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**Incubation continuity and the advantage of cryptic egg coloration to Mourning Doves.**—

Researchers primarily have addressed two hypothesized functions of egg coloration: (1) that when in direct sunlight, uniformly light-colored eggs are less likely to overheat than are darker eggs because light colors generally reflect solar radiation more efficiently (Montevecchi, *Behaviour* 58:26–39, 1976a), and (2) that scattered dark spots or scrawls benefit eggs by making them less conspicuous to predators (Lack, *Ibis* 100:145–166, 1958). Montevecchi (1976a) suggested that these potential functions of egg coloration are opposite selective forces; Bakken et al. (*Science* 200:321–323, 1978) found that the particular pigments used for cryptic coloration minimize heat absorption from direct insolation.

Little research has been done to document the effectiveness of cryptic egg coloration. Tinbergen et al. (*Behaviour* 19:74–117, 1962) and Montevecchi (1976a) placed cryptic and white eggs in meadows visited by avian predators and found that cryptic eggs suffered less predation. Bertram and Burger (*Ibis* 123:207–210, 1981) had similar results when they placed white vs brown Ostrich (*Struthio camelus*) eggs on bare ground. In contrast, Kruijt (*Arch. Neerl. Zool.* 12:565–567, 1958) found that egg speckling did not reduce predation by Herring Gulls (*Larus argentatus*) on artificial nests. In none of these studies were the eggs attended by adult birds.

Pigeons and doves (Columbidae) are unusual among open-nesting birds because they lay relatively conspicuous eggs of a uniform white or buff color. Columbids incubate continually (Kendeigh, *Ill. Biol. Monogr.* 22, 1952), so selective pressure for egg crypticity probably is weak. White eggs and constant incubation make columbids ideal for studies of egg coloration because a researcher can control both egg color (by painting eggs) and continuity of incubation (by flushing parents from the nest at regular time intervals). Here, we report on a test of the value of cryptic egg coloration to Mourning Doves (*Zenaida macroura*) under regimes of continual vs interrupted incubation. Unlike earlier studies of egg crypticity, our study involved natural nests with parents actively attending them.

*Methods.*—Before we began field work, we tested the effect of brown tempera paint on egg viability by measuring the evaporation rate of Ringed Turtle-Dove (*Streptopelia risoria*) eggs before and after they were spattered with paint. Laboratory results indicated that painting did not affect gas exchange.

Field work was done from May through early August 1983 at Big Creek State Park, Polk County, Iowa. The park contained several km of windbreaks, most of which consisted of a multiflora rose (*Rosa multiflora*) hedge flanked on one or both sides by double rows of jack pine (*Pinus banksiana*) or white pine (*P. strobus*). Most trees were less than 6 m tall, and land between windbreaks was either fallow or used to grow corn, alfalfa, or oats.

We found nests by walking between pine rows and flushing parents. We determined the age of eggs by candling (Hanson and Kossack, *Ill. Dept. Conserv. Tech. Bull.* 2, 1963). In addition, several nest-site features were recorded: light intensity above the nest (measured with a light meter and expressed as a percentage of ambient light intensity), average nest visibility from 5 m away (subjectively evaluated on a scale of 1–4 [poor to excellent] from the four cardinal directions), height of vegetation above nest level (tree height minus nest height). Relative light intensity above the nest was used as an index of overhead visibility. Previous analyses indicated that these variables may influence nesting success (Westmoreland and Best, *Auk* 102:774–780, 1985).

Each nest was assigned randomly to one of four treatments: (1) incubation interrupted and eggs cryptic, (2) incubation interrupted and eggs white, (3) incubation continual and eggs cryptic, and (4) incubation continual and eggs white. Immediately after a nest in treatments 1 or 3 was discovered, eggs were spattered with brown tempera paint (using a

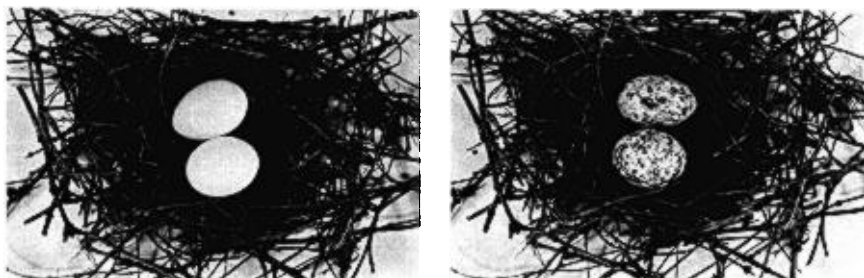


FIG. 1. A clutch of dove eggs before and after being painted.

watercolor brush) to simulate cryptic coloration (Fig. 1). Incubation was interrupted (treatments 1 and 2) by flushing parents from each nest every 3 days. We checked continually incubated nests from about 5 m away (using binoculars) at the same interval, taking care not to approach so closely that the parent flushed. Nest checks in all treatments continued until the nest failed or the eggs hatched.

When a nest was found empty but intact, we attributed the failure to avian predators (Best and Stauffer, *Condor* 82:149–158, 1980 and references therein). Common Crows (*Corvus brachyrhynchos*) were seen frequently in the area and are known to carry dove-sized eggs away from nests (Montevocchi, *Behaviour* 57:307–320, 1976b). Mammalian (probably raccoons [*Procyon lotor*] and weasels [*Mustela* spp.]) predation was assumed when the nest was partially or completely destroyed. Snakes and chipmunks (*Tamias striatus*) were seen infrequently in the study area, so predation by them probably was rare. Small nocturnal mammals (mice and shrews) were not considered important predators because one Mourning Dove adult usually is present at the nest overnight. Failures due to factors other than predation (i.e., wind blowing eggs from the nest or nest abandonment) were not included in the analysis.

Incubation was interrupted when nests were initially discovered. Thus, for continually incubated nests (treatments 3 and 4), we eliminated from analysis all data on the interval between nest discovery and the subsequent visit. As a result, comparisons of nesting success between continual and interrupted-incubation regimes are biased and are not discussed here (but see Westmoreland and Best, *Auk*, 1985). Comparing nesting success between cryptic vs white-egg clutches within each incubation regime, however, was valid. We calculated the daily nest survival probability (Mayfield, *Wilson Bull.* 87:456–466, 1975) for each treatment and compared them by using one-tailed statistical tests (Hensler and Nichols, *Wilson Bull.* 93:42–53, 1981). Analysis of variance was used to test for differences in nest-site features among treatments.

**Results.**— We found 130 active nests. One nest failed due to high winds; 12 clutches with cryptic eggs and two clutches of white eggs were abandoned. Eleven of the cryptic-egg abandonments occurred immediately after the eggs were painted; only once did parents initially accept a modified clutch and abandon it later. McClure (*Auk* 62:270–272, 1945) painted 10 Mourning Dove clutches various bright colors and observed the returning parents; all but one resumed incubation without hesitation. Seven of the cryptic-egg abandonments occurred at nests with interrupted incubation, and the remainder (5) at nests with continual incubation.

Nest-site features (mean vegetation height above nest level =  $2.3 \pm 0.1$  m [SE], treatments pooled; relative light intensity =  $19.2 \pm 1.5\%$ ; nest concealment =  $2.8 \pm 0.1$ ) and the age

TABLE 1  
NEST SUCCESS DATA FOR CLUTCHES OF CRYPTIC VS WHITE EGGS UNDER DIFFERENT  
INCUBATION REGIMES

	Incubation interrupted		Incubation continual	
	Cryptic	White	Cryptic	White
Number of nests	29	36	19	31
Number of failures	8	18	2	7
Daily nest survival probability	0.957 ± 0.015 <sup>a</sup>	0.915 ± 0.019	0.980 ± 0.014	0.958 ± 0.016
Estimated success <sup>b</sup>	54%	29%	75%	55%

<sup>a</sup> Difference is significant ( $P < 0.05$ ) by Hensler and Nichols (1981) test. Survival probability ± SE.

<sup>b</sup> Based on an incubation period of 14 days (see Mayfield 1975).

of eggs at nest discovery ( $6.8 \pm 0.6$  days) did not differ significantly ( $P > 0.05$ ) among treatments. These results suggest that nesting success for treatments was not affected by factors other than egg color and incubation regime.

Cryptic coloration significantly ( $P = 0.04$ ) reduced clutch losses when incubation was interrupted, but did not significantly influence clutch success when incubation was continual (Table 1). Avian predators, probably Common Crows and Common Grackles (*Quiscalus quiscula*), caused 85% of the clutch failures.

*Discussion.*—Our results suggest that cryptic egg coloration has strong adaptive value even when incubation is interrupted infrequently and for short periods. We attempted to determine return times for flushed adults, but were unable to find a method that did not cause abandonment or further increase the risk of predation. Casual observations, however, indicated that birds usually return to the nest within 3 h. McClure (1945) recorded return times of 3–50 min and suggested that most returns are within 1 h.

We found no evidence that Mourning Doves are exposed to selection for egg colors that reduce solar heating. Our cryptically painted clutches were often exposed to incident radiation during adults' absences, but all eggs not taken by predators hatched normally.

Columbid eggs may have originally been cryptic, and lost their color because constant incubation eliminated selection for the trait; conversely, columbids may have evolved constant incubation to cover their white eggs. We believe that the former is unlikely. Cryptic eggs probably would afford some selective value, even to continually incubating columbids, when parents are flushed from the nest by predators. In our study, survival of cryptic eggs was greater than that for white eggs even when incubation was continual. Although this difference was not significant ( $P = 0.15$ , Table 1), the hypothesis that cryptic egg coloration is valuable to continually incubating columbids should not be rejected, because the power of the test is low (0.37).

Some aspects of columbid incubation behavior strengthen the notion that continual incubation evolved, at least partially, as a mechanism to reduce the conspicuousness of white eggs. When incubating Mourning Doves are approached, they crouch on the nest and do not flush until almost in contact with the intruder (e.g., Laub, M.S. thesis, The Ohio State Univ., Columbus, Ohio, 1956; Walsberg and Voss-Roberts, *Physiol. Zool.* 56:88–93, 1983). Brightly colored male Purple-crowned Pigeons (*Ducula spilorrhoea*) also remain on the nest

when approached, but shift positions to keep a patch of cryptic undertail feathers oriented toward intruders (Crome, *Emu* 75:172-174, 1975).

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**Effects of old nests on nest-site selection in Black-crowned Night-Herons and Snowy Egrets.**—The use of old nests has been reported for Black-crowned Night-Herons (*Nycticorax nycticorax*) (Gross 1923), Little Blue Herons (*Egretta caerulea*) (Burger and Miller 1977), Green-backed Herons (*Butoroides striatus*) (Meyerriecks 1960), Cattle Egrets (*Bubulcus ibis*) and Tricolored Herons (*E. tricolor*) (Jenni 1969); however, the effect of old nests on nest-site selection during the following breeding season has not been investigated quantitatively. Nests of Black-crowned Night-Herons and Snowy Egrets (*E. thula*) survive the winter in large numbers at the Clark's Island heronry, Plymouth, Massachusetts, particularly when they are located in the dense foliage of eastern red cedars (*Juniperus virginiana*). During the spring of 1981 I attempted to determine the effect of old nests on nest-site selection in these two species.

*Study area and methods.*—The Clark's Island heronry (colony 324001, Osborn and Custer 1978) supports a breeding population of 500-600 pairs, mostly Black-crowned Night-Herons and Snowy Egrets (Davis and Parsons 1982).

On 28 March, 43 red cedar trees were divided into a group of 21 experimental trees from which all 52 old nests were removed and the sites of the old nests marked (hereafter "old sites"), and a group of 22 control trees, in which 53 nests were marked but left in place. No herons were observed on the island when the nest removal and tagging were done. All red cedars that contained at least one nest encountered in a transect through the colony were included in the study, and assignment to group was randomized by designating the group in which the next encountered tree would be placed. Nest density was comparable in control and experimental trees. Trees were examined at approximately weekly intervals (Fig. 1) beginning on 18 April, when 2 complete and 11 partial clutches were found. On each visit new eggs were marked, all new nest building noted, and the use of old nests recorded. A nest was considered active if one or more eggs were present. Species was determined by egg size (Snowy Egret eggs are smaller than those of night-herons) and confirmed after hatching. Statistical analysis was by  $\chi^2$  tests.

*Results.*—The date of the median active nest for Snowy Egrets was three weeks later than for Black-crowned Night-Herons in both the control and experimental trees (Fig. 1) (median test,  $P < 0.05$ ).

Black-crowned Night-Herons built more nests in control trees than in experimental trees (14 nests/22 trees vs 12 nests/21 trees), as did Snowy Egrets (35 to 24), but the differences were not significant ( $P > 0.05$ ). In control trees, Black-crowned Night-Herons used old nests in 86% of the cases, Snowy Egrets used them 60% of the time (Table 1). In the first nesting in each tree, Black-crowned Night-Herons used old nests in 85% of the cases, Snowy Egrets