EXPERIMENTAL PARASITISM OF AMERICAN COOT NESTS[1]

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BROOD parasitism has evolved in seven groups of five families of birds involving 80 or more species (Lack, 1968: 82). Many complex structural and behavioral adaptations have resulted, but the selective forces that have induced this mode of life are obscure. It is obvious that the host is an important factor in the successful evolution of this behavior (Hamilton and Orians, 1965; Lack, 1968: 96–97).

Only one completely parasitic species has precocial young, the Black-headed Duck (*Heteronetta atricapilla*) of temperate South America. The major hosts of this species are coots, especially the Red-fronted Coot (*Fulica rufifrons*) (Weller, 1968). Young Black-headed Ducks are hatched successfully and rear themselves so that differences in feeding and parental behavior are insignificant. Some species of waterfowl lay parasitically but also build nests; these have been termed semiparasites (Weller, 1959). Those with strong parasitic tendencies are the Redhead (*Aythya americana*) and the North American Ruddy Duck (*Oxyura jamaicensis*) (Low, 1941, 1945). Their hosts are almost exclusively other ducks with plain, lightcolored eggs, whereas Black-headed Ducks parasitize hosts with eggs of any size or color. Ruddy Ducks only rarely parasitize nests of American Coots (*Fulica americana*) (Weller, 1959; Fredrickson, pers. comm.), and there is one record of a Redhead parasitizing a coot nest (Bryant, 1914).

The great abundance of nests of American Coots in marshes frequented by semiparasitic Redheads and Ruddy Ducks would appear to be a perfect evolutionary inducement for successful parasitism. Moreover coots seem well-suited as hosts by their nesting behavior. They are extremely broody and both members of the pair incubate with the result that nest and egg success are extremely high. Coots have large clutches, and incubation does not start until the 4th or 5th egg, so there is considerable time when parasitic eggs could be deposited and be incubated fully.

That these species occur together without the evolution of a host-parasite relationship might be a result of: 1) lack of response of the parasite to the coot's spotted, tan egg so that parasitic eggs are not deposited, 2) a negative response of the host to the parasitic egg so that the egg does not hatch, or 3) that the young do not survive because they are not completely independent as are young Black-headed Ducks. Because these possibilities have a

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bearing on cause and mode of evolution of parasitism, a series of experiments was designed to test the more simple of the alternatives, the response of coot hosts to conspicuous foreign eggs.

Studies were conducted on Dan Green Slough in Clay County, Iowa in 1967 and 1969, in Rush Lake in Palo Alto County, Iowa in 1967 and 1968, and at Dewey's Pasture (Palo Alto County) in 1969. Robert Bergman did much of the field work during 1967 and 1968, and Steven Byers, Charles Hall, and Charles Steffen assisted in 1969. I am indebted to Leigh H. Fredrickson for his valuable comments on the manuscript.

Methods

In 1967 and 1968 one fresh, white ("Grade A Large") chicken egg was placed in each nest when it was found, regardless of the stage of incubation of the host's nest. Nests were rechecked at irregular intervals to determine acceptance and fate of the parasitic eggs. Like most commercial chicken eggs today, these were infertile but the time the egg was left in the nest bowl was used as an indication of potential hatching. Water levels were recorded because burial of parasitic eggs of Black-headed Ducks was associated with flood-induced nest building in Argentine coots (Weller, 1968).

In 1969 parasitized nests were checked more often to determine the precise fate of the parasitic eggs in relation to the host's nesting cycle. Each parasitic egg was checked one day after being placed in the nest to determine whether it was accepted by the host.

In addition unparasitized nests were used as controls in 1969 to determine the influence of parasitic eggs on nest success. Nests were parasitized in two areas by using slightly different systems. In Dewey's Pasture, each of the first 22 nests found was parasitized with one chicken egg. Additional nests found during the same week in the same area served as controls. Because of the tendency to visit experimentally parasitized nests more often to check on parasitic eggs, experiments at Dan Green Slough involved parasitizing every other nest regardless of its stage in the nesting cycle and using alternate nests as controls. Thus, both parasitized and unparasitized nests were checked on each visit and each nest received the same amount of disturbance.

To associate responses to the parasitic egg with stage of the host's nest, nests were placed in the following categories: laying and early, mid, and late incubation. These categories were determined by changes in numbers of eggs, by backdating from hatching dates, or by egg flotation based on data on pheasants by Westerskov (1950). Some nests were followed from the laying stage to hatching to determine more precisely the relationship between egg position in water and stage of incubation. Such data then were used to correct previous estimates.

Initial Response of Host to the "Parasitic" Egg

In 1969 each parasitic egg was placed in the center of the host's clutch. Nests were revisited the following day to determine whether the eggs were accepted or ejected. In 42 of 43 instances the egg was in the nest bowl and was being incubated, indicating acceptance of the conspicuous egg (Table 1). This is not surprising based on the findings of many workers who have performed similar experiments to study incubation behavior of birds (Tin-

TABLE 1
ACCEPTANCE AND POSITION OF "PARASITIC" EGG IN COOT NESTS 24 HOURS AFTER "PARASITISM," 1969

Place	No. parasitized	In nest bowl	At edge	Partially buried
Dan Green Slough	21	20	20/21	3
Dewey's Pasture	22	22	17/19	0
TOTALS	43	42	37/40	3

bergen, 1960: 147–159). Recognition of the egg as different was inferred because of 40 observed cases, 37 (92 per cent) of the chicken eggs were moved from central to a lateral position in the nests even though they were larger and heavier than coot eggs (Figure 1). In three instances eggs were so far to the edge of rather flat nests that they obviously were not incubated and were cool. In three nests at Dan Green Slough, the egg was partially buried and, in one of these, it was out of the nest bowl. Two of the nests were in the hatching stage; one female was laying. Thus, coots responded the same to parasitic eggs whether hens were in early laying or in late incubation. This suggests that coots at all stages of the nesting cycle recognize eggs distinctively different, but incubate them.

Figure 1. Coot nest showing chicken egg at the edge of the nest 24 hours after being placed in center.

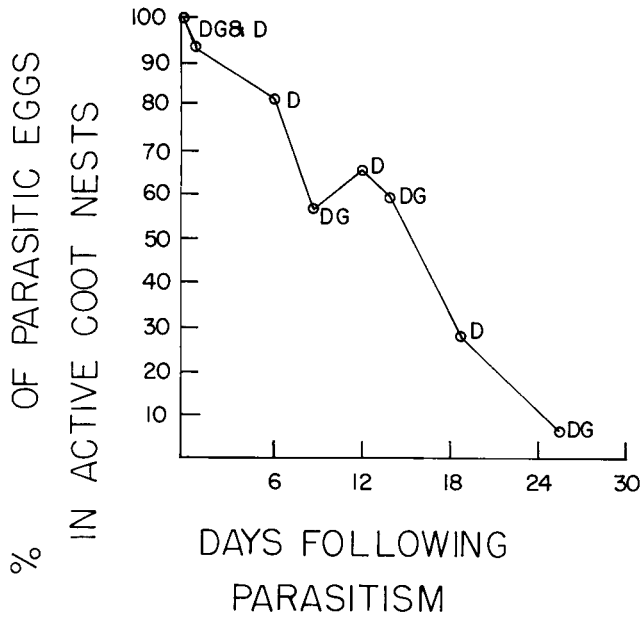

Figure 2. Relationship between time and the loss of parasitic eggs via burial or ejection from active nests. (D = Dewey's Pasture nests; DG = Dan Green Slough nests.)

Fate of Parasitic Eggs

There appears to be a general relationship between the chance of burial or ejection and the length of time the parasitic egg is in the nest. Data were insufficient to correlate burial of parasitic eggs and the stage of the nesting cycle, but parasitic eggs seemed more susceptible to burial during the host's laying stage and to ejection during the hatching stage. Ignoring stages of incubation, a gross correlation is suggested in Figure 2.

The fate of the 43 parasitic eggs from the 1969 experiments is shown in Table 2. Although 14 (32 per cent) were left in the nest bowl after all

TABLE 2
Fates of 43 "Parasitic" Eggs in Coot Nests in Two Study Units, 1969

Place	No.	Nest deserted	Ejected or buried early	Ejected or buried at hatching	Left in bowl at hatching
Dewey's Pasture	22	1	6	6	9
Dan Green Slough	21	1	14	1	5
Totals	43	2	20	7	14

TABLE 3
FATE OF "PARASITIC" EGG IN RELATION TO WATER FLUCTUATIONS, 1967 AND 1968

	Total nests	Egg missing	Egg buried	Egg incubated
Rising Level				
1967	19	8	11	0
1968	11	0	1	0
Subtotal	20	8	12	0
Declining Level				
1967	16	3	4	9
1968	11	4	4	3
Subtotal	27	7	8	12
TOTALS	47	15	20	12

coot eggs had hatched, none were incubated thereafter and most disappeared from the nest. The net result was that no parasitic egg induced maintenance in incubation behavior beyond the normal period, and the presence of these eggs did not deter coots from building brood ramps over their nests.

The causes of egg loss are suggested by the following observations: During 1967 and 1968, coot nests were parasitized at all stages of incubation. Observations were irregular and determined only the presence of the parasitic egg after hatching of the coot eggs. By chance, nests early in the season were subjected to a 5-inch water level rise, which later nests were not. Coots built up their nests during such floods and, in those nests flooded, no parasitic eggs remained in the nests at hatching. In those nests not flooded, 26 per cent of the parasitic eggs were left in the nests until hatching (Table 3).

During 1969 some nest building resulted from less dramatic water level increases than in 1967–1968 but there was a gradual 3-inch rise in water levels. There also were losses from the normal building common to the laying period. A higher loss of eggs in the Dan Green Slough sample than at Dewey's Pasture (Table 4) evidently was due to the fact that more nests were in the laying stage at Dan Green Slough and possibly the increase in water level was more rapid.

TABLE 4
RELATIONSHIP OF FATE OF "PARASITIC" EGG TO WATER LEVELS, 1969

Place	No.	Ejected or buried before flood	Ejected or buried after flood
Dewey's Pasture	22	4	2
Dan Green Slough	21	8[1]	5
TOTALS	43	12	7

[1] A higher percentage of nests were in early stages so that building was more prevalent.

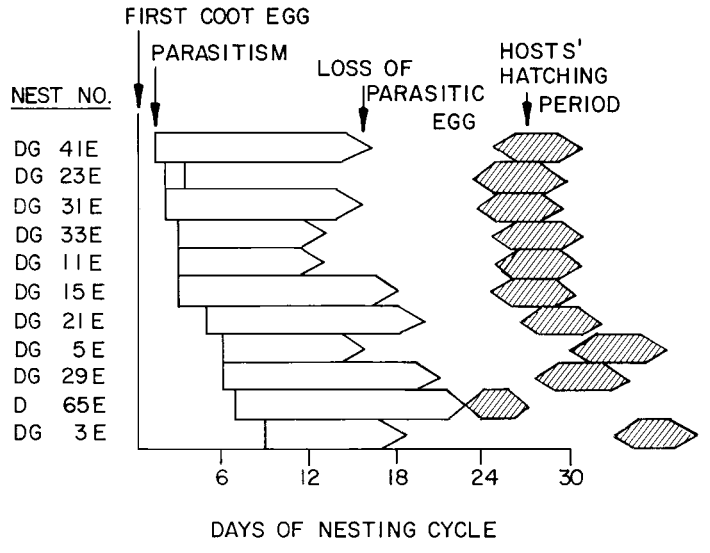

Figure 3. Maximal time periods parasitic eggs remaining in nests parasitized during the hosts' laying period.

Many parasitic eggs disappeared from the nest and, because fresh eggs sink, they were not found in the deep water. Some were buried and found during nest inspections. Presumably some eggs were ejected intentionally, especially at hatching when all unhatched coot eggs were ejected by the coots before relining the nest for the brood. However in 14 of 43 instances, the nest was deserted with only the chicken egg remaining, suggesting that chicken eggs were less likely to be ejected when the brood hatched. Some of these nests later were rebuilt as brood ramps, and the absence of a buried egg suggested that the egg eventually had been ejected into the water where it could not be found.

To hatch, a parasitic egg must be laid sufficiently early in the host's nesting cycle to provide for the normal incubation period of the parasitic egg. It appears that eggs of Black-headed Ducks may be hatched in nests of coots and White-faced Ibis (*Plegadis falcinellus*) during brooding of the young after all of the host's eggs have hatched (Weller, 1968). In 1969, at least 11 chicken eggs were placed in coot nests during the laying period, but none remained in the nest bowl long enough to have hatched if one assumes a 25-day incubation period for the parasite (Figure 3). Rarely did incubation of the parasitic egg exceed 14 days. Thus, the chance of hatching of parasitic eggs was nil, regardless of when nests were parasitized.

Water level fluctuations were a detrimental factor to parasitic eggs in

TABLE 5
NEST SUCCESS OF EXPERIMENTALLY PARASITIZED AND CONTROL COOT NESTS, 1969

Location	Control		Parasitized	
	No.	No. successful	No.	No. successful
Dewey's Pasture	22	19	22	21
Dan Green Slough	21	21	21	20
TOTALS	43	40 (93%)	43	41 (95%)

nests at Rush Lake and Dan Green Slough but were less significant to nests in Dewey's Pasture. Although 100 per cent of the parasitic eggs failed, possibly some would have remained long enough to hatch if deposited during the host's laying period and if water level increases had not induced further nest building and the resultant burial of parasitic eggs. This would necessitate more careful timing of laying on the part of the parasite.

THE INFLUENCE OF PARASITISM ON NEST SUCCESS

Although the presence of a conspicuous egg might be thought to induce desertion or predation, coots are known to be tolerant and broody, and to have low nest loss. A comparison of nest success of control and experimental nests shows comparable nest success: 93 per cent for control and 95 per cent for experimental nests (Table 5). It can be concluded that parasitic eggs did not influence nest success in this sample. Moreover, although the number of trips to control nests was greater at Dan Green's Slough than at Dewey's Pasture, there was no significant difference in nest success to suggest detrimental effects of the increased numbers of visits (Table 5).

DISCUSSION

Although the nesting behavior of coots and the density of their nesting populations appear to make the coot an ideal host species, the success of the parasitic eggs must be sufficient for parasitic laying to be perpetuated in the genetic makeup of the potential parasite. Based on these experiments, egg success was too low to have aided production of a semiparasite or a parasite. But it is not impossible that higher success would result in years with declining water levels.

Several possibilities might explain the lack of this host-parasite relationship in the wild. Redheads and North American Ruddy Ducks may not normally be stimulated to lay by the sight of coots' eggs, and possibly they have not "experimented" naturally to the extent that was done artificially in this study. Although the aggressive behavior of the coot is well known, it is not a deterrent to a specialized parasite like the Black-headed Duck

which parasitizes the larger and very aggressive Red-gartered Coot (*Fulica armillata*) (Navas, 1960). Or, it might be assumed that semiparasitic ducks once did lay parasitically in coot nests, but that either egg success or survival of young was so low that the generic strain to continue this unproductive act was eliminated.

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