

stated that King Vulture nests are found in a hollow tree or rock fissure and that 1 egg is laid. In Panama Lundy (1957) found a young bird incapable of flight, possibly having fallen from a hole in a tree, and Wetmore (1965) saw a juvenile perched in a large tree.

On 13 February 1985 we found a King Vulture nest in the Andean piedmont near the town Tucupido (Portuguesa State), Venezuela. The vegetation of the area is dry tropical forest. The nest was in a hole in the limb of a saman tree (*Pithecolobium saman*) 10.5 m above the ground. The hole was 1.2 m high and 60 cm wide. A nestling inside was covered with white down and had a naked, black head (Fig. 1a). We made ten more visits at intervals of 7–10 days and recorded the appearance of the nestling, its behavior, and the behavior of the adults when present.

Incubation time for King Vultures in captivity is 56–58 days (Brown and Amadon 1968). The egg probably was laid around the end of November or the beginning of December. This corresponds to the end of the rains and beginning of the dry season.

We believe the nestling was 2–3 weeks old at our first visit. Its condition was comparable to stage 1 of the California Condor (*Gymnogyps californianus*) described by Nice (in Brown and Amadon 1968). Its appearance did not change until 8 March (day 23) when black primary and secondary pinfeathers were present on the wings (Fig. 1b). A slight growth of the nasal excrescence was also observed. On the seventh visit (29 March, day 44) black teleoptiles were present on the back and shoulders (Fig. 1d). At the eighth visit (8 April, day 54) we noted a collar of black feathers on the neck, two tracks of black feathers on the back where the wings meet the body, and black rectrices 10 cm long. All the primaries and secondaries of the wings were growing (Fig. 1e). At the ninth visit (16 April, day 62) only two tracts of down were found on the back. The breast, abdomen, and wings were still covered with down (Fig. 1g). Due to a fire, the trunk of the tree was burning at its hollow base, and a burnt branch near the nest had fallen. Never-

theless, the nestling stayed in the nest unharmed. At the tenth visit (26 April, day 72) the young bird was found outside the nest perched on a branch. Its back was almost completely covered with feathers, while the breast and abdomen retained white down. It was probably capable of flight (Fig. 1h). By the last visit on 1 May the tree had fallen, and there was no sign of the young bird.

When observers were present, the nestling vocalized continuously while bowing. The head and neck approached its feet (Fig. 1c, d). When an attempt was made to touch the nestling, it attacked, using its talons and bill. This behavior was observed during the first 7 visits. From mid-April on the nestling no longer lowered its head and neck toward its feet, but remained erect with its head and neck folded onto its breast (Fig. 1f, g). This behavior also was seen when the bird was outside the nest.

Adults were seen during only 3 of the 11 visits to the nest. On one occasion 3 adults perched in the nest tree. One left, and the remaining two went nervously from one branch to another as the observer climbed to the nest. On another occasion an adult perched about 8 m from the nest. The third time 2 adults circled overhead and landed in nearby trees.

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Estimating Female Settlement from Nesting Data

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Testing predictions of mate-choice models often requires knowing the time a female settles in a particular territory. Because the effort necessary to observe settlement usually precludes direct observation of a large sample of females, researchers often rely on indices of settlement such as the onset of egg laying or nest building (e.g. Crawford 1977, Orians 1980, Yasukawa 1981, Yasukawa and Searcy 1981, Roskaft and Jarvi 1983, Alatalo et al. 1984, Muldal et al.

1985, Leonard and Picman 1986, Wooten et al. 1986, Lightbody and Weatherhead in press). Obviously, the reliability of those indices are of critical importance. We report on two studies that assessed the reliability of indices of female settlement. We also attempt to determine the factors that influence reliability in our own and in previously published studies to provide guidelines for future studies that use such indices.

The time from settlement on a territory to clutch

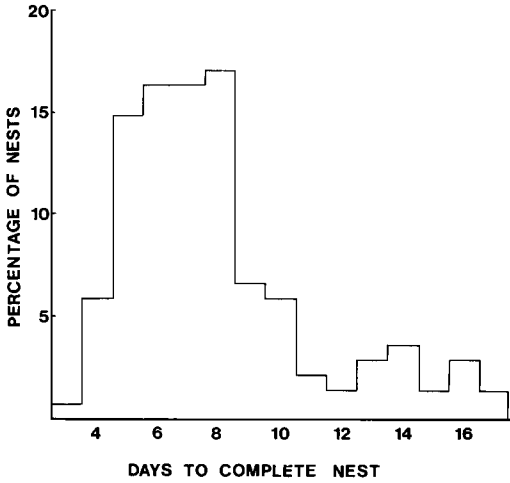


Fig. 1. Number of days between the initiation of nest construction and appearance of the first egg shown as a percentage of all Stage 1 Great-tailed Grackle nests.

initiation can be divided into two components, settlement to nest initiation and nest building to egg laying. Individual variation in either component will reduce the accuracy of estimates of settlement data based on either nest or clutch initiation. We examined variability in the duration of nest building (nest initiation to clutch initiation) in Great-tailed Grackles (*Quiscalus mexicanus*). We also studied variability in the time from settlement to nest initiation and the time from settlement to clutch initiation in Red-winged Blackbirds (*Agelaius phoeniceus*).

Duration of nest building in Great-tailed Grackles.—We studied Great-tailed Grackles between 13 April and 6 May 1986 on the Welder Wildlife Refuge near Sinton, Texas. Grackles nest locally in cattails (*Typha latifolia*) and bulrushes (*Scirpus californicus*) around open bodies of water (Tutor 1962). These areas were searched daily, and nests were marked and classified according to the following stages:

- Stage 1.—A few strands of wet vegetation woven among cattails or bulrushes (almost certainly began that day).
- Stage 2.—Obvious nest start, but nest cup not yet formed (possibly started that or previous day).
- Stage 3.—Nest cup clearly defined.
- Stage 4.—Exterior of nest complete but not yet lined with grass (characterized by mud bottom).
- Stage 5.—Nest complete but containing no eggs.

Nests were then checked daily to determine the date of clutch initiation.

Because Great-tailed Grackles breed colonially, we expected that proximity to other females might influence the speed with which females constructed nests

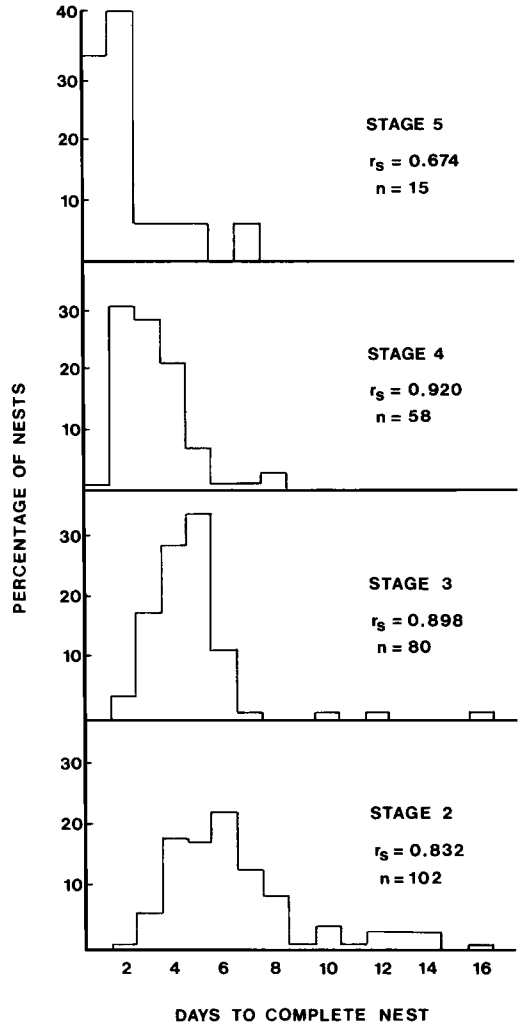


Fig. 2. Number of days between finding a nest and the appearance of the first egg for Great-tailed Grackle nests found at Stages 2-5. Spearman rank coefficients refer to the correlation between dates that nests were found and dates that first eggs were laid.

and began egg laying. Females may vary nest-building time to increase synchrony with neighbors. Therefore, for each nest studied we estimated the distance to the nearest active nest (0-1, 1-3, 3-5, 5-10, >10 m) when the nest was found and when the first egg was laid.

We found 135 nests in Stage 1. Although the correlation between the dates of nest initiation and clutch initiation for these nests was high ($r_s = 0.801$, $P < 0.001$), substantial variation occurred in the duration of nest building (Fig. 1). Forty-five percent of the nests were completed in 5-8 days, and 13% took longer than 12 days.

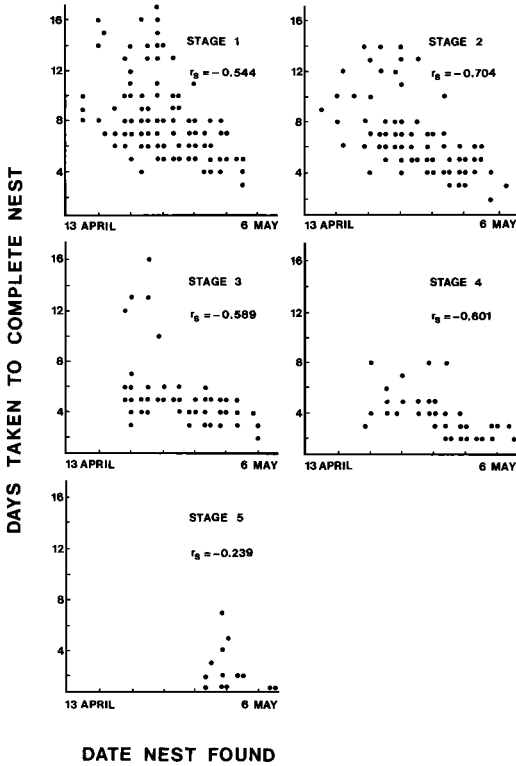


Fig. 3. Relationship between dates that Great-tailed Grackle nests were found and the number of days until the appearance of the first egg. All correlations are significant ($P < 0.05$) with the exception of Stage 5 nests ($P > 0.05$).

For nests in Stages 1-4, the closer a nest was to completion when found, the higher the correlation between the date of discovery and the date of clutch initiation (Figs. 1 and 2). The lower correlation for Stage 5 nests may be due in part to the smaller sample size.

One factor associated with the variability in nest-building duration was the time in the season that the nest was initiated. The later in the season a nest was found, the less time was taken for the nest to be completed. A negative correlation existed between date of discovery and duration of nest building for all five stages (Fig. 3).

Neither the distance from the nearest neighbor at the onset of building (Stage 1 nests only, $n = 135$) nor at clutch initiation (all nests combined, $n = 392$) affected the time taken to complete a nest ($r_s = 0.021$ and -0.093 , respectively; both P 's > 0.50).

Duration of pre-nest building and nest building in Red-winged Blackbirds.—This study was conducted between 1 April and 18 May 1986 near the Queen's University Biological Station in eastern Ontario. We monitored 17 territories daily to detect the settlement

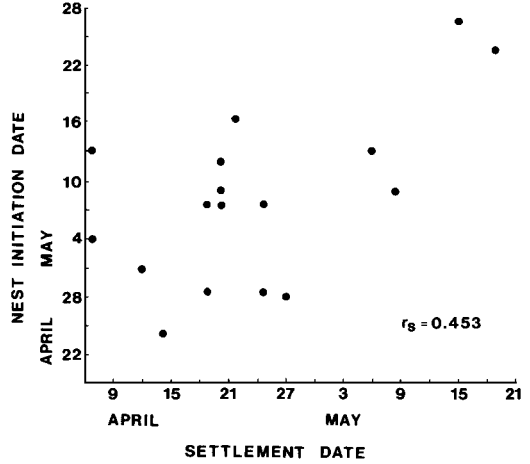


Fig. 4. Relationship between date of settlement and date of nest initiation for 17 female Red-winged Blackbirds ($P < 0.05$).

of first females. Because females were unbanded, we defined the day on which a female was seen on a particular territory and on all subsequent visits as the settlement date. All territories were located along roadsides and shared no boundaries with other territories, thereby making the determination of the presence or absence of a female on a territory unambiguous.

Once females had settled on territories we checked for nests every 2 days and subsequently monitored nests through egg laying. In early spring roadside territories are usually centered on small patches of cattail, the only available substrate for building nests. This allowed us to detect nest building as soon as it began.

Settlement dates were correlated positively with the date of nest initiation, although considerable variability was observed (Fig. 4). The correlation was lower between settlement date and the date of clutch initiation, indicating variability in the duration of nest building (Fig. 5). A separate analysis of nest building produced a significant, positive correlation between the date of nest initiation and the date of clutch initiation ($r_s = 0.912$, $P < 0.05$, $n = 17$).

As in the Great-tailed Grackle study, the date of settlement was strongly associated with the time taken by females to initiate clutches. The earlier a female settled, the longer the period between settlement and nest initiation (Fig. 6).

Discussion.—For both species the time between the initiation of a nest and the initiation of the clutch can be quite variable. In addition, there was considerable variation among female Red-winged Blackbirds in the time from settlement to nest initiation. Thus, estimates of female settlement date from the date of the first egg may be unreliable for many purposes. Sev-

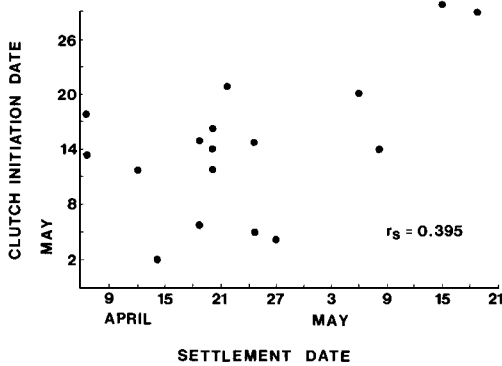


Fig. 5. Relationship between date of settlement and date of clutch initiation for 17 female Red-winged Blackbirds ($P < 0.05$).

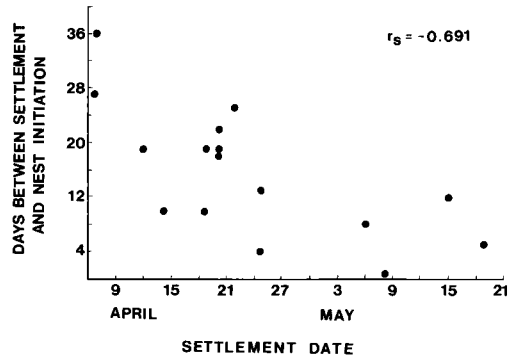


Fig. 6. Period between settlement and nest initiation in relation to settlement date for 17 female Red-winged Blackbirds ($0.05 < P < 0.10$).

eral patterns emerged, however, that suggest that in certain circumstances the reliability of estimating settlement dates could be increased. For example, nest initiation dates are superior indices of settlement dates because they avoid variation in nest-building duration. Also, because we found that females proceed more rapidly from settlement to nest building to egg laying as the breeding season progressed, for females that settle once nesting is underway, first-egg dates may be more reliable as an index of settlement date. Similarly, for species or populations with short intervals between the arrival of females and the onset of nesting (e.g. populations with short breeding seasons), first-egg dates will be better indices of settlement dates than in populations where females settle long before nesting.

These generalities are supported by other studies. For example, Lightbody and Weatherhead (in press) found a high correlation ($r_s = 0.84$, $P < 0.001$) between the order territories were settled by females and the order of first eggs in those territories in a population of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). In that population the breeding season is short, and females begin nesting a few days after settling. On the other hand, Stutchbury and Robertson (1987) found a very low correlation ($r_s = 0.22$, $P > 0.10$) between settlement date and clutch initiation in Tree Swallows (*Tachycineta bicolor*). They suggested that strong competition for nest sites in this hole-nesting species forces females to settle and secure a nest site long before laying begins. These results differ markedly from those found for another hole-nesting species, the Pied Flycatcher (*Ficedula hypoleuca*), in which only about 10 days separate female settlement from clutch initiation ($r_s = 0.86$, $P < 0.001$; Spearman ranks calculated from values presented by Alatalo et al. 1984: fig. 1). In contrast to the correlation of 0.395 between settling date and clutch initiation in Red-winged Blackbirds found in our study, Lenington (1980) found a correlation of 0.231 between

the two in a more southern population. Because this latter correlation was based on only five marked females, however, the results should be interpreted cautiously.

If there are advantages to nesting at a particular time during the breeding season, either because it coincides with nesting by other females or because of resource availability, females might adjust nest-building rates accordingly. In both Red-winged Blackbirds and Great-tailed Grackles we found strong correlations between the date of nest initiation and the time taken to complete the nest. Similar patterns have been found in Bobolinks (*Dolichonyx oryzivorus*) (Wittenberger 1978), Pied Flycatchers (from Alatalo et al. 1984: fig. 1), and Tree Swallows (Stutchbury and Robertson 1987).

Because it is difficult to observe female settling patterns directly, we expect that indices of these patterns will continue to be used in assessing mate choice and habitat selection decisions. We encourage investigators to assess the accuracy of such indices by considering the prelaying phase of the reproductive cycle of their study species. In particular, the variability in the time between settling and nest initiation and between nest initiation and clutch initiation will have obvious effects on the reliability of indices.

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Clutch-size Dependent Asynchronous Hatching and Brood Reduction in *Junco hyemalis*

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Asynchronous hatching of eggs may allow a reduction in number of offspring through starvation (brood reduction) to match the amount of food supplied by adult birds to the nest (Lack and Lack 1951, Lack 1954). Experimental manipulations of hatching synchrony generally have not supported the brood-reduction hypothesis (reviewed by Amundsen and Stokland 1988), and other explanations have been proposed for asynchronous hatching that are independent of brood reduction (reviewed by Clark and Wilson 1981). In particular, Clark and Wilson (1981) offered a "nest failure" hypothesis, closely related to Hussell's (1972) "predation" hypothesis, that asynchronous hatching in small birds, especially passerines, reduces the probability of total nest failure (see also Richter 1982; Slagsvold et al. 1984; Clark and Wilson 1985; Hussell 1985a, b; Slagsvold 1985, 1986a, b). This polemic concerning asynchronous hatching and brood reduction in passerines has tended to focus on between-species comparisons, obscuring potentially important within-species variation that is known to occur (Clark and Wilson 1981). I present evidence that suggests the Dark-eyed Junco (*Junco hyemalis*), a ground-nesting montane emberizid, employs both asynchronous hatching and brood-reduction strategies that depend on the number of eggs laid.

A total of 103 nests of "Pink-sided" Dark-eyed Junco (*J. h. mearnsi*) was found during 5 breeding seasons in northern Utah (Smith and Andersen 1982, 1985). The fate from eggs to termination was known for 83 clutches. At least 1 egg hatched in 65 nests, and the day on which all eggs within a clutch hatched was known for 44 clutches. Masses of nestlings within 1-2 days of hatching were known for all nests included in the analysis.

To determine the rate of asynchronous hatching among clutch sizes, I made three assumptions. First, the last-hatched egg was laid last (e.g. Zach 1982). Second, differences in hatching times of 24 h or more between last and penultimate nestlings reflected incubation beginning before clutch completion (Clark and Wilson 1981). Finally, differences of more than 1.0 g between the two smallest nestlings during the first 3 days after hatching represented asynchronous hatching, whereas differences of less than 0.5 g between the two smallest nestlings represented nearly synchronous hatching. In all cases where hatching times and masses were known, last-hatched nestlings in asynchronously hatched clutches were <1.0 g lighter than nest mates. Juncos weigh approximately 1.75 g at hatching (Smith and Andersen 1982), and only females incubate eggs.