McArthur, P. D. 1982. Mechanisms and development of parent-young vocal recognition in the Pinyon Jay (*Gymnorhinus cyanocephalus*). Anim. Behav. 30:62–74.

Department of Biological Sciences, North Arizona University, Flagstaff, Arizona 86011. Received 21 January 1985. Final acceptance 15 July 1985.

The Condor 87:561–562

SAGE THRASHERS REJECT COWBIRD EGGS

TERRELL RICH

AND

STEPHEN I. ROTHSTEIN

Actual and potential hosts of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) can be classified as either rejecters or accepters of cowbird eggs (Rothstein 1975, 1982a, b). Few North American species show intermediate responses (Rothstein 1982a). Rothstein (1982b) reasoned that once the rejection behavior appears in a species, it has such a high adaptive value that it is rapidly fixed. Whatever the cause, this dichotomy between accepters and rejecters makes it possible to determine the response of a given species by experimentally manipulating the contents of relatively few nests.

It is desirable to continue accumulating evidence on the responses to brood parasitism of untested species because no absolute criteria that explain why some species are rejecters and others accepters have yet been identified (Rothstein 1975). Although Rothstein (1975) failed to find a strong relationship between taxonomy and response to non-mimetic parasitic eggs, knowledge of the host response in all members of a family would be useful because many variables related to morphology, behavior, and evolutionary history would be somewhat controlled.

The Mimidae have several features that make the family a good group for study of response to brood parasitism. In particular, they have at least four of the six characteristics suggested by Rothstein (1975) as contributing to the formation of rejection behavior. Their eggs are unlike cowbird eggs, their beak is large, their nest is large and easily found, and they practice good nest sanitation (Bent 1948). Yet, three North American mimids accept eggs of the Brown-headed Cowbird: Northern Mockingbird (*Mimus polyglottos*; Rothstein 1975), Le Conte's Thrasher (*Toxostoma lecontei*), and California Thrasher (*T. redivivum*; Rothstein, pers. observ.). Among North American mimids, three species eject cowbird eggs from their nests: Gray Catbird (*Dumetella carolinensis*), Brown Thrasher (*T. rufum*; Rothstein 1975, 1982a), and Crissal Thrasher (*T. dorsale*; Finch 1982). A neotropical mimid, the Chalk-browed Mockingbird (*Mimus saturninus*), is also known to eject parasitic eggs (Mason 1980, Fraga 1982).

The Sage Thrasher (*Oreoscoptes montanus*) may have accepted a cowbird egg in the only known case of parasitism (Friedmann 1963), but most of the evidence suggests that this species may be a rejecter. Rich (1978) found no cowbird eggs in 21 Sage Thrasher nests in an area frequented by cowbirds, where at least two other sympatric species were parasitized. Also, Rich (pers. observ.) has examined about 40 other thrasher nests in Bingham and Blaine counties, Idaho, and found neither cowbird eggs nor nestlings. In Mono County, California, both cowbirds and Sage Thrashers are locally common and sometimes forage at the same horse corrals (Rothstein et al. 1980). Rothstein has seen a large number of fledgling cowbirds being fed by other passerine species, but has seen none associated with Sage Thrashers.

We experimentally parasitized Sage Thrashers to determine their responses to cowbird eggs. We wanted to determine whether few cases of parasitism are reported because Sage Thrashers are not parasitized or, in part at least, because they remove cowbird eggs before observers find them. The differing appearances of cowbird and Sage Thrasher eggs indicate that a bird could distinguish between them easily. Cowbird eggs are white with numerous small brown and gray spots, whereas Sage Thrasher eggs are blue-green with red-brown blotches.

We located Sage Thrasher nests in basin big sagebrush (*Artemisia tridentata tridentata*) habitat in Blaine County, Idaho, during April and May, 1984. Nest contents were manipulated between 08:00 and 14:00, with most manipulations being performed between 09:00 and 10:00. At each nest, we exchanged or added an artificial cowbird egg quickly and then left the area so as to minimize disturbance of adult thrashers. These eggs were made of plaster of Paris and measured 21.1 × 16.3 mm. They were identical to eggs in Rothstein's (1975) study and closely resembled real cowbird eggs found in southern Idaho (Rich, pers. observ.). Nests were checked between 1 h and several days after the manipulation to determine responses. Unless noted otherwise, all nests were subjected to only one experimental manipulation.

In ten nests, we removed a thrasher egg and replaced it with an artificial cowbird egg. Five of these nests were found during egg-laying, and five were found during incubation. Although most natural cowbird parasitism occurs during the host's egg-laying period, nest stage has little or no relation to response in most rejecter species (Rothstein 1976, 1977), a trend also indicated by our results. Nine of the 10 eggs were ejected. The tenth egg remained in the nest, which was deserted. The last nest was the only one where there had been only a single egg laid at the time of manipulation. At an eleventh nest, we added an artificial cowbird egg to a clutch of four eggs. This egg was also ejected along with two thrasher eggs, and the nest was subsequently deserted.

Cowbird eggs were usually ejected quickly, but not always immediately; artificial cowbird eggs were still present at one nest after 2 h and at another after 3 h. The earliest known ejections occurred within 1, 2, and 3 h, and two within 4 h, although in no case did we watch a bird remove an egg. Only one of 17 ejected eggs was found, and that was at a distance of 3 m from the nest. The egg bore no evidence of pecking, thereby matching previous findings that most species that eject eggs do so by holding eggs in their bills, rather than by spiking them (Rothstein 1975).

We performed nine additional experiments with two types of eggs intermediate between cowbird and Sage Thrasher eggs to get some indication of the factors that Sage Thrashers use to distinguish among egg types. Single, real, thrasher eggs that were painted to resemble cowbird eggs were ejected from four nests. These results suggest that the difference in size between thrasher (24.8 × 16.8 mm, Bent 1948, p. 429) and cowbird eggs (21.8 × 16.8 mm, Bent 1958, p. 451) is not a necessary releaser for rejection behavior.

Artificial eggs identical in size to the artificial cowbird eggs, but colored an immaculate blue (identical to egg type "S" in Rothstein 1982a), were accepted at two of five nests. Birds at three of these nests were incubating and had ejected artificial cowbird eggs 44 to 48 h before the blue egg

was added. Blue eggs were accepted during incubation at one nest where thrashers had ejected a cowbird egg earlier and during egg-laying at another nest where thrashers had no known prior experience with foreign eggs.

Because a blue egg was accepted in two of five cases, it appears that Sage Thrashers, like other rejecters (Rothstein 1982a), will accept some egg types that are distinguishable from their own eggs. Such tolerance may be adaptive in that it reduces the chances of a host's rejecting unusual eggs of its own. Indeed, Sage Thrashers occasionally lay immaculate blue eggs (Rich, pers. observ.) which are similar to the experimental blue egg, except for the former's slightly larger size. Ejection of three artificial blue eggs shows that Sage Thrashers are capable of subtle discrimination. Because of the small sample size, however, more tests with blue eggs are necessary before conclusions can be drawn.

Sage Thrashers clearly reject cowbird eggs by ejection. The Sage Thrasher has at least five of the six characteristics that Rothstein (1975) identified as being in common among rejectors: (1) its eggs are unlike cowbird eggs in size, color, and maculation; (2) it practices nest sanitation, as nests are completely free of excrement and other extraneous material (Rich, pers. observ.); (3) thrasher nests are large and relatively easy to find (The mean dimensions of nine newly built nests were: outside diameter at rim, 20.8 ± 1.0 cm, and depth, 12.2 ± 1.8 cm.); (4) although the Sage Thrasher is the smallest mimid, its beak is large enough to manipulate eggs at least as large as its own; and, (5) with territories of about 1.0 ha (Reynolds and Rich 1978) and the large range of the species (Bent 1948), population size must be considered as moderate to large.

The sixth characteristic, history of sympatry, may also favor the evolution of rejection in Sage Thrashers. Although some cowbirds occur in the continuous expanses of sagebrush occupied by Sage Thrashers, they are today most common in more favorable islands of habitat, such as riparian growth and livestock pastures, that exist within sagebrush. Cowbirds thus occur with Sage Thrashers at numerous points within the latter's range. This co-occurrence in the Great Basin is probably not recent (Grinnell 1909). Before settlement of the West by Europeans, cowbirds in the Great Basin may have been sustained in part by the foraging afforded by large herds of bison. Two other species that are broadly sympatric with Sage Thrashers in sagebrush habitat, the Sage Sparrow (*Amphispiza belli*) and the Brewer's Sparrow (*Spizella breweri*), may reject cowbird eggs through desertion (Rich 1978). Experimental verification of such a response is necessary (Rothstein 1975), however, because desertion does not provide clear evidence of a response to cowbird parasitism. Thus, the three passerines most closely tied to sagebrush habitat may have had long periods during which they could have evolved host defenses.

It would be valuable to determine the responses to cowbird eggs of those mimids so far untested. We would then be able to compare all the species in a family whose characteristics suggest that they should be largely preadapted to reject cowbird eggs, but which have had varying amounts of historical contact with cowbirds.

This note was improved by the constructive comments of H. Mayfield, D. Finch, and an anonymous reviewer.

LITERATURE CITED

BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195.

BENT, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U.S. Natl. Mus. Bull. 211.

FINCH, D. M. 1982. Rejection of cowbird eggs by Crissal Thrashers. Auk 99:719–724.

FRAGA, R. M. 1982. Host-brood interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. Ph.D. diss., Univ. of California, Santa Barbara.

FRIEDMANN, H. 1963. Host relations of the parasitic cowbirds. U.S. Natl. Mus. Bull. 233.

GRINNELL, J. 1909. A new cowbird of the genus *Molothrus*. Univ. Calif. Publ. Zool. 5:275–281.

MASON, P. 1980. Ecological and evolutionary aspects of host selection in cowbirds. Ph.D. diss., Univ. of Texas, Austin.

REYNOLDS, T. D., AND T. D. RICH. 1978. Reproductive ecology of the Sage Thrasher (*Oreoscoptes montanus*) on the Snake River Plain in southcentral Idaho. Auk 95:580–582.

RICH, T. D. 1978. Cowbird parasitism of Sage and Brewer's sparrows. Condor 80:348.

ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77: 250–271.

ROTHSTEIN, S. I. 1976. Experiments on defenses Cedar Waxwings use against cowbird parasitism. Auk 93: 675–691.

ROTHSTEIN, S. I. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull. 89:21–32.

ROTHSTEIN, S. I. 1982a. Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? Behav. Ecol. Sociobiol. 11:229–239.

ROTHSTEIN, S. I. 1982b. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. Am. Zool. 22:547–560.

ROTHSTEIN, S. I., J. VERNER, AND E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97:253–267.

U.S. Bureau of Land Management, Shoshone District, P.O. Box 2B, Shoshone, Idaho 83352; Department of Biological Sciences, University of California, Santa Barbara, California 93106. Present address of first author: U.S. Bureau of Land Management, P.O. Box 1229, Dickinson, North Dakota 58602. Received 1 February 1985. Final acceptance 12 July 1985.