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FACTORS AFFECTING RENESTING IN AMERICAN COOTS[1]

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Abstract. I studied renesting behavior of American Coots (*Fulica americana*) in southwestern Manitoba during 1987–1991. Coots were persistent renesters, replacing 68% of 281 destroyed clutches. Renesting rates varied annually and seasonally, but were unaffected by previous investments in egg formation or incubation. Renest intervals averaged 2.1 ± 1.8 days (1 SD; $n = 127$) following clutch loss during laying and 6.4 ± 1.1 days ($n = 28$) following clutch loss during incubation. Renest intervals did not vary, or varied only slightly ($r^2 \leq 0.11$), with respect to year, date, supplemental feeding, number of previous nesting attempts, previous clutch size, previous egg size, and stage of incubation. Clutch size of renests was usually one to two eggs smaller than clutch size of initial nests, but this was entirely an artifact of later nest initiation dates for renests. Clutch and egg sizes of renesting coots were unaffected by levels of previous investment in egg formation or incubation. After controlling for seasonal effects, approximately 30% of the variation in renest clutch size and 65% of the variation in renest egg size were attributable to individual females (i.e., within-season repeatability). These observations suggest that renesting coots are constrained by time or habitat quality, but not by the amount of food or nutrient reserves available for egg production.

Key words: American coot; clutch size; egg size; Fulica americana; *nutrient limitation; renesting; supplemental feeding.*

INTRODUCTION

Loss of nest contents to predators represents a major source of mortality in many bird populations (Ricklefs 1969). Birds often cope with high rates of nest predation by producing replacement clutches following failure of initial nesting attempts (Scott et al. 1987, Nesbitt 1988, McAuley et al. 1990). Although these replacement clutches contribute substantially to annual productivity in several species of birds (Parker 1981, Stoudt 1982, Cowardin et al. 1985), there have been very few studies of the factors that affect renesting abilities of individual birds. In this paper, I document the effects of habitat conditions, food availability, previous investments in egg formation, and timing and stage of nest loss on the renesting ability of American Coots (*Fulica americana*).

STUDY AREA AND METHODS

Research was conducted from 1987–1991 at the Minnedosa Substation of the Delta Waterfowl and Wetlands Research Station (50°16′N, 99°50′W), located about 10 km SE of Minnedosa, Manitoba. The area has been described in detail by Stoudt (1982). Study area size, coot density, and number of coot nests varied among years, partly in response to changing water levels (Table 1).

Nest searches were conducted every 4–9 days (depending on year) throughout the peak nest-initiation period, but searches became more infrequent later in the breeding season due to scheduling conflicts with other research activities. Some additional visits were made to most nests between normal nest searches. In all years except 1990, coot pairs on approximately half of

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TABLE 1. Annual and seasonal variation in water depths and peak annual counts of American Coots at Minnedosa, Manitoba.

Year	Mean water depths (cm)[a] May	June	July	Coot numbers[b]
1987	84.1	74.5	60.4	165
1988	72.6	65.5	41.3	289
1989	33.5	27.1	19.9	31
1990	54.4	52.4	41.1	110
1991	48.7	48.4	31.8	107

[a] Mean water depths are from the same 12 semipermanent wetlands sampled at the same specific locations on or near the first day of each month (M. Anderson and R. Emery, pers. comm.).

[b] Coot numbers are from a standardized 21-km roadside survey of 68 wetlands (T. Arnold, unpubl. data).

the study area wetlands were provided with supplemental food. In 1987 supplemental food consisted of steam-rolled corn and/or trout chow provided in a 2 × 2 factorial design, but coots only responded to the supplemental corn (Arnold 1990). In all other years supplemental food was a mixture of steam-rolled corn, layer diet for chickens, rabbit chow, oystershell, and grit. Supplemental corn and mixed diets had similar effects on coots (Arnold 1990), and the two diets are treated as equivalent in this study.

Nest losses were both natural and experimental. Natural losses were due to predation, flooding, and abandonment (some abandonment was caused by investigator disturbance, but these losses could not be distinguished reliably from natural causes of abandonment). Experimental losses included three nests in 1988, 31 nests in 1990, and 16 nests in 1991 where I removed all eggs from active nests to induce renesting (removals were conducted under permit from the Canadian Wildlife Service). Egg removals were completed before 10:00 and included nests at all stages of the laying and incubation cycle. Nest bowls were not destroyed during experimental egg removals, and were rarely destroyed as a result of natural clutch losses, but only one out of 281 coots renested in the same nest bowl.

Nests were identified as renests and assigned to particular coots based on three criteria: (1) timing of nest initiation in relation to a previous nest loss, (2) spatial proximity of the nest to a previously destroyed nest, and most importantly, (3) comparison of egg color and marking patterns between nests (Arnold 1992). Newly found nests were identified as renests only when all available data supported such a classification. Renests had to be initiated at least one day after a previous nest was abandoned or destroyed, but nests were not excluded as potential renests if renest intervals appeared excessively long. Suspected renests also had to be adjacent to a previously destroyed nest. Adjacent was defined in terms of relative proximity, not in terms of linear distance. Thus, if another simultaneously-active nest was juxtaposed between a previously destroyed nest and a newly-initiated nest, then the newly-initiated nest was not considered a renest. Finally, coots lay uniquely-patterned eggs, which can be used to identify individual females (Arnold 1990, Lyon 1991). In 1990, I visited 43 suspected renests and compared the eggs with six pairs of eggs that I brought with me in an egg carton. One pair of eggs was from the previously destroyed adjacent clutch and represented a potential match with the suspected renest clutch; the other five pairs were from nests on distant wetlands and represented impossible matches with the renest clutch. Eggs were marked on the apex only, and I was not able to see these markings during egg comparisons. After visually comparing the six pairs of eggs with eggs in the suspected renest, I selected the pair of eggs (if any) that matched the eggs in the suspected renest. In 35 trials (81%) I selected eggs from the previously destroyed adjacent clutch as an obvious match with the suspected renest, in three trials (7%) I selected these eggs as a possible match, and in five trials (12%) I concluded that none of the eggs matched. In no cases did I conclude that eggs from another wetland matched the eggs of the suspected renest. In 1991, I compared eggs of 14 suspected renests with their supposed initial nest, but these were not blind comparisons. Thirteen comparisons supported my original designation and one comparison rejected it. Additional blind performance trials conducted in an experimental setting further verified my ability to correctly identify individual females based on egg characteristics (Arnold 1990: Appendix 2).

Inter-nest distances between initial nests and renests, and between nearest neighbors, were measured using a Hip-Chain® distance measurer (Forestry Suppliers Inc., Jackson, Mississippi). Renesting propensity was defined as the proportion of abandoned or destroyed coot nests that were subsequently replaced by a renest. A renest interval was the time, in days, between failure of a previous nest and laying of the first egg in a replacement nest. Previously, I defined renest delay as the number of non-laying days between successive nesting attempts (Arnold 1992), but this definition is inconsistent with earlier definitions of renesting delay that also include the day on which the first egg of the renest is laid (Sowls 1955). Renesting intervals in this paper are therefore one day longer than those of Arnold (1992). Clutch size refers to a complete set of eggs that was incubated for at least two days following deposition of the last-laid egg. Analyses based on "number of eggs laid" include data from complete as well as incomplete clutches. Egg size was estimated from linear measurements of length and maximum breadth (L and B, ±0.05 mm) using Hoyt's (1979) equation: Egg volume = $0.000507^*(LB^2)$. Daily egg-laying rates were based on the number of detected laying skips divided by the number of observation days (laying skips could only be detected in the interval between two nest visits, where both visits occurred during the egg-laying period); the standard error of this proportion was calculated using Johnson's (1979) equation.

I used logistic regression (PROC CATMOD, SAS Institute, Inc. 1985) to assess renesting propensity in relation to year, season (date of previous clutch initiation, date of previous clutch destruction), supplemental feeding (fed vs. control), nest loss type (natural vs. experimental), general stage of nest loss (laying vs. incubation), specific stage of nest loss (number of eggs laid or number of days since clutch completion), and previous investment in egg formation (number of eggs in preceding clutch, average egg volume of preceding clutch, total number of previous clutches, and number of eggs in all previous clutches). I used a forward-selection criterion to identify the best multi-variable predictive model in CATMOD. If two or more predictor variables were significant ($P \leq 0.05$), I also tested all possible interactions among these variables. Backward-elimination was not used for this analysis because many of the predictors were highly correlated (e.g., number of eggs in the previous clutch and total number of previous eggs) and interaction terms were therefore inestimable and/or nonsensical. I used one-way ANOVA and simple linear regression (PROC GLM) to assess the possible effects of the preceding predictor variables on length of renest intervals. I compared clutch size of renests versus initial nests using two-way ANOVA to control for year effects, and using ANCOVAs (PROC GLM) to control for variation associated with laying date and supplemental feeding (Arnold 1990). A paired t-test was used to compare mean egg size of initial clutches with their known renests. To determine whether clutch and egg sizes of renest clutches were related to the initial clutch and egg sizes of individual coots, I compared clutch and egg sizes within and among individuals using nested ANOVAs (PROC NESTED). These analyses are equivalent to within-season repeatability estimates for clutch- and egg-size variation (Lessells and Boag 1987). Means are presented ±1 SD.

Some of the data in this paper have been presented elsewhere in the context of indeterminate laying patterns in coots (Arnold 1992; data from 1990–1991 clutches that were destroyed during laying). A few analyses have been duplicated (e.g., the relationship between previous egg production and renesting intervals), but the present analyses include additional data from 1987–1989.

RESULTS

Distances between initial nests and their suspected renests were smaller than nearest-neighbor distances between simultaneously-active nests (renests: 24.3 ± 19.0 m; nearest neighbors: 80.6 ± 59.5 m; $t = 6.30$, $P < 0.0001$). Eighty percent of suspected renests were ≤40 m from their initial nest, whereas only 23% of nearest-neighbor distances were ≤40 m.

Individual coots renested from 0–4 times per season. Overall, they replaced 67.6% of lost clutches (190/281). Renesting propensity was affected by date of clutch loss ($\chi^2 = 28.48$, $P < 0.0001$), year ($\chi^2 = 15.54$, $P = 0.004$), and the interaction between these two variables ($\chi^2 = 14.18$, $P = 0.007$) (Table 2). This model provided a good fit to the data (lack-of-fit test: $\chi^2 = 99.93$, 105 df, $P = 0.62$). Renesting propensity was unaffected by supplemental feeding, number of previous clutches, number or size of eggs in the preceding clutch, total number of eggs laid in all previous clutches, number of days the preceding clutch had been incubated, and whether the preceding clutch had been destroyed naturally or experimentally ($\chi^2 < 1.38$, $P > 0.24$). Monthly renesting rates were negatively correlated with monthly changes in water levels (Fig. 1; $r = -0.63$, $P = 0.07$, $n = 9$).

Renest intervals averaged 2.1 ± 1.8 days (range 1–12, $n = 127$) following clutch loss during laying and 6.4 ± 1.1 days (range 4–9, $n = 28$) following clutch loss during incubation ($t = 12.35$, $P < 0.0001$). For clutches lost during laying, renest

TABLE 2. Annual and seasonal variation in renesting propensity of American Coots in southwestern Manitoba. Data are percent of clutches replaced (number of lost clutches).

Year	Loss date				Pooled[a]
	≤19 May	20–29 May	30 May–8 June	≥9 June	
1987	81 (16)	62 (13)	0 (1)	0 (1)	68 (31)
1988	57 (14)	50 (12)	75 (8)	25 (4)	54 (41)
1989	91 (11)	17 (12)	0 (13)	0 (2)	30 (40)
1990	100 (4)	100 (36)	79 (14)	61 (36)	81 (90)
1991	93 (15)	88 (41)	54 (13)	25 (4)	79 (79)
Pooled	82 (60)	77 (114)	49 (49)	51 (47)	68 (281)

[a] Includes 11 nests for which loss dates were imprecisely known.

intervals increased slightly with date of clutch loss, number of eggs in the preceding clutch, and total number of eggs in all previous clutches (Table 3; Fig. 2), but the latter variable was not significant after variation due to date of clutch loss was statistically controlled ($P = 0.78$). Renest intervals of clutches lost during incubation were affected by supplemental feeding ($F_{1,26} = 4.85$, $P = 0.04$), but anomalously, the small sample of supplementally-fed birds required more time to initiate renests (fed: 7.7 ± 1.5 days, $n = 3$; control: 6.2 ± 1.0 days, $n = 25$). Renest intervals were weakly correlated with date of clutch loss and incubation stage (Fig. 3; $P = 0.08$), but were unaffected by other variables (Table 3).

Renest clutches were smaller than initial clutches during all five years of the study (Table 4). However, after controlling for variation due to laying date, year, and supplemental feeding, adjusted clutch sizes of initial nests and renests were almost identical (Table 5). Clutch size of renests was unrelated to initial clutch size for 29 coots that laid 2 or more complete clutches, but this relationship became significant after controlling for variation in laying date (Table 6).

There were no differences between initial nests and renests in mean egg size (28.6 vs. 28.4 cm^3, respectively; $t_{120} = 1.28$, $P = 0.20$). Most variation in egg size was attributable to individual females (63%) or individual eggs (26%; includes effects of intraclutch egg-size variation [see Arnold 1991] and random error); only a small portion of the variation in egg size (10.7%) was attributable to different nesting attempts by the same female (Table 6).

Laying rates of renesting coots were 0.961 ±

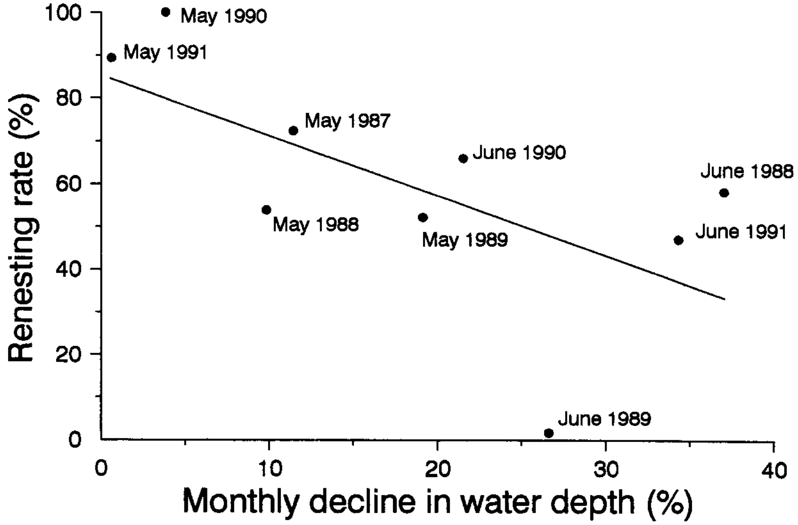

FIGURE 1. Renesting rates of American Coots (% of failed nests that were subsequently replaced, data from Table 2) in relation to seasonal water-level dynamics (% decline in mean depth, data derived from Table 1). Data points represent each month of the study in which ≥10 coot nests were destroyed. The relationship is nearly significant ($r = -0.63$, $P = 0.07$).

TABLE 3. Factors affecting renest intervals of American Coots.[a]

Effect	Clutches lost during laying				Clutches lost during incubation			
	b	*F*	*P*	*n*	b	*F*	*P*	*n*
Year	—	0.52	0.72	134	—	1.63	0.20	28
Loss date	0.05	6.42	0.01	134	0.06	3.21	0.09	28
Supplemental food	−0.47	1.70	0.19	134	1.43	4.85	0.04	28
Number of previous clutches	0.24	0.93	0.34	132	0.12	0.02	0.89	28
Number of eggs in previous clutch	0.16	5.47	0.02	134	−0.06	0.21	0.65	28
Previous egg size	−0.02	0.06	0.81	101	−0.06	0.35	0.56	28
Total number of previous eggs	0.07	3.82	0.05	134	−0.04	0.09	0.77	28
Number of days incubated	—	—	—	—	0.06	3.37	0.08	28

[a] Data are from one-way ANOVAs or simple linear regressions of renest intervals versus single predictor variables.

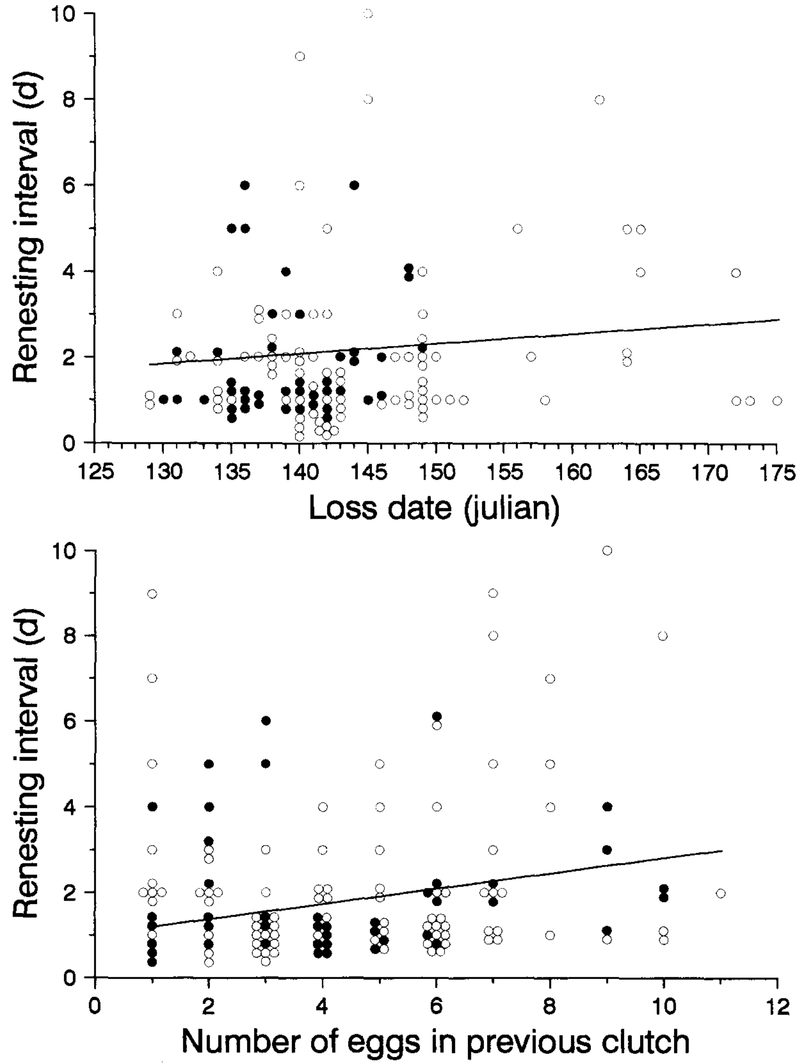

FIGURE 2. Renesting intervals of American Coots following clutch loss during egg laying. Renesting intervals increased with date of clutch loss (top) and number of eggs laid in the previous clutch (bottom), but the latter relationship was not significant if date of clutch loss was statistically controlled (see text). Filled circles indicate supplementally-fed coots and open circles indicate unsupplemented coots, but supplemental food did not affect renesting intervals (see Table 3).

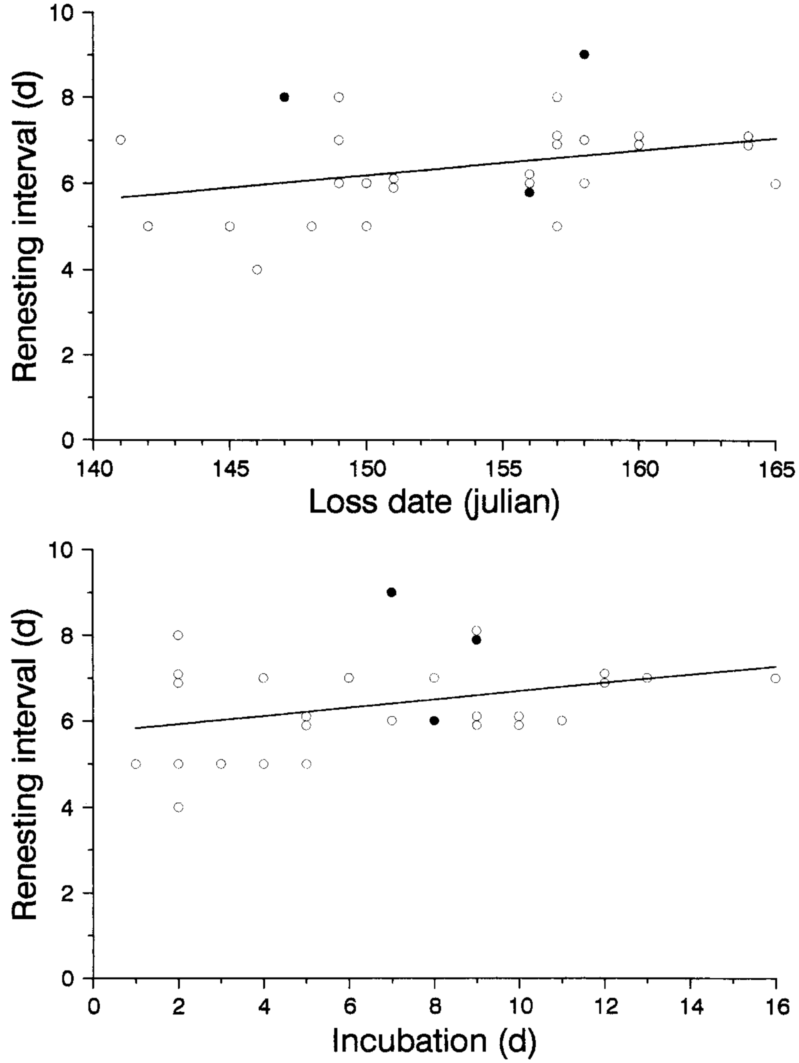

FIGURE 3. Renesting intervals of American Coots following clutch loss during incubation. Renesting intervals increased with date of clutch loss (top) and number of days the clutch had been incubated (bottom), but neither relationship was significant ($P = 0.09$ and 0.08). Filled circles indicate supplementally-fed coots, which had significantly longer renest intervals (Table 3).

0.015 (1 SE) eggs per day ($n = 156$; all years combined). This proportion did not differ from that of initial nesters (laying rate = 0.967 ± 0.004, $n = 1{,}892$ days; Fisher's Exact Test, $P = 0.78$).

DISCUSSION

Coots were persistent renesters, as shown by earlier studies (Ryder 1957, Lyon 1991). Renesting propensity was affected by date of clutch loss, year, and the interaction between these two variables. These effects may have been associated with annual and seasonal variation in water levels (Fig. 1). Water levels have also been shown to affect renesting propensity in Mallards (*Anas platyrhynchos*; Krapu et al. 1983, Cowardin et al. 1985).

Failure to renest did not result from energetic considerations associated with egg formation or incubation, because renesting propensity was unaffected by supplemental food, number of previous nests, total number of previous eggs, number or size of eggs in the preceding nest, or number of days the previous clutch had been incubated. For Mallards, research with captive birds on ex-

TABLE 4. Mean annual clutch sizes of American Coots in initial nests versus renests.

Year	Initial clutches	Renest clutches	t	P
1987	9.56 ± 1.98 (103)[a]	8.21 ± 2.08 (14)	2.38	0.02
1988	9.06 ± 2.04 (280)	7.32 ± 2.36 (19)	3.58	0.0004
1989	9.14 ± 2.55 (29)	7.14 ± 2.04 (7)	1.92	0.06
1990	9.74 ± 1.46 (69)	9.00 ± 2.74 (40)	1.84	0.07
1991	11.03 ± 2.12 (118)	9.85 ± 3.00 (26)	2.38	0.02
1987–1991[b]	9.60 ± 0.11 (599)	8.43 ± 0.21 (106)	5.17	0.0001

[a] Data are $\bar{x} \pm 1$ SD (n).

[b] Least squares means (±1 SE) controlling for significant annual variation in clutch size ($F_{4,619} = 27.02$, $P < 0.0001$). There was no interaction between year and nesting attempt ($F_{1,698} = 0.50$, $P = 0.73$).

perimental diets has revealed an effect of food quality on the likelihood of renesting (Eldridge and Krapu 1988), but for wild-nesting American Coots, the likelihood of renesting seems to be related to the chances of successfully hatching a nest and raising a brood, and these chances appear to be affected most strongly by water levels (Arnold, unpubl. data).

Coots required slightly more time to replace clutches that were lost late in the nesting season. Alliston (1979a) observed a similar pattern among renesting Redheads (*Aythya americana*). Seasonal declines in reproductive performance (e.g., clutch size, fledging success) are often attributed to declining food availability (Lack 1947; but see Daan et al. 1988). In this study, supplementally-fed coots did not have shorter renest intervals, suggesting that food availability did not proximately influence renesting. Longer renest intervals later in the nesting season may reflect a more unpredictable environment for renesting, or they might indicate the onset of the photorefractory period in part of the population.

Renest intervals also increased with the number of eggs laid in the previous clutch for females that lost clutches during egg laying (this effect was only marginally significant in Arnold 1992). This result was attributable to five coots that had exceptionally long delays (7–12 days) after losing clutches at the 7–10 egg stage (Fig. 2). Although they were classified as layers, these five birds could have laid the last egg of their clutch on the day their nests were destroyed, and hence may have had longer renesting intervals because they had to reinitiate follicle development. An alternative explanation, that these long delays were a function of large energetic expenditures towards egg production, was not supported by other analyses involving supplemental food and renest clutch size.

Coots that lost clutches during incubation required about four more days to initiate renests than did coots that lost clutches during laying. This difference was undoubtedly related to follicle development. Coots that lost clutches during laying would have had additional developing follicles with which to produce an immediate renest, whereas coots that lost clutches during incubation would have had to reinitiate follicle development. Coot follicles require from 4–7 days

TABLE 5. Adjusted mean annual clutch sizes of American Coots in initial nests versus renests. Means are least squares estimates controlling for effects of laying date, supplemental feeding, and any significant interactions.[a]

	Initial clutches	Renest clutches	Clutch effect		Date•clutch		Food•clutch	
Year	$\bar{x} \pm 1$ SE	$\bar{x} \pm 1$ SE	F	P	F	P	F	P
1987	9.31 ± 0.19	8.60 ± 0.57	6.18	0.01	6.28	0.01[b]	0.40	0.53
1988	8.89 ± 0.09	8.95 ± 0.39	0.02	0.88	0.01	0.92	0.16	0.69
1989	8.67 ± 0.30	7.85 ± 0.65	1.30	0.26	0.69	0.45	0.03	0.87
1990	9.22 ± 0.27	9.86 ± 0.38	1.46	0.22	0.01	0.91	—	—[c]
1991	10.71 ± 0.18	12.00 ± 0.41	7.33	0.008	0.73	0.39	5.05	0.03[d]
1987–1991[e]	9.32 ± 0.10	9.65 ± 0.23	1.92	0.16	1.63	0.20	1.78	0.18

[a] Date effects were highly significant in all five years; supplemental feeding effects were significant in 1987, 1988, 1991, and overall; date•feeding effects were nonsignificant (Arnold 1990, unpubl. data); other interactions are listed in the table.

[b] For initial nests: CS = 30.4 − 0.16•DATE, $r^2 = 0.44$, $P = 0.0001$; for renests: CS = 11.7 − 0.024•DATE, $r^2 = 0.01$, $P = 0.72$. DATE is julian initiation date (1 = 1 Jan.).

[c] Supplemental food was not provided in 1990.

[d] Least square means ± 1 SE: unfed initial nets, 10.26 ± 0.21; fed initial nests, 11.16 ± 0.29; unfed renests, 10.64 ± 0.48; fed renests, 13.36 ± 0.60.

[e] Year•date effect was highly significant ($F = 9.47$, $P = 0.0001$); all other interactions involving year were nonsignificant ($P > 0.59$).

TABLE 6. Repeatability of clutch size and egg size between first and second nesting attempts for individual American Coots.

Trait	Female effect				Clutch effect				% Error variance
	r_i	df	F	P	r_i	df	F	P	
Clutch size	13.4	28, 31	1.32	0.23	—	—	—	—	86.6
Adj. clutch size[a]	29.1	28, 31	1.85	0.049	—	—	—	—	70.9
Egg size	63.3	88, 119	11.93	0.005	10.7	119, 1,081	3.31	0.005	26.0

[a] Clutch size adjusted for variation in laying date, i.e., residuals from annual regressions of clutch size on laying date.

to mature (Alisauskas and Ankney 1985, Arnold 1990).

Among prairie nesting ducks (*Anas* and *Aythya*), renest intervals increased with the length of time that previous clutches were incubated (Sowls 1955, Doty et al. 1984). This is sometimes interpreted as a response to gonadal recrudescence or to depletion of nutrient reserves during incubation. This relationship also tended to occur among coots (Fig. 3; $P = 0.08$), but was much weaker than relationships derived from similar sample sizes of prairie ducks (Sowls 1955, Doty et al. 1984).

Although average clutch size of renests was smaller than that of initial nests, this difference did not persist after correcting for variation associated with laying date. A similar pattern has been observed in captive Mallards (Batt and Prince 1979), captive Northern Pintails (*Anas acuta*; Duncan 1987), wild Redheads (Alliston 1979b), and Eurasian Sparrowhawks (*Accipiter nisus*; Newton and Marquiss 1984). Many previous researchers have hypothesized that seasonal declines in clutch size are due, at least in part, to smaller clutches laid by renesting birds (see review in Murphy 1986). This hypothesis is not tenable for coots, however, because causality appears to be reversed: clutch sizes of renests are smaller because of their later laying dates. Neither do my data support the hypothesis that clutch size is smaller in renests due to energetic constraints associated with producing a previous clutch (Rohwer 1992). Elsewhere (Arnold 1992), I used some of the 1990–1991 data on continuation nesting to argue that clutch size of American Coots is not constrained by egg-formation costs (cf. Alisauskas and Ankney 1985). The larger data set employed in this paper supports this previous analysis.

Renest clutch size was independent of initial clutch size for 29 females that laid two or more complete clutches. However, after controlling for annual and seasonal variation, about 30% of the remaining clutch-size variation was attributable to individual females (i.e., within-season repeatability). Thus, a female that laid a large initial clutch was also likely to lay a large renest clutch (relative to neighboring coots initiating nests at the same time). Because females renested in the same territories, this repeatability could also represent a consistent territory effect.

Most variation in egg size was due to female effects (63%). There was no systematic difference in egg size between initial nests and renests, even though approximately 10% of the variation in egg size was associated with nesting attempt (i.e., some individuals laid smaller eggs in renests and some laid larger eggs). Although this variation with nesting attempt may have been partly due to misidentification of renest clutches, a nearly identical pattern of among-female variation in relative egg size of renests was observed among radio-marked Blue-winged Teal (*Anas discors*; Rohwer 1986).

Ankney and Afton (1988) predicted that renesting prairie ducks would have slower laying rates than would initial nesting individuals due to depletion of nutrient reserves among renesting birds. Their hypothesis does not apply to American Coots, however, as there was no difference in laying rates between initial nests and renests.

Collectively, these data showed that American Coots were persistent and capable renesters. They were constrained primarily by the amount of time remaining in the nesting season. Annual and seasonal variation in renesting performance may have been related to water levels, suggesting that coots fine-tuned their renesting effort based on the likelihood of future success in hatching a nest or raising a brood. Renesting was essentially unaffected by factors associated with previous egg production, suggesting that egg-formation costs were unimportant for shaping renesting strategies.

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