

DIFFERENTIAL PREDATION ON EGGS IN CLUTCHES OF NORTHWESTERN CROWS: THE IMPORTANCE OF EGG COLOR^{1,2}

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Abstract. In the majority of clutches of Northwestern Crows (*Corvus caurinus*) one of the eggs is frequently slightly to much paler than the others. I address the question why this may be so and I test the hypothesis that this egg, once a predator is at the nest, draws attention to itself and is thus subject to selective predation by conspecifics. In three-, four- and five-egg clutches, last-laid eggs were significantly smaller than all the other eggs in each clutch and second-laid eggs were generally the largest. In 74% of the clutches in which a pale egg was present this was the last-laid egg, while the first-laid egg was the palest one in 18% of the clutches. The larger the clutch, the greater the chance that one of the eggs was a pale one. In completed clutches, the first egg to be taken by a predator was significantly more often (a) the first- or last-laid egg in the clutch than a central egg and (b) the palest egg. The mean volume of depredated eggs did not differ significantly from the others so size per se was not the reason why they were taken. Last-laid eggs are particularly expendable as they have a significantly reduced hatching success due to asynchronous hatching.

Key words: Northwestern Crow; Corvidae; egg color; egg size; differential egg predation; hatching success.

INTRODUCTION

Several experimental studies have shown that egg color provides camouflage and enhances an egg's chance of escaping predation (Tinbergen et al. 1962, Croze 1971, Montevecchi 1976b, Bertram and Burger 1981). Other studies (Dice 1947, Mueller 1968, Ohguchi 1981) have shown that "the odd one out" is subject to selective predation.

Northwestern Crows (*Corvus caurinus*) lay a clutch of three to five eggs with a mean of 4.0 ± 0.7 eggs (Butler et al. 1984). The background color of the eggs ranges from light blue to dark green with blotches of brown to black. In some clutches all eggs are of the same color but in the majority of clutches one of the eggs is slightly to very much lighter than the others. Holyoak (1970) reported the same phenomenon in the Carrion Crow (*C. corone*) and a number of other species of *Corvus*.

In this paper I test the hypothesis that the light-colored egg, because it is the odd egg in the clutch, draws attention to itself once a predator is at the

nest, and is therefore subject to selective predation compared to the other eggs in the clutch.

METHODS

All eggs were numbered with India ink in the sequence in which they were laid. If I found a nest for the first time and it contained two or more eggs then these were given the same number. For instance, if there were three eggs, all were inscribed with the number 3. Subsequent eggs in that clutch were numbered in the order in which they were laid, i.e., 4 and 5 in the case of a five-egg clutch. Once the clutch was completed all the eggs for which the laying sequence was known were measured with vernier calipers to one decimal place. Egg volume was determined using the formula: volume = length \times width² \times 0.51 (Hoyt 1979). Eggs were laid in a row, on a brown cloth that resembled the color of the nest lining, with the first-laid egg on the left and the last-laid egg on the right and a color photograph was taken of the clutch. The slides were later projected and the eggs within each clutch scored for color relative to each other. I tried to measure and photograph on the same occasion to reduce disturbance but for various reasons this often was impossible. When a female crow is flushed from the nest she will leave silently and settle in a nearby tree top from where she monitors the

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² This paper is dedicated to Frank A. Pitelka on the occasion of his retirement.

TABLE 1. Volume ($\bar{x} \pm SD$) of eggs in completed clutches of three, four, or five eggs (number of each clutch size in parentheses) of Northwestern Crows on Mitlenatch Island, in which the volume (cm^3) and the sequence of each egg in the clutch was known. Statistical comparisons were done using standardized data (see text).

	Clutch size		
	3 ^a (<i>n</i> = 18)	4 (<i>n</i> = 28)	5 (<i>n</i> = 19)
1st egg	17.08 ± 1.52	15.77 ± 1.23	15.99 ± 1.66
2nd egg	17.12 ± 1.37	16.22 ± 0.82	16.52 ± 1.43
3rd egg	16.14 ± 1.40	15.95 ± 1.11	16.28 ± 1.44
4th egg		15.28 ± 1.01	15.96 ± 1.52
5th egg			15.25 ± 1.37
\bar{x}	16.78 ± 1.44	15.88 ± 1.23	16.00 ± 1.55

^a Significance levels of paired comparisons (Tukey test) within clutches as follows: three-egg clutches: 1 vs. 2, ns; 1 vs. 3, $P < 0.05$; 2 vs. 3, $P < 0.01$; four-egg clutches: 1 vs. 2, $P < 0.02$; 1 vs. 3, ns; 1 vs. 4, $P < 0.01$; 2 vs. 3, $P < 0.01$; 2 vs. 4, $P < 0.001$; 3 vs. 4, $P < 0.001$; five-egg clutches: 1 vs. 2, $P < 0.02$; 1 vs. 3, ns; 1 vs. 4, ns; 1 vs. 5, $P < 0.01$; 2 vs. 3, ns; 2 vs. 4, $P < 0.01$; 2 vs. 5, $P < 0.001$; 3 vs. 4, $P < 0.01$; 3 vs. 5, $P < 0.001$; 4 vs. 5, $P < 0.001$.

situation. If you stay near the nest too long she will return to the area and make alarm calls, which may attract her mate and other crows. Furthermore, eggs were photographed in bright light, which often meant that I had to take them to the forest edge. In some cases the distance involved was such that I ran the risk of giving the crow the impression that I had left the area. The crow finding the nest empty on her return would likely have abandoned it. This problem could only be avoided by having an assistant stay near the nest while I photographed, but an assistant was not always available. Thus, in some cases I was forced to measure and photograph on separate days, which meant that in some cases predation occurred before the eggs were measured or photographed, whichever occurred first. Sample sizes for the various components of this study are thus not the same. Once the eggs were measured and photographed, the nest was visited as little as possible (every 3.98 ± 1.42 days) to keep disturbance to a minimum, until all eggs had hatched or had had ample time to do so. The incubation period is 18 days (Butler et al. 1984). The data were gathered on Mitlenatch Island, British Columbia, during 1983–1986.

RESULTS

EGG VOLUME

The mean intraclutch egg volume differed in the order of laying in each clutch size (Table 1). As interclutch variation obscured the real difference between successive eggs within each clutch I did an ANOVA on adjusted values, obtained by subtracting the intraclutch mean volume from the volume of each egg within the clutch. Egg volume (Table 1) was significantly influenced by laying

order (for three-egg clutches $F = 10.50$, $df = 2$, $P < 0.001$; four-egg clutches $F = 14.42$, $df = 3$, $P < 0.001$; five-egg clutches $F = 12.55$, $df = 4$, $P < 0.001$). Using adjusted values, the mean egg volume of first and second eggs in three-egg clutches was significantly (Table 1) larger than the mean volume of third eggs (Tukey test). Similarly, second eggs differed significantly from first, third, and fourth eggs in four-egg clutches and from first, fourth, and fifth eggs in five-egg clutches. In three-, four-, and five-egg clutches last-laid eggs were significantly smaller than all others in their respective clutch size (Table 1). Clutches of three, four, and five eggs differed significantly in mean egg volume (ANOVA $F = 4.17$, $df = 2$, $P < 0.025$). Mean egg volume in three-egg clutches was significantly larger than in four-egg clutches (Tukey test, $q = 4.01$, $df = 2$, $P < 0.01$) and five-egg clutches ($q = 2.94$, $df = 2$, $P < 0.05$), but mean volume in four- and five-egg clutches did not differ significantly.

Relative to the mean volume of each clutch, second eggs were largest in five-egg clutches and smallest in three-egg clutches (Fig. 1). First eggs in four- and five-egg clutches and fourth eggs in five-egg clutches were as heavy as the mean weight of all eggs in their respective clutch size. The heaviest eggs were the first and second in three-egg clutches and the second and third in four- and five-egg clutches (Fig. 1).

EGG COLOR

In those clutches ($n = 82$) for which the color of the eggs in the laying sequence was known, the last-laid egg was the palest in 53 clutches (64.6%), followed by the first egg ($n = 13$, 15.9%), while

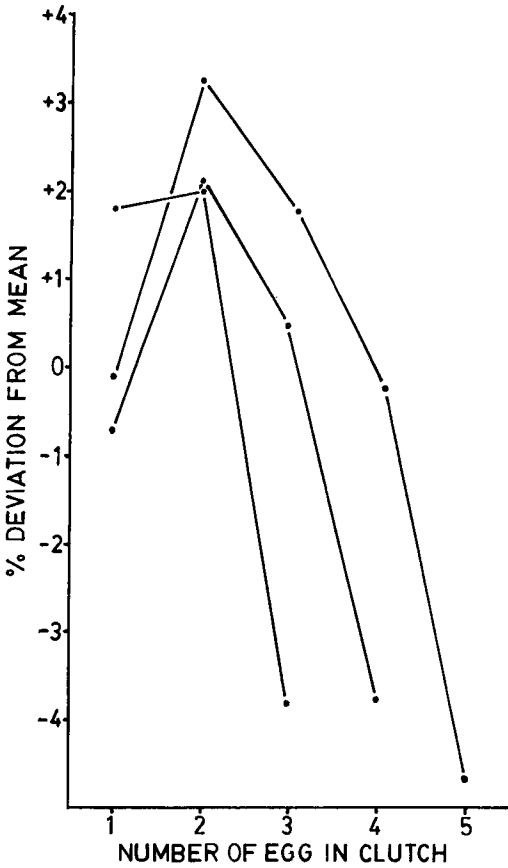


FIGURE 1. Intraclutch variation in egg size of Northwestern Crows in clutches of three ($n = 18$), four ($n = 28$), and five eggs ($n = 19$).

very few central eggs (all other eggs in a clutch except the first and the last) ($n = 6$, 7.3%) were the palest egg in the clutch (Table 2). In 10 clutches (12.2%) the eggs within each clutch were of the same color (Table 2). The highest proportion of these occurred in three-egg clutches (21.7%) and the lowest in five-egg clutches (4.3%), with four-egg clutches lying in between (11.1%). The relative frequency of pale eggs among first, central, and last eggs (Table 2) differs significantly ($\chi^2 = 167.8$, $df = 2$, $P < 0.001$) from expected. Excluding clutches within which all eggs were of the same color (Table 2), significantly more first eggs were the palest egg in the clutch than central eggs ($\chi^2 = 11.5$, $df = 1$, $P < 0.005$), while last-laid eggs were significantly more often the palest than first-laid ($\chi^2 = 40.6$, $df = 1$, $P < 0.001$) and central eggs ($\chi^2 = 111.2$, $df = 1$, $P < 0.001$, Table 2).

TABLE 2. The position of the palest egg within each of 82 clutches of three, four, or five eggs of the Northwestern Crow on Mitlenatch Island.

Clutch size	No. of clutches	No. of clutches in which all eggs had the same color	No. of clutches in which the palest egg was number				
			1	2	3	4	5
3	23	5	4	2	12		
4	36	4	5	3	1	23	
5	23	1	4	0	0	0	8

The degree to which the light-colored egg differed from the other eggs in each clutch was variable. Clutches in which all the eggs in the clutch were of the same color or in which one egg was only slightly paler than the others, predominated in nests with three eggs. The largest percentage of very pale to extremely pale eggs were found in five-egg clutches, while the proportion of medium-colored eggs remained about the same in each clutch size (Fig. 2).

PREDATION

The potential predators on Mitlenatch Island were coast garter snakes (*Thamnophis elegans*), river otters (*Lutra canadensis*), Glaucous-winged Gulls (*Larus glaucescens*), and Northwestern Crows themselves. As Mandarte Island, where this study was begun, lacked snakes, yet egg predation occurred there, I think it highly unlikely that garter snakes took crow eggs on Mitlenatch Island. Additionally, the crows are quite capable of catching and killing garter snakes (Butler 1979, James and Verbeek 1984, unpubl. data). Otters may have taken the eggs from some ground nests but as they would almost certainly have taken the whole clutch they are of no concern in this study (see below). Gulls would certainly eat crow eggs if they came across a nest, and they would likely take all the eggs, but as the crows nested in clumps of trees and in dense shrubbery the gulls had no access to the nests. This leaves the crows themselves. I have seen crows in the act of stealing crow eggs and on many occasions I have seen empty crow eggshells at sites to which crows take eggs to deal with them at leisure (Verbeek 1982).

In this study I was interested in a subset of depredated clutches ($n = 22$), that were known to be complete, had not been depredated prior to completion and from which only a single egg had disappeared upon my return visit. Whether

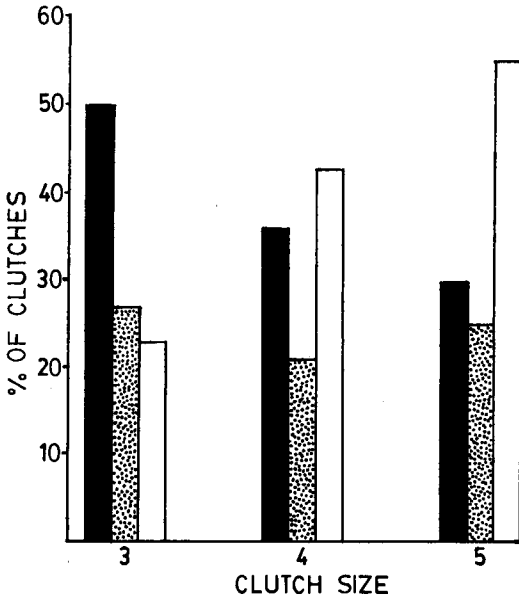


FIGURE 2. The proportion of clutches in which (1) all the eggs were of the same color or in which one egg was only slightly paler than the others (black bar), (2) one of the eggs was much to very much paler than the others (open bar), or (3) the difference in color of the palest egg in the clutch was intermediate compared to the other eggs in the clutch (stippled bar), in clutches of three ($n = 23$), four ($n = 36$), and five eggs ($n = 23$).

or not subsequent to my return visit to the nest additional eggs disappeared from some of these 22 clutches (and some did), was of no interest to this study. From this subset I ask the question, given a complete clutch, which egg does a crow take first? As eggs were marked in the sequence in which they were laid, results were tabulated (Table 3) to determine whether the missing eggs were taken from clutches at random or by selective predation, thereby indicating that some eggs were more vulnerable to predation than others. The relative proportion of depredated eggs among first, central, and last eggs, in all clutches combined, departs significantly from expectation ($\chi^2 = 13.5$, $df = 2$, $P < 0.005$). Significantly ($\chi^2 = 9.5$, $df = 1$, $P < 0.005$) more first eggs (nine out of 22) than central eggs (four out of 44) were taken by the predators and significantly ($\chi^2 = 9.5$, $df = 1$, $P < 0.005$) more last eggs (nine out of 22) than central eggs.

Among the 22 completed clutches that lost a single egg (Table 3), the eggs within each of three

TABLE 3. Position of the depredated egg in the laying sequence of eggs first taken by Northwestern Crows from 22 completed clutches of three, four, or five eggs.

Clutch size	No. of clutches	Position of egg in the laying sequence				
		1	2	3	4	5
3	6	2	1	3		
4	10	4	1	0	5	
5	6	3	2	0	0	1

clutches were of the same color, therefore the predators could not have chosen on the basis of color, and in two clutches the depredated eggs were lost before I photographed them, hence I had no record of their color. Of the remaining 17 clutches, 12 (70.6% of 17 eggs) lost their palest egg (four first, seven last, and one central egg) and five (9.6% of 52 eggs) had eggs other than the palest taken (Table 4), which is significant ($\chi^2 = 25.6$, $df = 1$, $P < 0.001$). Of the 12 nests that lost their palest egg, eight had been scored for the degree of paleness (for the other four I knew that the palest egg in each nest had disappeared but I did not know how pale they were relative to the other eggs in their respective clutch). Of the eight pale eggs, three were scored very pale and three extremely pale.

To test whether egg size was important, I compared the mean volume ($15.83 \pm 1.24 \text{ cm}^3$) of the single depredated egg in each clutch ($n = 10$, because for the other 12 of the 22 single eggs taken I did not have the volume) with the mean volume ($16.11 \pm 1.36 \text{ cm}^3$) of the nondepredated eggs ($n = 28$) in those same 10 clutches. The comparison between means was done on standardized data as explained earlier. Although depredated eggs were on average smaller than nondepredated eggs, the difference between the means was not significant (ANOVA, $F = 0.62$, $df = 1$, 37 , $P > 0.05$).

HATCHING

Eggs that failed to hatch (infertile or the chick did not manage to get out of the egg) remained in the nest for several days before they disappeared. Hatching failure was investigated in all completed clutches (regardless of whether I knew their volume or not) that were not preyed on. In these clutches, the proportion of eggs that did not hatch, 5 out of 48 (10.41%) eggs in three-egg clutches ($n = 16$), 14 out of 180 (7.77%) in four-

egg clutches ($n = 45$), and 16 out of 110 (14.55%) in five-egg clutches ($n = 22$), did not differ significantly ($\chi^2 = 3.33$, $df = 2$, $P > 0.05$). In three of 30 clutches in which eggs failed to hatch I did not know the position of the unhatched egg in the clutch. In the remaining 27 clutches, 32 eggs failed to hatch (one second and two last-laid eggs failed to hatch in three three-egg clutches, three first, one second, three third, and six last-laid eggs in 12 four-egg clutches and three first, two second, two third, four fourth, and five last-laid eggs in 12 five-egg clutches). Hatching success was significantly influenced by the position of the egg in the laying sequence ($\chi^2 = 7.52$, $df = 2$, $P < 0.025$). Significantly ($\chi^2 = 6.97$, $df = 1$, $P < 0.005$) more last-laid eggs (13 out of 27) failed to hatch than central eggs (13 out of 63) and first-laid eggs (6 out of 27, $\chi^2 = 3.98$, $df = 1$, $P < 0.05$). First-laid eggs and central eggs did not differ significantly ($\chi^2 = 0.02$, $df = 1$, $P > 0.05$) in the number of eggs that failed to hatch.

To investigate the possibility that egg size (volume) might have influenced hatching success I compared the mean volume of hatched ($n = 170$) and unhatched eggs ($n = 27$) in all unpredated clutches in which the volume of all eggs was known. The means did not differ significantly. A similar comparison between the 85 heaviest hatched eggs and the 14 heaviest unhatched eggs and between the 85 lightest hatched eggs and the 13 lightest unhatched eggs also showed no significant difference.

DISCUSSION

In a number of corvids (Slagsvold et al. 1984), including Northwestern Crows (Table 1), the last-laid egg in the clutch is on average noticeably and statistically smaller than the others. The corvids share this phenomenon with larids (Verbeek 1982, 1988; Slagsvold et al. 1984). In addition, incubation starts before clutch completion. In three-egg clutches, incubation starts when on average 1.82 ± 0.57 eggs have been laid and in four- and five-egg clutches incubation starts after 2.43 ± 0.77 and 2.50 ± 0.50 eggs have been laid, respectively (Butler et al. 1984). Thus in all clutches one or more young hatch later than the others and because they hatch from slightly smaller eggs they may be substantially smaller than earlier hatched young which may have been fed and growing for a day or more before later siblings hatch. Last eggs thus have a double dis-

TABLE 4. The number of completed Northwestern Crow clutches of three, four, or five eggs, in which the laying sequence and the color of the eggs in each clutch was known, as well as the color of the one egg in each clutch that was taken by a predator.

Clutch size	No. of clutches	Total eggs	No. of palest eggs		No. of darker eggs	
			Available	Taken	Available	Taken
3	4	12	4	4	8	0
4	8	32	8	7	24	1
5	5	25	5	1	20	4
Total	17	69	17	12	52	5

advantage. There may be an additional disadvantage due to small size, namely differential predation.

Egg loss can be quite high in *Corvus*: 27% in *C. corone* (Yom-Tov 1974) and 9.4% in the Northwestern Crow (Richardson et al. 1985). Intraspecific predation is the main reason for this. Wittenberg (1966) stated that most of the egg loss in the Carrion Crow was caused by non-breeding conspecifics. The same applies to the roving groups of yearlings, as well as neighboring adults, in this study. Intraspecific predation is thus common and it is made easier in Northwestern Crows because nests are close together (Butler et al. 1984) and the birds are well acquainted with the location of each other's nests (pers. observ.). Yom-Tov (1974) too found that predation was higher in those areas where the internest distance was small. Although female crows sit tight when incubating, the average inattentive period of 5.6 ± 3.3 min ($n = 65$, Butler et al. 1984) seems more than long enough to allow another crow to take an egg.

The possibility remains that female crows removed their own eggs but this seems unlikely. Yom-Tov (1976) showed that Carrion Crows did not remove the eggs of other Carrion Crows, Rooks (*C. frugilegus*), and domestic hens (*Gallus domesticus*) when these were placed in their nest during incubation, starting 3 days after the crows had completed their own clutch. Yom-Tov (1976) did find that when he introduced cracked eggs they were removed. It may be suggested that paler eggs are not as sturdy as normal-colored eggs and therefore more likely to be damaged and thus removed by the female. When handling eggs and while writing numbers on them I did not find paler eggs more easily damaged than the

others. Unhatched eggs might stay in the nest for up to a week before they were removed, presumably by the parents (Bingal and Withers 1989). Some of these eggs were pipped but the chick had been unable to emerge.

As Montevecchi (1976a) showed, *C. brachyrhynchos* tends selectively to take small eggs when presented experimentally with a choice between large and small ones. Northwestern Crows prey heavily on the eggs of cormorants (*Phalacrocorax* sp.) and are often seen flying with intact whole cormorant eggs in their bills (Verbeek 1982). As cormorant eggs are much larger than Northwestern Crow eggs, the crows should be able to carry off the entire range of available crow egg sizes. Although egg size per se thus does not appear to be an important determinant of predation in this study (mean volume of depredated eggs was not significantly different from that of non-depredated eggs), this does not negate the possibility that size is nevertheless important, particularly as speed may be a factor during the act of predation. A stronger case can be made for the importance of color.

Presumably birds' eggs are colored to camouflage them in the nest, particularly in open ground nests. Tinbergen et al. (1962) and Montevecchi (1976a) provided evidence to support this. *Corvus caurinus* lines its nest with strips of cedar bark (*Thuja plicata*) and this, along with a generally well-hidden nest, provides for a dark, shady background against which light-colored eggs tend to stand out. In *C. caurinus* these pale eggs are typically the last laid in the clutch, and occasionally the first-laid eggs (Table 2), precisely those eggs that suffer the most predation (Table 4, see also Verbeek 1988). It is not the size of the depredated egg that is important in making it more vulnerable but apparently the color, particularly the oddity of the egg's color relative to the others in the clutch.

As crow eggs appear to suffer frequent intraspecific predation, I wondered which eggs in the clutch were of the least value to the crows and therefore most expendable? This study and that of Richardson et al. (1985) shows that last-laid eggs in completed clutches have a significantly greater chance of not hatching when compared to first-laid eggs and central eggs. One reason for this is that incubation begins before the clutch is completed and asynchronous hatching often results in the neglect of the last-laid egg, the young

of which frequently does not manage to hatch. My results do not show that hatching success is related to egg size (volume), as is the case in *C. corone* and Black-billed Magpies, *Pica pica* (Rofstad and Sandvik 1985). Hatching success in *C. caurinus* thus appears to be dependent on the position of the egg in the clutch and not on the size of the egg. I am suggesting, as I did earlier for Glaucous-winged Gulls, *Larus glaucescens* (Verbeek 1988), that these eggs stand out because they are very pale. In both gulls and crows, intraspecific predation is common.

Clutches of three eggs contained proportionally fewer pale eggs than those of four- and five-egg clutches (Fig. 2). Arguably, this may be an indication that females that lay large clutches run out of pigment. However, as 20% of first eggs were the palest in the clutch this may indicate that pigment production at times runs behind schedule or that it takes time for the pigment glands to become functional. If females are running out of pigment, they are able to recover quickly because eggs in 10 repeat clutches (laid 13.6 ± 1.2 days after the loss of the first clutch [Butler et al. 1984]) are similar in color to those in the original clutches (Holyoak 1970, pers. observ.). The notion that females run out of pigment is not supported by an experiment I did with Glaucous-winged Gulls, in which third eggs were usually paler than the first two eggs in the clutch. If the first three eggs were removed in the order of laying, and the gulls continued to lay, then the last egg (sixth) was generally the palest (Verbeek, unpubl.). Another possibility is that the processes responsible for pigmentation are physiologically controlled. Both Paludan (1951) and Parsons (1972, 1976) suggested that the laying and partial incubation of the first two eggs in three-egg clutches of Herring Gulls (*L. argentatus*) inhibits the processes of egg production thus resulting in the smaller third egg. A similar process may inhibit the functioning of the pigment glands resulting in reduced pigmentation (Verbeek 1988). Regardless of the mechanism, running out of pigment or physiological control, and I do not envisage that the birds have the ability to deliberately produce a pale egg, most last eggs and some first eggs are paler than the others. This study clearly shows that the position of some eggs in the clutch and their concomitant paleness results in reduced hatching success and selective predation.

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