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NESTS WITHOUT EGGS: ABANDONMENT OR CRYPTIC PREDATION?

J. DYLAN MADDOX¹ AND PATRICK J. WEATHERHEAD

*Program in Ecology and Evolutionary Biology, University of Illinois, 606 East Healey Street,
Champaign, Illinois 61820, USA*

ABSTRACT.—We determined whether nests that did not receive eggs was attributable to cryptic nest predation (i.e. predation of eggs laid between nest checks) or nest abandonment in Common Grackles (*Quiscalus quiscula*). Nest predation was extremely low (~2%), whereas more than 44% of 427 nests found during nest building never received an egg; this indicates that nest abandonment accounted for most nests without eggs. Nest construction was completed for 32% of nests that were abandoned. Few nests known to have received eggs were abandoned. As the breeding season progressed, both nest abandonment and time from nest completion to first egg decreased. It has been proposed that the delay in egg laying early in the season allows females to optimize timing of egg laying. Nest abandonment may also serve this purpose, but seems an unnecessarily expensive mechanism. Alternatively, nest abandonment could be involved with mate switching. Understanding why nests are abandoned requires data on the associated ecological circumstances, in addition to accurate identification of instances of abandonment. The latter requires distinguishing abandonment from cryptic predation. Rates of nest abandonment can be estimated for populations by using rates of known nest predation during egg laying. For individual nests, however, distinguishing abandonment from cryptic predation requires detailed observation (e.g. video cameras), except in circumstances such as ours, where predation is extremely low. *Received 18 October 2004, accepted 26 June 2005.*

Key words: Common Grackle, nest abandonment, nest predation, *Quiscalus quiscula*.

Nidos sin Huevos: ¿Abandono o Depredación Críptica?

RESUMEN.—Determinamos si la observación de que algunos nidos no reciben huevos en *Quiscalus quiscula* es atribuible a depredación críptica de los nidos (i.e. depredación de los huevos puestos durante los intervalos entre una revisión y otra) o al abandono de éstos. La depredación de los nidos fue extremadamente baja (~2%), mientras que el 44% de los 427 nidos encontrados durante la etapa de construcción nunca recibieron huevos. Esto indica que el abandono de los nidos fue la causa responsable de la mayoría de los nidos sin huevos. La construcción de los nidos fue finalizada para el 32% de los nidos que fueron abandonados. Pocos de los nidos para los que se conocía que recibieron huevos fueron abandonados. Conforme la temporada reproductiva avanzó, el abandono de los nidos y el tiempo entre la finalización del nido y la puesta del primer huevo disminuyó. Se ha propuesto que el retraso en la puesta de los huevos al principio de la temporada permite a las hembras optimizar el tiempo de la puesta. El abandono de los nidos también podría contribuir a dicho propósito, pero sería un mecanismo innecesariamente costoso. Alternativamente, el abandono de los

¹E-mail: jmaddox@uiuc.edu

nidos podría estar relacionado con los cambios de pareja. Además de la identificación precisa de los casos de abandono, el entendimiento de por qué los nidos son abandonados requiere información sobre las circunstancias ecológicas asociadas con este fenómeno. Identificar las causas del abandono de los nidos requiere que los casos de abandono sean distinguidos de casos de depredación críptica. La tasa de abandono de nidos puede ser estimada a nivel poblacional utilizando la tasa de depredación ya conocida para la etapa de puesta de huevos. Sin embargo, distinguir el abandono de la depredación críptica para cada nido requiere de observaciones detalladas (e.g. cámaras de video), excepto bajo circunstancias como las de este estudio, en donde la depredación es extremadamente baja.

A SUBSTANTIAL PROPORTION of ornithological research focuses on breeding biology, where the goal is often to quantify factors affecting nesting success. Critical to these efforts is that researchers correctly classify the fate of nests. Because nests are typically checked every 3–4 days (Martin and Geupel 1993), researchers must infer nest fate by evidence (or lack thereof) at the nest, which creates uncertainty regarding the correct classification of nest fate. Nevertheless, methods are available that can account for some uncertain and ambiguous nest fates (e.g. Manolis et al. 2000, Shaffer 2004). More problematic, however, is classifying nests that apparently have been abandoned because they never received eggs after they were built.

Nest building can be temporally and energetically costly (Stanley 2002). Thus, abandonment of an apparently suitable nest and the subsequent building of another nest should be rare, at least in species that do not build dummy nests that presumably serve some function (e.g. Metz 1991). Despite the costs, nest abandonment may be common and highly variable. For example, in Red-winged Blackbirds (*Agelaius phoeniceus*), Westneat (1992) found that 20% (34 of 171) of nests monitored during nest building were abandoned, whereas Weatherhead and Sommerer (2001) found that only 3% (19 of 557) of nests were abandoned. Weatherhead and Sommerer (2001) hypothesized that the disparity in nest abandonment between the two studies could have resulted from differences in the incidence of nest predation during egg laying, where a predator removes eggs laid between consecutive nest checks (i.e. before the eggs are seen by a researcher), leading the researcher to incorrectly classify the nest as abandoned. This scenario (hereafter “cryptic nest predation”) seems particularly relevant when predators that can remove eggs without disturbing the nest are

abundant (Hernandez et al. 1997, Larivière 1999, Pietz and Granfors 2000, Thompson and Burhans 2003). In ornithological studies, completed nests that never receive eggs are typically classified as abandoned and excluded from further analyses. If a substantial proportion of “abandoned” nests were actually preyed on, rates of nest predation would be underestimated. Our goal here is to provide accurate estimates of nest abandonment by Common Grackles (*Quiscalus quiscula*; hereafter “grackles”) and consider factors that might underlie this behavior.

Two approaches could be used to obtain reliable estimates of nest abandonment. First, miniaturized video cameras could be placed at nests before nest building is completed to determine how often first-laid eggs are removed by predators between nest visits. This method is impractical, because nests must be found during nest building (a challenging task in many species) and video cameras are expensive and labor-intensive to operate. If cryptic predation or abandonment are relatively uncommon, a very large number of nests would have to be videotaped to obtain adequate sample sizes. The second approach is to eliminate nest predation or find a population lacking nest predation. This method has the advantage of avoiding having to distinguish between cryptic nest predation and abandonment, because apparent abandonment must in fact be true abandonment. Here, we use the second approach to document patterns of nest abandonment in a population of grackles where nest predation was extremely low.

STUDY AREA AND METHODS

We studied grackles in 2003–2004 at Ridge Road Tree Farm (RRTF) near Philo, Illinois. Situated in the row-crop-dominated landscape

of east-central Illinois, RRTF is an actively managed 8-ha Christmas-tree farm that was converted in 1994 from an agricultural field. Since its establishment, ~15,000 trees of 12 species have been planted. Because trees are harvested before exceeding 4 m in height, and grackles nested in trees 2–3 m tall, nests were easy to find and monitor.

We systematically searched all trees of appropriate height for nests 2–4 times per week. Nests were marked and classified as either under construction or completed. Once nests were found, we checked and reclassified them daily. We continued daily checks of nests without eggs for a minimum of three weeks. Nest searching spanned the full period of nest initiations in this population in both 2003 (2 April to 5 May) and 2004 (31 March to 29 May).

RESULTS

Over two years, we found 507 nests without eggs and 51 nests with eggs. Of nests found without eggs, 427 (84%) were found prior to completion of nest building and, thus, before eggs would have been laid. In total, 187 (43.8%) nests found while being built never received an egg. Of the 80 nests that we found completed, 71 (89%) subsequently received an egg, producing a total of 196 nests that never received an egg. These accounted for 35% of all nests found over the two years. Cryptic predation appears unlikely to account for most of these cases. Only 1.1% ($n = 4$) of grackle nests found during nest building and that subsequently received at least one egg were preyed on during egg laying. Only 1.8% ($n = 7$) of nests with eggs found prior to or during egg laying were preyed on during incubation. Predation rates during the nestling stage were similarly low in 2003 (2.4%; 4 of 164). Exclusive of one week in which several nests were preyed on (apparently by a transient coyote [*Canis latrans*]), nestling-stage predation was also low (0.6%; 1 of 155) in 2004. Low rates of predation were probably a consequence of RRTF existing in the midst of habitat (row crops) unsuitable for predators.

Given the low rate of nest predation, we refer to nests that never received an egg as having been abandoned. Nest abandonment was 37.0% (87 of 235) in 2003 and 40.1% (109 of 272) in 2004. Of the abandoned nests, 133 (67.9%) were abandoned before nest building was completed.

Abandonment after the first egg was laid was extremely rare compared with abandonment prior to egg laying. Of 362 nests that received at least one egg, 9 (2.5%) were never incubated or incubation ended prematurely and the eggs never hatched.

For both years combined, abandonment decreased as the breeding season progressed, where nests are grouped by the date nest building was completed (logistic regression: $\chi^2 = 20.57$, $df = 1$, $P < 0.0001$; Fig. 1). For nests that were not abandoned, females laid their first egg 5.4 ± 6.1 (mean \pm SD) days ($n = 311$) after nest completion. The mean time from nest completion to first egg decreased exponentially as the breeding season progressed (square-root [y] transformed: $F = 126.59$, $df = 1$, 309, $P < 0.0001$; Fig. 2).

DISCUSSION

Of the large number of nests monitored here, most were found prior to completion of nest building and nearly half of those never received an egg. Although most of the nests that did not receive an egg were never completely built, construction was completed for a substantial (32%) proportion. Our failure to observe eggs in these nests could have resulted from an egg being laid and then preyed on between our daily nest inspections (i.e. cryptic nest predation) or because the nests were abandoned prior to egg laying. If the cause was cryptic predation, nests without eggs should have occurred at a frequency similar to that of known egg predation during laying (i.e. ~1%). However, that the frequency of nests without eggs was more than an order of magnitude higher indicates that in nearly all instances these nests were abandoned. In our study population, therefore, nest abandonment before egg laying was a common occurrence.

Before considering possible adaptive explanations for the high rate of nest abandonment we observed, we consider two alternative explanations. First, abandonment may have been unnaturally high, because grackles were disturbed by daily nest checks or by farm activity at RRTF such as mowing and tree pruning. However, nest abandonment during egg laying and incubation was rare, despite most nests being monitored (and thus disturbed) during those stages. Furthermore, farm-related

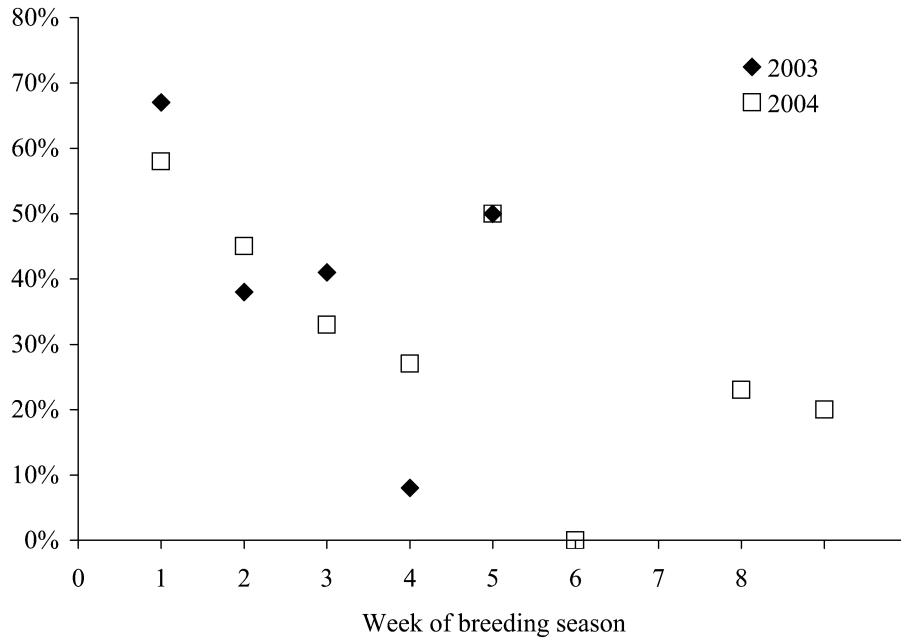


FIG. 1. Percentage of Common Grackle nests abandoned in relation to the week that nest building was completed. Week 1 began 2 April in 2003 and 31 March in 2004.

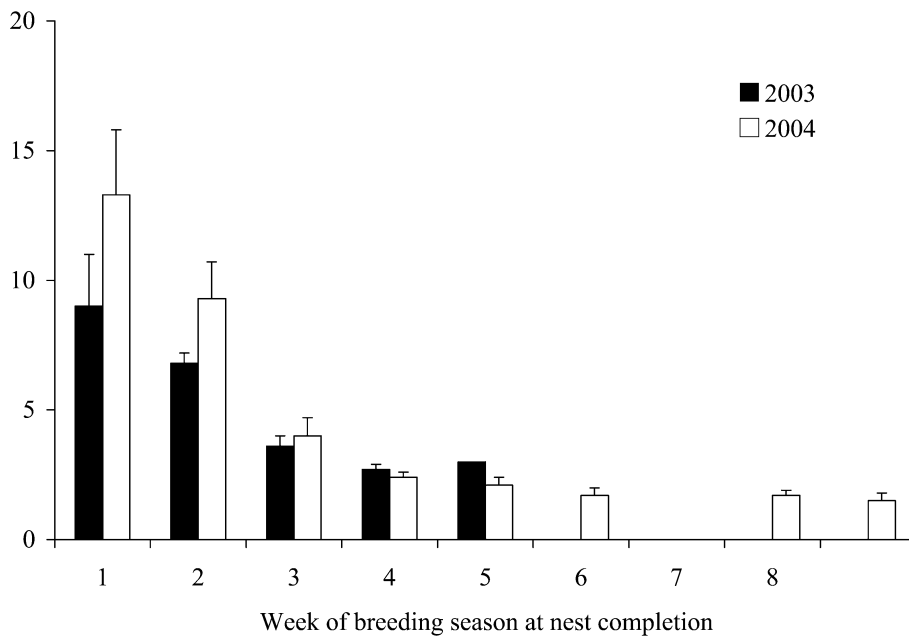


FIG. 2. Average number of days (\pm SE) between nest completion and first-egg date of Common Grackles in relation to week of nest completion for 2003–2004. Week 1 began 2 April in 2003 and 31 March in 2004.

activities increased through the season, which should have increased rates of abandonment as the season progressed, exactly the opposite pattern from that we observed. Thus, it seems unlikely that abandonment was an artifact of human disturbance.

The second possibility is that nests we considered abandoned were actually constructed as "dummy" courtship nests by males (Peer and Bollinger 1997). The suggestion that male grackles build dummy nests originates from a study that reported a single observation of a male grackle holding nesting material while perched at a nest (Petersen and Young 1950). The male was never observed actually building the nest. We are unaware of any direct evidence that male grackles build nests and never observed such behavior ourselves, so we consider this explanation implausible.

Consistent with birds abandoning nests because of natural causes were the similar seasonal declines in nest abandonment and delays in egg laying following completion of nest building. Previous studies have also found that time between nest building and egg laying declines seasonally (Wittenberger 1978, Alatalo et al. 1984, Stutchbury and Robertson 1987, Teather et al. 1988). Teather et al. (1988) proposed that females might delay egg laying early in the nesting season to enhance synchrony with other females or with resources. Similar reasoning could explain high nest abandonment early in the season, though abandoning a nest and rebuilding a new nest seems unnecessary if the purpose is only to delay egg laying. It is possible that nest abandonment is associated with mate abandonment in grackles, where building a new nest is inexpensive in relation to the advantage of obtaining a better mate. Because grackles are single-brooded in our study population (also see Peer and Bollinger 1997), mate switching should decline as the nesting season progresses because females would run out of time to start new nests. We have no data on what females did after they abandoned nests prior to egg laying, but with a marked population it would be possible to determine whether abandonment is associated with switching mates.

Our results have biological and methodological implications. Biologically, it seems surprising that so many females expend time and energy building nests they never use, presumably at the cost of having to start over. If abandonment

is associated with changing mates, as suggested above, then it is surprising that so many females would make inappropriate mate choices initially. American Robins (*Turdus migratorius*) provide an interesting contrast to the grackles. Also abundant at our study site, American Robins almost never abandon nests prior to egg laying (K. Cavey pers. comm.). American Robins also have a much longer breeding season than grackles. If length of the breeding season affected abandonment rates, however, it would seem that a shorter season should constrain abandonment because there would be less time available for starting a new nest.

Understanding why nests are abandoned will require detailed study of the ecological circumstances associated with nest abandonment by individuals and with variation in rates of nest abandonment among populations and species. Methodologically, both approaches will require accurate estimates of nest abandonment. Because predation rates in most studies are much higher than in our study, nests without eggs are likely to include cases of abandonment and cryptic predation. Rates of known egg predation during egg laying can be used to estimate the frequency of cryptic predation. In addition to providing more accurate estimates of abandonment rates, estimates of predation will also be improved. Although valuable for documenting the frequency of these phenomena at the level of populations, however, distinguishing abandonment from cryptic predation remains difficult for individuals. If the goal is to identify ecological circumstances associated with specific instances of nest abandonment, videotaping nests remains the only alternative.

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