jellyfish, were fed to a colony of snappers, the snappers avoided the unpalatable ones after a few trials.

LEARNING THE PLACE

Foraging on wing over the landscape, the hummingbird is confronted with a maze of landmarks. But this expert marksman locates the object of its search with precision, be it a choice bed of larkspur, a lantana bush, honey-feeder, or even a single flower among many like it. Should the bird perchance discover a single flower containing more sweet food than is to be found in others like it, that flower will be singled out for special attention.

By means of a simple experiment let us observe the procedure by which the bird

locates an object or site once discovered. The subject was a female adult Black-chin, who had yet to taste honey from feeders that other hummingbirds had discovered weeks ago. The target was a yellow nasturtium bloom. After pinching off its spur, the experimenter inserted the flower into a vial of honey, leaving the corolla exposed. The vial, a reservoir of honey diluted with water, served as an artificial nectary. The disguised feeder was fastened to a stick which was concealed in a nasturtium plant whose foliage was arranged to leave no clue that might serve as a reference point once the decoy flower was discovered.

The bird arrived and, darting from flower to flower, accidentally came in contact with the decoy into whose corolla she thrust her bill. Surprised at finding so much honey in a single flower that resembled others she had been probing, she bounced back, paused before the decoy, and immediately lunged forward to take another drink. A half dozen sips followed in quick succession before the bird flew away.

Returning a half hour later, the bird flew straight to the decoy from which she took a long drink. If she searched for the flower while descending, her movements gave no indication of it. Twice she visited the flower and located it each time without apparent difficulty.

After the third trip the decoy flower was removed, leaving the vial and top of the stick exposed. A half hour later the bird arrived and flew directly to the site of the flower, but finding a strange vial in place of the flower paused a few seconds, then cautiously sampled it. A succession of short sips followed. Thereafter the bird visited the vial in routine manner, locating it accurately on each trip.

The vial was then placed on a white stand ten inches higher than the stick and two feet south of the original site. The stick was discarded. The white pedestal supporting the vial stood in sharp contrast against a background of green vegetation. When the bird arrived, she flew straight to the old site as though the vial were still there, but finding no feeder, became bewildered and excited. She searched for the vial, but either it escaped her attention or she failed to associate vial-on-stand-two-feet-away with the original vial-on-stick pattern. Frantically she probed a half dozen nasturtiums in the immediate vicinity of the stand, returned to the old site, and continued the search for the vial. A minute or two of futile exploration ended, the bird flew to a nearby fence, eight feet away, where she perched listlessly on a cross wire. A few seconds later she left.

Not certain how strongly the bird had been conditioned to the vial and fearing that she would give up further attempts to find the feeder if withheld too long, the experimenter returned it to the original site and attached it to the stick. On her next trip the bird flew straight to the old site and found the feeder.

Vial and stick were then moved one foot south of the old position, where the feeder was easily discovered, but finding it in a new position, the bird paused a few seconds before thrusting her bill into the honey. The vial was next placed on a white stand in place of the stick; it was discovered and the characteristic behavior of hesitation and bewilderment ensued before the bird decided to drink.

Thereafter vial and stand were gradually moved to various sites in the order shown in the accompanying sketch (fig. 2), and the bird discovered them at each new site in much the same manner in which the previous discoveries were made.

Starting with vial-on-stick at 1, the bird followed the feeder to 2 where she learned to associate it with the stand. Each new site was learned by exploration. At position 8 she learned to feed from the hand of the experimenter who was seated in a chair adjacent to the stand. When the experimenter, chair, and stand were removed and the bird

deprived of the feeder, she flew to site 8, though the closest landmark was the hedge fence ten feet from the site.

If a feeder was removed from a feeding site which she was in the habit of visiting, the bird would search the spot, then fly to other familiar sites where she sought the missing feeder. At first, with two to four sites learned, when the feeder was removed the bird would visit the sites in the order opposite to that in which they had been learned. Later, as the pattern acquired the full quota of nine sites, the bird would make no systematic search and short cuts were taken. Not only all the old sites were visited and re-visited but as the bird grew more and more excited, she would try any place that impulse prompted her.

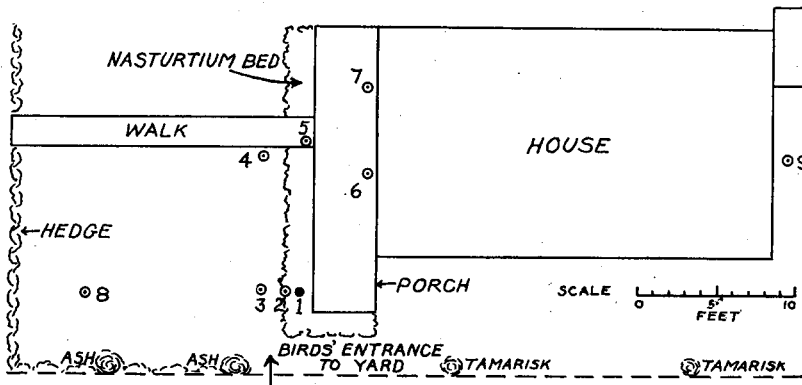


Fig. 2. Study area, showing order of location of feeders visited by an adult female Black-chin used as a subject in experiment on place learning. Distances between successive sites vary from 1 to 50 feet.

Of significance is the fact that the bird can locate accurately a site in the absence of the feeder or stand. The path to a site is taken quickly and with no apparent hesitation, save for a momentary pause preceding the actual search for the feeder. The bird has acquired a memory of old sites which she recognizes upon entering the yard.

After making one trip to an object, the bird retraces the path to it with seeming facility. If the bird must search for the object as she arrives in the yard, her flight does not indicate it, although the search may be so rapid that it can not be detected by the experimenter. It is much more rapid than the habits of orientation acquired by Noddy and Sooty terns that attempt to locate their nests when these are removed. Watson and Lashley's (1915) investigation of orientation in Noddy and Sooty terns nesting in a densely populated colony on Key West, Florida, led them to conclude that "Kinaesthetic-motor habits are formed with no such rapidity as to suggest that birds can retrace a path by memory of its direction and distances when these have been experienced only once."

Differences in rapidity of orientation between a hummer and a tern might be attributed, among other things, to differences in the learning situation. Nesting in a densely populated colony, a tern has to locate its nest among others similarly constructed and in close proximity to it, so that when the nest is removed a few feet from its original site, the tern finds its nest with difficulty. Still, the nest configuration facing the tern appears no more complex than the pattern of the flower bed in which a hummingbird singles out a flower similar in form and color to those surrounding it. Yet the hummer quickly locates that flower after the first trip. However, a hummer, like a tern, is thrown

into confusion when the position of its goal is changed. Then it must search until the goal is found, and the length of time spent in such exploration varies according to the distance the goal is moved from its original site.

Differences in the manner of locomotion may account for the difference in rate of fixing the path to a goal. A hummer explores the path and finds its way to the goal *wholly on its wings*; whereas a tern must explore partly by flight and partly by walking. Because it has an aerial view of the configuration all the way to the goal, a hummer can spot it with greater facility than can a tern, which, after alighting in the vicinity of its territorial preserve, must pick its way to the nest on foot, getting only a horizontal view of the path to it.

That an aerial perspective or what amounts to the same thing, an unobstructed view of the total configuration, facilitates perception of spatial relations has been demonstrated by experiments on apes solving simple problems of perception (Kohler, 1925). Such observations, of course, are more suggestive than conclusive and hence may be regarded only as a possible explanation of the situation in question.

The third explanation may be found in the hummer's adeptness at maneuvering in air. When the hummer is intent on visiting a source of favorite food, as a honey glass, it descends swiftly to the site of its objective and only momentarily does it hover before beginning to feed. The act preceding actual feeding is comparable to the tern's flight to the territorial preserve, after which the tern walks to its nest. Swiftens of flight, maneuverability, and ability to explore as it poises in mid-air appear to facilitate the hummer's perception of the goal configuration.

The comparative observations set forth indicate that for the study of orientation in hummingbirds, something finer than mere number of trips or trials as a measure of proficiency is needed; for in every case in which the source of food was visited only once, the second trip to it was made by the hummer without perceptible hesitation.

For the purpose of comparing place learning of hummingbirds with that of other animal forms, three methods of investigation are available. With winged insects and birds, a frequent procedure is one in which the configuration of the goal or the position of the goal itself is changed and the animal's reaction noted. Another procedure adapted for winged creatures is the investigation of homing flights, whereby the subjects are removed to a distant, alien locality and the speed with which they return to their nests, if they return at all, and their behavior are recorded. For animals adapted for terrestrial locomotion the most widely used learning device is the maze. The investigation of place learning for comparative purposes is thus seen to be complicated by the mode of locomotion of the learners, the nature of the goal sought, and the kind of learning device used.

PROBLEM-SOLVING

The desire to reach a source of food or a nest, or to preserve its freedom against possible confinement, motivates the animal's learning behavior. So long as these goals are attained, a state of well-being accompanies the learning activity; but should the path to the goal be blocked by an obstacle or barrier, the animal experiences a strong emotional state, the degree of emotion experienced depending on the extent to which the animal is thwarted in attempting to reach its goal. The obstacle creates (1) a problem which makes demands on the cerebral processes and (2) an emotional state whose function it is to reinforce those activities that are directed in pursuit of the goal. In the experiment to be described we propose to show that the mental and instinctive-emotional processes in a problematic situation are sometimes incompatible and hence inhibit the fulfillment of the learning task.

A feeder was placed in a box 18" \times 12" \times 12" (see fig. 3), open on top, with an open window 6" \times 4" on one side to permit the subject's entrance. The box was placed on a small table at the same place on the porch where previously the subjects had been feeding. On each side of the box was placed a feeder mounted on a stand. The purpose of these feeding stands was to restrict the experimental area to the porch and to attract to the box the subjects, B1 and B2, two adult female Black-chinned Hummingbirds.

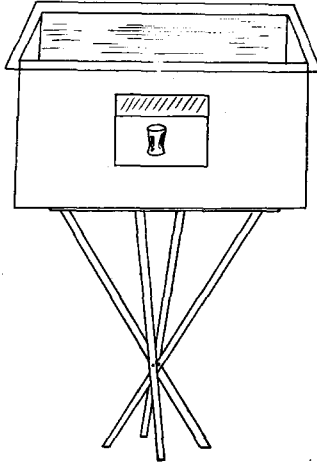


Fig. 3. Problem box used in experiments with hummingbirds.

When B1 arrived, she drank from one of the feeders and, as was expected, examined the box. B2 did likewise. The feeders were then taken from the stands and one of them was placed in the box. This preliminary phase disposed of, the experiment proper was begun.

To illustrate the inhibiting factors in the learning process, the column on the right in table 5 records the instinctive-emotional counterpart of the learning activities given in the column at the left. The impulse to feed is not of equal intensity at all times but increases or decreases according to the internal state of the bird. Increasing intensity is designated by "feeding-excitation," which means that the food-getting instinct dominates the birds. "Defense-excitation" indicates that response to confinement is dominant. Both the food-getting and defense instincts have their antagonistic correlates in "feeding-inhibition" and "defense-inhibition," respectively. The instinct of defense is manifested as a response to actual or potential confinement, as when the bird flies out of the box without drinking or when it cuts short its drink from the glass in the box.

So far we can hardly call this situation problematic; it entails learning of the most primitive, direct sort. Once the birds catch sight of the feeder in the box, the path to it can easily be grasped, whether the birds discover the feeder by spotting it from atop the box or at the side through the window. Since the top covers a larger area, both birds perceived the path to the feeder from atop the box. This discovery was made quickly, after random, exploratory movements about the porch. B1 found it in four trips to the porch, in exactly three minutes, and B2 on her second trip, in one minute.

More significant than the matter of solving this simple problem in this phase of our investigation is the role of instincts and their emotional correlates in the learning process. In the first place, the excess energy released by the emotional state is intended

Table 5
Learning behavior of two female adult Black-chins attempting to locate feeder in box

Time of Arrival	Learning behavior	Instinctive-emotional state
2:32	B1 arrives and searches for feeder, flying all over porch.	Feeding-excitation
	Departs without finding feeder in box.	Feeding-inhibition
2:33	B1 undertakes another search as above.	Feeding-excitation
	Departs without finding feeder.	Feeding-inhibition
2:34	B1 undertakes another search as above.	Feeding-excitation
	Departs without finding feeder.	Feeding-inhibition
2:35	B1 discovers feeder in box and looks at it suspiciously from atop the box.	Feeding-inhibition, defense-excitation
	Swings before box in pendulum fashion.	Feeding-excitation, defense-excitation
	Departs without entering box.	Feeding-inhibition, defense-excitation
2:36	B1 flies to box and inspects it.	Feeding-excitation, defense-inhibition
	Enters via top.	Feeding-excitation, defense-inhibition
	Refuses to drink; leaves box.	Feeding-inhibition, defense-excitation
	Repeats above acts three times.	Preceding two states repeated three times
2:41	B1 enters box via top, takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out of box.	Feeding-inhibition, defense-excitation
	Enters and takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out.	Feeding-inhibition, defense-excitation
	Enters and takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out.	Feeding-inhibition, defense-excitation
	Enters and takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out.	Feeding-inhibition, defense-excitation
2:48	B1 flies to box, hovers before it.	Feeding-inhibition, defense-excitation
	Flies to experimenter, seated ten feet from box, and hovers about his face, squeaking.	Feeding-inhibition
	Returns to box and enters via top.	Feeding-excitation, defense-inhibition
	Refuses to drink, flies out instantly.	Feeding-inhibition, defense-excitation
	Repeats above acts of entering box and flying out instantly without taking drink six times.	Preceding two states repeated six times
	Enters box and takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out instantly.	Feeding-inhibition, defense-excitation
	Inspects exterior of box.	Feeding-inhibition
	Enters box via top, takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out and inspects exterior of box.	Feeding-inhibition, defense-excitation
	Enters via top, takes quick sip.	Feeding-excitation, defense-inhibition
	Flies out and surveys surroundings.	Feeding-inhibition
2:50	B1 arrives and examines the interior of box, inspects table on which box sits, and looks underneath table. Then inspects stand at the side of the box.	
	Flies away without feeding.	Feeding-inhibition, defense-excitation
2:57	B1 returns and enters box, taking quick sip.	Feeding-excitation, defense-inhibition
	Flies out.	Feeding-inhibition, defense-excitation
	Repeats above acts three times.	Preceding two states repeated three times
2:58	B2 flies to vicinity of box but fails to see feeder in box.	
	Flies to experimenter and squeaks.	Feeding-excitation
	Departs without finding feeder.	Feeding-excitation
		Feeding-inhibition
2:59	B2 returns and flies to experimenter, squeaking.	Feeding-excitation
	Flies to box and discovers feeder, enters box via top, taking quick sip.	Feeding-excitation, defense-inhibition

for the benefit of the contending instincts—one driving the birds to feed, the other impelling them to stay clear of the menacing box. The clash of these instincts is evident in the rhythmical excitatory and inhibitory processes in which nervous and motor energy is expended. The obstacle, namely the box, calls into action the mental processes, but the instinct of defense persists in shunting it out of action intermittently, and not until the feeding instinct grows stronger and the birds become somewhat accustomed to the experimental situation do the mental processes gain sufficient control to direct the birds to the feeder. In time the birds reach their goal if but to take quick, cautious sips of honey.



Fig. 4. Adult female Black-chinned Hummingbird extracting nectar from blossoms of honeysuckle; this hummer designated B1 in experiment dealing with problem-solving.

There can be no doubt that perception of the path to the feeder, insight, intelligence, or whatever we call the process, is not wanting in birds. What keeps the mental processes from functioning smoothly is the difficulty of conquering fear. What is there about this open box that arouses fear in the birds? The way of escape is simple and perceivable to the most elementary mind. Yet the birds hesitate to enter and are dissatisfied with the easy avenue of escape open to them. They must critically examine top, bottom, and sides of the box. They swing in pendulum fashion before it. Under the stress of emotion they make useless, diffuse movements, all of which contribute nothing toward the attainment of their goal, save perhaps in the most remote way. What is the meaning of all this? From observations such as these it is evident that not the least important factor in learning is control of the instincts and deep-seated desires; perception of the path to the goal is not enough.

Up to this point neither bird had made any attempt to reach the feeder via the window. By placing a glass pane over the top of the box, we created a more complex problem than the preceding one. There was then only one path available to the feeder and this path could be perceived in two ways. The direct method was the simplest and to carry this through the birds needed only to come up to the window, catch sight of the feeder, and enter. This problem was the same as the preceding one. Another method would require that the birds, upon hovering atop the box, perceive the indirect or "roundabout" path to the feeder. A person would reason thus: "From atop the box I see the feeder six inches from the window. By going to the side I can enter through the window and thus reach the feeder." But this problem is difficult for the hummer, as table 6 discloses.

Table 6

Time of Arrival	Birds' behavior
3:14	B1 encounters B2 on porch and drives her off.
3:15	B1 makes no attempt to enter box; instead flies to the experimenter and hovers about his head.
3:17	B2 arrives and flies to box, tries to enter but is stopped by glass pane. Looks at box in bewilderment.
3:18	Tries again to enter box but is stopped by glass pane.
3:20	B1 makes no attempt to enter box; fails to see the feeder through the open window.
3:21	Tries to enter box via top but is stopped by glass pane. Flies to experimenter and squeaks.
3:24	B1 flies all over porch, investigating prospective sites for trace of feeder. Gives up search and flies to flowers nearby, probing a few blooms. Then flies to box, tries to enter via top. She gets very excited as she beats her body against the glass pane in the effort to reach the feeder.
3:27	Tries to get into box via top. Then flies to experimenter and squeaks.
3:28	Same behavior as above.
3:30	Same.
3:31	Same.

Both birds failed to solve this simple problem. B1 failed to see the connection in eight trips and B2 in two. Instead of going to the window, they beat their bodies against the glass pane. Before the pane was placed over the top of the box, they would enter with fear and sip honey nervously. But when entrance via the top was barred by the pane, they frantically strove to get into the box at all costs. The strong defense instinct, which had played a prominent role in inhibiting learning at first, was completely absent. Even stronger than before was the emotional state. B1, who had hardly noticed the experimenter up to this point, now flew to him greatly excited, squeaking loudly, after which she returned to the box and beat her body futilely against the glass pane. B2, on the other hand, was less demonstrative, but she, too, bumped her body against the glass in the attempt to make a direct entrance. But, strangely enough, she was not as emotionally upset now as she had been when faced with an open top.

Apparently, the birds' failure to solve this simple problem of entering must be attributed to one or both of these factors: (1) the problem was too difficult, (2) the emotional state blinded the mental processes, preventing effective learning.

The problem was simplified by moving the feeder up to the window, so that the birds could hardly miss sight of the feeder at the window. The bird needed only to fly accidentally to the window and catch sight of the feeder, part of the rim of which protruded from the window.

B1 arrived at 3:42 and instead of catching sight of the feeder in its new position, looked into the box from the top. Then she flew to the experimenter, squeaking. A minute later, at 3:43, she returned, looked at the feeder from atop the box, then flew to the window where she quickly discovered the feeder and took a long drink. The sound of her wings resounding in the box momentarily frightened her.

B1 solved the problem in the direct manner, but B2's behavior indicates that she found the solution in a "roundabout" way. She looked at the feeder from atop the box as she struck the pane and in a moment was at the side facing the window and the feeder, where she took a long drink.

The feeder was moved away from the ledge of the window back to its original position. We now have the same configuration as existed in the preceding situation, but this time both birds had been conditioned to the window, and hence we should expect that on their next trip they would fly directly to the window.

When B1 arrived at 3:44, she paused before the window, finally mustering enough courage to enter. Instead of drinking honey when she got into the box, however, the bird became excited and pushed up against the glass pane. The experimenter lifted the pane one foot above the box, but still the bird pushed against it frantically. Not until the pane was moved to one side did the bewildered and frightened bird escape.

B2 arrived at 4:27, flew to the window of the box, hesitated as did B1, then entered. She, too, became panic-stricken and tried to escape by pushing against the glass pane. The experimenter reached into the box; the bird's wings stopped beating at the same time—"playing possum." The helpless bird allowed herself to be grasped. Once out of the box, the bird struggled frantically to escape. Upon her release she at once flew to a high perch on an ash tree where she preened her feathers. B2 refused to approach the box thereafter.

In order to ascertain to what extent the birds profited from the fearful experiences of the preceding day, the experimenter moved the problem box out on the lawn, leaving the glass pane and feeder in the box intact. B2 did not enter, but B1 overcame her timidity and entered the box via the window on three different occasions, leaving the same way she entered it; but once in the box she refused to touch the honey.

How can we account for this successful exit, an exit she had failed to make the day before? In the preceding experiment B1 became panic-stricken the moment she entered the box, whereas the next day she saw the way of escape instantly upon entering. We have here a learning behavior that is comparable to that exhibited by B2 when she had quickly learned to avoid the salt solution after a rest interval of fourteen hours. B1's sudden solution of the simple entrance and exit might be attributed (1) to sudden *insight* into the problem, (2) to getting the solution before fear had a chance to nullify her perception, (3) to practice and rest, and (4) to slight change in the configuration of the problematic situation through placing the box on the lawn and giving the bird a different perspective.

It would seem that the instinct of defense and its emotional correlate, fear, was so strong the day before that the bird became flustered. On the instinctive side we observed acts of interest and significance. First, the instinctive tendency is to take the line of least resistance to a goal which may result in direct learning. Moreover, the fact that escape takes the direction of upward flight, together with the presence of fear, blinded the bird's perception of the path of escape. It is probable that the diminished fear of the next day made possible a clearer perception of the means of escape. Then, too, the bird's inexperience with glass and its inability to recognize it had contributed to the bird's failure the day before. Had there been an opaque partition on top of

the box, the flight of escape would not have been vertical but probably horizontal. We noticed that the birds tried repeatedly to get into the box by bumping onto the pane, while in attempting to get out they bumped upward against the pane. B2's death feint shows that a sense of helplessness inhibits all movements, resulting in the cessation of learning activity.

SUMMARY

While adaptation and specialization of feeding mechanisms determine the direction feeding behavior will take, the feeding habits of hummingbirds are modified by experience. The feeding mechanism is not fully developed in young hummingbirds until at least two weeks after they leave the nest. The earliest responses related to food-getting are probing with bill and tongue, first while perched and later while hovering. The recognition of flowers as sources of food appears after the young have acquired sufficient strength for sustained flight. The hummingbird's acceptance or rejection of flowers as sources of food is governed by experience.

The hummingbird exhibits no special sense for detecting nutriment in a food source at a distance but perceives the quality and quantity of nutriment after contact. It can discriminate the color, taste, and form of flowers and through association learn to recognize and locate them.

Hummingbirds learn to associate sites with specific sources of food and return to the site though the food source be removed. Apparently but one visit to a food source is necessary to establish an associational pattern.

Two female hummingbirds learned to visit a feeder in an open-top box with a side entrance. When a glass cover was placed over the top, both birds failed to solve the problem of reaching the food through the open side entrance after attempts to reach it from the top were thwarted. When the feeder was lifted to view from the side entrance, both birds found it. In both instances, however, feeding was inhibited once the bird entered the box by efforts to escape inclosure.

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