

ONSET OF INCUBATION AND PATTERNS OF HATCHING IN THE AMERICAN COOT

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Abstract. Examining incubation behavior during laying and that behavior's consequences on patterns of hatching can help discriminate among hypotheses competing to explain the evolution of asynchronous hatching. Consequently, I documented nest attentiveness and patterns of hatching of American Coots (*Fulica americana*) nesting in southwestern Manitoba from 1986 to 1991. Coots gradually increased their nest attentiveness from laying of the first to the sixth egg, and attentiveness to late-season clutches peaked earlier during laying, but it was unaffected by clutch size, first vs. replacement nest, or supplemental food. Nest attentiveness during laying was effective at initiating embryo development, as evidenced by a strong positive correlation between the order of laying of eggs and order of hatching of chicks. These results are most consistent with hypotheses that nest attentiveness during laying evolved to protect eggs or maintain viability of embryos. Clutch-initiation date had the most pronounced effect on patterns of hatching, with late-laid clutches hatching sooner and more asynchronously. Very large clutches took longer to hatch, whereas renesting and supplementally fed coots hatched early-sequence eggs more quickly. Despite large clutches and pronounced asynchrony, there was no evidence that neglect of last-laid eggs delayed their hatching. Observed variation in patterns of hatching provided little support for hypotheses that asynchrony of hatching has evolved to produce a hierarchy within a brood (e.g., brood reduction, reduction of peak loads) but strongly supported hypotheses that hatching asynchrony serves to minimize risks to unincubated eggs (e.g., egg viability, nest protection, and nest failure).

Key words: *American Coot, clutch size, Fulica americana, hatching asynchrony, incubation onset.*

Inicio de la Incubación y Patrones de Eclosión en *Fulica americana*

Resumen. El examen del comportamiento de incubación durante la puesta y de las consecuencias del comportamiento para los patrones de eclosión puede ayudar a discriminar entre hipótesis que compiten entre sí para explicar la evolución de la asincronía de la eclosión. Consecuentemente, documenté la atención al nido y los patrones de eclosión de individuos de *Fulica americana* que estaban anidando en el sudoeste de Manitoba entre 1986 y 1991. Los individuos de *F. americana* aumentaron gradualmente su atención al nido desde que pusieron su primer huevo hasta que pusieron su sexto huevo. La atención a las puestas de estación aumentó a principios de la puesta, pero no fue afectada por el tamaño de la nidada, el intento de anidación o el alimento suplementario. La atención al nido durante la puesta fue efectiva para iniciar el desarrollo del embrión, lo cual se evidenció por la existencia de una fuerte correlación positiva entre el orden de la puesta de los huevos y el orden de eclosión de los pichones. Estos resultados son más consistentes con las hipótesis de que la atención al nido durante la puesta evolucionó para proteger los huevos o para mantener la viabilidad de los embriones. La fecha de inicio de la nidada tuvo el efecto más pronunciado en los patrones de eclosión, de modo que las nidadas puestas tardíamente eclosionaron antes y de modo más asincrónico. Las nidadas muy grandes tomaron más tiempo en eclosionar, mientras que las aves que repitieron la anidación y las alimentadas suplementariamente presentaron la eclosión de los primeros huevos de la secuencia más rápidamente. A pesar de las nidadas grandes y de una asincronía pronunciada, no hubo evidencia de que la falta de atención a los últimos huevos puestos demorase su eclosión. La variación observada en los patrones de eclosión no apoyó las hipótesis de que la asincronía de la eclosión ha evolucionado para producir una jerarquía dentro de la camada (e.g., reducción de la camada, reducción de las cargas pico de alimento), pero apoyó fuertemente las hipótesis de que la asincronía en la eclosión sirve para minimizar los riesgos de falta de incubación de huevos (e.g., viabilidad de los huevos, protección de los nidos y fracaso de los nidos).

INTRODUCTION

Incubating birds face several important and often conflicting selection pressures: obtaining sufficient nutrients to meet their own energetic needs (Moreno 1989), maintaining a favorable

thermal and gaseous environment for embryonic development (Carey 1983), and avoiding predation risks to their eggs and themselves (Ricklefs 1969, Devries et al. 2003). Additionally, incubation behavior during laying largely determines patterns of hatching during the nestling period, which can have

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important consequences for fledging success (Stoleson and Beissinger 1995).

Most detailed studies of nest attentiveness during laying reveal that birds gradually increase the constancy of incubation over several days rather than transitioning directly into full incubation (Haftorn 1981, Anderson 1997, Loos and Rohwer 2004). This “partial incubation” can lead to embryo development and to asymmetries of development within the clutch (Wiebe et al. 1998). Partial incubation occurs even among precocial species whose chicks exit the nest synchronously within a few hours of hatching (Afton and Paulus 1992, Loos and Rohwer 2004). However, such behavior could be adaptive if it maintains embryo viability (Arnold et al. 1987), allows incubating parents to defend their nests against predators or brood parasites (Clotfelter and Yasukawa 1999), or minimizes predation risk by allowing chicks to depart the nest earlier (Hepp 2004). However, it also has associated costs for precocial broods because these asymmetries of development must be overcome so that all offspring can leave the nest simultaneously shortly after hatching (Davies and Cooke 1983, Persson and Andersson 1999).

American Coot (*Fulica americana*) chicks are precocial and able to leave the nest within a few hours of hatching, but unlike other precocial species such as waterfowl, shorebirds, or gallinaceous birds, they hatch asynchronously over several days and are critically dependent on their parents for food for at least the first 10 days after hatching (Lyon 1993). This pattern creates conflicting demands on parents because incubating unhatched eggs in the nest bowl and feeding already hatched young outside the nest are mutually incompatible, although biparental care potentially allows parents to partition these activities. Clutch size is large and highly variable (Arnold 1994), and up to half of all hatched chicks starve (Lyon

1993, Amundson and Arnold 2010). But losses also occur from selective factors operating during egg laying, including nest predation, intraspecific brood parasitism, intraspecific nest destruction, and egg inviability (Arnold 1990, Lyon 1993).

At least seven general hypotheses could explain the coot’s pattern of asynchronous hatching (Table 1). These hypotheses offer contrasting predictions about optimal incubation behavior during egg laying in response to variation in clutch size, date of laying, first vs. replacement nest, and supplemental feeding (Table 1), and hence an examination of proximate factors influencing the onset of incubation can be a fertile way to discriminate among competing explanations for the evolution of asynchronous hatching (Stoleson and Beissinger 1995).

The hormonal-constraints hypothesis views asynchronous hatching as an epiphenomenon of reliance upon the same hormonal mechanism for both onset of incubation and inhibition of ovulation (Mead and Morton 1985). The hypothesis was first advanced to explain why in passerines full nocturnal incubation often begins with the penultimate egg (Mead and Morton 1985), but similar arguments could be advanced to explain why the onset of incubation is gradual rather than sudden if the same hormonal mechanism that sequentially shuts down a series of developing follicles is also responsible for sequentially increasing attentiveness to incubation. For coots, the hormonal-constraints hypothesis might predict a gradual increase in partial incubation over the last five to seven eggs in each clutch, the laying of which represents the typical duration of rapid follicle growth in coots (Arnold and Rohwer 1991), combined with full incubation beginning with the penultimate egg (Mead and Morton 1985; Fig. 1a).

According to the energetic-constraints hypothesis (Nilsson 1993b, Ardia et al. 2009), birds are limited in their

TABLE 1. Hypotheses to explain hatching asynchrony in birds, with specific predictions about onset of incubation by the American Coot.

Hypothesis ^b	Critical period ^b	What pattern of hatching is most adaptive? ^a	Optimal timing of onset ^a	How onset of incubation is affected by . . . ^a			
				Larger clutch size	Later laying date	Previous nesting attempts	Access to supplemental food
Hormonal constraints	Laying	Not applicable	Penultimate	Later	—	—	—
Energetic constraints	Laying	Greater asynchrony ^c	Earlier	Later	Earlier	Later	Earlier
Egg viability	Laying	Synchrony, ambivalent	Near-first	—	Earlier	—	—
Nest protection ^d	Laying	Ambivalent	First	—	—	—	—
Nest failure ^e	Both	Full asynchrony	First	—	Earlier	Earlier	—
Peak-load reduction ^f	Nestling	Full asynchrony	First	Earlier	—	—	—
Brood reduction	Nestling	Partial asynchrony	Near-last	Later ^g	—	—	Later

^aPredictions are based on each hypothesis acting alone; earlier and later are relative to sequence of laying, with later meaning that coots postpone incubation until more eggs have been laid, whereas earlier means that coots start incubation earlier during laying.

^bAfter Stoleson and Beissinger (1995), with slight modifications (see text).

^cUnder this hypothesis, a greater degree of asynchrony is optimal, but it is constrained by competing demands of egg laying.

^dIncludes a variety of hypotheses that posit a protective function of early nest attendance but not necessarily incubation.

^ePredictions are specific to the American Coot and based on greater nest loss later in the season and for replacement nests.

^fMaximal asynchrony is favored in all cases, but benefits are greater for large clutches.

^gPresumes variation in clutch size is a function of individual optimization and supplemental food is a reliable cue.

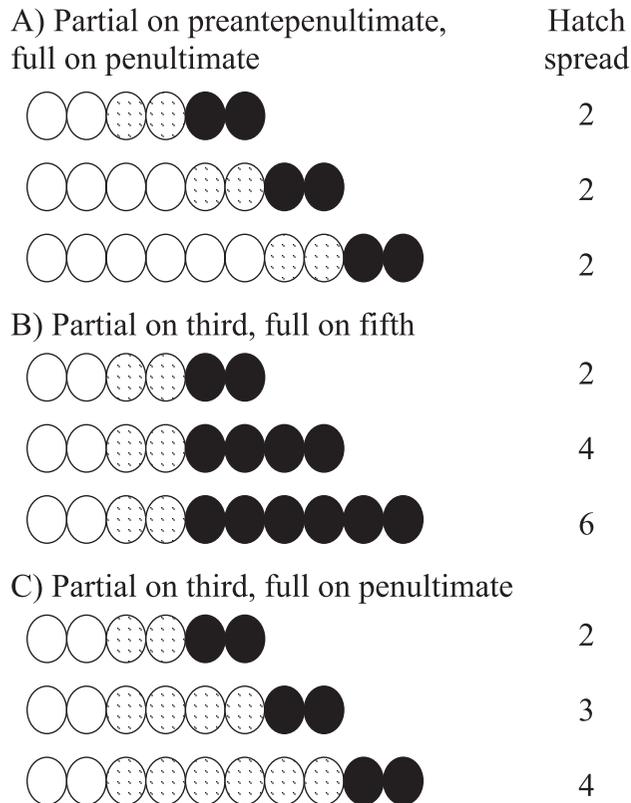


FIGURE 1. Each illustration represents onset of incubation during the laying period for a species with large and variable clutch size (e.g., 6, 8, or 10 eggs; daily egg laying assumed). There are many intermediate incubation strategies involving partial incubation (stippled eggs) preceding full incubation (black eggs). Full and partial incubation during egg laying are presumed to lead to 1.0 and 0.5 days of asymmetry in development, respectively. Pattern A represents a strategy where partial incubation begins as follicle development terminates and full incubation begins with the penultimate egg, a variant of the hormonal-constraints hypothesis. This leads to three offspring hatching late regardless of clutch size (hatching 0.5, 1.0, and 2 days after the eggs hatching first), which might be adaptive under the brood-reduction or insurance-egg hypotheses. Pattern B, where onset of incubation is timed relative to the first-laid egg, suggests that there is selection for an early start to incubation (e.g., nest failure) or highly asynchronous hatching. Pattern C suggests a benefit of early nest attendance but a cost to asynchronous hatching, with partial incubation used as a strategy to maintain egg viability while minimizing asymmetry in development.

ability to increase the asynchrony of hatching by the competing demands of egg formation versus incubation. This hypothesis is most applicable to species in which egg formation is expensive and only females incubate (Nilsson 1993a). The importance of egg formation costs to coots is debatable (Alisauskas and Ankney 1985, Arnold and Ankney 1997), and biparental incubation further minimizes its influence, but the hypothesis nevertheless makes very clear predictions about individual variation in the onset of incubation (Table 1).

Female coots should delay incubation when they produce larger, more expensive clutches (Alisauskas and Ankney 1985), advance incubation when they nest later and food is presumably more abundant (Arnold and Ankney 1997), delay incubation in replacement nests (if nutrient reserves have been depleted; Rohwer 1986), and, most importantly, advance incubation with supplemental feeding (Nilsson 1993b).

The egg-viability hypothesis (Arnold et al. 1987, Veiga 1992) posits that birds begin incubation prior to clutch completion in order to maintain the viability of eggs laid early in the clutch. It predicts that the onset of incubation should be timed relative to when the viability of unincubated eggs begins to decline but should be unaffected by variation in clutch size, first vs. replacement nest, or food availability. It predicts earlier onset of incubation for later-season clutches, provided that warmer ambient temperatures are more deleterious for maintaining embryo viability (Arnold 1993a, Stoleson and Beissinger 1995, Viñuela 2000). It makes no predictions about the utility of asynchronous hatching and was first advanced to explain limitation of clutch size in waterfowl, in which asymmetric development was viewed as maladaptive (Arnold et al. 1987). It is perhaps the only hypothesis that predicts that partial incubation (Fig. 1c) might be adaptive as a means of maintaining embryo viability while minimizing asymmetric development (Hepp 2004, Loos and Rohwer 2004, Beissinger et al. 2005).

The “nest-protection hypothesis” represents my amalgamation of several very similar hypotheses that suggest that birds begin incubation early during egg laying in order to enhance protection from predators that might steal unattended eggs (Bollinger et al. 1990), from brood parasites that might lay eggs in unattended nests (Lombardo et al. 1989, Hepp 2004), or from competitors that might usurp limited nest sites (Beissinger et al. 1998). These hypotheses are all ambivalent about the adaptiveness of asynchronous hatching, and it is important to note that it is possible to protect eggs and nest sites without applying heat to eggs (Haftorn 1978). Hence, if asynchronous hatching itself is maladaptive, these selective forces should favor nest guarding without incubation. However, if asynchronous hatching is neutral or beneficial, these factors could act in concert with other factors to help promote it (Stoleson and Beissinger 1995). Unfortunately, predictions of this hypothesis are largely identical to those of the egg-viability hypothesis (Table 1).

The nest-failure hypothesis (Hussell 1972, 1985, Clark and Wilson 1981) is similar to the nest-protection hypothesis, but here the benefit is not defending the nest but speeding up the date of fledging of at least some chicks. Magrath (1988) added the caveat that incubating parents speed up the hatching of some chicks by increasing their own vulnerability to predation by spending more total time incubating, provided that incubating places a parent at higher risk of mortality (Devries et al. 2003). If food supplies for nestlings are at risk of falling precipitously at the end of the breeding season, the nest-failure hypothesis is qualitatively similar to the “hurry-up hypothesis”

(Hussell 1972, Slagsvold 1986). Incubating coots are at some direct risk to predators, especially the mink (*Neovison vison*) and Great Horned Owl (*Bubo virginianus*), but rates of adult mortality are low relative to those of nest failure early during laying, and hence for coots the nest-failure hypothesis predicts early onset of incubation (unpubl. data).

According to the peak-load-reduction hypothesis, asynchronous hatching is adaptive because it limits the demands for parental care that would be maximized if all offspring hatched at once (Hussell 1972). This hypothesis has not received much empirical support (Stoleson and Beissinger 1995), but three features make it potentially attractive for coots: (1) it should have a stronger influence among species with large clutches (Mock and Schwagmeyer 1990), (2) biparental care allows coots to overcome some of the major costs of asynchrony (i.e., concurrent laying and incubation, or concurrent incubation and chick care), and (3) coot chicks transition rapidly from total dependence on parents during the first 10 days of life to relative independence over the next 10 days (Desroschers and Ankney 1986, Lyon 1993). Young coot chicks are fed primarily aquatic insects, atypical food for adult coots, so a bottleneck in prey availability could arise (Driver 1988). The peak-load-reduction hypothesis is qualitatively similar to the dietary-diversity hypothesis, which predicts that brood size might be limited by the ability of parents to provide a specific food needed at a critical stage of offspring development and that asynchronous hatching can help by staggering the demand for that food (Magrath 1990, Hébert 1993). Both the peak-load-reduction and the dietary-diversity hypotheses are clear in predicting maximal asynchrony under virtually all conditions (Table 1), although one should not presume that any of these hypotheses acts alone (Stoleson and Beissinger 1995).

Finally, Lack's (1947) brood-reduction hypothesis posits that asynchronous hatching is adaptive because it facilitates efficient brood reduction under conditions of food shortage but allows all chicks to survive under conditions of food abundance. It typically predicts partial asynchrony, that parents should begin incubation part way through laying at a point where they can be fairly certain of fledging all the chicks that hatch in concert but are uncertain about the prospects of chicks that hatch later. These later chicks can also serve as insurance against failure to hatch or random mortality of earlier chicks (Cash and Evans 1986, Forbes 1990). The predictions of the insurance-egg hypothesis are virtually identical to the predictions of the brood-reduction hypothesis (Stoleson and Beissinger 1995); all that differs is when and why the asynchronously hatched offspring become liabilities rather than assets. If variation among individuals in clutch size is adaptive (Perrins and Moss 1975), the brood-reduction hypothesis predicts delayed onset of incubation of larger clutches (Table 1). Furthermore, if food availability during laying is a reliable cue to food availability during brood rearing, the brood-reduction hypothesis is the only hypothesis that predicts later onset of

incubation when birds are given access to supplemental food (Table 1).

Stoleson and Beissinger (1995) admonished ornithologists to pay more attention to incubation behavior during laying in order to assess the mechanisms of asynchronous hatching and identify the selective pressures responsible for it. My primary objectives in this study were to examine proximate sources of variation in onset of incubation and patterns of hatching of American Coots in relation to order and date of laying, clutch size, first vs. replacement nest, and supplemental feeding in order to discriminate among these competing hypotheses about the possible adaptive significance of asynchronous hatching. In addition, I explored sources of variation in duration of incubation since this is a time of high energetic demands and risk of predation.

METHODS

From 1986 to 1991, I studied the incubation behavior of coots near Minnedosa, Manitoba, Canada (50° 10' N, 99° 47' W). The study area contains a high density (>40 km⁻²) of small (0.1–3.0 ha) wetlands and supports a large population of breeding coots except during years of extreme drought. I searched emergent vegetation systematically for coot nests every 4–6 days (Arnold 1994). Upon first discovering a nest, I numbered all eggs with a black permanent marker and tracked them through hatching. For nests found during laying, I determined clutch-initiation dates and clutch sizes by backdating, assuming one egg was laid per day (Arnold 1993), excluding any obvious parasitic eggs (approximately 6% of all nests; unpubl. data). I identified attempts at renesting on the basis of timing and proximity to previous nests and comparison of egg color and markings (Arnold 1993b). During 1987, 1988, 1989, and 1991 I provided a random sample of ponds with supplemental food throughout the nesting period (Arnold 1994). I measured eggs (length [*L*] and maximum breadth [*B*], 0.1 mm) with dial calipers and calculated egg size as $0.000507LB^2$.

I visited most nests infrequently during laying, making estimates of the eggs' sequence and date laid imprecise, but when I visited nests daily I knew the sequence and dates exactly. Dates were measured as Julian dates – 120, so that 1 May = 1 (this was approximately the earliest observed date of nest initiation). From 55 additional clutches visited every second day during laying, I knew the position in sequence to ± 0.5 for another 256 eggs, and I assigned midpoint values to these eggs (e.g., new eggs 3 and 4 laid 10–11 May would both be assigned a position of 3.5 and a date of 10.5).

In 1990 and 1991 I measured attentiveness at 362 nests by handling two or three haphazardly selected eggs during 1890 routine diurnal nest visits, holding them to my cheek (Clotfelter and Yasukawa 1999), and subjectively categorizing them as warm (near body temperature; warm to the touch), intermediate (warmer than ambient), or cool (at or below ambient

temperature). I assigned orders and dates of hatching on the basis of daily or twice daily nest visits. If multiple eggs hatched between visits, I assigned each hatched egg the mean order of all eggs hatching during that interval (e.g., if eggs 1, 2, 3, and 5 were the first four eggs in a clutch to hatch, I assigned all four a mean order of 2.5). In 1991, I collected most eggs and placed them in an artificial incubator after they began pipping, and typically measured the time of hatching to ± 2 hr (e.g., 30.5 indicates that an egg hatched at 12:00 on 30 May).

STATISTICAL ANALYSIS

I interpreted egg-temperature categories (warm, intermediate, cool) as full incubation, partial incubation, and unincubated and assigned them values of 4, 0, and -4 , respectively. These values simulated use of a logistic regression, giving back-transformed proportions of 0.98, 0.5, and 0.02, which I used to keep predictions of diurnal nest attentiveness between 0 and 1. I used mixed linear models (Proc MIXED, SAS Institute, Inc., Cary, NC) to test predictions about nest attentiveness (Table 1) as a function of year, nest-initiation date, clutch size, initial vs. replacement nest, and food supplementation, analyzing the laying period (first to last laid egg, hereafter "laying-stage nest attentiveness"), incubation (clutch completion to first hatch, hereafter "incubation attentiveness"), and the hatching period (first to last hatched egg, hereafter "hatching-stage nest attentiveness") separately. I used nest number as a random effect to account for possible non-independence of replicate observations from the same nest. For the laying and hatching periods, I included number of eggs already laid or number of unhatched eggs remaining, respectively, as covariates, and I considered quadratic and cubic terms to allow for nonlinear relationships in order to better model the onset or decline of nest attentiveness. I began modeling with a full model including all main effects, quadratic or cubic terms for laying or hatching order, and all possible 2-way interactions. Interactions with the eggs' sequence or number of eggs remaining to hatch were of particular importance, as they indicated factors affecting variation in the onset of incubation or terminal-egg neglect, respectively. I deleted nonsignificant predictor variables ($P > 0.05$, df based on Satterthwaite method) from the model sequentially, beginning with the least-significant predictor, until all remaining variables were significant, except that I retained nonsignificant effects whenever they were nested within a significant higher-level interaction effect and included lower-order linear or quadratic effects whenever there were higher-order polynomial terms. Model predictions and their 95% CI were transformed from logit values to give estimates of diurnal nest attentiveness bounded between 0 and 1.

I used a simple Pearson correlation to determine if eggs hatched in the same order that they were laid, which would indicate that laying-stage nest attentiveness was effective at initiating embryo development (Wiebe et al. 1998). If this correlation was a reliable predictor of the order in which eggs

were laid, it also allowed me to infer the length of incubation of additional eggs whose order of laying was imprecisely known (see beyond). To examine sources of departure from a perfect 1:1 relationship between the sequences of laying and hatching, I fit a mixed linear model of the sequence of hatching versus laying (including quadratic and cubic terms), year, clutch size, clutch-initiation date, first vs. replacement nest, supplemental food, and all two-way interactions (fixed effects) as well as nest number (random effect). I removed nonsignificant variables following the same protocol described above for the analysis of incubation attentiveness.

I calculated incubation periods as the interval between laying and hatching of each individual egg, so they include periods when eggs were unattended or partially incubated. Because most nests were not visited daily during laying, I typically inferred the order in which eggs were laid from the order in which they hatched (72%); however, the preceding analysis revealed that laying order was highly correlated with hatching order when both were known exactly ($r = 0.97$; see also Horsfall 1984, Lyon 1991). Moreover, most departures from a perfect concordance between laying and hatching order arose because of synchronous hatching (80%), and this would not lead to errors in length of incubation, except for egg-specific attributes like egg size. Nonconcordance also arose because of earlier eggs failing to hatch (9%; e.g., if egg 5 hatched third because eggs 3 and 4 failed to hatch) as well as actual transpositions in laying and hatching order (11%; e.g., if eggs 4 and 5 both hatched, but egg 5 hatched before egg 4). I excluded eggs from clutches where two or more eggs laid earlier in the sequence failed to hatch, thereby limiting errors in estimation of incubation periods due to hatching failure to ≤ 1 day. Failure to recognize transpositions in laying and hatching order should not affect estimates of mean incubation periods because each unknown transposition involved one egg that was incorrectly recorded as hatching too early, balanced against another egg that was recorded as hatching too late (i.e., these two errors cancel each other); however, such errors would lead to an underestimate of the variance in incubation periods.

I analyzed variation in egg-specific incubation periods with respect to nest (random effect) and year, position in sequence (linear and quadratic), clutch size, egg size, clutch-initiation date, first vs. replacement nest, supplemental food, and all two-way interactions (fixed effects), using linear mixed modeling procedures identical to those described for nest attentiveness and hatching order. Asynchronous hatching can lead to scheduling conflicts because parents are unable to simultaneously feed offspring already hatched and incubate unhatched eggs (Cash and Evans 1986, Stoleson and Beissinger 1995), so I tested for terminal-egg neglect by examining the duration of incubation of the last four eggs in each clutch, while controlling for all other factors that affected incubation duration. I generated predicted values and their 95% confidence intervals with Estimate statements in SAS.

RESULTS

DIURNAL NEST ATTENTIVENESS

Nest attentiveness increased monotonically throughout laying and was best described as a quadratic function of laying sequence [Fig. 2; $\text{logit}(\text{attentiveness}) = -5.27 \text{ (SE } 0.16) + 1.41 \text{ (SE } 0.06) \times S - 0.066 \text{ (SE } 0.005) \times S^2$, where S is the sequence of laying]. Attentiveness was unaffected by clutch size ($F_{1,998} = 0.03, P = 0.87$), renesting ($F_{1,1043} = 0.42, P = 0.52$), or supplemental feeding ($F_{1,955} = 2.79, P = 0.09$) but did vary with clutch-initiation date (date: $F_{1,900} = 10.22, P = 0.001$; date-by-sequence: $F_{1,1371} = 4.49, P = 0.03$). Laying-stage nest attentiveness increased more rapidly for late-season clutches than for early-season clutches (Fig 3).

Incubation attentiveness was high throughout the interval between laying of the last egg and hatching of the first chick (Fig. 2; $\bar{x} = 0.964, 95\% \text{ CI} = 0.955\text{--}0.971, n = 121$ nests) and did not vary significantly with any measured covariate. During the hatching period, nest attentiveness was best modeled as a cubic function of how many eggs remained to hatch rather than by how many eggs had already hatched [Fig. 2; $\text{logit}(\text{attentiveness}) = -0.41 \text{ (SE } 0.40) + 1.28 \text{ (SE } 0.24) \times R - 0.16 \text{ (SE } 0.04) \times R^2 + 0.0064 \text{ (SE } 0.0021) \times R^3$, where R is the number of eggs remaining]. Hatching-stage nest attentiveness was further affected by year, clutch-initiation date, and an interaction between remaining eggs and clutch-initiation date (Fig. 4).

CORRELATION BETWEEN SEQUENCES OF LAYING AND HATCHING

For 177 eggs of precisely known laying and hatching sequence, eggs hatched in the general order they were laid (Fig. 5;

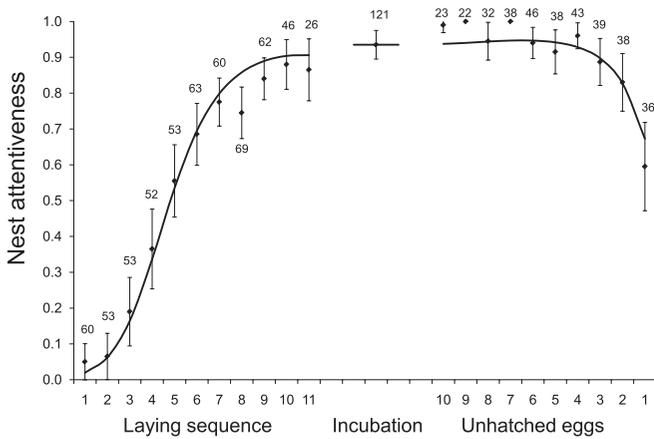


FIGURE 2. Diurnal nest attentiveness by American Coots during the laying, incubation, and hatching periods in relation to number of eggs laid and number of eggs left to hatch. “Incubation” extends from the last-laid to first-hatched egg and typically lasts 14 days for an 11-egg clutch (duration not drawn to scale). Symbols and 95% confidence intervals are based on actual means and standard errors (sample size above error bars), whereas lines represent best-fitting polynomial-regression models (see text).

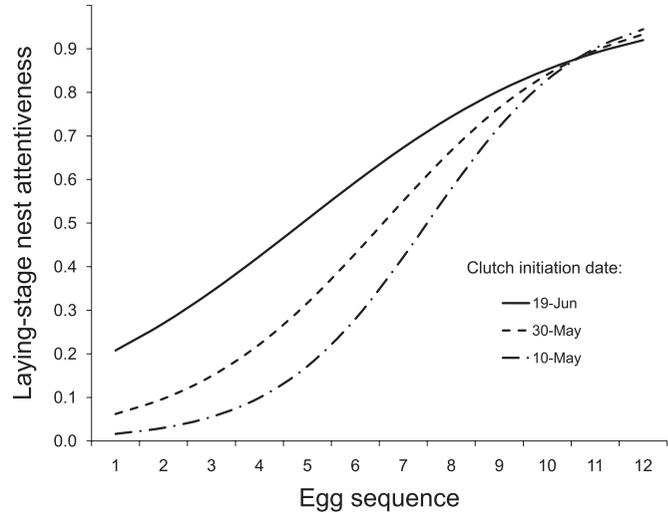


FIGURE 3. Model-based estimates of laying-stage nest attentiveness by American Coots in relation to egg sequence (S , range: 1–14), clutch-initiation date (1 May = 1; observed range 6–53), and their interaction: $\text{logit}(\text{attentiveness}) = -5.487 \text{ (SE } 0.536) \pm 2.23(\text{random effect}) + 0.702 \text{ (SE } 0.071) \times S + 0.076 \text{ (SE } 0.024) \times \text{date} - 0.0072 \text{ (SE } 0.0034) \times S \times \text{date}$.

$r = 0.97$). Imprecision in this relationship was attributable to three factors: (1) two or more eggs hatching in synchrony ($n = 82$ eggs in 36 clutches; errors of ± 0.5 to ± 3 eggs), (2) early-sequence eggs failing to hatch, which resulted in an advancement of hatching order of later-laid eggs ($n = 9$ eggs in 4 clutches; directional bias of 1–3 eggs), or (3) actual transpositions in the sequence of eggs being laid and hatching ($n = 11$

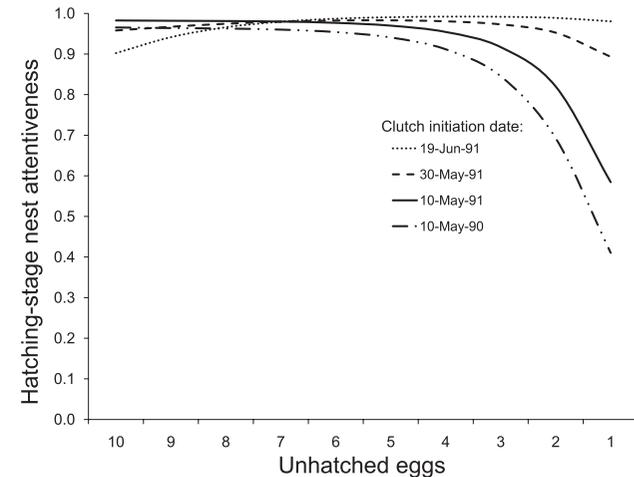


FIGURE 4. Model-based estimates of hatching-stage nest attentiveness by American Coots as a function of number of unhatched eggs (R), year (1990 = 0, 1991 = 1), and clutch-initiation date (1 May = 1): $\text{logit}(\text{attentiveness}) = -2.912 \text{ (SE } 0.609) \pm 0.117(\text{random effect}) + 0.704 \text{ (SE } 0.244) \times \text{year} + 0.104 \text{ (SE } 0.020) \times \text{date} + 1.839 \text{ (SE } 0.251) \times R - 0.188 \text{ (SE } 0.040) \times R^2 + 0.0071 \text{ (SE } 0.0019) \times R^3 - 0.015 \text{ (SE } 0.0004) \times \text{date} \times R$.

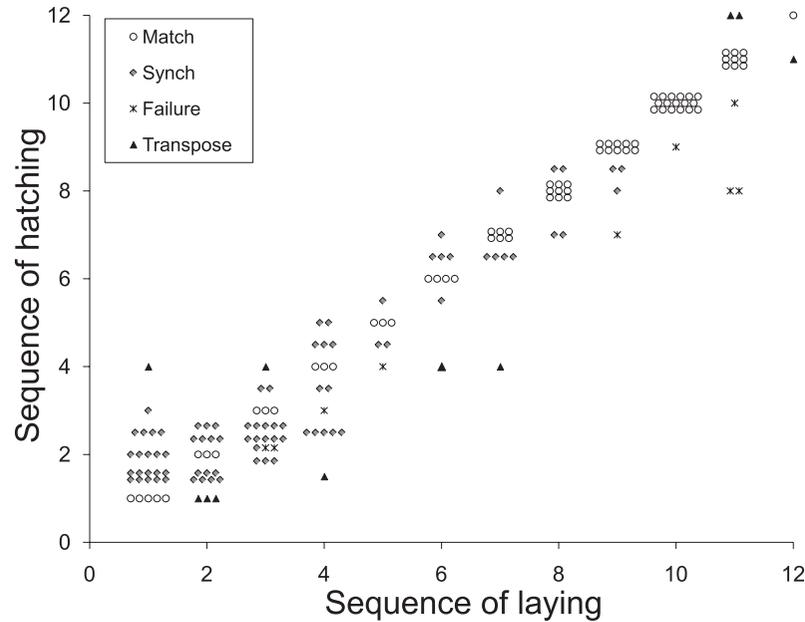


FIGURE 5. Relationship between position in sequences of hatching and laying for 177 American Coot eggs for which these values were precisely known (2 matches at 13 and 15 not shown). When eggs hatched in synchrony, they were assigned tie values equal to the average rank (e.g. if eggs 1–4 hatched in synchrony, they all received the value 2.5). Values are shifted slightly to allow all data points to show.

eggs in 5 clutches; errors of ± 3 eggs). Errors due to synchrony and transpositions tended to occur among eggs laid earlier in the clutch ($\bar{x} = 3.5$, $SD = 2.3$; $\bar{x} = 5.5$, $SD = 4.1$), whereas errors due to hatching failure tended to occur among those laid later ($\bar{x} = 7.5$, $SD = 3.6$). When laying order was known less precisely (± 0.5 eggs), the correlation was identical ($r = 0.97$, $n = 433$), so I used this larger sample for assessing potential correlates of imprecision between laying order and hatching order. Hatching order was a quadratic function of laying order [HO = $0.393 (0.116) + 0.831 (0.040) \times LO + 0.0096 (0.0030) \times LO^2$] but was not affected by any other covariates ($P > 0.05$).

EGG-SPECIFIC INCUBATION PERIODS

The interval between laying and hatching of an individual egg varied with respect to the sequence in which it was laid, year, clutch-initiation date, clutch size, first vs. replacement nest, supplemental food, and numerous interactions among these variables (Table 2). Variation among clutches was pronounced, with 64% of the variation in incubation periods occurring among nests and only 36% among eggs within the same nest. Sequence of laying had the strongest fixed effect (Table 2). Egg-specific incubation periods declined steadily for eggs 1–6, reflecting incomplete incubation during early laying; however, all differences between mean incubation periods of adjacent pairs of eggs were significantly smaller than 1 day, the predicted difference if there were no incubation and no development occurring during the laying period (Fig. 6). Incubation periods declined for later clutch-initiation dates, especially among early-sequence eggs (Fig. 7). Clutch size had minimal

TABLE 2. Duration of incubation of individual American Coot eggs in relation to the sequence in which they were laid (egg, range 1–17), clutch size (CS, range 5–20), clutch-initiation date (date; range 2 May–20 Jun, with 2 May = 2), supplemental food (food; fed = 1, unfed = 0), and nesting attempt (renew = 1, initial nest = 0). Clutch effects were controlled with random effects ($\sigma^2_{\text{among}} = 0.732$, 95% CI: 0.598–0.918; $\sigma^2_{\text{within}} = 0.413$, 95% CI: 0.384–0.446).

Variable	B	SE	F	df ^a	P
Intercept ^a	28.293	0.533	2818.55	880	0.0001
Year ^b	0.000	—	8.32	297	0.0001
Egg	-1.000	0.116	74.30	1470	0.0001
Egg ²	0.066	0.009	56.40	1462	0.0001
CS	0.034	0.033	1.08	952	0.30
Date	-0.220	0.036	37.82	967	0.0001
Date ²	0.0029	0.0009	10.56	795	0.001
Food	-0.856	0.122	49.14	824	0.0001
Renest	-5.516	1.931	8.18	229	0.005
CS × egg	0.016	0.008	4.49	1491	0.03
CS × egg ²	-0.0029	0.0005	27.77	1462	0.0001
Date × egg	-0.0008	0.0078	0.01	1459	0.92
Date × egg ²	0.0013	0.0006	4.12	1474	0.04
Date ² × egg	0.00024	0.00020	1.42	1461	0.23
Date ² × egg ²	-0.00005	0.00002	6.60	1484	0.01
Date × reneat	0.387	0.134	8.29	235	0.004
Date ² × reneat	-0.0073	0.0022	10.63	245	0.001
Food × egg	0.113	0.011	100.40	1487	0.0001
Food × reneat	1.537	0.474	10.50	219	0.001
Renest × egg	0.213	0.065	10.69	1439	0.001
Renest × egg ²	-0.0094	0.0048	3.84	1434	0.05

^aDenominator df based on Satterthwaite method; numerator df = 1 except year (df = 5).

^bEffect size in 1991; values ranged from -0.68 (SE = 0.17) in 1987 to 1.25 (SE = 0.39) in 1989.

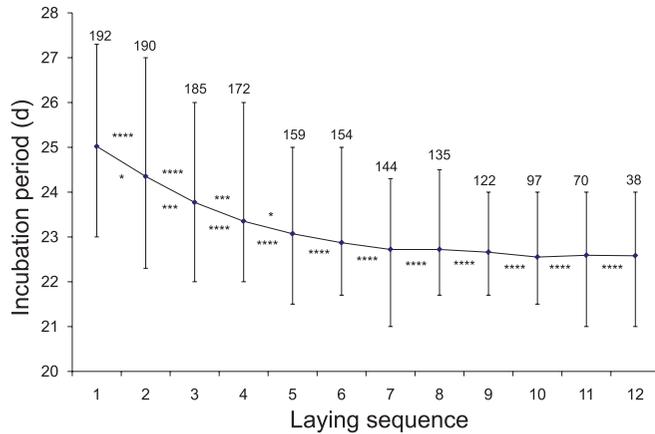


FIGURE 6. Interval between laying and hatching for individual eggs of American Coots according to the sequence in which they were laid for combined clutches of all sizes. Confidence intervals exclude the lowest and highest 5% of observed values (i.e., 90% ranges; sample sizes noted above each interval). Comparisons (2-sample *t*-tests; ****, $P < 0.0001$; ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$) above the line test the null hypothesis that differences between adjacent means are zero (i.e., that continuous incubation begins on or before this egg), whereas comparisons below the line test the null hypothesis that differences are 1 day (i.e., no effective incubation between sequentially laid eggs). The data indicate that continuous incubation begins by egg 5, with gradually increasing partial incubation between eggs 1 and 5.

influence on length of incubation, except among the very largest clutches (>12), in which all eggs took up to 0.5 days longer to hatch regardless of the sequence in which they were laid. Early-laid eggs (1–4) of supplementally fed coots hatched

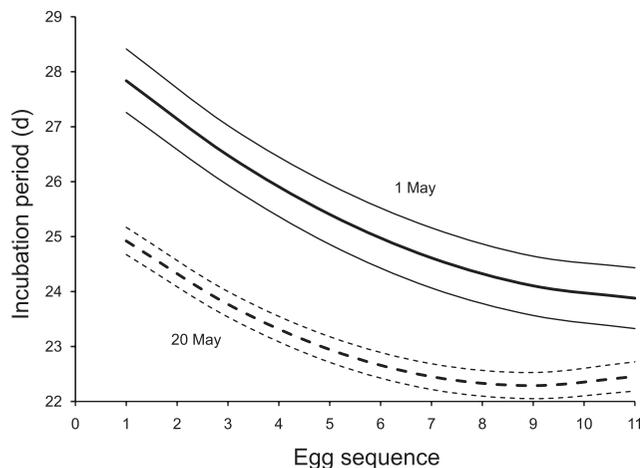


FIGURE 7. Model-based estimates of the effect of nest-initiation date (1 vs. 20 May) on incubation duration of American Coot eggs laid at different positions in the sequence (estimates based on Table 2, solved for an 11-egg initial clutch in 1991 without supplemental food). The pronounced seasonal reduction among early-sequence eggs is due to earlier onset of incubation, but the ~1.5-day reduction among late-sequence eggs is due to more rapid development.

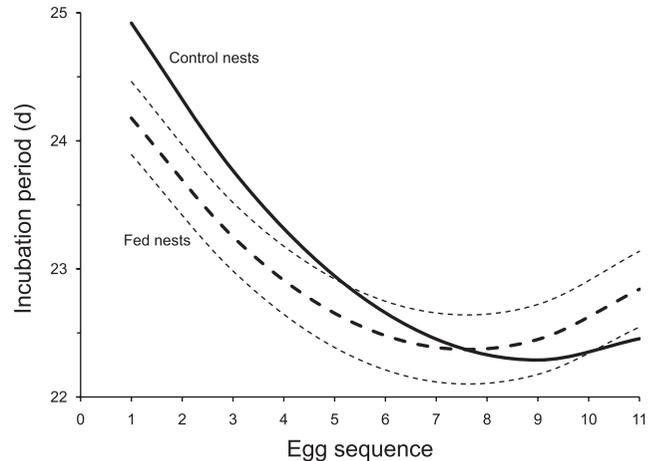


FIGURE 8. Model-based estimates of the effect of supplemental food on incubation duration of American Coot eggs laid at different positions in the sequence (thick dashed line), including 95% confidence intervals (thin dashed lines). Incubation periods of unfed coots (solid line) are shown for comparison. Year was set to 1991, clutch size to 11, clutch-initiation date to 20 May, and renest to 0 (initial nest; Table 2).

sooner than eggs of unfed coots, but eggs later in the sequence did not differ (Fig. 8). Among renesting coots the effect was similar (not shown). Annual variation in incubation periods was slight, except in 1989 when eggs required 1.25 (SE = 0.39) additional days to hatch, on average. Egg size had no discernable effect on length of incubation periods ($F_{1,1452} = 1.01$, $P = 0.32$). There was no evidence of terminal-egg neglect on incubation duration among the last four eggs to hatch in each clutch ($F_{4,1480} = 2.24$, $P = 0.06$); the near significance of this effect was due to slightly shorter incubation periods among last-laid eggs (least-square means \pm SE: terminal egg, 23.3 ± 0.2 ; penultimate egg, 23.5 ± 0.1 ; antepenultimate egg, 23.6 ± 0.1).

DISCUSSION

ONSET OF INCUBATION

American Coots' nest attentiveness increased gradually throughout the egg-laying period. The net outcome of laying-stage nest attentiveness was that most coot eggs hatched asynchronously in the same order that they were laid, except for the first two to four eggs, which often hatched in relative synchrony. These results were qualitatively similar to results obtained from the Eurasian Kestrel (*Falco tinnunculus*; Wiebe et al. 1998), Green-rumped Parrotlet (*Forpus passerinus*; Grenier and Beissinger 1999), Tree Swallow (*Tachycineta bicolor*; Clotfelter et al. 2000), and Barn Swallow (*Hirundo rustica*; Saino et al. 2001). However, Bortolotti and Wiebe (1993) observed numerous transpositions in the sequences of laying versus hatching in the American Kestrel, which they attributed to inefficient incubation due to the relatively large clutch mass and small body size of female kestrels.

Laying-stage nest attentiveness was unaffected by clutch size; thus, as clutch size increased, so did the span of hatching. This observation is difficult to reconcile with the brood-reduction hypothesis (Stoleson and Beissinger 1995), unless all eggs in excess of ~6 represent insurance eggs, but this seems unlikely given that most coots in this population laid clutches of ≥ 10 eggs (Arnold 1994) and that individuals laying large clutches were better able to raise large broods (unpubl. data). According to the individual-optimization hypothesis (Perrins and Moss 1975), much of the within-population variance in clutch size is due to real variation in ability to raise offspring. Thus, coots laying 12 eggs might have hatched 9 eggs in synchrony and 3 eggs asynchronously, whereas coots laying 8 eggs might have hatched 5 synchronously and 3 asynchronously to reflect this difference in parenting skill (the important distinction being that onset of incubation is determined relative to the last-laid egg and hatching spans remain more or less invariant across clutch sizes; Fig. 1A). However, coots timed onset of incubation relative to the first-laid egg (Fig. 1B), and this pattern is inconsistent with the brood-reduction, hormonal-constraints, and energetic-constraints hypotheses; it is most consistent with the egg-viability, nest-protection, and nest-failure hypotheses (Table 1). In the Burrowing Owl (*Athene cunicularia*), Wellicome (2005) observed that hatching spans increased by about 0.5 days for each 1 egg increase in clutch size, a rate about a third of the 1.5-day interval at which it lays, suggesting that partial incubation during egg laying may function as a compromise to protect eggs via initiation of incubation while minimizing asynchronous hatching.

The only covariate that affected laying-stage nest attentiveness was clutch-initiation date, with coots increasing attentiveness more rapidly among late-season nests than among early-season nests. This result was most consistent with the egg-viability and nest-failure hypotheses (Table 1). Several studies have demonstrated that unincubated eggs remain less viable later in the season (Veiga 1992, Cooper et al. 2006) or as ambient temperatures increase (Arnold 1993a, Viñuela 2000; but see Stoleson and Beissinger 1999), and coot eggs are affected similarly (Arnold 1990; unpubl. data). However, temperature alone did not adequately explain viability decline in the Pearly-eyed Thrasher (*Margarops fuscatus*; Beissinger et al. 2005), and date or temperature may simply be a correlate for risk of bacterial infection (Beissinger et al. 2005, Cook et al. 2005). If seasonal advancement of the onset of incubation is due to temperature-mediated declines in egg viability, then laying-stage nest attentiveness should be responsive to ambient temperature, a prediction that has received mixed support in studies of cavity-nesting birds (Ardia et al. 2006, Wang and Beissinger 2009).

Nest survival declined seasonally in this population of coots, and rates of nest failure were highest during early laying when nests were unattended (unpubl. data), so earlier onset of nest attentiveness among late-season nests might also be an adaptation to minimize risks of nest predation. Given

that the nest-failure and egg-viability hypotheses both make similar predictions with respect to clutch-initiation date, and that both sources of embryo loss can be substantial, it seems likely that seasonal advancement in incubation onset may be a coordinated response to both egg viability and nest predation. Stoleson and Beissinger (1995) effectively combined these two hypotheses in an illustrative model to explain onset of incubation in the House Sparrow (*Passer domesticus*).

Supplemental feeding did not affect diurnal nest attentiveness, but it did lead to earlier hatching among early-sequence eggs, a result that supports the energetic-constraints hypothesis (Nilsson 1993b). Given that energetic constraints have been implicated primarily for species with uniparental incubation (Nilsson 1993a, Wang and Beissinger 2009), it would be instructive to observe how male and female coots apportion nest attentiveness during the egg-laying period. And because male and female incubation roles appear to differ by day and night (Gullion 1954), it will be important to compare nocturnal as well as diurnal incubation patterns with more sophisticated measures of incubation behavior (e.g., Wang and Beissinger 2009).

TERMINAL-EGG NEGLECT

Nest attentiveness was extremely high from clutch completion throughout hatching, except for the last one or two eggs to hatch, which were noticeably cooler, especially among early-nesting coots. This suggests that breeding adults may have experienced scheduling conflicts due to extremely asynchronous hatching; i.e., parents were unable to feed earlier-hatched offspring and tend unhatched eggs simultaneously, and they responded by ignoring the last one or two eggs in the clutch. However, this apparent neglect did not affect the hatching time of last-laid eggs, as there was no evidence for longer incubation periods among terminal eggs, as observed in some other species that frequently neglect their eggs (Evans 1990, Nuechterlein and Buitron 2002; but see Wang and Beissinger 2009). Late-stage embryos may be sufficiently cold-hardy to withstand incubation neglect during the last few days of development (Nuechterlein and Buitron 2002), and the reduced evidence of terminal-egg neglect among late-season clutches (Fig. 4) might be an artifact of warmer ambient temperatures (i.e., eggs are still neglected by parents, but embryos can generate enough heat to prevent noticeable temperature declines). Late-stage coot embryos vocalize in response to cooling, which may be an adaptation to solicit incubation or communicate to parents that the embryo is still alive (Bugden and Evans 1991).

EGG-SPECIFIC INCUBATION PERIODS

Laying-stage nest attentiveness is the mechanism by which birds purportedly affect asynchronous hatching, but hatching patterns are a measure of the actual effectiveness of this behavior (Bortolotti and Wiebe 1993). About two thirds of

the variation in egg-specific incubation periods was among rather than within clutches, not surprising given that eggs within a clutch share a common incubation environment for most of their development period. Unrecognized transpositions in orders of laying and hatching would also lead to a reduction in within-clutch variability, so some of this effect may be a methodological artifact. Within-clutch consistency could also be due to genetic or maternal effects (Schwabl et al. 2007), but discriminating between this alternative and a shared incubation environment would require either reciprocal transplant experiments (Ricklefs and Smeraski 1983) or a common garden experiment using artificial incubators (Arnold 1993a). American Coots often reject eggs laid by conspecifics (Lyon 1993), and their eggs hatch poorly when incubated artificially (unpubl. data), so they are poor candidates for such research questions.

Incubation periods were affected by supplemental feeding, especially for early-sequence eggs, suggesting that coots altered their incubation behavior in response to food abundance or energetic limitations. Unlike the American Kestrel, which hatches its clutches more synchronously when food is more abundant during egg laying (Wiebe and Bortolotti 1994), American Coot clutches hatched less synchronously when parents had access to supplemental food, which is more consistent with energetic-constraints than with brood reduction (Nilsson 1993b). Manipulating food availability during laying is somewhat ambiguous because food availability might function as either a proximate constraint on the energy budgets of incubating birds or as an ultimate cue used to predict food availability during brood rearing. By manipulating the thermal environment of nest boxes, Ardia et al. (2009) showed that Tree Swallows alter incubation behavior in a manner most consistent with energetic limitations.

Incubation periods of late-sequence (≥ 6) eggs decreased by up to 2 days for clutches initiated late in the nesting season. This decline was not due to earlier onset of incubation, because egg-specific incubation periods reached an asymptote with the sixth egg. Seasonal reductions in incubation periods appear to be widespread in birds (Feldheim 1997, Cooper et al. 2005, Wang and Beissinger 2009) and have often been interpreted as a result of warmer ambient temperatures that create a more favorable environment for embryo development. However, Arnold (1993a) and Wells-Berlin et al. (2005) found the same effect for dabbling duck eggs incubated in artificial incubators, suggesting that there might be inherent differences among late-season eggs that favor more rapid embryo development (MacCluskie et al. 1997, Schwabl et al. 2007, Liedvogel et al. 2009).

Clutch size had a slight but significant effect on total duration of incubation. The mean incubation period for late-sequence (≥ 6) eggs increased from 22.5 days for 6-egg clutches to 23.5 days for 16-egg clutches. Although this increase may seem trivial, one additional day of predation risk could have important implications for clutch-size optimization (Arnold

1999). Similar effects of clutch size on incubation duration have been found in other species (Moreno and Sanz 1994, Feldheim 1997), but Ardia et al. (2006) observed the opposite pattern in the Tree Swallow.

Egg size had no influence on incubation duration in coots, which is consistent with previous studies that found minimal or no effect of egg size on intraspecific variation in incubation (Martin and Arnold 1991). Although egg size in coots varies with laying order, declining among last-laid eggs (Arnold 1991), this variation does not appear to be an adaptation to help synchronize hatching (Flint et al. 1994) or avoid terminal-egg neglect, because smaller eggs did not hatch more quickly, even across the much larger range of variation among females in egg size (Reed et al. 2009).

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