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## SENSE OF SMELL IN THE BLACK-CHINNED HUMMINGBIRD

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The sense of smell in most birds is considered to be relatively unimportant, and with a few exceptions, it has been little studied. In an extensive anatomical survey of 151 species in 23 orders, Bang and Cobb (1968) and Bang (1971) measured the relative diameters of the olfactory bulb and ipsilateral hemisphere, finding a 12-fold variation in the ratio of these dimensions. Behavioral studies on Rock Doves (*Columba livia*; Michelsen 1959, Henton et al. 1966, Shumake et al. 1969, Oley et al. 1975, Keeton 1979) as well as on the Turkey Vulture (*Cathartes aura*; Stager 1964), the Brown Kiwi (*Apteryx australis*; Wenzel 1971a), and various procellariiforms (Grubb 1979, Hutchison and Wenzel 1980) indicate a sense of smell in these species. Electrical activity has been recorded in the olfactory system of numerous birds, including species with a very small bulb/hemisphere ratio (see Wenzel 1971b, 1973 for reviews).

We report here behavioral experiments which indicate that the Black-chinned Hummingbird (*Archilochus alexandri*) has a functional olfactory apparatus. Although hummingbirds feed from flowers, a general characteristic of the hummingbird-pollinated flowers, particularly of western North America, is their relative absence of fragrance. This leads to the inference that hummingbirds do not perceive odors (Grant and Grant 1968). We are unaware, however, of any previous experimental efforts to demonstrate a sense of smell in hummingbirds.

### METHODS

Our experiments were done in conjunction with more extensive studies of color discrimination by hummingbirds, and were conducted at the Southwestern Research Station of the American Museum of Natural History in the Chiricahua Mountains of southeastern Arizona during late May, 1979. Four feeders about 4 m apart were strung on a line over open ground at a height of about 0.7 m. Each feeder consisted of a 125-ml plastic wash bottle, with the conical tip to its spout removed, suspended upside down in a cradle constructed from a wire coat hanger. The birds drank from the feeders while hovering in front of them. Two of the feeders were filled with a 30% solution of sucrose; the other two with 3% saline, which, like water, the birds find mildly aversive. Sugar bottles alternated with water bottles on the line, and, as described below, the positions were exchanged at regular intervals to prevent learning of position. The same bottles were used for all three experiments described, and the fluid levels were kept approximately equal.

A small glass vial with a cotton plug and a short strip of white paper towel for a wick was secured with rubber bands to the vertical part of the stem of each bottle. Each vial contained about 3 ml of benzyl benzoate, a solvent frequently used for organic odorants in psychophysical experiments on the olfactory system. Two of the vials contained in addition a few drops of ethyl butyrate, to whose odor—suggestive of “juicy fruit” chewing gum—the birds were trained (see below). The line of feeders was kept at right angles to the breeze, and oriented so that the birds fed from the upwind side.

An observer sat to the side of the feeding line, viewing the feeders through binoculars or a spotting scope, and counting as visits only those approaches in which a bird inserted its bill or tongue into the orifice of a feeder. The birds would frequently sample more than one feeder before leaving the immediate area; consequently, during a test period we tabulated only the initial visit that a bird made on arrival. Further details on scoring visits can be found in Goldsmith and Goldsmith (1979).

During both training and testing, the positions of the scented and unscented feeders were interchanged after every 10–25 visits to the array. More extensive tests with the feeders used in visual discrimination experiments at a site less than 100 m away showed that for the size of the population of birds in the area, this was sufficiently frequent to prevent the birds from learning the positions of the sucrose bottles (Goldsmith and Goldsmith 1979, Goldsmith 1980, Goldsmith et al. 1981).

### RESULTS

In addition to Black-chinned Hummingbirds, Blue-throated (*Lampornis clemenciae*) and Rivoli's (*Eugenes fulgens*) hummingbirds also came to the feeders, but the former was the most frequent visitor, and we report results only for this species.

In the first experiment, the birds were trained to associate the odor of ethyl butyrate with sugar solution, while the bottles with saline solution had no fragrance. Training started the morning of day 1 and the schedule of reinforcement continued for two and one-half days. Compared with color discrimination, the birds learned this task slowly and imperfectly. The results are shown in Table 1. Out of 140 consecutive visits tabulated at the end of the second and beginning of the third days, 60% were correct, but a  $\chi^2$  test indicates this is a significant departure from chance. By contrast, birds of this species can master almost any visual wavelength discrimination we have set them with greater accuracy and in about one-third the time (Goldsmith and Goldsmith 1979).

The second experiment was a control, designed to establish whether the birds were detecting the sugar bottles by some cue other than the odor of ethyl butyrate. Immediately following completion of the first experiment, the odor was placed at all four bottles and 100 visits were scored. During this test period, the positions of the sucrose and saline bottles were alternated at regular intervals, as described above. The results are shown in the second row of Table 1. With the fragrance at all four bottles, discrimination fell to chance, indicating that the small effect observed in the first experiment was a learned association of the odor with the food bottles.

A third experiment was undertaken on the following day, in which the odorant was placed at the saline bottles, with only solvent in the vials on the sugar bottles. Training

TABLE 1. Selection of sucrose solution by Black-chinned Hummingbirds.

Experiment	Cue	Fraction correct	n	$\chi^2$	P
1	+	0.60	140	5.6	0.018
2	0	0.51	100	0.04	0.84
3	-	0.68	100	12.96	$\ll 0.01$

+ : ethyl butyrate odor associated with sucrose solution; no odorant at salt solution.

0 : control; after training with + reinforcement, ethyl butyrate odor was placed at both sucrose and saline bottles.

- : ethyl butyrate odor associated with salt solution; no odorant at sucrose solution.

began in the morning; counting started in the late afternoon and continued the next morning. The results are shown in the bottom row of Table 1. With this pattern of reinforcement, the birds' performance climbed to nearly 70% correct, and the departure from chance was highly significant.

Bang and Cobb (1968) and Bang (1971) tabulated the relative lengths of the olfactory bulb and hemisphere for a large number of species of birds, but they reported no values for hummingbirds. We have therefore made corresponding measurements on a preserved specimen of a male Ruby-throated Hummingbird (*Archilochus colubris*) in the collection of the Peabody Museum of Yale University. The skin was peeled from the head, which was then placed in 2% nitric acid for a day to decalcify the skull. The dorsal surface of the brain was then exposed and measured with a binocular dissecting microscope and an ocular micrometer. The olfactory bulbs are unfused in this species and were about 0.81 mm long and 0.57 mm wide. The olfactory nerves were clearly evident and about 80  $\mu$ m in diameter. The longest dimension of the hemispheres was about 5.8 mm, giving a bulb/hemisphere ratio of 14%.

#### DISCUSSION

These experiments show that Black-chinned Hummingbirds have a functional sense of smell, yet they raise more questions than we have been able to address. The difficulty that the birds exhibited in learning a positive correlation of odor with food does nothing to shake the belief that vision is much more important than olfaction in the foraging behavior of hummingbirds. It is risky, moreover, to draw sweeping conclusions on the basis of experiments involving only a single odorant. Similarly, one might be tempted to read some ecological significance into the observation that a negative association of food with odor seemed to be more easily effected than a positive association. The birds could simply have become more familiar with the rules of the game by the time experiment 3 was done (although our experience with training the birds to make visual discriminations does not lead us to believe that this explanation is necessarily correct), or the results could have been determined by the specific odorant used. Clearly, more work will be necessary to establish the role of olfaction in the normal lives of hummingbirds.

The bulb/hemisphere index of 14% is modest compared with a mean value of 29% for 10 species of procellariiforms (which use olfactory cues in feeding) and is somewhat smaller than the mean value of 20% found for Rock Doves or 19% observed in several species of swifts. On the other hand, this index is several times larger than those for many (but not all) passerines that have been examined (Bang and Cobb 1968). By this gross anatomical criterion, therefore, *Archilochus* compared with other birds has only a moderate olfactory system.

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