COWBIRD PARASITISM AND EGG RECOGNITION OF THE NORTHERN ORIOLE

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Little information exists on host-parasite interactions between the Northern Oriole (*Icterus galbula*) and the parasitic Brown-headed Cowbird (*Molothrus ater*) (Friedmann 1963) even though both species are abundant and broadly sympatric. The small number of nests known to have been parasitized is not due to a scarcity of observations on oriole nests; e.g., parasitism was observed at only 8 (2.5%) of 318 oriole nests in Ontario (Peck 1974). Alternative explanations can account for the scarcity of observed parasitism: (1) Northern Orioles typically accept cowbird eggs but are rarely parasitized; or (2) Northern Orioles typically eject cowbird eggs causing a large proportion of cowbird eggs to disappear before observers see them. Under the first explanation, the frequency of observed parasitism would equal the frequency of actual parasitism. But under the second, incidences of observed parasitism would always be less than incidences of actual parasitism and orioles might be frequently parasitized even though parasitism is rarely seen.

If orioles typically eject cowbird eggs, the cases of natural parasitism most likely to be seen would be those rare ones in which parasitic eggs are accepted. Thus observations of natural parasitism do not give reliable data on the frequency with which birds eject cowbird eggs. Reliable data on ejection can be derived by experimentally placing cowbird eggs into nests because the experimenter can determine the fate of all the cowbird eggs within a sample. In 1968 I placed an artificial cowbird egg in a Northern Oriole nest. The egg was ejected within 24 h. This was one of a series of experiments on many species. These experiments demonstrated little intraspecific variation in response to experimental cowbird parasitism (Rothstein 1975a, 1975b). Thus species were easily divided into 2 discrete groups—accepters and rejecters. Based on the 1 experiment and on several reports of ejections of naturally deposited cowbird eggs (Friedmann 1963, Smith 1972), I tentatively designated the Northern Oriole as a rejecter species. New experiments on 27 additional nests reported here demonstrate that this designation was correct. Experiments on 2 nests also deal with behavioral mechanisms responsible for the oriole's egg recognition.

MATERIALS AND METHODS

Artificial eggs.—Artificial cowbird eggs (Fig. 1) made of plaster of Paris were used in most experiments. These eggs are identical to ones described elsewhere (Rothstein 1975a, 1975c) except that eggs used in nests whose number begins with "74-" or "75-"

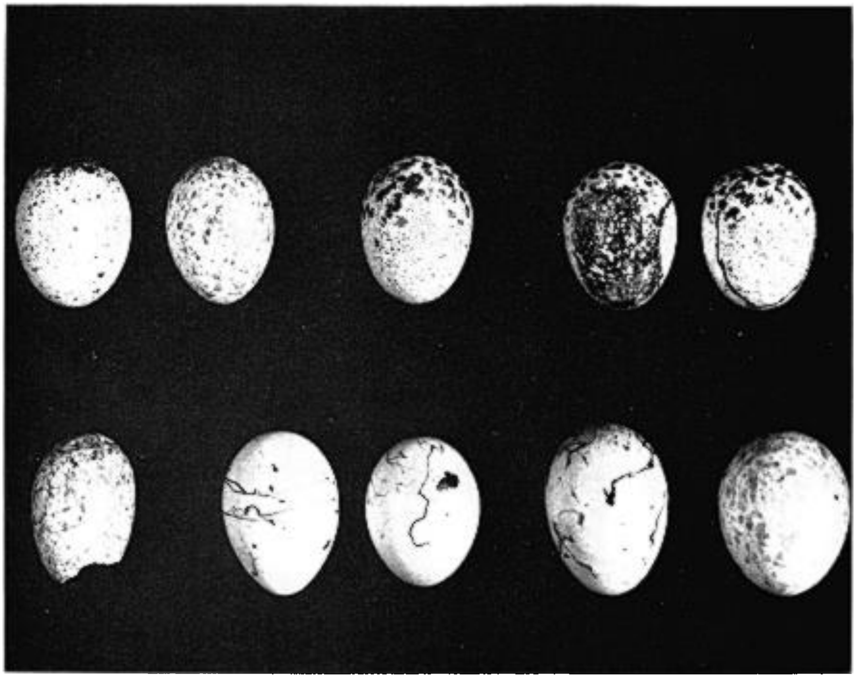

FIG. 1. Egg Types Mentioned in Text. Top row: 2 cowbird eggs; an artificial cowbird egg; 2 artificial cowbird eggs damaged by orioles (The surface of the artificial egg on the left has been blackened so as to better reveal the peck marks. The most heavily damaged area of the egg on the right is within the black lines.). Bottom row: House Sparrow egg after being ejected from nest 75-81; 2 Northern Oriole eggs; Red-winged Blackbird egg; Loggerhead Shrike egg from same clutch as eggs placed in nest 74-86.

were coated with a clear acrylic polymer gloss medium, not with shellac. Controls performed on other species show birds do not reject these eggs because they are artificial (Rothstein 1975a, 1975c). I performed controls on orioles by experimentally parasitizing nests with a real cowbird egg or with real House Sparrow (*Passer domesticus*) eggs. The latter simulate cowbird eggs in color and size (Fig. 1, see data in Bent 1958).

Experimental procedures.—During a single visit to each nest, one "parasite" egg was added and one "host" (oriole) egg was removed. I experimentally parasitized most nests between 12:00 and 18:30. Elsewhere (Rothstein 1975a) I discussed differences between my procedures and those usually employed by cowbirds; but these differences have no detectable influence on the incidence of rejection. Experimentally parasitized nests were usually checked within 24 ± 2 h. If an experimental egg was not ejected I left it in the nest for at least 7 days except at nest 73-01 where nest checks ceased after 3 days.

Nest stage.—Most naturally parasitized nests receive cowbird eggs during the host's laying period (Friedmann 1963). The question of whether there is a correlation between host response and nest stage can be answered by parasitizing nests throughout the cycle. I divided nests into 3 stages. Those known to be parasitized on or before the day

TABLE 1

NORTHERN ORIOLE NESTS SUBJECTED TO EXPERIMENTS SIMULATING COWBIRD PARASITISM

Nest Number	Experimental Egg Type	Clutch Size[a]	Date Nest Parasitized	No. of Eggs Present When Parasitized	Nest Stage When Parasitized	Type of Rejection	Days For Rejection	Oriole Eggs Missing (M) or Damaged (D)
68-220	A	≥ 6	May 27	5	L	E	0–1	None
74-88	A	≥ 5	May 6	2	L	E	0–7	None
75-101	A	≥ 5	May 19	5	L	D	0–1	4M
75-112	A	≥ 4	May 22	2	L	D	0–1	None
75-123	A	≥ 3	May 29	2	L	D	0–1	None
73-33	A	≥ 5	May 10	5	L-I	D	0–1	4M
74-79	A	≥ 6	May 6	6	L-I	E	0–7	None
74-86	A	≥ 5	May 6	5	L-I	D	0–7	None
74-94	A	≥ 4	May 13	4	L-I	E	0–1	1M, 1D
75-105	A	4	May 20	4	L-I	D	0–1	3M
72-01	A	≥ 3	June 14	3	I	D	0–1	2M, 1D
74-81	A	6	May 6	6	I	D	0–7	2M
74-93	A	5	May 13	5	I	D	0–1	4D
74-96	A	5	May 13	5	I	D	0–1	3M
74-97	A	4	May 13	4	I	D	1–7	1D
75-107	A	≥ 2	May 21	2	I	D	0–1	1M
75-108	A	5	May 21	5	I	D	0–1	None
73-01	A	4	June 10	4	?	D	0–3	2D
75-81	HS	≥ 5	May 10	5	L-I	E	0–1	None
75-88	HS	5	May 11	5	L-I	E	0–1	None
75-84	HS	5	May 11	5	I	E	0–1	1M
75-103	HS	4	May 20	4	I	E	0–1	None
75-109	CB	5	May 21	5	L-I	E	0–1	None

Note: Prefixes of nest numbers equal year in which experiment was conducted. A = artificial cowbird egg; HS = House Sparrow egg; CB = real cowbird egg; E = egg ejected; D = egg damaged and left in nest.

[a] Additional eggs could have been laid in nests where "≥" precedes clutch size. Uncertainties exist for various reasons, e.g. visits to one nest ceased before it was certain that egg laying was completed (68-220). At other nests parasitized during the laying stage, egg disappearance may have been impossible to detect because eggs lost could have been replaced by eggs laid between nest checks.

the last oriole egg was laid were in the laying stage, "L" in Table 1. Nests at which no additional oriole eggs appeared after parasitization were in the incubation stage, "I," if the oriole egg I removed contained an embryo. The third stage was intermediate, "L-I," and consisted of nests at which no additional eggs appeared but at which the removed oriole egg was fresh and lacked an embryo. I estimate nests in the L-I stage were parasitized between the day the last egg was laid and 2 or 3 days later.

Study areas.—Most nests were studied during May 1974 and May–June 1975 within 18 km of Shandon, San Luis Obispo Co., California. Nests studied in other areas are as follows: 68-220, Woodbridge, New Haven Co., Connecticut; 72-01, Delta, Manitoba; 73-33, Goleta, Santa Barbara Co., California; 73-01, Chaffey's Locks, Ontario, and 75-103, Tupman, Kern Co., California.

RESULTS OF EXPERIMENTS SIMULATING NATURAL COWBIRD PARASITISM

Responses to experimental parasitism.—Rejection occurred at all 5 nests where I added a real cowbird or cowbird-like egg (Table 1). In addition, Raleigh J. Robertson and Richard Norman (pers. comm.) added real cowbird eggs to 5 oriole nests at Delta, Manitoba. Each was rejected. As Robertson and Norman's techniques differed slightly from mine, I do not include their data in statistical tests that follow. Because rejection of real eggs occurred at 10 of 10 nests, I assume rejections of artificial cowbird eggs at 18 other nests (Table 1) were not in response to artificiality of the eggs. Thus, orioles rejected at each of 28 nests sampled. The 95% confidence interval for percent rejection in the total population is 86 to 100% (determined from Owen 1962). All the real eggs in my experiments were ejected whereas only 4 of 18 artificial eggs were ejected; the remainder were damaged and left in the nest. The incidence of ejection differs significantly for the 2 egg types ($P < 0.02$; Fisher exact test, Bailey 1959 and tables in Owen 1962. All subsequent probabilities also involve this test.). I searched for ejected eggs in an area 3 to 5 m around the point below each nest but failed to find them except in 1 case in which I watched the oriole eject (next section). Most of the damaged artificial eggs had numerous shallow peck marks (Fig. 1). To determine the total number of pecks I counted the peck marks in an area centered around the equator of the egg from nest 74-81. This egg had undergone moderate to heavy damage. I extrapolated this figure to the entire egg (using a formula in Romanoff and Romanoff 1949 for surface area). During the 7 days it was in the nest at least 196 pecks were inflicted, or half this number if each peck was with the bill open. Besides these shallow peck marks, most of which did not penetrate the paint to the underlying plaster, the eggs from 3 nests also had gouges up to 1 mm into the plaster indicating these birds concentrated pecks at specific sites.

Observations of rejection behavior.—After parasitizing a nest I usually left the area as quickly as possible, not returning until a subsequent day. I did watch 6 nests immediately after I inserted the experimental egg and at 2 other nests I returned within an hour: (1) At 18:30 I parasitized nest 75-81 (Table 1) with a House Sparrow egg while a female scolded. About 4 min after I left the nest the female landed on the nest rim, looked into the nest for several sec and then "up-ended," clinging to the inside of the nest wall with her body roughly perpendicular to the ground and her tail protruding from the nest. The motion of her tail indicated she began to peck immediately at the eggs. Pecking continued for about 75 sec; then she flew from the nest and fluttered within several m of it for about 30 sec. She then returned to the nest, immediately up-ended and began to peck. After about 40 sec she left the nest with the House Sparrow egg in her bill and flew to a branch about 10 m away. Upon landing she seemed to immediately wipe the egg across a twig and then dropped it. I retrieved the sparrow egg from the ground and found part of the shell at the pointed end missing (Fig. 1). The missing shell may have remained in the tree. At 18:57 I returned to the nest, and added an artificial cowbird egg. Until 19:04 the female fluttered within 5 m of the nest, frequently looking into it. She then flew to the nest, immediately up-ended as before and began to peck. She stayed in the nest about 2 min, frequently pecking in rapid series of 2–4 pecks. She then left the nest and fluttered nearby only to return at 19:10 again up-ending immediately and pecking until she left at 19:12. She had not returned to the nest when I ceased observations at 19:15. Pecks against the artificial cowbird egg were delivered with such force that they were audible about 6 m away. During these observations I did not see or hear a second oriole.

(2) At 10:53 a real House Sparrow egg was inserted into nest 75-84, while the female scolded. For the next 34 min the female fluttered within 3 to 10 m of the nest, vocalizing frequently. Several times she perched about 1 m over the nest, tilted her head and apparently inspected the nest contents. She was evidently reluctant to return to the nest, perhaps frightened by a rope we had tied to a nearby branch and by occasional disturbances from a nearby house. We removed the rope between 11:27 and 11:31. At 11:42 the female landed on the nest rim, stood there and began to frequently bend over and peck into the nest. She did not up-end as did the bird at 75-81, probably because this nest was not as deep. At 11:44 she flew from the nest, landed about 12 m away and began to bill wipe for several min. At 11:48 and 11:50 she again stood on the nest rim, pecked into the nest and then flew suddenly. In none of her 3 departures were we able to determine whether she carried an egg. At 11:55 we inspected the nest. The House Sparrow egg and one oriole egg were missing. Pieces of oriole eggshell were found beneath the branches the female flew to after her second and third pecking sessions. Perhaps the sparrow egg was removed after the first pecking session and the oriole egg

was broken while the bird tried to eject the sparrow egg. A second oriole was not detected.

(3) I added a real cowbird egg to 75-109 at 15:45 while 1 or 2 orioles scolded. At 15:47 a female landed on the nest, up-ended and began to peck. She flew after about 90 sec but I couldn't see if she carried an egg. This performance was repeated about 1 min later and again I couldn't detect whether an egg was carried away. At 15:50 the female went to the nest and began to incubate. At 16:02 I ceased my observations, chasing the female from the nest which now contained only 4 oriole eggs. A striking feature at nests 75-81, 84, and 109 was the speed with which the females left the nest after most pecking sessions. I suspect they carried eggs or parts of eggs on these departures and left quickly so as to avoid dropping eggs back into the nest.

(4) Nest 75-112 was parasitized at 11:00 with an artificial egg. An adult male scolded while I was at the nest. I watched the nest until 11:14. During this time the male stayed in the tree with the nest but never came within 2 m of it. As the male was not scolding and showed no "nervous" behavior, my presence about 25 m away was probably not responsible for his failure to go to the nest. A female was not detected.

(5) At 15:24 I added an artificial egg to nest 75-123 while scolded by a female. I did not see the female arrive at the nest but 3.5 min later I noticed her, up-ended and pecking into the nest. After about 30 sec she flew to a tree roughly 60 m away and was joined by an adult male. About 30 sec later she returned to the nest, up-ended for about 90 sec and then went all the way into the nest and apparently sat on the eggs. I flushed the female from the nest at 15:34.5. The cowbird egg had 15–30 peck marks. The one oriole egg I had left in the nest was undamaged.

(6) I parasitized nest 75-101 at 18:08, flushing a female from the nest. The nest was watched until 18:20 but no orioles were seen.

(7) Nest 75-88 was parasitized with a House Sparrow egg at 18:15. A male and female scolded while the egg was inserted. The sparrow egg was missing when I returned at 18:49 and a female was incubating.

(8) I parasitized nest 75-103 at 10:25 with a House Sparrow egg. No orioles were detected. When I returned at 10:35 a bird was on the nest and the undamaged sparrow egg was present. At 11:00 the egg was gone and a bird was again on the nest.

These observations suggest ejection usually occurs shortly after a female returns to her nest as was the case at nests 75-81, 84, 109, and 123. The speed with which birds carried ejected eggs made it impossible to determine how the eggs were carried. Pecking motions that preceded ejections indicate eggshells were pierced before removal but whether the eggs, still virtually intact, were speared on the bill or whether the eggs were broken in the nest and pieces carried away separately is uncertain. The former is more likely but the latter may have occurred at 75-109 as the oriole made 2 rapid departures from the nest. My observations indicate most ejected eggs are dropped at least several m from the nest. Orioles are known to drop naturally deposited cowbird eggs directly from the nest (Friedmann 1963, Smith 1972) but these cases of natural parasitism were detected only because eggs were dropped from the nest. Each of the 4 rejections I observed was by a female, suggesting males do not usually reject. Furthermore a male, but not a female, was present and scolded when I parasitized nest 75-112, yet the male did not inspect the nest as had females at other nests. Whether males totally lack rejection behavior remains an important question and is critical to the population genetics of the rejection trait (Rothstein 1975b).

Breakage and disappearance of oriole eggs.—Some but not all oriole eggs disappeared from or were broken in 11 of 18 nests parasitized with artificial eggs. I suggest orioles broke their own eggs while attempting to eject artificial eggs and that they later removed some of these broken eggs. Birds remove their own eggs if these have holes (Poulsen 1953, McClure 1945). This interpretation is supported by several lines of evidence. The incidence of missing or broken oriole eggs at nests parasitized with real eggs (1 in 5) is significantly ($P < 0.05$) less than for nests that received artificial eggs. That orioles removed their own broken eggs is suggested by the fact that at some nests, eggs seen to be damaged on one nest check were missing on a subsequent check. Finally the female at nest 75-81 ejected a House Sparrow egg without breaking any of her own eggs. I then added an artificial egg. The next day the nest contained a damaged artificial egg and pieces of oriole eggshell. Pieces of oriole eggshell were also on the ground beneath the nest, which was deserted. Breakage of oriole eggs probably occurred when an oriole's bill or the plaster egg rebounded against the oriole eggs during pecking or when a plaster egg was dropped on the oriole eggs. Possibly orioles actively pecked their own eggs during redirected behavior occurring when their frustrated attempts to eject the plaster egg conflicted with another tendency such as incubation.

Effects of nest stage.—As orioles parasitized during all 3 nest stages rejected (Table 1) there is no correlation between nest stage and acceptance or rejection of cowbird eggs. However, there is a possible correlation between nest stage and amount of effort exerted in rejection. The fact that artificial eggs can't be ejected easily provides a measure of rejection effort because different amounts of effort may produce different results. By contrast, with real cowbird eggs, rejection effort, even if it does change with the breeding cycle, may always be sufficiently strong to result in the same response—rapid ejection. In response to artificial cowbird eggs, intense rejection effort is likely to lead to ejection, rather than only egg damage. The incidence of missing oriole eggs may be correlated with rejection effort because the more intense the attempts to eject the plaster egg the more likely oriole eggs will be damaged. Results from the 13 nests that received artificial eggs and were checked on day 1 (24 h after parasitization) are relevant. On day 1, 5 of 7 L and L-I nests showed ejection of the plaster egg or disappearance of at least 1 oriole egg whereas these events occurred at none of 6 I nests ($P < 0.025$). This suggests rejection effort decreases after the first 3 days of incubation.

THE NORTHERN ORIOLE AS A REJECTER SPECIES

Because rejection occurred at each experimental nest the Northern Oriole conforms to the responses of previously designated rejecter species. These species reject cowbird eggs at rates of 88 to 100% (Rothstein 1975b). Experiments on orioles were conducted in 4 widely spaced regions (California, Ontario, Manitoba, Connecticut) suggesting rejection is characteristic of the entire species. However, because only 1 nest was tested in 2 regions and because the species is polytypic in morphology (Rising 1970, Misra and Short 1974) experiments in other regions should be done.

There is little doubt that orioles that damaged artificial eggs would have ejected real ones. This must mean that the natural parasitism that is observed is just a fraction of the actual parasitism that occurs. The rapidity with which cowbird eggs can be ejected is shown by nests observed immediately after they were parasitized experimentally. The point is also demonstrated by the fact that rejection occurred within 24 h at 17 of 18 experimental nests visited on day 1 (Table 1). Methods to estimate the rate of natural parasitism are described elsewhere (Friedmann et al. 1977).

The Northern Oriole's status as a rejecter contrasts with other Icteridae. Two well studied icterids, Red-winged Blackbird (*Agelaius phoeniceus*) and Common Grackle (*Quiscalus quiscula*) are accepter species (Rothstein 1975a). The contrast between the oriole and Red-wing is especially interesting because their eggs are similar (Fig. 1). The presence of a definite rejecter species within the Icteridae strengthens the generalization (Rothstein 1975a) that species within a family often differ as regards rejecter-accepter status.

COMPARISONS BETWEEN THE NORTHERN ORIOLE AND OTHER REJECTER SPECIES

Fourteen of 18 (77.8%) oriole rejections of artificial cowbird eggs were by damage. Only 6 of 201 (3.0%) rejections of artificial cowbird eggs by 7 other rejecters were by damage and all of these were by the Cedar Waxwing (*Bombycilla cedrorum*) (data in Rothstein 1975a). Orioles rejected by damaging significantly ($P < 0.005$) more frequently than every other rejecter species, except the Western Kingbird (*Tyrannus verticalis*), for which I tested only 2 nests. The waxwing and oriole differ in the type of damage they inflicted. In contrast to the numerous shallow peck marks on cowbird eggs damaged by orioles, eggs from waxwing nests had nearly all the damage restricted to several large depressions dug into the plaster. Damaged eggs were probably more prevalent among orioles because this species ejects cowbird eggs by spiking them. Other rejecters usually lift cowbird eggs in their mandibles (Rothstein 1975a). While the occurrence of damaged cowbird eggs left in nests is probably an artifact of using plaster eggs (i.e., real cowbird eggs would have been removed) it leads to the discovery that the oriole differs from other rejecters in its ejection technique—a finding that would not have resulted as easily from experiments using real cowbird eggs.

Ejection by spiking would not seem to be as adaptive as ejection by carrying eggs in the mandibles. Even if a broken egg is quickly removed it may leak its contents and this endangers the other eggs (Rothstein 1975a). A bird spiking an egg might cause the egg or its bill to rebound against other eggs, thereby breaking them. Why then does the Northern Oriole eject by spiking instead of by carrying eggs in its bill? I suggest a bird would have difficulty removing an egg from the deep pendant nest characteristic of orioles unless the egg were securely impaled on the bird's bill. Otherwise, the egg might fall back into the nest and damage the bird's own eggs. By contrast other rejecter species I studied have the cup-shaped, shallow nests typical of most passerines. Corroborative evidence is provided by N. G. Smith's findings (pers. comm.; see also Smith 1968) that oropendolas and caciques, whose nests are even deeper than those of the oriole, also eject by spiking. The shape of the oriole's bill may also introduce some difficulties in ejection. Other rejecters have either slightly decurved or hooked bills but the oriole's bill is straight and this may make it difficult for orioles to lift eggs. Also, among known rejecters the oriole has the smallest bill after the Cedar Waxwing.

The oriole and waxwing differ from other rejecters in the incidence with which some but not all of their own eggs were found broken or missing from the nest. Missing or damaged "host" eggs occurred at 12 of 23 (52.2%) oriole nests and at 25 of 58 (43.2%) waxwing nests subjected to experimental cowbird parasitism. Breakage or disappearance of host eggs occurred at only 5 of 190 (2.6%) experimental nests of the other rejecters (Rothstein 1976).

The loss of oriole eggs in experimentally parasitized nests is not totally lacking in biological significance. One nest parasitized with a real egg (75-84, Table 1) lost an oriole egg during the ejection process. The remaining oriole eggs had wet egg contents on them and this may have caused further losses. Another nest I parasitized with a real egg (75-109) showed a potential for the loss of oriole eggs. About 15 min after the female ejected a real cowbird egg, 2 of the 4 oriole eggs had wet egg white on them. A third had a small feather and some cottony nest lining glued to it. These eggs were incubated successfully but my handling may have decreased the likelihood that they would be glued to one another or the nest. I suggest that orioles reject cowbird eggs at some risk to their own eggs. This risk explains the possible reduction in the oriole's rejection effort during the I stage (see above). Selection may favor a reduction in rejection effort during the I stage because cowbird eggs laid then pose little threat to the oriole's reproductive output but sustained efforts to eject such eggs could result in loss of oriole eggs. A similar explanation accounts for the fact that Cedar Waxwings shift from 87.5% rejection during the L and L-I stages to 40.0% rejection during the I stage (Rothstein 1976).

TRUE EGG RECOGNITION VERSUS RECOGNITION ON THE BASIS OF DISCORDANCY

Oriole and "parasitic" eggs in experiments reported above differed in appearance and numerical representation in the clutch (the parasitic eggs were outnumbered by oriole eggs). Thus do orioles reject eggs on the basis of appearance or on the basis of which egg is in the minority? I shall refer to these 2 mechanisms as true egg recognition and recognition on the basis of discordancy. If the latter occurs orioles should reject their own egg if it is outnumbered by foreign eggs. Experiments on other species demonstrated true egg recognition (Victoria 1972, Rothstein 1975c).

Data for 2 nests (75-107 and 123) in Table 1 indicate true egg recognition. Artificial cowbird eggs were rejected even though only 1 oriole egg was present. Thus the orioles at these nests rejected the foreign egg even though it and their own egg type were represented equally.

After artificial cowbird eggs had been rejected, experiments were conducted at 2 nests to distinguish between the 2 modes of egg recognition. On 13 May nest 74-79 (Table 1) contained 5 oriole eggs. At 16:55 I replaced 4 of these with 3 Loggerhead Shrike (*Lanius ludovicianus*) eggs. When next checked, on 14 May at 14:11, the nest contained only an undamaged oriole egg. The nest was still active as 2 orioles scolded intensely. I found no trace of the missing shrike eggs in an area 3 to 5 m around the point under the nest. When next visited on 20 May the nest was abandoned and curiously the still intact oriole egg was buried under 10 to 25 mm of new nesting material. On 13 May, nest 74-86 contained 4 oriole eggs and one heavily damaged cowbird egg (Table 1). I removed the latter at 12:16 and at 12:50 I replaced 3 oriole eggs with 4 shrike eggs. At 13:27 I removed 1 shrike egg because the combined mass of 4 shrike and 1 oriole egg was too large for the eggs to lie on the nest floor in 1 layer. The eggs were being incubated when checked at

13:27. When next visited on 14 May at 18:35 the nest contained only the oriole egg. The egg was cold and had a hole that measured about 3 by 2 mm. No orioles were in attendance. The shrike eggs were not found beneath the oriole nest.

The orioles at nests 74-79 and 74-86 demonstrated true egg recognition. Both nests were probably eventually abandoned because the single oriole egg that remained was not a sufficient stimulus to release incubation behavior. The shrike eggs were larger than the orioles' eggs. At nest 74-79 the oriole egg left with the shrike eggs measured 22.67 × 15.95 mm. Measurements are unavailable for the 3 shrike eggs placed in the nest but 2 eggs from the same shrike clutch measured 23.70 × 18.40 and 24.92 × 18.97 mm. Measurements are unavailable for the shrike eggs used at nest 74-86 but these eggs were also larger than the oriole egg (unpubl. photograph). Thus these experiments present no evidence that orioles prefer large eggs or that large eggs are a supernormal stimulus, as has been found in some nonpasserines (see Tinbergen 1951).

SUMMARY

Experiments on 28 Northern Oriole nests showed this species does not tolerate cowbird parasitism. Artificial or real cowbird eggs or real House Sparrow eggs, which simulate cowbird eggs, were rejected at every nest. Real eggs were ejected whereas most artificial (plaster) ones were damaged and left in the nest. Observations at nests immediately after they were parasitized showed: (1) 4 of 4 rejections were by females, (2) cowbird eggs are often ejected within min, (3) cowbird eggs are usually dropped at least several m from the nest. The oriole's rapid removal of cowbird eggs indicates that the natural parasitism that is observed is a fraction of the total parasitism that occurs.

The Northern Oriole corresponds closely to species previously designated as rejecters —these species reject cowbird eggs at rates close to 100%. But other rejecters usually remove artificial cowbird eggs whereas most orioles damaged them and left them in the nest. This difference demonstrates orioles eject cowbird eggs by spiking although other species do so by lifting the egg in their mandibles. The oriole's special ejection technique is probably an adaption to its pendant nest. Although orioles reject cowbird eggs throughout the egg stage, the effort exerted in rejection seems to weaken during incubation. This decrease in rejection effort may have been selected for because cowbird eggs laid during the oriole's incubation pose little threat to the oriole's offspring but ejecting them endangers the oriole's own eggs. Orioles correctly distinguished between their own and foreign eggs even when the latter outnumbered their eggs, as orioles at 2 experimental nests ejected 3 and 4 real Loggerhead Shrike eggs even though only 1 oriole egg was present.

ACKNOWLEDGMENTS

Much of the data could not have been gathered without the able and indispensable field assistance provided by Donald A. Schroeder. The generosity and hospitality of Clare Hardham, Ian and Donald McMillan, and many other ranchers made it possible for me to conduct my studies near Shandon. These individuals also provided valuable information on local ecological conditions. Richard S. Miller kindly conducted the experiment on nest 72-01 and gathered data on additional oriole nests. Sharron Elliott and Raleigh J. Robertson conducted the experiment on nest 73-01. The manuscript profited from critical reviews by Lloyd F. Kiff, Dennis M. Power, Donald A. Schroeder, and Robert A. Wallace. I am thankful to all these individuals who have helped me at various stages of this project. Financial aid was provided by a Faculty Research Grant from the University of California.

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ACCEPTED 20 JAN. 1976.