RESPONSES OF YELLOW WARBLERS TO EXPERIMENTAL INTRASPECIFIC BROOD PARASITISM

SPENCER G. SEALY, KEITH A. HOBSON,[1] AND JAMES V. BRISKIE[2]

Department of Zoology
University of Manitoba
Winnipeg, Manitoba R3T 2N2, Canada

Abstract.—Examination of over 1500 completed clutches of the Yellow Warbler (*Dendroica petechia*) between 1974 and 1987 revealed only four nests that received more than one egg/d and seven nests that contained abnormally large clutches (i.e., more than five eggs). Since the latter clutches could have been laid by one female, these data suggest intraspecific brood parasitism was rare. To determine whether Yellow Warblers discriminate and reject conspecific eggs, we experimentally parasitized nests with other warbler eggs. Single Yellow Warbler eggs introduced experimentally into 53 warbler nests (without removing a host egg) during the pre-laying (lined but empty) through incubation stages were accepted. Eggs introduced into unlined nests were buried because of continued nest-building behavior (n = 16) or deserted (n = 1). Switched eggs at 11 additional nests introduced during the laying stage were accepted. "Parasitized" females did not reduce their clutch sizes in response to our manipulations. These results suggest that the low rate of intraspecific parasitism we observed was not due to egg rejection but to a low rate of actual parasitism.

RESPUESTAS DE *DENDROICA PETECHIA* A PARASITISMO INTRAESPECÍFICO EXPERIMENTAL

Resumen.—El examen de más de 1500 camadas de huevos de *Dendroica petechia* entre 1974 y 1987 reveló que solo 4 nidos recibieron más de 1 huevo por dia y 7 nidos contenían camadas anormalmente grandes, i.e., más de 5 huevos. Ya que las camadas grandes pudieron haber sido puestas por una sola hembra los datos sugieren que el parasitismo intraespecífico es raro. Para determinar si *Dendroica petechia* discriminaban y rechazaba huevos de conespecíficos, se parasitaron experimentalmente nidos con otros huevos de *petechia*. El huesped aceptó huevos de su propia especie colocados por nosotros experimentalmente en 53 nidos (sin remover un huevo del huesped) durante pre-puesta (nido revestido/vacio) y etapas de incubación. Huevos colocados en nidos no revestidos (listos) fueron enterrados debido al comportamiento de construcción del nido (n = 16) o fueron abandonados (n = 1). Huevos intercambiados a 11 nidos adicionales durante la etapa de puesta de huevos fueron aceptados. Las hembras parasitadas no redujeron sus camadas de huevos como respuesta a nuestra manipulación. Estos resultados sugieren que la tasa baja de parasitismo intraespecífico que observamos no se debío al rechazo de huevos sino a la propia tasa baja de parasitismo.

Intraspecific brood parasitism occurs when a female lays one or more eggs in a conspecific's nest without contributing subsequent parental care (Yom-Tov 1980). Perhaps as a result of the difficulty in documenting this behavior, intraspecific brood parasitism is considered rare among altricial birds (see Yom-Tov 1980 for a review, Brown 1984, Dhindsa 1983, Fleischer et al. 1985). Because the costs of raising offspring are great in altricial birds, selection should favor the evolution of defenses against parasitism in any population that is regularly subjected to either

inter- or intraspecific brood parasitism (Lanier 1982). Hosts have three possible defenses once a parasite's egg has been laid: (1) ejection of the foreign egg, (2) burial of the foreign egg along with any host eggs present at the time (actually a form of desertion except that only the clutch is deserted not the nest-site), or (3) desertion. Ejection requires the host to discriminate between its eggs and those of the parasite while burial and desertion require the host only to recognize that parasitism has occurred.

Usually, the ability of a species to discriminate between eggs is tested by switching eggs between conspecifics (Burtt 1977, Hoogland and Sherman 1976, Lanier 1982, Peek et al. 1972, Victoria 1972). Although egg-switching can demonstrate egg discrimination, it does not simulate intraspecific brood parasitism by parasites that do not habitually remove a host's egg prior to laying. Birds that cannot discriminate between eggs nevertheless may respond to parasitism through changes in clutch size or the appearance of an egg laid out of sequence with their own laying schedule (see Murton and Westwood 1977).

Between 1974 and 1987 we monitored over 1500 completed clutches of the Yellow Warbler (*Dendroica petechia*) on our study area in southern Manitoba. We never observed intraspecific brood parasitism directly in any of these nests; however, two lines of evidence suggest that it may occur, albeit infrequently. First, we recorded the appearance of more than one egg per day in four nests. Since no female birds are known to lay more than one egg per day (Sturkie 1976), these nests probably were the victims of brood parasitism. Second, we observed abnormally large clutches in 7 other nests (6 of 6 eggs, 1 of 7 eggs). Yellow Warblers on our study area generally lay either 4 or 5 eggs per clutch (Goossen and Sealy 1982). Since the larger-than-average clutches possibly were laid by one female, this evidence is less convincing.

Alternatively, if Yellow Warblers reject conspecific eggs or desert parasitized nests then we would rarely detect cases of intraspecific brood parasitism. We investigated this possibility by recording responses of Yellow Warblers to experimental intraspecific brood parasitism. Our objectives were to determine whether warblers discriminate and reject other Yellow Warbler eggs that appear in their nests and whether or not their response depended upon the timing of parasitism.

METHODS

We tested Yellow Warblers nesting in the dune-ridge forest that separates Delta Marsh from Lake Manitoba, Manitoba (description in Mackenzie 1982, Sealy 1980), and in an oak woodlot 3 km to the southeast on the southern edge of Delta Marsh. We collected Yellow Warbler eggs in late May and June 1986 and 1987 and introduced them into 70 nests during the pre-laying ($n = 38$), laying ($n = 21$), and incubation ($n = 11$) stages. During the pre-laying stage alien eggs were added to both unlined ($n = 17$) and lined nests ($n = 21$). Lined nests were characterized by the presence of a cotton or feather lining while unlined nests comprised only a shell of woven fibers. No host eggs were removed during these sets of

experiments. The behavior of the returning female was noted at 7 nests. We then selected 11 additional nests where we switched eggs between clutches during laying. In all cases, one egg, identified by a small pencil mark, was switched with one of the host's eggs. Nests were then checked daily for 3 consecutive days or until clutches were complete, after which unburied experimental eggs were removed. Eggs were recorded as accepted if they were being incubated by a female when the nest was checked or they were warm when touched.

RESULTS

Foreign Yellow Warbler eggs were added to 17 unlined and 21 lined, but empty warbler nests. Sixteen of the eggs added to unlined nests were buried, the other nest was abandoned. In the lined nests, all 21 eggs were accepted, although one nest was preyed upon 48–72 h after the egg was added. Warbler eggs added to unlined nests were buried more often than when added to lined but empty nests ($\chi^2 = 34.1$, df = 1, $P < 0.0001$). Female warblers initiated their own clutches in all 21 lined and 16 of the unlined nests.

All eggs added to nests during laying at the one- ($n = 5$), two- ($n = 4$), three- ($n = 8$), and four- ($n = 4$) egg stages were accepted. The same prevailed for nests where we switched eggs at the one- ($n = 4$), two- ($n = 1$), three- ($n = 4$), and four- ($n = 2$) egg stages. Laying continued uninterrupted in all nests parasitized during the laying period. Warbler eggs added to unlined nests were buried more often than when added to nests that contained eggs ($\chi^2 = 34.1$, df = 1, $P < 0.0001$).

Clutches were completed before experimental eggs were removed in 18 nests. Including the foreign egg, 13 pairs accepted 6 eggs and 5 accepted 5 eggs. Since clutch size in experimental nests ($\bar{x} = 4.72$) did not differ from the modal clutch size for this population (4.50, $n = 144$ [Goossen and Sealy 1982]; Mann-Whitney: $U = 996$, $P > 0.05$), Yellow Warblers did not appear to reduce their clutches in response to parasitism.

Nests parasitized during incubation all had five-egg clutches but the stage of incubation was unknown. In all cases the alien eggs were accepted (11 egg additions).

In seven egg-addition experiments we noted that the returning female first inspected the nest contents and then proceeded to incubate.

DISCUSSION

The Yellow Warbler does not discriminate between its own eggs and those of conspecifics. Neither the timing of parasitism (once a nest was lined) nor the sudden increase in clutch size seemed to elicit any sort of rejection behavior. Thus, Yellow Warblers accept parasitism whether or not a host egg is removed in the process.

One potential cost to a parasitized host that accepts a foreign egg is the increased effort required to raise the extra offspring. If this demand cannot be met then the host risks losing its own young through brood reduction or producing young in a poorer condition. Hosts unable to

prevent or reject parasitism nonetheless may reduce the consequences by adjusting downwards their own clutch size. The Yellow Warblers we parasitized during laying did not reduce their clutches in response to our manipulations; however, it is possible that the increase in effort needed to raise an additional parasitic young is not great enough to favor a reduction in their own clutches.

Yellow Warblers frequently respond to interspecific brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) by burying the parasite's eggs along with any of their own under a new nest lining (Clark and Robertson 1981, Graham 1988, but see Rothstein 1975). In contrast, we found that burial of conspecific eggs occurred only when the foreign eggs were introduced into unfinished nests. This suggests that egg burial resulted from continued nest building of an unfinished nest rather than as a response to the introduced egg *per se* (see Hobson and Sealy 1987). In a similar fashion, Emlen (1941) found that if eggs or young were introduced into unfinished Tricolored Blackbird (*Agelaius tricolor*) nests, normal nest-building behavior was not interrupted. Our results also suggest that Yellow Warblers can discriminate between warbler eggs and those of the Brown-headed Cowbird. Interestingly, Brown-headed Cowbird eggs often are similar in color and spotting to Yellow Warbler eggs (pers. obs.). Sometimes the only obvious difference between the eggs of the two species is size; cowbird eggs are roughly twice the volume of warbler eggs. It is possible that Yellow Warblers recognize foreign eggs using size alone, but this hypothesis needs to be tested further.

Experimental additions of conspecific eggs to nests and clutches of other species have produced mixed results. Some species, such as the European Starling (*Sturnus vulgaris*), rejected parasitic eggs only before any eggs of their own were laid (Stouffer et al. 1987). Eggs added after clutch initiation were removed only rarely, which suggested that these species no longer recognized they had been parasitized or that they could not distinguish between foreign eggs and their own (see also Emlen and Wrege 1986, Mumme et al. 1983, Vehrencamp 1978). On the other hand, the Village Weaver (*Ploceus cucullatus*) has well-developed discriminative abilities based upon intraspecific variability in egg coloration and pigmentation patterns (Victoria 1972; see also Arnold 1987, Bertram 1979, Buckley and Buckley 1972, Shugart 1987, Tschantz 1959). Finally, a number of species have shown no response to conspecific eggs, although not all conditions were tested in every study (Briskie and Sealy 1987, Burtt 1977, Grzybowski 1979, Hoogland and Sherman 1976, Lanier 1982, Peek et al. 1972).

Intraspecific brood parasitism is expected to be more likely in colonial than in non-colonial species due to the ease of locating similar nests at the same stage of the nesting cycle (Hamilton and Orians 1965). The Yellow Warbler is not colonial but it nests at densities in the dune-ridge forest up to 15 pairs/ha and clutches are initiated synchronously (Goossen and Sealy 1982; Sealy, unpubl. data). Nevertheless, natural intraspecific brood parasitism appears to be rare in our population. While Yellow

Warblers remain susceptible to intraspecific brood parasitism, other be-
havior such as intraspecific aggression, particularly among females, may
effectively prevent its occurrence (see Hobson 1988; Robertson and Nor-
man 1976; see also Hobson and Sealy, in press).

ACKNOWLEDGMENTS

LITERATURE CITED

ARNOLD, T. W. 1987. Conspecific egg discrimination in American Coots. Condor 89:675–
676.
BERTRAM, B. C. R. 1979. Ostriches recognize their own eggs and discard others. Nature,
Lond. 279:233–234.
BRISKIE, J. V., AND S. G. SEALY. 1987. Responses of Least Flycatchers to experimental
inter- and intraspecific brood parasitism. Condor 89:899–901.
BROWN, C. R. 1984. Laying eggs in a neighbor's nest: benefit and cost of colonial nesting
in swallows. Science 224:518–519.
BUCKLEY, P. A., AND F. G. BUCKLEY. 1972. Individual egg and chick recognition by adult
Royal Terns (*Sterna maxima maxima*). Anim. Behav. 20:457–462.
BURTT, E. H., JR. 1977. Some factors in the timing of parent-chick recognition in swallows.
Anim. Behav. 25:231–239.
CLARK, K. L., AND R. J. ROBERTSON. 1981. Cowbird parasitism and evolution of
anti-parasite strategies in the Yellow Warbler. Wilson Bull. 93:249–258.
DHINDSA, M. S. 1983. Intraspecific nest parasitism in two species of Indian Weaverbirds
Ploceus benghalensis and *P. manyar*. Ibis 125:243–245.
EMLEN, J. T., JR. 1941. An experimental analysis of the breeding cycle of Tricolored
Red-wing. Condor 43:209–219.
EMLEN, S. T., AND P. H. WREGE. 1986. Forced copulations and intra-specific parasitism:
two costs of social living in the White-fronted Bee-eater. Ethology 71:2–29.
FLEISCHER, R. C., M. T. MURPHY, AND L. E. HUNT. 1985. Clutch size increase and
intraspecific brood parasitism in the Yellow-billed Cuckoo. Wilson Bull. 97:125–127.
GOOSSEN, J. P., AND S. G. SEALY. 1982. Production of young in a dense nesting population
of Yellow Warblers, *Dendroica petechia,* in Manitoba. Can. Field-Nat. 96:189–199.
GRAHAM, D. S. 1988. Responses of five host species to cowbird parasitism. Condor 90:
588–591.
GRZYBOWSKI, J. A. 1979. Responses of Barn Swallows to eggs, young, nests, and nest
sites. Condor 81:236–246.
HAMILTON, W. J., III, AND G. H. ORIANS. 1965. Evolution of brood parasitism in altricial
birds. Condor 67:361–382.
HOBSON, K. A. 1988. Protection of genetic parentage in the Yellow Warbler (*Dendroica
petechia*). M.S. thesis. Univ. Manitoba, Winnipeg. 125 pp.
————, AND S. G. SEALY. 1987. Cowbird egg buried by a Northern Oriole. J. Field
Ornithol. 58:222–224.
————, AND ————. 1989. Female-female aggression in polygynously nesting Yellow
Warblers. Wilson Bull. 101:84–86.
HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank
Swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46:33–58.
LANIER, G. A., JR. 1982. A test for conspecific egg discrimination in three species of
colonial passerine birds. Auk 99:519–525.

MacKenzie, D. I. 1982. The dune-ridge forest, Delta Marsh, Manitoba: overstory vegetation and soil patterns. Can. Field-Nat. 96:61–68.

Mumme, R. L., W. D. Koenig, and F. A. Pitelka. 1983. Reproductive competition in the communal Acorn Woodpecker: sisters destroy each other's eggs. Nature, Lond. 306: 583–584.

Murton, R. K., and N. J. Westwood. 1977. Avian breeding cycles. Clarendon, Oxford. 594 pp.

Peek, F. W., E. Franks, and D. Case. 1972. Recognition of nest, eggs, nest site and young in female Red-winged Blackbirds. Wilson Bull. 84:243–249.

Robertson, R. J., and R. F. Norman. 1976. Behavioral defenses to brood parasitism by potential hosts of the Brown-headed Cowbird. Condor 78:166–173.

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

Sealy, S. G. 1980. Breeding biology of Orchard Orioles in a new population in Manitoba. Can. Field-Nat. 94:154–158.

Shugart, G. W. 1987. Individual clutch recognition by Caspian Terns, *Sterna caspia.* Anim. Behav. 35:1563–1565.

Stouffer, P. C., E. D. Kennedy, and H. W. Power. 1987. Recognition and removal of intraspecific parasite eggs by starlings. Anim. Behav. 35:1583–1584.

Sturkie, P. D. 1976. Avian physiology. 3rd edition. Springer-Verlag, New York. 400 pp.

Tschantz, B. 1959. Zur Brutbiologie der Trottlelummer (*Uria aalge* Pont.). Behaviour 14:1–100.

Vehrencamp, S. L. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga sulcirostris*). Behav. Ecol. Sociobiol. 4:1–33.

Victoria, J. K. 1972. Clutch characteristics and egg discriminative ability of the African Village Weaver *Ploceus cucullatus.* Ibis 114:36–376.

Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. Biol. Rev. 55:93–108.