

EVIDENCE OF CONSPECIFIC NEST PARASITISM AND EGG DISCRIMINATION IN THE SORA¹

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Conspecific nest parasitism (CNP) is relatively frequent among precocial species and several hypotheses for this pattern have been suggested (Rohwer and Freeman 1989, Lyon and Eadie 1991, Sorenson 1992). I report here observations made at the nest of a Sora, *Porzana carolina*, which suggest both the occurrence of CNP as well as very fine egg discrimination in this species. Recognition and rejection of parasitic eggs is a well documented defense in some hosts of obligate brood parasites (e.g., Rothstein 1975, Davies and Brooke 1989) but may also evolve as a response to CNP (Freeman 1988; Jackson, in press). Intraspecific egg discrimination, however, has been verified in very few species (Arnold 1987). The following observations were made near Minnedosa, Manitoba, an area characterized by high densities of small wetlands and breeding waterfowl (see Kiel et al. 1972).

On 25 June 1986, I found a Sora nest in dense white-top grass, *Scholochloa festucacea*, in 20 cm of water along the edge of a small (0.65 ha), shallow wetland. Twelve eggs were visible in a single layer in the nest bowl whereas three additional eggs were partially buried in the nest material under the rest of the clutch. These three eggs were slightly different in appearance from the other 12, having fewer and smaller spots, a slightly lighter background color, and less glossy appearance. The latter was perhaps a consequence of having been buried and not in contact with the plumage of the incubating bird. The three buried eggs were also the smallest in the nest, ranging from 8.49 to 8.61 cm³ compared to 8.80 to 9.37 cm³ for the other 12 eggs (volume calculated as $0.51 \times LW^2$, Hoyt 1979). The three buried eggs were distinctly cooler to the touch than the other 12. I immediately suspected that these eggs were laid by another female, but because of the very slight differences in egg color and markings, I carried out the following series of impromptu experiments.

(1) I marked the three buried eggs with a single black dot on the large end of the egg and marked the re-

maining 12 eggs with a dot on the small end. I then placed three of the 12 presumed "host" eggs in the depression in which the three "odd" eggs were found. I left the remaining nine "host" eggs and three "odd" eggs in one layer in the nest bowl. On 26 June, only 12 eggs were visible in the nest. Finding none outside of the nest, I removed the 12 remaining eggs and carefully spread the nest material apart. I found the three missing eggs buried at least 3 cm below the level of the nest bowl; two of the eggs were at water level. These were the same three eggs that were partially buried when the nest was originally found. In addition, my marks on the 12 "host" eggs had become very faint whereas the dots on the three buried eggs were not worn at all, suggesting that they had been buried soon after the incubating bird returned to the nest on the previous day. (2) Attempting the experiment again, I removed three of the "host" eggs from the nest site and left nine "host" eggs and the three "odd" eggs in a single layer in the nest bowl. By 27 June, the same three eggs were again deeply buried in the nest material and nine "host" eggs remained in the nest bowl. (3) I returned the three "host" eggs taken away on the previous day and removed the three buried eggs from the nest site. On 29 June, all 12 "host" eggs were still in the nest bowl. (4) With a red, permanent marker, I colored over and slightly enlarged about 30 spots on one of the 12 "host" eggs. On 30 June, this egg was buried out of sight but only slightly below the level of the nest bowl. I retrieved the egg and left it with the rest of the clutch.

Also on 30 June, at least five days after any other egg was laid, a new egg (the 16th overall) appeared in the nest. This egg was smaller (7.86 cm³), more pointed, and had a darker background color and smaller spots than any of the other 15 eggs. This last egg was not buried during the next three days, although it was perhaps less like the "host" clutch than the three eggs that were originally buried. On 3 July, all 13 eggs (12 "host" eggs and the 16th egg) remained in the nest bowl. The egg I marked with red dots (now mostly faded) occupied a low position in the center of the clutch. By 8 July, the nest was destroyed. Several shells were found scattered around the nest and one hatchling or near-hatch embryo was found in the water.

The most likely explanation for these results is that a second female parasitized the nest with three eggs which were then buried by the nesting female or pair. The 16th egg, laid well into the incubation stage, can almost certainly be attributed to a female other than the nest owner (see Yom-Tov 1980). The possibility

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that the nesting female laid all 15 eggs originally in the nest and buried three of her own eggs because they were inviable is unlikely for several reasons. (1) There was no evidence that the buried eggs were cracked, rotting, or defective in any way. (2) Selective burial of the egg I modified indicates an ability to discriminate among eggs on the basis of external appearance alone. (3) A clutch of 15 eggs is unusually large for Soras: for 8 annual data sets reviewed by Tanner and Hendrickson (1956) and Lowther (1977), mean clutch size was 10.4 eggs ($n = 133$; range 5–16) with clutches as large as 15 eggs reported only twice. (4) Spotting pattern and background color of the three buried eggs were discernibly different from the 12 “host” eggs. Observations of consistency within and variability among females in egg characteristics (e.g., Lyon 1993a) suggest that the buried eggs were laid by a second female.

The observations reported here are consistent with studies of other rallids. CNP occurs in several species (Gibbons 1986, Rohwer and Freeman 1989, Lyon 1993b), and American Coots, *Fulica americana*, reject parasitic eggs by burying them (Arnold 1987, Lyon 1993b). Observations of egg laying sufficiently detailed to detect CNP (e.g., Greenlaw and Miller 1983) are generally lacking for Soras. Pospichal and Marshall (1954), however, recorded two new eggs in one day at one Sora nest and two Virginia Rail, *Rallus limicola*, nests, and clutches of up to 16 eggs have been reported for the Sora (Lowther 1977). Parasitism of a Virginia Rail nest by a Sora (Tanner and Hendrickson 1954) and CNP in Soras (Allen 1939) have been noted but no details were given in either study. I found no evidence of CNP in five other Sora nests with completed clutches of 7 to 10 eggs.

The egg rejection behavior I observed was impressive in two respects. First, the Sora selectively buried three particular eggs in the existing nest material while keeping the rest of its clutch in the small nest bowl. Eggs were buried very deeply after my manipulations and were no longer visible without digging into the nest material (perhaps contributing to the lack of previous documentation of CNP in Soras). American Coots also selectively bury odd eggs (Arnold 1987). In contrast, some passerine hosts of obligate brood parasites may bury their own eggs along with the parasitic egg and then lay a new clutch (e.g., Sealy 1995). Second, egg discrimination was apparently based on very slight differences in egg color, markings, and perhaps size. This fine discrimination suggests that CNP was the context in which egg rejection evolved in the Sora (cf. Davies and Brooke 1989). When parasitic eggs are very similar to those of the host, as in the case of CNP, hosts should be less tolerant of eggs that differ only slightly from their own (Rothstein 1982).

Experimental studies of conspecific egg discrimination have found that only a portion of introduced eggs are rejected (Victoria 1972; Arnold 1987; Jackson, in press) and this was the case even in this single Sora nest. A variety of factors may influence the likelihood of egg rejection, including the nesting female's previous experience with her own eggs (Lotem et al. 1992) and the degree of difference between host and parasitic eggs (e.g., Victoria 1972, Rothstein 1982). Perhaps the most likely explanation of the failure to reject the 16th egg

in this Sora nest is that birds become more tolerant of mismatched eggs as incubation proceeds (Rothstein 1982; but see Davies and Brooke 1989). Finally, variation among Sora nests in egg rejection might be related to nesting vegetation. Selective egg rejection by burial was probably facilitated by the relatively loose structure resulting from construction with whitetop grass but might be more difficult in nests constructed of cattail (*Typha* spp.) or sedge (*Carex* spp.), the typical nesting vegetation used by Soras (Pospichal and Marshall 1954; Lowther 1977). Additional studies of CNP and egg discrimination in the Sora and other rails would be of great interest.

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LITERATURE CITED

- ALLEN, A. A. 1939. The Golden Plover and other birds. Comstock Publishing, Ithaca, NY.
- ARNOLD, T. W. 1987. Conspecific egg discrimination in American Coots. *Condor* 89:675–676.
- DAVIES, N. B., AND M. DEL BROOK. 1989. An experimental study of co-evolution between the cuckoo, *Cuculus canorus* and its hosts. I. Host egg discrimination. *J. Anim. Ecol.* 58:207–224.
- FREEMAN, S. 1988. Egg variability and conspecific nest parasitism in the *Ploceus* weaverbirds. *Ostrich* 59:49–53.
- GIBBONS, D. W. 1986. Brood parasitism and cooperative nesting in the moorhen, *Gallinula chloropus*. *Behav. Ecol. Sociobiol.* 19:221–232.
- GREENLAW, J. S., AND R. F. MILLER. 1983. Calculating incubation periods of species that sometimes neglect their last eggs: the case of the Sora. *Wilson Bull.* 95:459–461.
- HOYT, D. F. 1979. Practical methods of estimating volume and fresh weights of bird eggs. *Auk* 96:73–77.
- JACKSON, W. M. In press. Egg-discriminating ability and egg-color variability in the Northern Masked Weaver. In S. I. Rothstein and S. K. Robinson [eds.], *Parasitic birds and their hosts: behavioral, ecological, and evolutionary interactions*. Oxford University Press, New York.
- KIEL, W. H., A. S. HAWKINS, AND N. G. PERRET. 1972. Waterfowl habitat trends in the aspen parkland of Manitoba. *Can. Wildl. Serv. Rep. Ser. No. 18*.
- LOTEM, A., H. NAKAMURA, AND A. ZAHAVI. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behav. Ecol.* 3:128–132.
- LOWTHER, J. K. 1977. Nesting biology of the Sora at Vermillion, Alberta. *Can. Field-Nat.* 91:63–67.
- LYON, B. E. 1993a. Tactics of parasitic American Coots: host choice and the pattern of egg dispersion among host nests. *Behav. Ecol. Sociobiol.* 33:87–100.

- LYON, B. E. 1993b. Conspecific brood parasitism as a flexible female reproductive tactic in American Coots. *Anim. Behav.* 46:911-928.
- LYON, B. E., AND J. M. EADIE. 1991. Mode of development and interspecific avian brood parasitism. *Behav. Ecol.* 2:309-318.
- POSPICHAL, L. B., AND W. H. MARSHALL. 1954. A field study of Sora Rail and Virginia Rail in central Minnesota. *Flicker* 26:2-32.
- ROHWER, F. C., AND S. FREEMAN. 1989. The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* 67:239-253.
- ROTHSTEIN, S. I. 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250-271.
- ROTHSTEIN, S. I. 1982. Mechanisms of avian egg recognition: which egg parameters elicit response by rejecter species? *Behav. Ecol. & Sociobiol.* 11:229-239.
- SEALY, S. G. 1995. Burial of cowbird eggs by parasitized Yellow Warblers: an empirical and experimental study. *Anim. Behav.* 49:877-889.
- SORENSEN, M. D. 1992. Comment: Why is conspecific nest parasitism more frequent in waterfowl than in other birds? *Can. J. Zool.* 70:1856-1858.
- TANNER, W. D., AND G. O. HENDRICKSON. 1954. Ecology of the Virginia Rail in Clay County, Iowa. *Iowa Bird Life* 24:65-70.
- TANNER, W. D., AND G. O. HENDRICKSON. 1956. Ecology of the Sora in Clay County, Iowa. *Iowa Bird Life* 26:78-81.
- VICTORIA, J. K. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaverbird *Ploceus cucullatus*. *Ibis* 114:367-376.
- YOM-TOV, Y. 1980. Intraspecific nest parasitism in birds. *Biol. Rev.* 55:93-108.

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DIFFERENCES IN SINGING BEHAVIOR BETWEEN RUFIOUS-COLLARED SPARROWS IN COSTA RICA AND NORTHWESTERN ARGENTINA¹

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The Rufous-collared Sparrow (*Zonotrichia capensis*) is one of the most common passerine species in Latin America, ranging from southern Mexico to Tierra del Fuego. Although there are studies on the vocal behavior of this species from several locations across South America (see King 1974, Nottebohm 1975, Tubaro et al. 1993), most have concentrated on populations in northwestern Argentina (Nottebohm 1969, King 1972, Handford 1988, Loughheed and Handford 1992). Males within these populations sing songs that have two distinct parts: an introductory theme, consisting of one to five usually dissimilar whistles, and a terminal trill, made from a series of repeated, morphologically similar notes (Nottebohm 1975). In northwestern and west-central Argentina, song dialects in Rufous-collared Sparrows are defined by quantitative variation in trill rate (Nottebohm 1969), and map closely onto patterns of original natural vegetation (Nottebohm 1975, Handford 1988).

Based on studies in Argentina, Rufous-collared Sparrows have been characterized as having a repertoire of one song type per individual; that is, although song

themes may vary considerably among individuals within a population, and trill rates may vary between populations in different habitats, there is little variation in the songs of a single individual. Nottebohm (1969) analyzed at least five songs (and occasionally up to 30 songs) from each of 523 Rufous-collared Sparrows from 29 populations in northern Argentina. He reported that only 19 birds (3.6%) sang more than one song type. Similarly, King (1972) studied song variation in three populations in northwestern Argentina and found that only five of 771 birds (0.6%) sang more than one song type. Other recent observations of Rufous-collared Sparrows in northwestern Argentina have also noted song stereotypy within individuals across a breeding season (S. C. Loughheed, pers. comm.).

Since studies investigating the vocal behavior of Rufous-collared Sparrows have almost exclusively concerned populations in northwestern Argentina, the generality of these observations is unknown. To determine if song stereotypy is common throughout their range, I recorded songs of Rufous-collared Sparrows from three localities in Costa Rica. My observations indicate that, unlike birds in northwestern Argentina, Rufous-collared Sparrows in Costa Rica commonly possess individual song repertoires and lack the terminal trill.

METHODS

I recorded songs from Rufous-collared Sparrows between 14-26 February, 1994, at three main sites in

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