AN EXPERIMENTAL STUDY OF CLUTCH SIZE OF THE AMERICAN COOT[1]

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MUCH information on laying behavior has appeared in the literature since Phillips (1887) performed his classical experiment by removing eggs daily from a flicker's nest. Lack (1947, 1948a, 1954) suggests a variety of factors that might influence clutch size, and he believes all factors are related to the maximum number of young a pair can rear successfully. Lack's ideas are based on studies of closely related species that nest over wide geographic areas.

Not all workers agree with Lack's theory on food as the mechanism for controlling clutch size. Skutch's (1949) observations on tropical nesting birds indicate that these birds rear fewer young than they can nourish. Wynne-Edwards (1962) proposes that populations are regulated by social behavior before food resources are depleted. The differences of opinion existing between workers may be attributable to different mechanisms that are effective in regulating animal populations in varying degrees under a variety of conditions (Weins, 1966).

Experimental studies of clutch size have been conducted on oceanic birds that are determinate layers. Clutch size has been manipulated in Laysan (*Diomedia immutabilis*) and Black-footed Albatrosses (*D. nigripes*) by Rice and Kenyon (1962) and in North Atlantic Gannets (*Sula bassana*) by Nelson (1964).

I know of no reports in the literature that describe responses to manipulations of clutch size of indeterminate layers after the clutch is complete and incubation has started. American Coots (*Fulica americana*) are indeterminate layers (Sooter, 1941) and both sexes normally incubate before the clutch is complete. The eggs hatch over a period of several days, and both sexes brood and feed the young. To gain an insight into the mechanism controlling clutch size in coots, the clutch was changed by adding or removing eggs during incubation after the clutch was complete. The manipulations of clutch size provided information on the number of eggs coots can incubate successfully and the number of young they can rear successfully.

METHODS

During the 4-year period from 1963 through 1966, 565 coot nests were examined in the Ruthven area of northwestern Iowa. Eggs in 223 nests were manipulated experimentally after the clutch was completed to increase or decrease the clutch size. To reduce the clutch to four, eggs were removed from one nest. All eggs that were re-

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TABLE 1
NEST SUCCESS OF EXPERIMENTAL AND CONTROL CLUTCHES OF AMERICAN COOTS IN 1963 THROUGH 1966

Year	Clutches				Hatched	
	Type	Number	Mean size ± SE	Range	Number	Per cent
1963	Large	2	14.0 ± 2.83	12–16	2	100
	Control	34	9.0 ± 2.04	6–16	34	100
	Small	None	—	—	—	—
1964	Large	36	15.6 ± 2.70	9–21	35	97
	Control	44	9.7 ± 2.13	6–17	33	75
	Small	35	4.0 ± 0.17	4– 5	29	83
1965	Large	44	13.8 ± 2.50	9–19	43	98
	Control	60	9.2 ± 1.74	6–17	56	93
	Small	41	4.0 ± 0.32	2– 4	40	98
1966	Large	25	15.4 ± 2.45	12–21	25	100
	Control	23	8.0 ± 1.54	4–16	18	77
	Small	42	4.0 ± 0.00	4	40	95
TOTAL	Large	107	14.8 ± 2.69	9–21	105	98
	Control	161	9.0 ± 1.68	4–17	141	88
	Small	118	4.0 ± 0.21	2– 5	109	92

moved were then added to another clutch. The resulting experimental clutches were termed either "large" or "small" and henceforth will be referred to as such throughout this report.

Experimental work was initiated each year as soon as nests in similar stages of incubation were located. Because of my absence from the study area early in 1965, pairing of nests according to initiation dates was not always possible. All eggs were marked with the corresponding nest number so their source was known. Nests were rechecked weekly to determine hatching success and to record any unusual behavior resulting from the manipulations. Nests were considered successful if one or more eggs hatched.

RESULTS

Control nests.—Careful records on hatching and nest success were maintained on 161 nests to provide information for comparison with the 223 nests used in experiments. Nest success seemed to vary with habitat, weather, and the timing of nesting in the annual breeding cycle, but no accurate data were obtained on hatching success of control clutches.

Large clutches.—During the study eggs were added to 107 nests to form large clutches (Table 1). These experimental nests contained 1,555 eggs or a mean clutch of 14.8 (range 9 to 21) eggs (Table 2).

Nest success was 98 per cent for the large clutches, or 10 per cent higher than for control clutches and 6 per cent higher than for small clutches (Table 1). Neither unsuccessful large clutch was deserted. When com-

TABLE 2
EGG SUCCESS OF LARGE EXPERIMENTAL CLUTCHES OF AMERICAN COOTS FROM 1963 THROUGH 1966

Year	Eggs		
	Number	Number hatched	Per cent hatched
1963	28	27	100
1964	532	485	91
1965	609	517	85
1966	386	376	97
TOTALS	1,555	1,405	90

pared with a Chi-square test, nest success of large clutches was significantly different from both control ($P < 0.005$) and small clutches ($P < 0.025$). Differences in success between small and control clutches were not significant.

Hatching success of large clutches varied from 85 to 100 per cent (mean 90 per cent) during the study (Table 2). Because nest success was high, the years of lowest hatching success indicated a situation in which fewer eggs hatched in nests rather than a complete nest failure. The cause of the lower hatching success was not determined. The mean number of eggs not hatched in the large clutches was 0.9 eggs per nest (Table 3).

Unusual circumstances associated with large clutches indicated the intense broodiness of coots. For example, one nest collapsed when decreasing water levels left the bowl of the nest high above the water surface; however, most of the eggs remained above the water. The pair formed a new nest structure with two bowls and successfully hatched the remaining eggs.

When clutches were increased in size, the coots enlarged the diameter of the nest bowl to accommodate the additional eggs. Occasionally eggs were buried, but in most instances the eggs were arranged in a single layer. The coot's brood patch was not sufficiently large to cover all eggs in large clutches simultaneously. On cool days eggs in the center of large clutches were warm but eggs on the periphery were cold. Despite this, the size of the brood patch did not limit the coot's ability to hatch a large clutch successfully. Evidently the eggs were rolled so that each received sufficient heat to complete development.

Gullion (1954: 386–387) suggests that the activity of seven or eight young coots provides a sufficient stimulus to adults to suppress incubation tendencies. If this were true, one would expect that coots would not hatch more than eight eggs. These data suggest that cessation of incubation probably was influenced by the lack of stimulation of the eggs remaining in the nest. Regardless of clutch size, the mean number of unhatched eggs in large clutches was less than one (Table 3). Of 107 large clutches, 35

TABLE 3

NEST AND EGG SUCCESS OF 104 LARGE CLUTCHES OF THE AMERICAN COOT IN RELATION TO CLUTCH SIZE

"Manipulated" clutch size	Nests				Eggs in Successful Nests				
	Total	Per cent of total	Number hatched	Per cent hatched	Total	Number hatched	Per cent hatched	Mean no. hatched/ nest	Mean no. not hatched
9	2	2	2	100	18	18	100	9.0	0.0
10	5	5	5	100	50	49	98	9.8	0.2
11	5	5	5	100	55	55	100	11.0	0.0
12	8	8	8	100	96	80	83	10.0	2.0
13	11	11	10	91	143	138	87	12.5	0.5
14	13	13	13	100	182	164	90	12.6	1.4
15	18	17	18	100	270	254	94	14.1	0.9
16	14	13	14	100	224	215	96	15.4	0.6
17	13	13	12	92	221	205	86	15.8	1.2
18	2	2	2	100	36	35	97	17.5	0.5
19	9	9	8	89	171	164	84	18.2	0.8
20	2	2	2	100	40	40	100	20.0	1.0
21	2	2	2	100	42	41	98	20.5	0.5
TOTALS	104		101		1,548	1,458		14.0	0.9

or 32 per cent of the clutches had an egg success of less than 100 per cent. The number of nests with unhatched eggs was as follows: 1964, 15 of 36 (42 per cent); 1965, 13 of 44 (24 per cent); and 1966, 6 of 25 (24 per cent). We found a total of 13 dead young in or near nests with large clutches during the study, indicating that some eggs hatched after incubation had terminated. Unhatched eggs were not examined to determine whether they were infertile or contained dead or incompletely developed embryos.

Small clutches.—Eggs in 118 coot nests were manipulated to form small clutches (Table 1); 116 of the nests contained four eggs, and 109 of the 118 nests (92 per cent) were successful. Presumably yearly differences in success of small clutches can be attributed partly to the varying interval between completion of the clutch and experimental manipulations of eggs. Because adults become more broody as incubation progresses (Gullion, 1954: 381–383), birds in later stages of incubation are less likely to be influenced by egg removal.

Hatching success in small clutches was very similar to success in large clutches. This situation may reflect the mechanism that terminates incubation behavior in the Rallidae, a family that initiates incubation before a complete clutch is laid. The change to brooding behavior occurs when the unhatched eggs no longer provide a sufficient stimulus for incubation behavior.

Some coots responded to removal of eggs from nests by starting a new laying cycle. During three of the years, coots laid additional eggs in 16 nests after the clutch was completed. The number of clutches in which additional eggs were laid varied as follows: 1964, 8 of 35 (23 per cent); 1965, 4 of 41 (10 per cent); and 1966, 4 of 42 (10 per cent). During these years the mean intervals between cessation of laying and experimental manipulations were: 1964, 5.54 days; 1965, 13.55 days; 1966, 8.26 days; overall mean, 9.59 days. When manipulation occurred just before hatching, less time was available for a new laying cycle to be initiated before the clutch hatched or perhaps birds were not affected by egg removal because of the increased broodiness near the termination of incubation. Therefore coots did not respond by laying additional eggs in clutches manipulated near the final days of incubation.

The original clutch size of nests used in experiments as small clutches varied from 5 to 13 eggs (Table 4). Additional eggs laid (after removal of some eggs) varied from 1 to 11 in the 16 nests. No recognizable relationship was obvious between the number of eggs in the original clutch and the number of additional eggs laid, nor did the length of time between completion of the clutch and egg manipulations follow a recognizable pattern. Some of the additional eggs may represent dump nesting by other

TABLE 4
EGG SUCCESS OF SMALL EXPERIMENTAL CLUTCHES OF AMERICAN COOTS FROM 1964 THROUGH 1966

Year	Not including additional eggs			Including additional eggs		
	Total	Number hatched	Per cent hatched	Total	Number hatched	Per cent hatched
1964	133	122	92	163	139	85
1965	170	154	91	178	162	91
1966	168	154	91	184	170	92
TOTALS	471	430	91	525	471	90

coots not associated with the nest under observation, but the pattern of laying in some small clutches suggested a second laying cycle.

Sowls (1955) found that waterfowl started a second nest when the entire clutch was removed or destroyed. These second nests he called renests. Some ducks responded to removal of the entire clutch by ending reproductive activity, but others built news nests and laid another clutch. Ducks initiated a laying cycle sooner if the first nest was incubated for only a short period. Ducks well along in the incubation period required a longer interval before renesting.

A second laying cycle can be initiated in the American Coot during incubation and after a clutch is complete without removing the entire clutch. Therefore these nests cannot be called renests. In such cases the interval between removal of eggs and the laying of additional eggs was not comparable to the pattern found in ducks. The mean time between egg removal and laying was 8 days. The first additional eggs were laid in nests with small clutches in from 2 days to as many as 14 days after egg manipulations (Table 5). When the switching was conducted within a week of hatching as in 1965, few additional eggs were laid. This pattern of laying additional eggs is unique when compared with other nonpasserine species. Not only are additional eggs laid without a consistent relationship to the stage of incubation but, in no instance in other nonpasserine species noted in the literature, did partial removal of a clutch induce additional laying as occurred in the coot.

Coots that laid additional eggs continued to incubate these eggs until they hatched. For several of the nests, the incubation period reached twice the normal period of 23 days. The extension of incubation did not seem particularly unusual when compared with the time that other species have spent on the nest when eggs did not hatch during the normal incubation period: Pintail, 62 days (Sowls, 1955), and Wood Duck, 62 days (Leopold, 1951). It was assumed that the coots were caring for the young that hatched from the original four eggs of the small clutch during the same

TABLE 5
DATA ON COOT NESTS WITH ADDITIONAL EGGS

Nest number	Number of original eggs	Number of days between finished clutch and manipulation	Number of days between manipulation and laying	Number of days between finished clutch and laying	Number of additional eggs
E-50	13	1	8	9	11
E-55	6	10	2	12	2
E-60	11	4	2	6	2
E-68	10	8	14[1]	22[1]	5[1]
E-71	10	9	7	16	11[1]
E-82	10	6	7	13	4
E-90	10	6	14[1]	20[1]	2[1]
E-156	10	1	14[1]	15[1]	1[1]
E-18	11	–[2]	7	7[1]	1
E-20	10	–	7	7[1]	2
E-56	6	–	5	5[1]	5
E-73	5	–	7	7[1]	8
E-33	12	0	9	9	9
E-37	13	–	12	12[1]	4
E-49	9	12	8	20	1[1]
E-57	10	–	7	7[1]	2[1]

[1] Number given is minimum.
[2] Unknown.

period. Additional eggs can be hatched successfully only in a species such as the coot in which both sexes incubate and brood the young.

Brood survival.—Data on brood survival were difficult to obtain. Coots with young often remained in or near vegetative cover where they are hard to watch. Because both parents feed and brood the young, it was difficult to obtain accurate brood counts. The most reliable data on survival of young were obtained on single pairs that nested on isolated potholes.

Survival of four broods was recorded but was restricted to the first few weeks after hatching. A nest located in an isolated pothole contained 12 eggs that all hatched. A count made 2 days after hatching indicated that nine young had survived, but the brood was reduced to eight by the fourth day after hatching.

All the eggs in a clutch of 16 hatched, but one dead young was found near the nest. One week later 11 young were on a brood ramp with the color-marked male, but none was with the female.

In a control clutch 9 of 10 eggs hatched. One adult associated with this nest was color-marked. Four of the nine young survived to an age of 5 weeks.

In an experimental clutch of 15 eggs, 12 eggs hatched, but after 7 days only 9 young were noted. Unfortunately, no complete counts on this brood were possible later in the season.

These results suggest that mortality of 25 to 31 per cent occurs in broods from large clutches during the first week after hatching; 11 was the maximum number of young known to survive for 1 week.

DISCUSSION

Experimental work has shown that coots can successfully incubate and hatch more eggs than they normally lay. As the study was made during only four nesting cycles, all conditions that limit the ability of coots to hatch eggs may not have been encountered. Over long periods of time, extreme weather or habitat conditions might limit the clutch size that can be incubated successfully.

Because the differences in nest success were statistically significant, the data suggest that coots have a greater drive to incubate large clutches than small or control clutches. The mean number of young produced per female was nearly 4 in successful small clutches and 13 in successful large clutches, or 90 per cent of the eggs hatched regardless of clutch size.

If we think of Gullion's (1954) figure of eight birds as the normal number of young to be hatched, we see that coots with large clutches were able to hatch five more young than normal. Preliminary experiments indicated that brood mortality in large clutches may be as high as 31 per cent during the first week after hatching. High mortality in large broods has been described for the Curve-billed Thrasher (*Toxostoma curvirostre*) by Ricklefs (1965) and in Leach's Petrel (*Oceanodroma leucorhoa*) by Huntington (1963).

Survival of young probably varies because of differences in habitat and weather conditions. Gullion (1954) reported that both parents spent much time brooding the young during the first days after hatching, but 11 observations in this study showed that most young were brooded by the male at night. Perhaps more young would survive if both sexes shared the nocturnal brooding duties equally.

High mortality in large broods during the first week after hatching suggests parents cannot rear all young hatched from larger than normal clutches. Experiments on Laysan and Black-footed Albatrosses by Rice and Kenyon (1962) showed an increase in mortality as the brood size increased. Both Herring Gulls (*Larus argentatus*) and Black-backed Gulls (*L. fuscus*) are unable to protect a large brood successfully from adverse weather (Harris and Plumb, 1965). This failure appears related to food or brooding tendencies of the parents. If brooding tendencies of coots are solely responsible for survival of young, Lack's emphasis on food as a determining factor of clutch size could be questioned.

While feeding young coots in captivity, I was surprised by the quantity of food each young consumed before it stopped begging. With extremely large broods, adults probably fed each young less than in smaller broods. Lack (1948b) found that starling nestlings were fed less often in large broods and that the band recovery rate for birds that survived 3 months was lower. Because young coots evidently require large quantities of animal matter during the first days after hatching, the availability of dragonfly nymphs and other aquatic invertebrates could determine the average number of young for which parents can find sufficient food, supporting Lack's theory on factors determining clutch size.

Some coots responded to small clutches by laying additional eggs, even after the clutch was completed and incubation had started. Evidently four eggs did not supply sufficient visual or tactile stimuli to maintain incubation drives. Experimentation to determine the mechanisms by which coots respond to a small clutch would be most interesting, but also most difficult, especially with free-living populations. Effects of tactile stimulation on the incubation response of coots appear most easily studied. Unfortunately the endocrine control of broodiness in the American Coot has not been studied. Both progesterone and prolactin may be involved in broodiness (Lehrman, 1961). Assuming that broodiness is related to the level of prolactin, bioassays or analytical determinations might be performed to determine prolactin concentrations. Possibly the small clutch reduces the tactile stimulus to the brood patch. If this reduced tactile stimulus decreases prolactin levels, the concentrations of prolactin could be compared with birds having larger clutches.

Additional aspects that need investigation include the ability of coots to feed young and the effects of the availability of food on this relationship. Studies of food habits of young coots seem necessary to understand this factor better as it affects rearing success; such a study should encompass an analysis of food availability as well as utilization.

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Summary

Experimental manipulation of clutch size showed conclusively that coots can incubate successfully more eggs than they normally lay. Success of both control and small clutches was lower and significantly different from

large clutches. Nest success was not statistically different between small and control clutches. Hatching success for all experimental clutches was 90 per cent regardless of clutch size.

Removal of eggs from nests after the clutch was completed and during the incubation period induced some coots to initiate a second laying cycle. More coots responded by laying eggs when the egg removal occurred early in the incubation period. No distinct pattern of laying additional eggs could be determined from the data collected.

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