EFFECTS OF SUPPLEMENTAL FOOD ON EGG PRODUCTION IN AMERICAN COOTS

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Abstract.—Previous researchers have suggested that egg production in American Coots (*Fulica americana*) is limited by food availability for the laying female. I studied patterns of variation in laying date, clutch size, egg size, and laying rate of American Coots from 1985–1991 in southwestern Manitoba. Annual variation was evident for all four of these traits. Clutch size declined seasonally during most years, but the rate of decline differed markedly among years. These temporal patterns of variation in laying performance provided a template for assessing the relative importance of food availability. I provided coots with supplemental food during four breeding seasons (1987–1989 and 1991) to determine whether variation in laying performance could be attributed to food availability for the laying female. Supplementally fed coots nested one to two days earlier and laid about one more egg than did controls, but this represented only 1 and 3% of the observed variation in laying date and clutch size, respectively. In contrast, annual effects accounted for 12% of the variation in laying date, and annual plus seasonal effects accounted for 38% of the variation in clutch size. Supplemental food did not affect egg size or laying rate. Feeding effects were independent of year and date, suggesting that most natural variation in laying performance was independent of food availability. I conclude that reproduction in American Coots was weakly limited by food availability for the laying female. Alternatively, supplemental food may have caused female coots to modify their laying date and clutch size in anticipation of future food abundance during the brood-rearing period, but this hypothesis will be difficult to test. *Received 14 April 1993, accepted 19 November 1993.*

Lack (1947) hypothesized that reproductive rates of birds with parentally fed young are limited by food availability during the brood-rearing period; however, the majority of brood-manipulation studies have demonstrated that parent birds can successfully raise experimentally enlarged broods (reviewed by Lessells 1986, Ydenberg and Bertram 1989, Arnold 1990, Dijkstra et al. 1990, VanderWerf 1992). Such results have often been attributed to trade-offs between brood size and adult or postfledging survival, but even these explanations cannot fully explain patterns of clutch-size variation in several well-studied bird populations (Nur 1986, 1988, Boyce and Perrins 1987, Reid 1987b, Gustafsson and Sutherland 1988, Pettifor et al. 1988, Daan et al. 1990, Hochachka and Smith 1991). The inability of the brood-rearing hypothesis to fully explain clutch-size variation has led some researchers to reexamine reproductive costs associated with egg formation (reviewed by Mur-

phy and Haukioja 1986, Martin 1987). Energetic costs associated with egg formation are often regarded as a critical limiting factor among birds with precocial self-feeding young (Lack 1968, Ankney et al. 1991, but see Arnold and Rohwer 1991), but egg-formation costs have rarely been implicated for birds with parentally fed young (but see Jones and Ward 1976, Winkler 1985). However, if birds time their breeding efforts to coincide with periods of peak food abundance for nestlings, then they must necessarily begin laying eggs when food is relatively less abundant (Lack 1956, Perrins 1970). Thus, although the daily energetic costs of egg formation for altricial birds are less than those incurred during brood rearing (Rohwer 1992), egg-formation costs might be extremely high in terms of relative energy availability (Perrins 1970). As Daan et al. (1988) have pointed out, Perrins' hypothesis implies that food limitation is a proximate constraint, because birds would increase their reproductive success if they could produce more eggs. One common method of testing whether egg production is limited by nutritional constraints is to manipulate food availability for the laying female. Although most supplemental-feeding experiments have dem-

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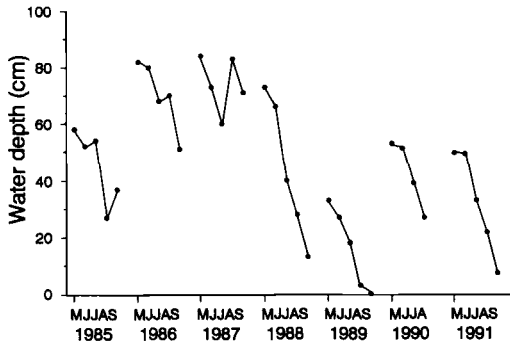
Fig. 1. Annual and seasonal variation in water depths of semipermanent wetlands at Minnedosa, Manitoba. Data points represent means from 12 wetlands sampled at permanent locations on or near first day of each month (May, June, July, August and September).

onstrated that birds advance their laying date in response to additional food, very few of these studies have demonstrated a concomitant increase in clutch or egg size (reviewed by Daan et al. 1988).

Here I report the results of supplemental feeding experiments conducted with wild-nesting American Coots (*Fulica americana*). Based on patterns of nutrient reserve usage, Alisauskas and Ankney (1985) concluded that clutch size and laying date in American Coots were constrained by nutrient availability for laying females. In contrast, Hill (1988) argued that female coots altered egg size, but not clutch size or laying date, in response to fluctuations in food availability during the laying period. In this paper, effects of supplemental food on laying date, clutch size, egg size, and laying rate are evaluated within the context of annual and seasonal variation in these traits.

STUDY AREA AND METHODS

Study area.—I studied American Coots from 1985–1991 on a study area approximately 10 km SW of Minnedosa, Manitoba, Canada (50°16′N, 99°50′W). The study area contains numerous small (0.1–3.0 ha) natural-basin wetlands that are dominated by cattail (*Typha* spp.) or, more rarely, by hardstem bullrush (*Scirpus acutus*). Wetland levels at the beginning of the breeding season were: relatively high in 1986–1988; relatively low in 1985, 1990, and 1991; and extremely low in 1989 (Fig. 1). These assessments are all relative to other years of the study. In comparison to long-term (1961–1991) water-level fluctuations, all years except 1986 were drier than average, and 1989 was

the driest year on record (U.S. Fish and Wildlife Service unpubl. data). Water levels declined seasonally in all years of the study, but these declines were most severe during 1988–1991 (Fig. 1). Upland habitats in the study area have been modified extensively by agriculture (primarily small grains and oil seeds). The study area has been described in detail by Stoudt (1982).

Study animal.—American Coots are monogamous (Fredrickson et al. 1977), and they defend exclusive territories that are used for all activities of the breeding cycle (Gullion 1953). Nests are constructed over-water in dense stands of emergent vegetation (primarily cattail and bullrush). Coots have one of the most variable clutch-size distributions of any bird (Arnold 1990). Energetic costs of clutch formation are high in coots (Alisauskas and Ankney 1985), and most begin laying well before the seasonal emergence of submerged aquatic macrophytes, which are their primary food (Jones 1940). Coots begin incubation midway through laying and, therefore, hatch is asynchronous (Fredrickson et al. 1977). Chicks are precocial and can leave the nest within hours of hatching, but they are critically dependent on their parents for food for at least the first two weeks posthatching (Ryan and Dinsmore 1979, Desrochers and Ankney 1986, Driver 1988). Chicks gradually acquire foraging skills of their own over the next two to three weeks, and fledging occurs at 60 to 70 days (Fredrickson et al. 1977, Desrochers and Ankney 1986).

Supplemental feeding.—Supplemental feeding experiments were conducted during 1987–1989 and 1991. In 1987, steam-rolled corn and trout chow (Martins 84G Grower Pellets; Martin Feed Mills, Elmira, Ontario) were provided independently in a 2 × 2 factorial design (presence or absence of corn and presence or absence of trout chow). Two varieties of supplemental food were employed to test whether coots were limited by lipid and/or by protein (Hill 1989, Ankney and Alisauskas 1991). Corn is very high in carbohydrates and provides an excellent diet for lipogenesis, whereas trout chow contains greater than 40% crude protein and includes a full complement of amino acids. Coots readily consumed supplemental corn, but not trout chow. Because trout chow had little or no effect on reproductive performance in coots (detailed analyses are provided in Arnold 1990), I treated the 1987 data as if only supplemental corn was provided. In 1988, 1989, and 1991, only one food supplement was provided; fed birds received a mixture of steam-rolled corn, rabbit chow (Nutrena Bunny Booster; Cargill Ltd., Winnipeg, Manitoba), layer diet for chickens (Co-op Layer Diet 20; Federated Cooperatives Ltd., Saskatoon, Saskatchewan), oyster-shell, and grit in an approximate 20:10:10:1:1 ratio. Complete nutritional information on each food supplement is provided in Arnold (1990:appendix 1).

Supplemental food was placed on floating platforms located within the territories of breeding coot

TABLE 1. Numbers of study ponds, numbers of American Coot nests, and dates that supplemental-feeding experiments were initiated at Minnedosa, Manitoba, 1987–1991.

	Unsupplemented			Supplemented			Date feeding began	No. days before laying[a]
Year	No. ponds	No. nests	Nests/ pond	No. ponds	No. nests	Nests/ pond		
1987	33	76	2.3	23	52	2.3	27 April	20
1988	62	205	3.3	56	213	3.8	27 April	21
1989	16	32	2.0	7	21	3.0	2 May	14
1991	24	98	4.1	16	71	4.4	27 April	21

[a] Number of days between onset of supplemental feeding and mean nest initiation date of unsupplemented pairs (Table 2).

pairs. Feeding began in late April or early May, after most birds had settled on territories, but two to three weeks before they began nesting (Table 1). Platforms were refilled every three to four days with approximately 0.75 kg of food; most visits occurred during regularly scheduled nest searches. In order to prevent food piracy among neighboring coot pairs, all pairs on a wetland received the same food supplement (i.e. food supplements were randomly assigned to wetlands, rather than coot pairs). Nest densities did not vary in response to feeding (Table 1; $t \leq 1.16$, $P \geq 0.20$ for each year), suggesting that supplemental food did not cause coots to move among wetlands. Coots were observed feeding from platforms on numerous occasions each year, but no quantitative data on frequency of feeder use were collected.

Reproductive performance.—Coot nests were found during systematic searches of emergent wetland vegetation conducted every four to six days. Most nests were visited one or more times during laying, and at each visit any unmarked eggs were numbered with permanent black ink. Initiation dates typically were determined by backdating from incomplete clutches found during laying. Occasionally, initiation dates were estimated by backdating from known hatching dates, or by floating or candling eggs to determine stage of embryo development (Westerkov 1950, Weller 1956).

Clutch size was determined two days after the last egg had been laid, provided the clutch was being incubated. Clutch size was adjusted for known cases of egg loss or brood parasitism. Parasitic eggs were identified based on: excessive laying rates (i.e. > one egg per day); eggs added more than two days after host clutch completion; or eggs that clearly mismatched the egg color and marking pattern of the host clutch (Arnold 1990, Lyon 1991). Renests were identified based on spatial and temporal proximity to nests that had been destroyed previously, and based on visual comparison of egg characteristics (Arnold 1993). Only data from first nesting attempts are included; data from renests are presented elsewhere (Arnold 1993). Eggs were measured with dial calipers to determine length and maximum breadth (L and B, ± 0.05 mm), and egg volume (V; cm³) was estimated

using Hoyt's (1979) equation:

$$V = 0.000507LB^2. \qquad (1)$$

This measure of egg size is highly correlated with fresh egg mass, dry egg mass, and energy content (Arnold et al. 1991). Analyses of egg-size variation are based on the mean volume for all measured eggs in a clutch (intraclutch egg-size variation has been treated elsewhere; Arnold 1991). Daily laying rates were calculated as the number of eggs laid divided by the number of days that nests were observed during laying (laying rates could only be calculated for interval between two nest visits, when both visits occurred during laying period). Coots lay at night (Sooter 1941, Arnold unpubl. data), whereas I visited nests during the day, so estimates of daily laying rates were not confounded by timing of nest visits. The standard error (SE) of daily laying rate was calculated using Johnson's (1979) formula.

Statistical analyses.—Annual variation in laying date, clutch size, and egg size was assessed using one-way ANOVA (unsupplemented pairs only). Supplemental feeding effects were evaluated for each year separately using one-way ANOVAs, and for all years combined using a two-way ANOVA (data from 1985, 1986, and 1990 were excluded because no food supplements were provided). Seasonal variation in clutch size was assessed using ANCOVA; year and/or supplemental feeding were the factor variables and laying date was the covariate. In analyses employing two or more predictor variables, higher-order interaction terms were also assessed. Test statistics for these analyses were based on Type III sums of squares (GLM procedure; SAS Institute 1985). Nonsignificant effects were deleted, beginning with the highest-order interaction terms, and probability values were recalculated for the remaining predictor variables. Nonsignificant predictors were deleted until all remaining variables were significant or included within a significant higher-order interaction term. I used F_{max} tests (Sokal and Rohlf 1973) to test for homogeneity of variance among years, and between fed and control birds. Annual variation in laying rates was evaluated using categorical data analysis (SAS CATMOD procedure). Within-year comparisons of supplementally
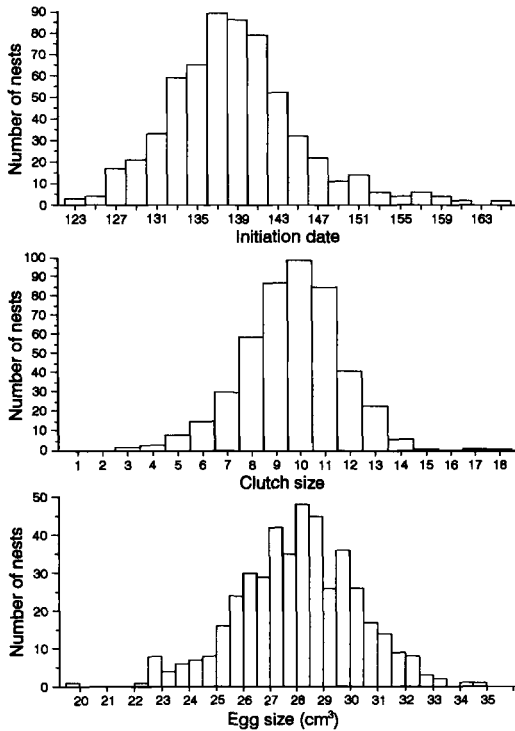
Fig. 2. Observed variation in nest initiation date (Julian date; 123 = 3 May, 163 = 12 June), clutch size, and egg size for American Coots nesting near Minnedosa, Manitoba from 1985–1991. Data from unsupplemented first-nesting attempts. Egg size is mean value for all measured eggs per clutch.

fed versus control nests were based on Fisher's exact tests. Means are presented ±1 SD, except for least-square means (which control for variation attributable to one or more covariates); these are presented ±1 SE. Regression lines were estimated using ordinary least squares. All statistical tests were two-tailed.

RESULTS

Natural variation.—First nesting attempts were initiated over a 42-day interval, but most nests (76%) were initiated in a two-week period between 11 and 24 May (Fig. 2). Completed clutch size ranged from 3 to 18 (Fig. 2; CV = 21.0%); however, the majority of coots (80%) laid 8 to 12 eggs. Mean egg size was less variable than clutch size (Fig. 2; CV = 7.9%), ranging from 19.5 to 34.5 cm^3 (a 1.8-fold difference). Clutch size accounted for 90% of the variation in total clutch volume (clutch size × mean egg size), whereas egg size accounted for the remaining 10%.

Mean annual date of clutch initiation varied by up to 10.5 days during the seven years of this study (Table 2; $F = 16.15$, $P = 0.0001$, unfed coots only). Variance in onset of nesting also differed among years ($F_{max} = 5.32$, $P < 0.01$); the 1987 nesting season was about twice as extended as the 1985 and 1991 seasons (Table 2). Annual variation was even stronger for mean clutch size, which varied by up to 2.6 eggs among years (Table 2; $F = 25.73$, $P = 0.0001$). Although it was statistically significant, annual variation in mean egg size was less pronounced than for laying date or clutch size (Table 2, $F = 3.89$, $P = 0.0008$). Laying rates also varied annually, from 1.00 eggs per day in 1985 to 0.94 eggs per day in 1987 (Table 3; $X^2 = 20.88$, $P = 0.002$). Annual changes in mean clutch and egg size were not accompanied by annual changes in variance ($F_{max} = 1.58$ and 2.15, respectively; $P > 0.05$).

Annual laying rates were positively correlated with mean annual clutch and egg sizes ($r = 0.86$, $P = 0.01$, $n = 7$ for both variables), but all other among-year correlations involving mean laying date, clutch size, egg size, and laying rate were nonsignificant ($P \geq 0.11$). Annual variations in laying date, clutch size, egg size, and laying rate were not correlated with any measured aspects of spring arrival chronology, breeding density, spring temperatures, or wetland water levels (Table 4; only 1 of 32 correlations was significant).

Clutch size declined seasonally in all years except 1985 and 1986 (Fig. 3). The lack of effect in 1985 was likely an artifact of small sample size and a short nesting season, because clutch size appeared to decline very steeply that year (Fig. 3). Although laying date accounted for much of the variation in clutch size within and among years, laying date did not ultimately determine clutch size because the shape of this relationship differed significantly among years (i.e. there were significant differences in slopes and intercepts among the annual regressions of clutch size on laying date; Table 5). Egg size increased slightly with clutch size ($r = 0.22$, $P = 0.0001$, $n = 350$; all years combined). There was a suggestion of a weak seasonal decline in egg size ($r = -0.11$ to -0.45) during all years except 1987 ($r = 0.31$), but these trends were not significant ($P > 0.13$) except for 1989 ($P = 0.02$). Laying rates did not vary seasonally ($F_{1,423} = 2.33$, $P = 0.13$), but laying skips were more frequent among coots laying smaller clutches ($F_{1,355} = 4.40$, $P = 0.04$) and smaller eggs ($F_{1,368} = 19.79$, $P = 0.0001$).

TABLE 2. Laying date, clutch size, and egg size of American Coots in relation to year and supplemental feeding.[a]

Year	Unsupplemented	Supplemented	F[b]
	Laying date		
1985	130.7 ± 3.6 (11)	—	—
1986	135.0 ± 4.6 (35)	—	—
1987	134.6 ± 8.3 (72)	131.6 ± 5.8 (52)	5.24*
1988	138.5 ± 6.5 (189)	137.4 ± 6.9 (169)	2.09
1989	136.3 ± 4.5 (28)	135.2 ± 6.4 (17)	0.39
1990	141.2 ± 9.1 (91)	—	—
1991	137.7 ± 3.8 (97)	136.2 ± 4.6 (71)	5.15*
Pooled[c]	136.7 ± 0.4 (386)	135.2 ± 0.4 (309)	9.70**
	Clutch size		
1985	11.00 ± 1.63 (13)	—	—
1986	11.05 ± 1.63 (91)	—	—
1987	9.02 ± 1.87 (61)	10.31 ± 1.93 (42)	11.61***
1988	8.49 ± 1.80 (138)	9.35 ± 1.95 (142)	14.44***
1989	8.65 ± 1.77 (17)	9.58 ± 3.32 (12)	0.97
1990	9.71 ± 1.49 (69)	—	—
1991	10.62 ± 1.97 (77)	11.76 ± 2.45 (41)	7.43**
Pooled[a]	9.24 ± 0.14 (294)	10.23 ± 0.16 (237)	31.47***
	Egg size		
1985	28.79 ± 1.69 (11)	—	—
1986	28.09 ± 1.86 (43)	—	—
1987	27.33 ± 2.06 (65)	27.73 ± 2.30 (48)	0.98
1988	27.81 ± 2.30 (141)	27.88 ± 2.15 (114)	0.07
1989	27.12 ± 2.48 (29)	26.99 ± 1.61 (16)	0.03
1990	28.64 ± 2.18 (120)	—	—
1991	28.16 ± 2.16 (76)	27.95 ± 2.52 (59)	0.26
Pooled[a]	27.60 ± 0.14 (311)	27.65 ± 0.16 (237)	0.09

[a] $\bar{x}$ ± SD (n).

[b] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; others not significant ($P > 0.05$).

[c] Common years only (1987–1989, 1991); data are least-squares $\bar{x}$ ± SE (n) controlling for significant year effects. No year-by-feeding interaction effects ($F = 0.85$, 0.41, and 0.40 for laying date, clutch size, and egg size, respectively; $P \geq 0.46$).

Supplemental feeding.—Laying date was significantly advanced among supplementally fed coots in 1987, 1991, and overall (Table 2). Similar trends were apparent in 1988 and 1989. Supplementally fed coots laid from 1.0 (1989) to 3.0 (1987) days earlier than did controls, but this slight annual variation in feeding effect was not significant (year-by-feeding interaction effect, $F = 0.85$, $P = 0.46$). On average, fed coots initiated nesting 1.5 days earlier than controls. Supplemental feeding led to reduced variance in laying date in 1987 ($F_{max} = 2.09$, $P < 0.01$),

TABLE 3. Laying rate (eggs per day) of American Coots in relation to year and supplemental feeding.

Year	Unsupplemented			Supplemented			P[c]
	$\bar{x}$ ± SE[a]	Nests	Days[b]	$\bar{x}$ ± SE	Nests	Days	
1985	1.000 ± 0.006[d]	16	114	—	—	—	—
1986	0.986 ± 0.008	38	222	—	—	—	—
1987	0.939 ± 0.017	39	198	0.973 ± 0.012	36	189	0.14
1988	0.953 ± 0.012	79	297	0.974 ± 0.009	73	313	0.19
1989	0.958 ± 0.041	16	24	0.939 ± 0.042	9	33	1.00
1990	0.983 ± 0.010	41	174	—	—	—	—
1991	0.983 ± 0.007	71	405	0.973 ± 0.010	48	259	0.42
Pooled[e]	0.963 ± 0.006	205	924	0.972 ± 0.006	166	794	0.34

[a] Laying rate = number of eggs/observation days; SE = ([(days − eggs) × eggs]/days³)[0.5]. After Johnson (1979).

[b] Number of observation days on which laying skips could have been detected had they occurred.

[c] Fisher's exact test (two-tailed) comparing unsupplemented and supplemented coots.

[d] SE calculated assuming 0.5 laying skips.

[e] Likelihood-ratio chi-square test of annual variation; for common years (1978–1989, 1991), there was no year-by-food interaction effect ($X^2 = 3.98$, $P = 0.26$).

TABLE 4. Annual variation in timing of spring coot migration (Julian dates), coot population size, spring temperature (°C), semipermanent pond depth (cm), and total pond counts for Minnedosa study area and southwestern Manitoba (top), and correlations with annual mean laying date, clutch size, egg size, and laying rate of unsupplemented coots (bottom).

| Year or variable | Minnedosa | | | | | | SW Manitoba | |
	Earliest arrival date	Peak arrival date	Peak coot count	April temper-ature	May temper-ature	May pond depth	May pond count[a]	May coot count[a]
				Statistics				
1985	105	—[b]	—[b]	4.3	10.5	58.1	103.6	10.3
1986	105	—[b]	—[b]	2.5	11.5	82.3	202.2	50.6
1987	105	119	210	6.7	12.7	84.1	133.9	41.1
1988	99	124	322	3.3	11.8	72.6	113.6	72.4
1989	109	129	42	2.3	11.4	33.5	47.2	9.8
1990	109	133	130	0.9	8.9	54.4	145.2	41.5
1991	105	136	118	5.0	11.8	48.7	114.0	41.3
				Correlations with				
Laying date	0.10	0.60	0.03	−0.51	−0.33	−0.20	0.07	0.52
Clutch size	0.13	0.74	−0.37	0.02	−0.24	0.10	0.51	−0.21
Egg size	0.02	0.63	0.07	−0.27	−0.70	0.00	0.38	−0.02
Laying rate	0.23	0.96**	−0.46	−0.35	−0.61	−0.24	0.26	−0.31

[a] Data from stratum 40 air-ground waterfowl surveys (U.S. Fish and Wildlife Service and Canadian Wildlife Service unpubl. data); values in thousands.

[b] Surveys not conducted in 1985 and 1986; remaining data are from Arnold (in press).

but patterns were inconsistent and nonsignificant during the other three years (Table 2).

Supplementally fed coots laid significantly larger clutches in 1987, 1988, 1991, and overall (Table 2). Small samples in 1989 precluded a significant result, but the effect size was similar to other years (year-by-feeding interaction effect, $F = 0.41$, $P = 0.74$). On average, fed coots laid one more egg than did controls. Supplemental food did not lead to reduced variance in clutch size (Table 2); in 1989, clutch-size variance was significantly larger among fed birds ($F_{max} = 3.52$, $P < 0.05$). Because fed coots initiated nesting about 1.5 days earlier than controls, and because clutch size declines season-ally, part of the increase in mean clutch size among supplementally fed coots could be due to earlier nesting, and not to larger clutch size per se (see Daan et al. 1988). Therefore, I used ANCOVAs to control for laying date while comparing clutch sizes of fed and control coots (Fig. 4). These analyses showed that about 30% of the increase in clutch size of fed coots was due to an advancement of laying date and about 70% was attributable to a direct effect on clutch size (Table 6). Supplemental food did not affect rates of seasonal decline in clutch size (Table 6; date-by-feeding interaction effects are all nonsignificant), even though these rates varied among years (Fig. 3).

TABLE 5. Annual covariation in laying date and clutch size for first-nesting attempts of American Coots at Minnedosa, Manitoba (unsupplemented coots only).

| Year | Clutch size[a] | Regression of clutch size on Julian laying date | | | |
		a	b ± SE	r²	P
1985	9.41 ± 2.19	39.21	−0.217 ± 0.233	0.110	0.38
1986	11.05 ± 0.29	11.63	−0.004 ± 0.056	0.000	0.94
1987	8.60 ± 0.25	24.91	−0.119 ± 0.027	0.350	0.0001
1988	8.69 ± 0.13	25.89	−0.125 ± 0.021	0.233	0.0001
1989	8.23 ± 0.41	75.39	−0.488 ± 0.104	0.613	0.0003
1990	10.23 ± 0.25	26.39	−0.118 ± 0.040	0.123	0.005
1991	10.70 ± 0.17	46.84	−0.263 ± 0.048	0.286	0.0001

[a] Least-square clutch size, $\bar{x} \pm 1$ SE, controlling for among-year variation in laying date (year effect, $F = 2.11$, $P = 0.06$; date effect, $F = 10.85$, $P = 0.001$; year-by-date interaction effect, $F = 2.60$, $P = 0.03$).
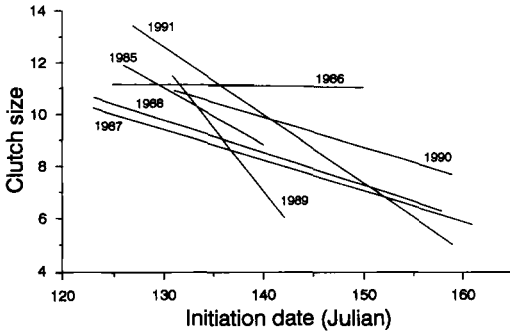
Fig. 3. Seasonal variation in clutch size of American Coots nesting at Minnedosa, Manitoba. Data for unsupplemented first-nesting attempts. Lines represent least-squares regressions of clutch size on Julian nest initiation date (Table 5; 120 = 30 April, 160 = 9 June). Slopes were significantly different from zero in all years except 1985 and 1986; annual variation among slopes and intercepts was significant (Table 5).

Egg size was unaffected by food supplementation (Table 2). Although egg size was positively correlated with clutch size for unsupplemented coots (see above), this relationship did

not occur in supplementally fed coots ($r = 0.03$, $P = 0.66$, $n = 171$; all years combined). This difference between unsupplemented and supplemented coots was significant (food-by-clutch size interaction, $F = 6.05$, $P = 0.01$; common years only). Laying rates were unaffected by supplemental food, although results were somewhat suggestive in 1987 and 1988 (Table 3).

DISCUSSION

Natural variation in reproductive performance.— There was enormous among-individual variation in the laying performances of female coots: first nesting attempts were initiated over a 42-day interval, clutch size ranged from 3 to 18, and egg size varied from 19.5 to 34.5 cm³. The extent of variation in these three traits is extremely high in comparison to other North Temperate birds (Arnold 1990, unpubl. data), suggesting that selection pressures acting on coots are more variable than those acting on other species of birds.
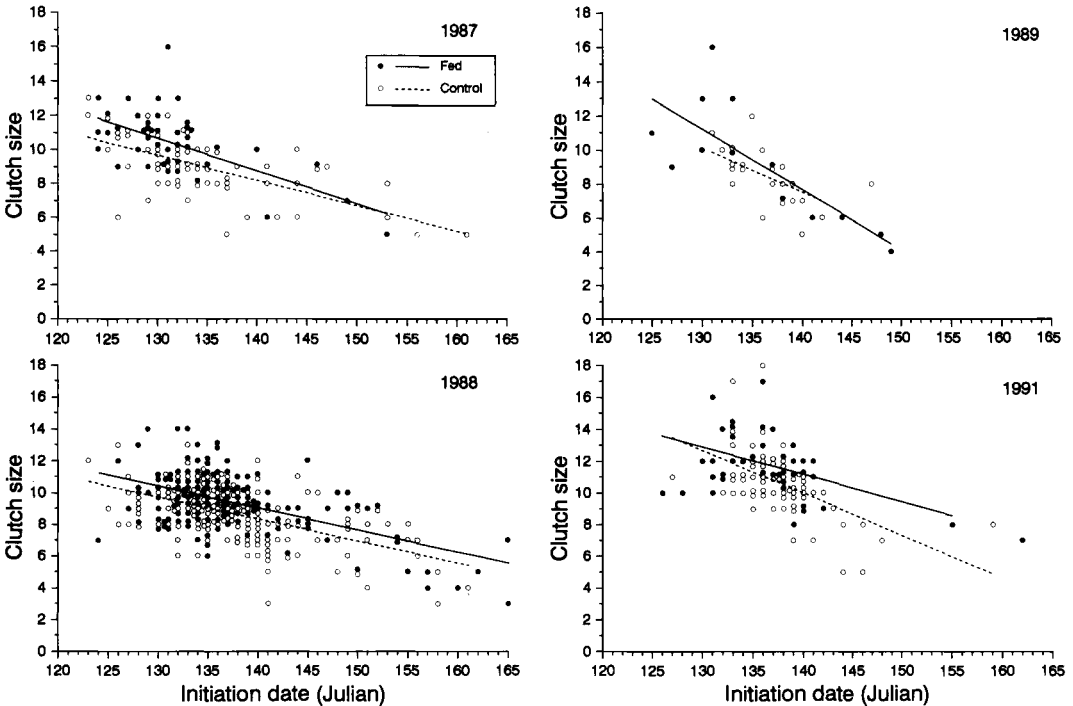
Coots exhibited significant annual variation

Fig. 4. Seasonal variation in clutch size for supplemented and unsupplemented American Coots in 1987, 1988, 1989, and 1991 supplemental-feeding experiments. Supplemental food increased clutch size in all years except 1989, but food did not affect rate of seasonal decline in clutch size during any year. Initiation dates are Julian dates (120 = 30 April, 165 = 14 June).

TABLE 6. Effects of year, laying date, and supplemental food on clutch size of American Coots at Minnedosa, Manitoba.[a]

Effect	F
Year[b]	5.13**
Laying date[c]	123.85***
Supplemental food[d]	27.25***
Year × date[e]	4.60**
Year × food	0.29
Date × food	0.11
Year × date × food	1.57
Model[f]	44.83***

**, $P < 0.01$; ***, $P < 0.001$; others not significant ($P > 0.05$).

[a] First-nesting attempts only; data are from 1987–1989 and 1991 ($n = 496$).

[b] Least-square $\bar{x} \pm$ SE: (1987) 9.05 ± 0.18; (1988) 9.03 ± 0.10; (1989) 8.59 ± 0.31; (1991) 11.23 ± 0.15. 1991 differed significantly from all other years ($P < 0.0001$).

[c] Clutch size declined by 0.213 eggs per day, on average.

[d] Least-square $\bar{x} \pm$ SE: (unfed) 9.28 ± 0.12; (fed) 10.10 ± 0.14.

[e] Rate of seasonal decline in clutch size in 1989 significantly larger than in all other years ($P < 0.05$).

[f] Model $R^2 = 0.424$.

in timing of breeding, clutch size, egg size, and laying rate. Annual variation in these traits is often attributed to annual fluctuations in food supply (e.g. Hussell and Quinney 1987), but I did not assess natural food abundance in this study. Annual changes in laying patterns of wetland birds have also been correlated with migrational chronology, spring temperatures, and wetland conditions (Krapu et al. 1983, Hammond and Johnson 1984, Perdeck and Cavé 1989). For example, Perdeck and Cavé (1989) demonstrated that early spring temperatures could explain approximately one-half of the annual variation in timing of breeding in a 21-year study of European Coots (*F. atra*) breeding in The Netherlands. However, the only significant correlation in this study was between laying rate and peak arrival date ($r = 0.96$, $P < 0.01$), and this relationship was likely spurious (32 different correlations are presented in Table 4). Annual variation in reproductive performance has also been correlated with population density (e.g. Arcese and Smith 1988, Perrins and McCleery 1989), but no such trends were apparent in my study. Alternatively, annual variation might reflect changes in the population age structure (Crawford 1980), or variation in the amount of nutrient reserves that coots brought with them from the wintering grounds (Alisauskas and Ankney 1985), but data from 1987 through 1989 did not support either of these hypotheses (Arnold 1990). Although annual variation in laying date and clutch size

was pronounced, it was not related to any measured environmental or demographic characteristic. Low statistical power is the most likely explanation for these results: with seven years of data, correlations would have to exceed 0.75 (or be less than −0.75) to be statistically significant. Most studies that have documented statistically significant correlates of annual variation in reproductive performance have continued for 10 or more years (e.g. Arcese and Smith 1988, Perdeck and Cavé 1989, Perrins and McCleery 1989).

Clutch size declined seasonally in six of seven years (although 1985 decline was not significant). Clutch size averaged 10 to 13 eggs at the beginning of each nesting season (during first two weeks of May), but then declined at different rates and for different lengths of time among years, such that clutch size averaged anywhere from 5 to 11 eggs at the end of the nesting season (Fig. 3). Seasonal declines in reproductive performance often are interpreted as responses to seasonally declining food resources, but the few studies that have simultaneously quantified both sets of variables do not provide much support for this hypothesis (reviewed in Daan et al. 1988; see also Murphy 1986, Hussell and Quinney 1987). Adult coots are primarily herbivorous (Jones 1940), although chick diets also include numerous aquatic invertebrates (Driver 1988). These food types tend to increase seasonally in North Temperate wetlands (Rohwer 1992, Arnold unpubl. data), while clutch size and brood size are concurrently declining. Thus, food availability does not appear to explain the seasonal decline in clutch size (see also results and discussion on supplemental feeding).

Although mean annual clutch size did not vary with annual fluctuations in water levels (Table 4), the annual rate of clutch size decline was negatively correlated with average May water depth (Fig. 5), suggesting that late-nesting coots may reduce their clutch size in response to lowered prospects for successful reproduction. For coots nesting at Minnedosa, nest success and brood survival were reduced during drought years, and nest success declined seasonally (unpubl. data). Coots may have reduced their clutch size later in the season in an attempt to complete their nesting attempts before habitat conditions further deteriorated (e.g. Clark and Wilson 1981), or they may have reduced their amount of parental investment be-

cause late hatched offspring have reduced likelihood of recruiting into the breeding population (Daan et al. 1988, 1990).

Effects of supplemental food.—Although I did not collect systematic data on feeder use by coots, several lines of evidence indicate that coots consumed substantial amounts of supplemental food. First, over 5,000 kg of supplemental food were dispensed during the four years and, aside from blackbirds (*Agelaius phoeniceus* and *Xanthocephalus xanthocephalus*), coots were the most frequent visitors to feeders during incidental observations. Second, I collected samples of male and female coots throughout the breeding season, and supplementally fed individuals had two to three times more body fat than control birds (Arnold 1990). Third, liver tissues of samples of fed and control birds were subjected to stable-isotope analysis (Hobson and Clark 1992), and coots with access to supplemental food had $^{13}C:^{12}C$ ratios that were characteristic of corn-fed birds and markedly different from control birds (Hobson et al. unpubl. data). Finally, supplemental food had strong effects on several aspects of breeding performance (e.g. brood survival and fledging mass; Arnold 1990, unpubl. data), albeit not on any of the factors discussed in this paper. Supplemental feeding was therefore effective and, thus, I conclude that the weak effects of supplemental food on clutch size and laying date can be attributed to the relative unimportance of food limitation during laying.

For the most part, supplemental food had little effect on the variance associated with laying date, clutch size, or egg size (1987 laying date and 1989 clutch size were the only 2 exceptions in 12 comparisons). This implies that any effects of supplemental food tended to occur among all supplemented individuals, rather than a particular subset of individuals (Schultz 1991). Thus, advancements in laying date or increases in clutch size were not restricted to individuals that otherwise would have done poorly (such a scenario occurred in Arcese and Smith's [1988] experiment with Song Sparrows, *Melospiza melodia*). A corollary to this argument suggests that most among-individual variation in laying date, clutch size, and egg size is not related to food availability for laying American Coots.

Supplementally fed coots nested approximately 1.5 days earlier and laid about one more egg than did unsupplemented coots. On average, nest success declined by 2% over a 1.5-day period, but fledging success and fledging mass
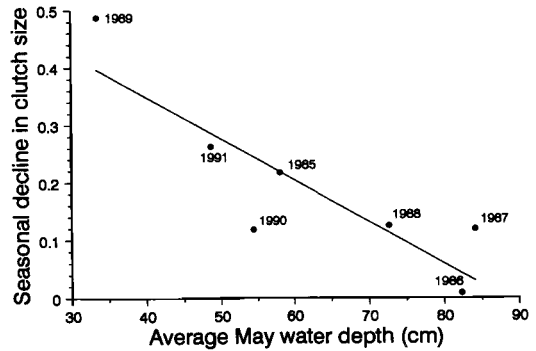
Fig. 5. Rate of seasonal decline in clutch size (eggs/day) of American Coots in relation to average water depth (cm) in May ($r = 0.87$, $P = 0.01$, $n = 7$).

were unchanged (unpubl. data). Hence, this slight advancement in laying date probably had minimal influence on nest and brood survival, given that the nesting season spanned up to 40 days in most years. However, average clutch size would have declined by 0.3 eggs in 1.5 days (Table 6; extremes range from 0.0 to 0.7 based on 1986 and 1989 data, respectively). Thus, the one-egg increase in clutch size among fed birds was due to an indirect effect of earlier nesting (0.3 eggs), as well as a direct effect of larger clutch size for any given laying date (0.7 eggs). I do not regard this clutch-size effect as trivial, but it is not easily interpreted either. Fed coots may have increased their clutch size because they were better able to produce eggs, or because they use current food availability to predict future availability and therefore "anticipated" that they would be able to raise more chicks (Daan et al. 1988). Based on other evidence suggesting that coots are not constrained by their ability to produce additional eggs (Arnold 1990, 1992a), but may be constrained by their ability to raise additional chicks (unpubl. data), I suspect that supplementally fed coots adjusted their clutch size because they anticipated better conditions for brood rearing. However, it will be very difficult to design field experiments capable of discriminating between these two contrasting explanations, given that clutch size increased by only one egg.

My findings differed from those of Horsfall (1984) and Hill (1988), who provided food supplements to nesting European Coots and American Coots, and found no effects of supplemental food on laying date or clutch size. Hill (1988) provided supplemental food to only three pairs
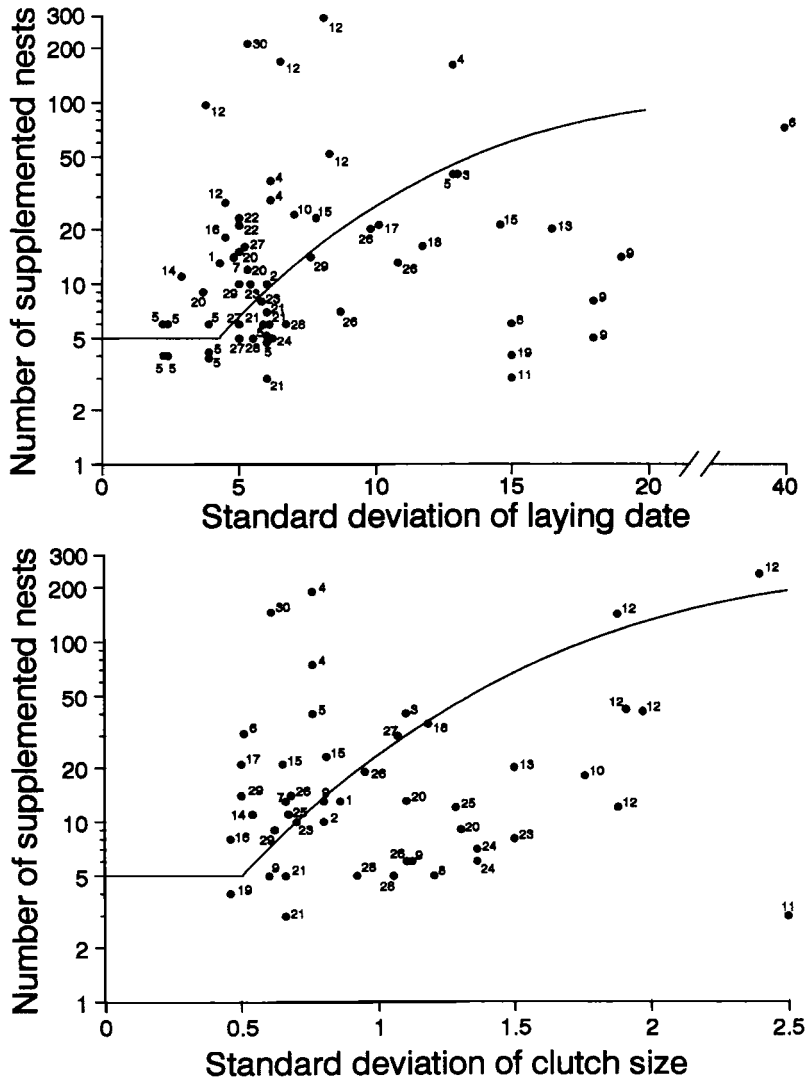
Fig. 6. Numbers of supplementally fed nests obtained during feeding experiments on laying-date (top) and clutch-size (bottom) variation in wild-nesting birds. Most studies had equal or larger numbers of control nests. Each dot represents one study or one experiment (some studies reported multiple experiments; i.e. $\geq$ 2 years or habitats). Curvilinear line represents minimum sample size required to detect significant two-tailed differences (i.e. $P \leq 0.05$) of five days (laying date) or 0.5 eggs (clutch size) with a probability of at least 80% (i.e. $\beta = 0.20$). Horizonal portion of line at $n = 5$ represents minimum sample requirement for Mann-Whitney U-test. Data from: (1) *Accipiter nisus*, Newton and Marquiss 1981; (2) *Aegolius funereus*, Korpimäki 1989; (3) *A funereus*, Hörnfeldt and Eklund 1990; (4) *Agelaius phoeniceus*, Ewald and Rohwer 1982 (SD from Crawford 1977); (5) *A. phoeniceus*, Wimberger 1988 (SD from Crawford 1977; Ewald and Rohwer 1982); (6) *Ardea herodius*, Powell 1983; (7) *Corvus corone*, Yom-Tov 1974 (SD from Loman 1984); (8) *Falco tinnunculus*, Dijkstra et al. 1982; (9) *F. tinnunculus*, Meijer et al. 1988; (10) *Fulica atra*, Horsfall 1984 (SD from Fjeldså 1973); (11) *F. americana*, Hill 1988; (12) *F. americana*, this study; (13) *Gallinula chloropus*, Eden et al. 1989 (SD from Gibbons 1986); (14) *Lanius collurio*, Carlson 1989; (15) *Larus fuscus*, Hiom et al. 1991; (16) *L. glaucescens*, Reid 1987a; (17) *Melospiza melodia*, Smith et al. 1980; (18) *M. melodia*, Arcese and Smith 1988; (19) *Pandion haliaetus*, Poole 1985; (20) *Parus caeruleus*, Clamens and Isenmann 1989; (21) *P. cristatus*, von Brömssen and Jansson 1980 (SD from Ekman and Askenmo 1986); (22) *P. major*, Kalländer 1974 (SD from Slagsvold 1984); (23) *P. major*, Clamens and Isenmann 1989; (24) *P. montanus*, von Brömssen and Jansson 1980 (SD approximated from other Paridae); (25) *P. palustris*, Nilsson 1991; (26) *Pica pica*, Högstedt 1981; (27) *P. pica*, Hochachka and Boag 1987; (28) *P. pica*, Dhindsa and Boag 1990; (29) *Prunella modularis*, Davies and Lundberg 1985 (assumed SD was 20% of range); (30) *Xanthocephalus xanthocephalus*, Arnold 1992b.

of American Coots and, thus, her results are not robust. Horsfall (1984) provided food to 24 pairs of European Coots and, although his sample sizes are comparable to other feeding experiments (references in Arcese and Smith 1988, Boutin 1990), they are small in comparison to my study. I did not detect any significant effects of supplemental food on clutch size or laying date in 1989, when my sample sizes approximated those of Horsfall, even though the magnitude of differences in mean clutch size and laying date during 1989 were similar to other years. This suggests that many previous supplemental feeding experiments have lacked sufficient statistical power to detect biologically meaningful differences in laying date or clutch size.

To explore this idea further, I extracted data on natural variation in laying date and clutch size from the avian supplemental-feeding literature, as well as sample sizes of fed individuals obtained in these experiments (sample sizes for controls were equal or larger in most instances). The most critical step in a statistical-power assessment is to specify a meaningful minimum effect size; I selected five days for laying date and 0.5 eggs for clutch size. I reasoned that effects of this size were large enough to have important evolutionary consequences, and yet not so small that these consequences could not be measured in a field study. I used a Type I error rate of 0.05 (two-tailed) and a Type II error rate of 0.20; I then estimated necessary sample sizes for any given level of natural variation in laying date or clutch size (Steel and Torrie 1980:118). Less than one-half of the previous supplemental-feeding experiments have had sufficient statistical power to detect effects of five days on laying date or 0.5 eggs on clutch size (Fig. 6). My own sample sizes for clutch-size variation were adequate in 1988 (n = 142) and overall (n = 237), but were inadequate in the remaining three years (n = 12 to 42). Investigators planning future supplemental-feeding experiments could easily determine the standard deviation of laying date or clutch size for their proposed study population and calculate the appropriate sample sizes required to reliably detect differences between supplemented and unsupplemented birds. Many North Temperate birds have standard deviations of 0.5 to 1.5 for clutch size and 5 to 15 days for laying date. This level of variation suggests that samples of about 40 to 60 fed individuals should be

adequate for most species (Fig. 6), but very few experiments have been conducted on this scale.

Although supplemental food affected both clutch size and laying date, it did not affect the relationship between these two variables. Thus, clutch size declined just as rapidly among fed coots as it did among unfed coots. This result is similar to the findings of other supplemental-feeding experiments that have controlled for variation in laying date (Meijer et al. 1988, Hörnfeldt and Eklund 1990, Nilsson 1991, Arnold 1992b; but see Arcese and Smith 1988). Because clutch size and laying date are often correlated (e.g. Klomp 1970 figs. 3 and 4), and because supplemental feeding typically affects laying date (reviewed by Arcese and Smith 1988), analyses that use laying date as a covariate are especially appropriate when assessing the effect of supplemental food on clutch size.

Supplemental food did not affect egg size or laying rates in American Coots. When data from all four years are combined, my analyses had an 80% chance of detecting differences as small as 0.41 cm³ for egg size (i.e. 1.5% of the mean) and 0.02 eggs/day for laying rates (McDonald 1977, Steel and Torrie 1980). Therefore, I conclude that supplemental food did not affect egg size or laying rates at any biologically meaningful level.

There was no annual variation in the effect that supplemental food had on any of the variables measured in this study (i.e. no year-by-food interaction effects), despite the fact that there were significant direct effects of both variables and reasonably large sample sizes were obtained in each of four years. This suggests that short-term studies may be sufficient to document the impact of supplemental food on breeding success, provided that sufficient samples can be obtained over the short term. It also indicates that annual variation in the nesting ecology of American Coots was not related to annual variation in food availability for laying females.

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