

**INTRACLUTCH EGG VARIATION:
THE UNIQUENESS OF THE COMMON TERN'S
THIRD EGG**

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Eggs of the Common Tern (*Sterna hirundo*) show considerable variability in size and color (e.g., Marples and Marples, 1934; Palmer, 1941). Gemperle and Preston (1955) emphasized that the third egg of a three-egg clutch (c/3) was usually distinctive in shape. This distinctiveness has also been noted for other species of Laridae (Coulson, 1963; Harris, 1964; Paludan, 1951; Preston and Preston, 1953). Common Terns have three brood patches and the usual clutch size is three, although birds nesting at times of low food availability or re-nesting late in a season, usually lay only one or two eggs (personal observation; Cooper et al., 1970). The third egg in the clutch is usually smaller than the others, and Nisbet (1973) reported that chicks hatching from such small eggs have a reduced likelihood of survival. Usually a pair of terns cannot successfully raise three young, and unless food is unusually abundant or an older sibling dies, the third chick is not likely to survive (Kremer, 1973; Langham, 1972; LeCroy and LeCroy, 1974; Nisbet, 1973). Similar findings have been reported for Herring Gulls (*Larus argentatus*) by Harris (1964) and Nisbet and Drury (1972). Further studies may provide quantitative information on the conditions under which a third chick may survive and on the costs and benefits of laying a third egg. Presumably the increased reproductive cost of laying the third egg is compensated in the long run.

The present study examines intraclutch variability in size and coloration of Common Tern eggs in 112 c/3 clutches. The rationale is partly methodological for it would be valuable to have some *a posteriori* criterion for recognizing 3rd eggs by their appearance. Such a criterion would greatly facilitate large scale studies where it is undesirable or unfeasible to make frequent visits to a colony. However, the main concern is to determine whether there is a consistent relationship between laying order and egg characteristics, for such a relationship is of considerable evolutionary and physiological interest. This study involves comparisons of the dimensions and ground coloration of eggs with respect to laying sequence.

METHODS

Observations in 1964, 1969, and 1970 confirmed the apparent distinctiveness of the last egg, and the data were obtained in 1971. The colony sites were at West End Beach, Nassau County and at Cedar Beach, Suffolk County, New York (Gochfeld, 1976). Colonies were visited about four times weekly and eggs were marked on each visit. I used a sample of 112 nests in which the laying sequence of the three eggs was known. Because two-egg clutches (c/2) may be physiologically complete or may arise from loss of an egg, they were ignored in this study.

The length and maximum width of eggs were measured with a dial caliper to the nearest 0.1 mm. A field assistant and I examined

the eggs, subjectively describing the ground color and determining which egg was the palest.

In evaluating egg color we found that our determinations varied with the intensity or angle of incident light (eggs appeared browner on sunny days or at noon and greener on cloudy days or in the morning). Moreover there was a strong aftereffect, whereby after examining a clutch of bright green eggs we found ourselves overestimating the "brownness" of the next clutch examined. Since this was a field study we were unable to use reflectance spectrophotometry. In view of these difficulties, I consider here only the paleness of the ground color. The amount and distribution of speckling, which Rowan et al. (1919) found related to egg width, are likewise not considered in this paper.

In only five of 112 clutches was there disagreement as to which egg was palest (due to difference in hue) and these were eliminated from the "paleness" analysis. In many cases the differences were quite subtle, and when one observer considered two eggs "slightly different" and the other considered them "identical," they were defined as identical. Finally, we made a judgment of which egg was the most unique in the clutch without regard for whether uniqueness was conferred by spots, size, shape, color, or some combination of these.

RESULTS

Table 1 shows how many of the 1st, 2nd and 3rd eggs were shortest or thinnest in the clutch. In only 57 clutches was the same egg both shortest and thinnest, and 48 (85.2%) of these were third eggs. From the first to the third egg there is a trend toward de-

TABLE 1.
Distribution of shortest and thinnest eggs by laying sequence
(n = 112 clutches).

	1st egg	2nd egg	3rd egg
Shortest	14	41	57
Thinnest	2	23	87
Shortest and thinnest	0	9	48

creasing both dimensions (Table 2), and this was most pronounced width. Differences between 1st vs. 2nd, 1st vs. 3rd, and 2nd vs. 3rd eggs were compared by *t*-tests. Third eggs were significantly shorter than first eggs ($P < .05$) and narrower than 1st or 2nd eggs. In 15 cases (13.4%) the third egg was neither shortest nor thinnest.

The distribution of "paleness" in 107 clutches is shown in Table 3. The third egg was palest in 54 of 107 clutches (50.5%) which differs significantly from a random expectation of 1/3 (Chi-square goodness of Fit test, $df = 2$; $P < .001$). In 11 additional cases the third egg was identical to one other egg and paler than the remaining egg, but in 40 cases one or both of the first two eggs was paler than the third. In 19 clutches the third egg was smallest in length and width and was also the palest. Assuming that egg size and color

TABLE 2.
Egg sizes for 112 clutches of the Common Tern.

	Egg length		Egg width	
	mean	S.D.	mean	S.D.
First egg	42.17	± 1.85	30.82	± 1.19
Second egg	41.90	± 1.96	30.35	± 0.99
Third egg	41.60	± 1.93	29.70	± 1.02

Probability Matrix based on *t*-tests

		Length		
		1st	2nd	3rd
Width	1st	—	> .20	< .05
	2nd	< .01	—	> .20
	3rd	< .001	< .001	—

are independent variables, their concordance will equal the product of their relative frequencies, giving an expected value of 22 for such third eggs. The observed value of 19 is not significantly

TABLE 3.
Distribution of egg paleness by laying sequence (n = 107 clutches).

	Number of clutches	
	Total	Subtotal
3rd egg palest in clutch	54	
1st and 2nd eggs identical		17
1st and 2nd eggs different		37
3rd egg and 1st or 2nd eggs paler than remaining egg	11	
3rd egg not palest in clutch	42	
All eggs identical		8
3rd egg darker than 1st and 2nd		9
1st or 2nd eggs darker than 3rd		25

different from this. In addition, in one clutch the second egg was shortest, thinnest, and palest. Thus in the present sample 21.6% of clutches had a single egg that was shortest, thinnest, and palest, and 95% of these were third eggs.

Egg uniqueness was judged subjectively for each clutch without regard for the actual clues influencing the decision. In 18 clutches it was not possible to distinguish a unique or most distinctive egg. In the remaining clutches 17 first eggs, 26 second eggs, and 51 third eggs were judged most distinctive (Goodness of Fit Test, *df* = 2; *P* < .001). This confirms the findings of Gemperle and Preston (1955), but clearly uniqueness alone is not an adequate criterion for distinguishing a third egg.

DISCUSSION

Distinctiveness of Third Eggs.—This study found that the third egg in a Common Tern clutch was more likely to be shorter, thinner, or paler than other eggs in the clutch. Size and ground color varied independently, a finding in agreement with work by Rowan et al. (1919) who found significant negative correlation between egg width and mottling, but no correlation between size and color. In 51 (45.6%) of clutches, the third egg was judged most distinctive. Preston (Gemperle and Preston, 1955) was able to recognize the 3rd egg in 19 of 22 clutches using thinness and bluntness of small end as criteria. Their test differed from the present study in that they attempted to identify third eggs by their shape without using color clues. Gemperle and Preston (1955) also noted that the third egg was actually longest in 15 of 22 clutches as well as narrowest in 16 of 22 cases. In the present study 3rd eggs were shortest in about half the clutches (57 of 112) and were longest in only 26% (29 of 112).

The actual size of tern eggs may vary geographically as suggested by Gemperle and Preston (1955), but is also subject to within-season and between-season as well as individual variation. In this study tern eggs were slightly longer and thinner than those reported by Gemperle and Preston (1955), and were longer than those reported for British Common Terns by Witherby et al. (1944). The measurements are very slightly larger than those reported by Bent (1922) for 82 tern eggs from various places.

Factors Influencing Egg Characteristics.—Romanoff and Romanoff (1949) have reviewed numerous papers on the factors influencing the size, shape, and color of eggs. They noted that as early as 1772, Gunther found that egg shape was influenced by tone of the oviductal muscles. Pearl (1909) demonstrated this with more refined studies. Subsequently Marble (1943) and Harper and Marble (1945) showed that a variety of endogenous and exogenous factors interact to influence oviductal muscle tone. In a biometrical study Schultz (1953) estimated the maximum heritability for egg shape in chickens to be 0.25 for the first and 0.18 for the second egg of a clutch, thus demonstrating that the relative contributions of genetic and environmental factors can vary within a clutch.

Egg size has received more attention. Huxley (1927) pointed out the general relationship between bird size and egg size for many species. Romanoff and Romanoff (1949) summarized studies of intraspecific size variation. For domestic fowl (*Gallus gallus*) abundant evidence relates egg size variation to age, age at first laying, health, season and clutch sequence. Seasonal variation in egg size was documented for poultry by Jull (1925). Kendeigh (1941) found that high temperatures appeared to decrease egg size of House Wrens (*Troglodytes aedon*). Food availability at the time of egg formation may be the most important proximate factor influencing egg size (e.g., Nisbet, 1973). Since larger eggs can hold more energy stores in the yolk and since chicks hatching from larger eggs appear to fare better than those from smaller eggs (Nisbet, 1973), a basic selective pressure favors larger eggs. This is limited,

however, by opposing factors such as limitations on the female's ability to obtain adequate food or to produce larger eggs. Moreover, Skoglund et al. (1948) demonstrated that smaller or larger eggs had significantly lower hatchability than "average sized" chicken eggs. Moreover, large eggs require longer incubation so that smaller eggs will be favored where a short incubation period is advantageous. Coulson (1963) and Preston (1958) among others reported a relationship between female age and egg size, size increasing and then finally declining in "old age."

Egg Coloration.—Common Tern eggs vary strikingly in coloration (e.g., Marples and Marples, 1934). Most are some shade of brown or green, although whitish and reddish eggs occur. Green pigments are subject to fading, for many clutches that we denoted initially as "bright green" subsequently became brownish green. Moreover, when green eggs are abandoned, the exposed upper surface becomes much browner than the concealed surface, a fact noted also by Marples and Marples (1934). Rowan et al. (1919), who examined egg variability biometrically, made a most provocative if unlikely suggestion. They believed that a Common Tern population might have a "green egg" and a "brown egg" gens with a moderate rate of egg dumping (laying of an egg in another bird's nest) accounting for the occurrence of clutches containing both greenish and brownish eggs. Currently it is unclear to what extent heredity, diet, or other factors might account for the observed variability in tern egg color. Punnett and Bailey (1920) discussed egg color heredity in fowl, and Newton (1893) long ago suggested that egg color darkens with advancing age of the female. Romanoff and Romanoff (1949) found little evidence confirming this phenomenon in fowl. Labisky and Jackson (1969) did find that some hen Ring-necked Pheasants (*Phasianus colchicus*) lay darker eggs with advancing age, although there is considerable within-season variability.

Preston (1957) described intraclutch variation in the markings of Common Tern and Laughing Gull (*Larus atricilla*) eggs, finding certain characteristic markings on the 3rd eggs. To some extent the intensity of the markings may relate to the size of the egg (e.g., Rowan et al., 1919) and to the amount of time it spends in the oviduct (Romanoff and Romanoff, 1949). In cases where egg passage through the oviduct is rapid, shells tend to be thinner and paler (Romanoff and Romanoff, 1949).

Why Are Third Eggs Paler?—The colors deposited on egg shells are bile pigment metabolites, and it is possible that during the laying period the "paint supply" of the female is depleted so that later eggs are lighter than early ones. This tendency could be modified by food intake or duration of time in the oviduct. There is no evidence that the third egg of a Common Tern clutch spends less time in the oviduct. In fact, the scant data on inter-egg intervals indicates that the interval between 3rd and 2nd eggs tends to be longer than between 2nd and 1st eggs (Cooper et al., 1970; Gochfeld, unpubl. data).

Holyoak (1970) reported that the final egg in the clutches of several species of European Corvidae was often the palest, and he

implicated pigment depletion as a cause. He speculated that since parental attendance at the nest is low during the laying period and approaches 100% after clutch completion, relaxation of predation pressure could account for the paler eggs. For example, if cryptic coloration is both important and physiologically expensive, and if predation pressure (of a sort affected by having cryptic eggs) declines once continuous incubation begins, one could account for the tendency for early eggs to be more cryptic than the final egg. This hypothesis, yet untested, is consistent with the frequent paleness of the third egg in the Common Tern and several other larids. Croze (1970) and Tinbergen et al. (1962) demonstrated the importance of cryptic coloration (and the conspicuousness of the white inside of the shell) in gull eggs. Schultz's (1953) report of differential heritability of egg shape indicates that selection could act with different force on the 3rd egg of a tern's clutch. Holyoak's (1970) speculation is attractive in linking an ecological and evolutionary process (predation pressure) with behavioral and physiological processes (nest attentiveness and pigment depletion). Although Common Terns do incubate prior to clutch completion, their attentiveness during the laying period is much less than during true incubation (Nisbet and Cohen, 1975). A direct test of differential predation, however, remains to be done.

Recognition of Third Eggs.—This study confirms the report by Gemperle and Preston (1955) that the 3rd egg is often distinctive, but in this case the 3rd egg could be recognized as such in only about half of the clutches. Although only 20 clutches (17.9%) contained a single egg that was shortest, thinnest, and palest, this egg proved to be the 3rd in 19 cases (95% of the subset). This is the most reliable of the relationships discovered in this study, and the only one of sufficient magnitude to be of any use in a field study where *a posteriori* identification of the 3rd egg is desired.

Hays and LeCroy (1971) described a means of estimating the incubation stage of tern eggs based on changes of specific gravity. This flotation technique readily distinguishes recently laid from well-incubated clutches, and in 8 of 19 cases I could distinguish three distinct flotation levels. In 11 of these known sequence clutches, I could not distinguish the 2nd egg from the 1st or from the 3rd, although in 9 of these cases I could distinguish the 3rd from the 1st. Most Common Terns spend some time incubating after laying their 1st egg, and this tendency increases after laying of the 2nd egg. Since usually two days intervene between layings, there is some opportunity for embryonic development to proceed during the laying period. Nisbet (1975) found this technique adequate for distinguishing clutch sequence in many cases, and it is certainly superior to any technique based on size, shape, or color.

Productivity and Value of Third Eggs.—LeCroy and LeCroy (1974) found that although a third chick had an improved chance of survival when raised in a brood of two, it did not fare as well as a second chick in a brood of two. Nisbet (1973) found that in the few cases where chicks fledged from 3rd eggs, the egg had been

larger than average for 3rd eggs. Since a third chick is at a disadvantage because it hatches from small eggs and must compete with older siblings, it is reasonable to view a third egg as a form of insurance in case one of the earlier eggs or chicks is lost. Occasionally all three chicks may be raised as a bonus, but usually a chick from a third egg survives to fledging only if an older sibling dies. Since the 3rd egg is often smaller than the others, it becomes reasonable to ask whether under some circumstances a bird might profit by investing in two larger-than-average eggs, foregoing the third egg.

CONCLUSIONS

In 112 clutches the third egg was thinnest in 77.7% and shortest in 50.8%; it was both shortest and thinnest in 42.9% of clutches. In 57 clutches where a single egg was both shortest and thinnest, it was the 3rd egg in 48 cases (85.2%). In 107 clutches there were 88 cases where one egg was paler than the others, and 54 of these (61.3% or 50.4% of total) were third eggs. In only 20 clutches (17.9%) was the same egg shortest, thinnest, and palest, and 19 of these (95% or 17% of total) were third eggs. In 51 clutches (45.6%) the 3rd egg was judged most distinctive. It is impossible to recognize confidently 3rd eggs by their uniqueness or by size or color alone, although this may prove possible in some populations.

It is possible that predation pressure, relaxed when parents begin full incubation, may lead to differential selection for crypticity, accounting in part for the paler coloration of the ultimate eggs. This may operate through proximate factors such as pigment depletion. The interactions among ecological, behavioral, and physiological processes are of sufficient interest to warrant direct study.

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