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1982

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Cole, Susan; Hainsworth, F. Reed; Kamil, Alan; Mercier, Terre; and Wolf, Larry L., "Spatial Learning as an Adaptation in Hummingbirds" (1982). *Avian Cognition Papers*. 13.  
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# Spatial Learning as an Adaptation in Hummingbirds

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## Abstract

An ecological approach based on food distribution suggests that hummingbirds should more easily learn to visit a flower in a new location than to learn to return to a flower in a position just visited, for a food reward. Experimental results support this hypothesis as well as the general view that differences in learning within and among species represent adaptations.

Learning is a mechanism by which animals modify their behavior to respond more efficiently to their environments. Like other adaptations, learning has evolved as the result of the interactions that occur between animals and their environments. From this perspective, the characteristics of learning should vary because the ecological and social conditions in which animals learn are varied. With sufficient information on the ecology of animals it should be possible to make a priori predictions about learning. We tested predictions about the ability of hummingbirds to learn different spatial patterns of food availability from individual flowers.

Hummingbirds obtain most of their energy from floral nectar, present in individual flowers in small, slowly renewed amounts (1). The small size of hummingbirds and their hovering flight while feeding make them dependent on short-term supplies of energy, requiring visits to many flowers (2). Their foraging efficiency depends on the difference between the rates of gain and expenditure of energy. Several experiments indicate that animals often approach maximum rates of net energy gain when they feed (3). Although learning may

enhance energy returns, only a few experiments have examined the impact of learning (4).

In their natural environment, hummingbirds returning to a recently emptied flower would have a lower rate of net energy gain than birds going to a flower that contains nectar. We hypothesized that a hummingbird reinforced for visiting a flower location should more easily learn to choose a different location during a subsequent foraging effort than learn to return to the same location.

We studied four female *Archilochus alexandri* (black-chinned hummingbird; 3 to 4 g), two male *Eugenes fulgens* (Rivoli's hummingbird; 8 to 10 g), and two male *Lampornis clemenciae* (blue-throated hummingbird; 8 to 9 g) captured wild in southeastern Arizona (5). They were maintained individually in 1-m<sup>3</sup> cages in an aviary with temperature controlled at 24° ± 2°C and with a photoperiod of 14 hours of light and 10 hours of darkness. The maintenance food was *Drosophila* and a 0.5M sucrose solution with vitamins, minerals, and amino acids (6). The birds maintained in this manner have remained healthy for more than a year and have completed at least one molt.

**Table 1.** Trials and errors to criterion and first-day performance of each hummingbird during shift and stay learning; S.E., standard error.

Hummingbird	Shift learning				Stay learning			
	Trials to criterion	Errors to criterion	Pct correct Day 1	Learning rate to criterion (pct/day)	Trials to criterion	Errors to criterion	Pct correct Day 1	Learning rate to criterion (pct/day)
<b>Stay first</b>								
<i>Archilochus</i> 1	160	82	20	6.7	640	239	40	1.2
<i>Archilochus</i> 2	180	96	25	6.5	620	238	35	1.4
<i>Eugenes</i> 1	96	42	38	11.6	282	130	29	4.9
<i>Lampornis</i> 1	144	43	50	5.4	624	273	50	1.5
Mean + S.E.	145 ± 17.9	65.7 ± 13.7	33.2 ± 6.8	7.6 ± 1.4	441.5 ± 104.5	220 ± 31.0	38.5 ± 4.4	2.2 ± 0.9
<b>Shift first</b>								
<i>Archilochus</i> 3	200	48	60	1.8	1240	506	40	0.9
<i>Archilochus</i> 4	80	25	70	2.0	360	138	30	2.6
<i>Eugenes</i> 2	24	5	79	4.0	360	149	25	4.5
<i>Lampornis</i> 2	96	24	67	5.2	790*	341*	35	2.8
Mean + S.E.	100 ± 36.7	25.5 ± 8.8	69.0 ± 3.9	3.2 ± 0.8	687.5 ± 210.2	283.5 ± 87.6	32.5 ± 3.2	2.7 ± 0.7

\* Did not reach criterion; this represents a minimum estimate.

Birds were deprived of food for 1/2 hour before the testing period each day. They were placed in a 1-m<sup>3</sup> cage with a perch. A 0.5M sucrose solution was provided in "flowers" made from yellow plastic syringe needles plugged with clay and fitted with a plastic corolla that extended 12 mm from the top of the syringe needle cap (7). Flowers could be presented at two locations, 12.5 cm to the right or left of the middle of a Styrofoam strip placed against the side of the cage opposite to the perched bird.

During the initial (information) stage of each trial, a single flower containing food was presented. The position of this flower varied randomly from trial to trial, except that the position was never the same for more than three consecutive trials. After the bird was fed, the strip was removed and the second (choice) stage of the trial was begun within 10 to 12 seconds. Two flowers were presented, one containing food and the other empty. The hummingbird was allowed to visit only one flower. A visit was defined as a bird inserting its bill into the corolla. If a correct response was made, the bird consumed the food, and the flowers were removed. If an incorrect response was made, the flowers were withdrawn immediately. In either case, the next trial was begun 3 minutes later. The *Eugenes* and *Lampornis* were given 24 trials per day and the *Archilochus* were given 20 trials per day for 5 days per week.

Two problems were presented. "Stay learning" required a return to the position that had been visited during the information stage of the trial in order to obtain a reward during the choice stage. "Shift learning" required going to the opposite position to obtain food. All birds were trained on both tasks. Four birds first

learned stay and then shift, while the other four birds learned the tasks in reverse order (Table 1). Training on each task continued until at least 80 percent of the choices were correct each day for three consecutive days.

Every hummingbird learned the shift task in a shorter time than it learned the stay task, regardless of the order of presentation of the two tasks (Table 1). The slowest shift learning by any bird (*Archilochus* 2, 180 trials and 96 errors) was much more rapid than the fastest stay learning by any bird (*Eugenes* 1, 282 trials and 130 errors). These differences between stay and shift learning were statistically significant for both groups (Wilcoxon matched pairs test,  $T=0$ ,  $P < .01$ ).

Two factors contributed to the more rapid achievement of criterion during shift learning: (i) different levels of shift and stay performance at the start of training and (ii) different rates of improvement on the two tasks. That the hummingbirds had a preexperimental bias toward shift behavior was evident during the first day of the experiment. They shifted about two times as often as they stayed, regardless of the task. Thus the birds being trained to shift were more often correct than those being trained to stay, on the first trial day (Table 1; Mann-Whitney  $U=0$ ;  $P < .05$ ).

An initial bias toward shifting, however, does not in itself account for the results. The average daily improvement (percentage improvement per day; Table 1) for each bird was significantly higher during shift learning than during stay learning ( $T=3$ ,  $P < .05$ ). This higher rate of shift learning also can be seen by comparing stay and shift learning when each was the second task to be learned. The birds showed virtually

identical percentages of correct responses during the first day ( $U=7$ ;  $P>.40$ ) because of previous training, but the shift task still was learned more rapidly ( $U=0$ ;  $P<.05$ ).

The differences in learning rates were notable in view of the similarity in the structure of stay and shift tasks. In each case, the only cue for location of nectar was the location of the flower that had just been visited, and in each case, the correct response was a visit to a specific location. The only difference between the tasks was the rule used to relate the correct location to the remembered location. Therefore, the reason for the differences in learning rates must be sought in something other than the structure of the tasks. Similar learning occurs in rats using position cues (9), and the ease of shift learning is not predicted by the traditional views of the effects of reinforcement on behavior (10).

These results support the hypothesis that spatial learning in hummingbirds is related to the spatial distribution of resources influencing rates of net energy gain. The preexperimental bias toward shift behavior of these wild-caught birds may have been innate or may have reflected their earlier field experiences. But the differences in learning rates, especially during the second stage of the experiment, are unlikely to represent these kinds of effects. It is possible that an evolved tendency for hummingbirds to shift locations of flower visits is manifested in starting performance as well as in differential rates of learning. For non-spatial cues, such as colors, sounds, and shapes, stay learning should be more rapid than shift learning. This difference may be due to the nature of position as a cue, for each position in space is unique.

Differences between and within species in the ease of shift and stay learning may depend on the influence of the spatial and temporal scale of resource depletion after feeding. Shift learning should occur whenever the positions are divided so finely that visits always produce depletion; stay learning should occur whenever visits do not result in appreciable resource depletion. In hummingbirds, for example, stay learning may occur more easily at patches of inflorescences. Temporal scales may also be important for resources that are renewed, since the rate of renewal should determine the value of a site for future visits.

An ecological approach to learning, based on an analysis of the problems animals face in their natural environments, can generate useful predictions about differences in learning between and within species. This is in contrast to the recent approach called biological

“constraints” on learning (11), which requires the analysis of apparent anomalies in arbitrary learning situations. Our results suggest that the ecology of food resource distribution in space and time generates important evolutionary influences on learning.

#### References and Notes

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5. The Department of Interior Fish and Wildlife Service, the Arizona Department of Fish and Game, and the New York State Department of Conservation provided the necessary permits.
6. Nutritional components were provided by K.-L. Schuchmann [see K.-L. Schuchmann, *Kolibris: Haltung, und Pflege* (Biotropic Verlag, Frankfurt, 1979)].
7. The *Archilochus* obtained 30  $\mu$ l per rewarded flower while the *Lampornis* and *Eugenes* obtained 20  $\mu$ l per flower. These amounts are much less than the average meal size for these birds so several trials could be conducted in a short time.
8. The rate of improvement in shift learning was much greater when the shift learning followed stay learning than when the shift learning came first. This may represent a ceiling effect, since those birds who learned to shift first and showed lower rates of improvement began training at relatively high levels of shift behavior. Alternatively, this difference could represent some more basic difference in the learning process.
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12. Supported by grants from the National Science Foundation and the Syracuse University Undergraduate Honors Program. We also acknowledge the Department of the Interior Fish and Wildlife Service and the Arizona Department of Fish and Game for permits. We thank C. L. Gass, T. Goldsmith, B. Heinrich, J. Krebs, S. E. G. Lea, W. Roberts, and S. Shettleworth for their comments on an earlier version of this report.