

# VARIATION IN THE APPEARANCE OF SWALLOW EGGS AND THE DETECTION OF INTRASPECIFIC BROOD PARASITISM<sup>1</sup>

CHARLES R. BROWN AND LORA C. SHERMAN

Department of Biology, Yale University, P.O. Box 6666, New Haven, CT 06511

**Abstract.** A method sometimes used to study avian intraspecific brood parasitism is to visually examine a clutch of eggs and infer parasitic egg laying if an egg of odd appearance is present in the clutch. Yet the degree to which individual females always lay eggs that look alike has seldom been evaluated quantitatively. We measured variation in egg appearance within and between 33 clutches of Barn Swallows (*Hirundo rustica*) and 35 clutches of Cliff Swallows (*H. pyrrhonota*) in southwestern Nebraska. Variables measured were egg length, breadth, shape, total amount of spotting, and degree of spotting in four separate sections of the egg. For both species within-clutch variance was significantly less than between-clutch variance for all variables except upper right and lower right spotting, when a sample size of 26-30 nests was used. Significant differences tended not to occur when small numbers of randomly selected nests (five to seven) were examined. Within-clutch variance for nests known to contain parasitic eggs did not differ from within-clutch variance for nonparasitized nests. Differences in egg appearance probably cannot be used safely to infer brood parasitism in Barn and Cliff swallows. Researchers should quantify within- vs. between-clutch variation in egg appearance before assuming that an individual of a given species always lays eggs that look more alike than do eggs from different individuals.

**Key words:** Barn Swallow; brood parasitism; Cliff Swallow; egg appearance; *Hirundo pyrrhonota*; *H. rustica*.

## INTRODUCTION

Intraspecific brood parasitism is known or suspected to occur in a variety of birds (e.g., Power et al. 1981; Andersson and Eriksson 1982; Andersson 1984; Brown 1984; Gowaty and Karlin 1984; Gibbons 1986; Emlen and Wrege 1986; Møller 1987; Brown and Brown 1988, 1989; review in Yom-Tov 1980a), and may represent a common alternative female reproductive strategy. To understand the evolutionary importance of brood parasitism one must be able to accurately identify when parasitic egg laying has occurred, in what nest, and the parasitic individual. Visual identification of parasitic individuals and their eggs is difficult on the intraspecific level, because eggs of conspecifics generally look alike. Nevertheless, intraspecific variation in egg appearance does exist in many species of birds, and this variation has been used to infer instances of intraspecific brood parasitism (e.g., Weller 1959, Yom-Tov 1980b, Littlefield 1981, Fetterolf and Blokpoel 1984, Colwell 1986, Earle 1986, Gibbons 1986, Møller 1987, Kendra et al. 1988). In a study of Ring-billed Gulls (*Larus delawarensis*),

Fetterolf and Blokpoel (1984) demonstrated that variance in egg dimensions between females was significantly greater than that for the same female, verifying for that species the widely held assumption that odd-looking eggs in a clutch probably are in fact parasitic.

However, despite Fetterolf and Blokpoel's (1984) work, there is little quantitative information in general on the extent of variability in egg characteristics of species believed to be intraspecific brood parasites. Whether between-clutch variance is greater than within-clutch variance has rarely been tested, and two recent studies on Common Moorhens (*Gallinula chloropus*; Gibbons 1986) and European Barn Swallows (*Hirundo rustica*; Møller 1987) both relied on the assumption that a given female always lays eggs that look similar. Gibbons (1986) and Møller (1987) identified specific females as being brood parasites by comparing odd-looking eggs within a clutch to the eggs in neighboring clutches. In each study it was concluded that the neighbors were the parasites because the odd eggs presumably matched the neighbors' own eggs in appearance. While this conclusion seems reasonable in each case, neither study quantified the degree of individual variation in egg appearance within and between clutches. In support of their

<sup>1</sup> Received 24 October 1988. Final acceptance 23 February 1989.

method, Gibbons (1986) and Møller (1987) cited other studies that also presented no quantitative information on variation (Wood 1974, Lanier 1982). In addition, Møller (1987) suggested, on the basis of the presence of presumably odd-looking eggs in museum collections, that Bank Swallows (*Riparia riparia*) may exhibit intraspecific brood parasitism, although Hoogland and Sherman (1976) found no evidence of parasitism in a field study of this species.

In the general absence of quantitative data on the degree of variation within and between clutches, using dissimilar egg appearance to infer brood parasitism or to assign parasitism to specific individuals seems problematic at best. A number of studies have demonstrated that the first egg or (more commonly) the last egg laid in a clutch often differs significantly in dimensions and appearance from the others in the clutch (e.g., Marble 1943, Preston and Preston 1953, Gemperle and Preston 1955, Koskimies 1957, Coulson 1963, Gochfeld 1977, Nolan 1978, Lowther 1988, see also Kendra et al. 1988). If the terminal egg in a clutch is routinely different in appearance and the exact sequence of laying is unknown, presence of an odd egg in a clutch cannot be used with certainty to infer parasitic egg laying. Compounding this difficulty is the fact that when within- and between-clutch variation in egg dimensions were quantitatively measured in larids, there was no evidence that eggs within a clutch were similar enough in appearance to accurately infer parentage among eggs (Preston and Preston 1953, Coulson 1963). Although several workers have asserted that eggs within a nest look alike (e.g., Marble 1943, Kendeigh et al. 1956, Van Bree 1957, Rosene 1969, Nolan 1978, Yom-Tov 1980a, Kendra et al. 1988), only Koskimies (1957), Baerends and Hogan-Warburg (1982), and Fetterolf and Blokpoel (1984) presented quantitative data suggesting that within-clutch variation in egg appearance was less than variation among all eggs in a sample.

In this study we examined the degree of variation in egg appearance within vs. between clutches in two congeneric species of swallows, the Barn and Cliff (*H. pyrrhonota*) swallows. Our goal was to determine if within-clutch variation in egg appearance was sufficiently low enough to potentially enable a researcher to accurately discriminate nonparental (parasitic) eggs within a clutch. Cliff Swallows are known brood parasites (Brown 1984; Brown and Brown 1988, 1989),

and egg appearance has not been used previously to study brood parasitism in this species. There is little evidence that Barn Swallows regularly brood-parasitize nests in North America (Shields and Crook 1987; Brown, pers. observ.), but in Europe brood parasitism apparently occurs often (Møller 1987). Eggs of both Barn and Cliff swallows are of cream color with variable reddish-brown speckling, potentially enabling researchers to discriminate eggs of different females.

## METHODS

### STUDY SITE

This study, part of continuing research on the social behavior of Cliff Swallows, was done in Keith County, Nebraska, near the University of Nebraska's Cedar Point Biological Station, during May and June 1987. Both Barn and Cliff swallows are abundant in Nebraska, and Cliff Swallows, at least, have probably always occurred there, nesting on bluffs and outcrops along the North Platte River and on cliffs in other parts of the state (Nichols, cited in Pearson 1917). Data reported here are all from swallow nests located in highway culverts, although some Cliff Swallows nested on bridges, buildings, and natural cliff sites in the study area. All Cliff Swallow data are from a colony of approximately 1,100 active nests, whereas the Barn Swallow data are from three separate nesting aggregations of 2, 4, and approximately 27 active nests.

### MEASURING EGG DIMENSIONS AND SPOTTING

The progress of each nesting attempt in our study colonies was observed throughout the season. Nests were numbered by writing symbols with chalk on the nearby concrete culvert wall. Nest contents were observed with a dental mirror and flashlight inserted through each nest's narrow neck in the case of Cliff Swallows, or positioned above the open nest in the case of Barn Swallows. For each nest we knew the date that egg laying and hatching began, clutch size, whether any eggs were lost during incubation, and whether any eggs had been added, presumably through brood parasitism. A nest was considered parasitized if more than one egg appeared per day during the egg-laying period (Brown 1984, Brown and Brown 1989), or if an egg was added to a nest (presumably by physical transfer) three or more days after laying had ceased yet still hatched in syn-

chrony with the clutch to which it was added (see Brown and Brown 1988).

For Barn Swallows, eggs in all active nests in each nesting aggregation were measured. For Cliff Swallows, we attempted to randomly select nests within the colony for egg measurements. Nests from both walls of the culvert and from each end and the middle of each wall were selected. Selection of a nest was based only on the knowledge that incubation there had begun. We did not preferentially select nests in which we knew a priori that brood parasitism had occurred, nor did we select nests that previously had been inspected visually for degree of similarity in egg appearance. We believe that our sample of Cliff Swallow nests was potentially nonrandom only in that nests that were completely surrounded on all sides by other nests were inaccessible to us. Removal of eggs required our access to one side of a nest (see below), and Cliff Swallow nests in the lower tiers of nests along the culvert wall were the most easily reached. Those nests also tended to be started later in the year than the nests along the upper tiers, but we have no evidence at present that late-starting Cliff Swallows are young birds or in any other ways drastically unrepresentative of our population (Brown, unpubl. data).

A hole, only narrow enough to insert two fingers through and remove the eggs, was cut in the side of each Cliff Swallow nest about 2.5 cm above the estimated bottom of the nest. Barn Swallow eggs were simply removed by hand from the completely open nests of this species. Eggs were placed in a dish lined with a cloth, temporarily removed from the colony, photographed, and then replaced in the nest. About 5 min were required to process and photograph each clutch after the eggs were removed. After Cliff Swallow eggs were replaced, we patched the hole in the nest with mud. There was no evidence that temporary removal of eggs for photography or our cutting and then repairing holes in the sides of nests caused any adults to abandon their nests or an increase in any form of nest failure.

Our methods of photographing and measuring eggs were similar to those of Mand et al. (1986) but less elaborate. Each clutch was photographed using a Pentax K1000 35-mm camera with Kodachrome 64 film against the same neutral gray background and with a ruler for determination of scale. The image size of each photograph varied slightly from clutch to clutch, so the subsequent measurements for each clutch were scaled

by the length of the ruler in each photograph. Photographs could be separated generally into two types by their image sizes: "small" photographs taken with the camera lens held about 50 cm from the eggs and "large" photographs taken with the camera lens held about 20 cm from the eggs. Eggs were not measured directly; all measurements were taken directly from the photographs and scaled appropriately. All measurements of egg images in the photographs were made to the nearest 0.05 cm. Egg dimensions measured were length, the longest axis of the egg; breadth, the widest point perpendicular to the length; and shape, based on the classical shape index of transverse diameter  $\times$  100/length (e.g., Pearl and Surface 1914, Marble 1943, Romanoff and Romanoff 1949, Coulson 1963), substituting the two-dimensional measurements of breadth and length from the photographs. Any absolute error in measurements introduced from using photographs was presumably constant from clutch to clutch, and should not have affected relative differences within and between clutches (that is, the variance in measurements).

Spotting of eggs was determined by superimposing a transparent grid over each egg. The grid was divided along the egg's length and breadth, resulting in four major sections for each egg (upper and lower left, upper and lower right sections). The blunt end of each egg fell into the upper and lower left sections, and the elongate end fell into the upper and lower right sections. The number of spots falling within each grid square in each section was counted. Only grid squares that fit entirely within the boundaries of the egg image were scored. A spot that fell into more than one square was counted as being in the square that was the farthest to the right and the farthest down. Spots/mm<sup>2</sup> were calculated for each major section of the egg and converted to scale using the following formula: spots/mm<sup>2</sup> = (spots  $\times$  0.25)/[squares  $\times$  (scale)<sup>2</sup>]. The area of each grid square was 4 mm<sup>2</sup>. Dividing the egg into four sections allowed a comparison of spot distribution, similar to that used by Baerends and Hogan-Warburg (1982). Speckled bird eggs (such as those of Barn and Cliff swallows) often show dark, "primary" spots and faint, "secondary" spots, reflecting differences in layering of the pigment. Baerends and Hogan-Warburg (1982) sanded gull eggs to discriminate between primary and secondary spots, which may be deposited on top of each other. We did not sand

eggs and did not discriminate between primary and secondary spots in our counts.

Color of both the egg background and the spots might also vary among Barn and Cliff swallow eggs. However, Baerends and Hogan-Warburg (1982) reported that color characterizations of the same gull egg by different observers differed 30% of the time. For this reason, and also because of potential chemical-related color differences resulting from development of the photographs, we did not score color of eggs in a clutch. Our subjective impression was that color varied little among eggs with the same degree of spotting, whether within the same clutch or among different clutches.

Measurements on Cliff Swallow clutches were made blind as to whether the clutches had received parasitic eggs. Thus, knowledge of parasitism in a nest did not bias our measurements of egg dimensions and degree of spotting. Eggs were not marked as they were laid, and therefore we had no information on how sequence of laying might have affected variability in egg appearance for these species.

#### STATISTICAL ANALYSES

Clutch size ranged from three to five for Cliff Swallows and from two to six for Barn Swallows. The mean and variance for each variable was determined for each clutch, using the standardized (scaled) values for each that were comparable between clutches. The average within-clutch variance for each variable was calculated, which served as the within-group variance for the subsequent *F*-test (Sokal and Rohlf 1969). For each variable the variance in the clutch means was calculated, which served as the between-group variance for the subsequent *F*-test. The ratio of the between-group to within-group variances led to an *F* statistic in a one-tailed test (Sokal and Rohlf 1969). That test evaluated whether within-clutch variance was significantly less than between-clutch variance for each variable. Using variance of the clutch means as between-clutch variance is preferable to using overall variance among all eggs (e.g., cf. Baerends and Hogan-Warburg 1982). Variance of clutch means more accurately measures the degree of variation between nests.

Average within-clutch variance for each variable was calculated for Cliff Swallow clutches known to have been parasitized by conspecifics ( $n = 5$ ) and for clutches in which parasitism was

not known to have occurred ( $n = 30$ ). Variance for parasitized nests and variance for nonparasitized nests were compared with an *F*-test for equality of variances (Sokal and Rohlf 1969). This test was one-tailed because we had a priori reason to suspect that the variance for parasitized nests was higher.

All statistical analyses were performed on a Macintosh SE personal computer using the SYSTAT statistical package (Wilkinson 1987) or on a Texas Instruments 59 programmable calculator. Significance was set at  $P = 0.050$ .

#### RESULTS

Egg dimensions and spotting were measured for 144 eggs from 35 Cliff Swallow clutches and 156 eggs from 33 Barn Swallow clutches. For Cliff Swallows, overall mean values ( $\pm$ SD) for each variable based on all eggs from all clutches were: length 2.11 cm ( $\pm$ 0.25); breadth 1.49 cm ( $\pm$ 0.18); shape 70.67 ( $\pm$ 4.38); total spots/mm<sup>2</sup> 0.40 ( $\pm$ 0.17); upper left spots/mm<sup>2</sup> 0.53 ( $\pm$ 0.23); lower left spots/mm<sup>2</sup> 0.50 ( $\pm$ 0.24); upper right spots/mm<sup>2</sup> 0.32 ( $\pm$ 0.18); lower right spots/mm<sup>2</sup> 0.30 ( $\pm$ 0.16). Comparable mean values ( $\pm$ SD) for Barn Swallows were: length 1.94 cm ( $\pm$ 0.16); breadth 1.43 cm ( $\pm$ 0.11); shape 74.20 ( $\pm$ 4.77); total spots/mm<sup>2</sup> 0.62 ( $\pm$ 0.28); upper left spots/mm<sup>2</sup> 0.83 ( $\pm$ 0.38); lower left spots/mm<sup>2</sup> 0.78 ( $\pm$ 0.37); upper right spots/mm<sup>2</sup> 0.48 ( $\pm$ 0.25); lower right spots/mm<sup>2</sup> 0.48 ( $\pm$ 0.25).

Within-clutch variance for each variable reflects the degree to which the same individual lays eggs that look alike, whereas between-clutch variance reflects the degree to which different individuals lay eggs that look alike. Within- and between-clutch variances for each variable, the *F* values, and tests of significance for each are shown in Tables 1 and 2. Although all measurements for all clutches regardless of egg image size in the photographs were standardized by scaling, we separated the clutches for analysis based on small (Table 1) and large (Table 2) photographs. This was done because spots were more visible on the photographs with larger images, and some spots may have been overlooked on the eggs represented by smaller images. Separating the clutches by approximate image size resulted in two separate data sets for each species, one relatively large and one relatively small in size. Other than photographic image size, there were no other a priori differences among these nests; thus, we also used these separate data sets to evaluate

TABLE 1. Comparison of variance within clutches vs. between clutches for variables measuring egg appearance in Cliff Swallows and Barn Swallows, based on photographs with small egg images (see text). Significant differences denoted by \*.

Variable	A. Cliff Swallow ( <i>n</i> = 30 clutches)				B. Barn Swallow ( <i>n</i> = 7 clutches)			
	Within-clutch variance	Between-clutch variance	<i>F</i> <sup>a</sup>	<i>P</i>	Within-clutch variance	Between-clutch variance	<i>F</i> <sup>b</sup>	<i>P</i>
Length	0.00673	0.0443	6.582	<0.001*	0.00500	0.00586	1.172	0.348
Breadth	0.00217	0.0224	10.322	<0.001*	0.00214	0.00197	0.921	0.494
Shape	8.644	14.029	1.623	0.043*	20.462	9.180	0.449	0.840
Total spots/mm <sup>2</sup>	0.00557	0.0129	2.316	0.001*	0.00343	0.00374	1.090	0.392
Upper left spots/mm <sup>2</sup>	0.0138	0.0259	1.877	0.012*	0.0201	0.00842	0.419	0.860
Lower left spots/mm <sup>2</sup>	0.0131	0.0263	2.008	0.006*	0.0174	0.00259	0.149	0.988
Upper right spots/mm <sup>2</sup>	0.0158	0.00976	0.618	0.929	0.0200	0.00790	0.395	0.876
Lower right spots/mm <sup>2</sup>	0.0121	0.00976	0.807	0.740	0.00829	0.00544	0.656	0.685

<sup>a</sup> *df* = 29, 93 for each.

<sup>b</sup> *df* = 6, 29 for each.

the effect of sample size on comparison of within- vs. between-clutch variance.

When the data sets with the larger sample sizes were considered, in both species between-clutch variance was significantly greater than within-clutch variance for all variables except upper and lower right spots/mm<sup>2</sup> (Tables 1A, 2B). In contrast, when the data sets with the smaller sample sizes were considered, within- and between-clutch variance differed significantly only for egg breadth in Cliff Swallows (Table 2A). There were no significant differences among variances for any of the variables in Barn Swallows (Table 1B). Finding significant differences (Tables 1A, 2B) apparently was unrelated to the image size of the photographs, because for Cliff Swallows the majority of significant differences resulted from data taken from small photographs, whereas for Barn Swallows all significant differences resulted from data taken from large photographs. This suggests

that sample size probably had the greatest effect on whether within- and between-clutch variances were found to differ significantly in these species.

When we compared average within-clutch variances for Cliff Swallow nests known to have been parasitized by conspecifics with those for nests not known to have been parasitized, within-clutch variance was significantly greater (barely) in parasitized nests for only one of the eight variables (Table 3). Thus, nests with known parasitic eggs in general did not show more within-clutch variation in egg appearance than nonparasitized nests.

## DISCUSSION

Our results suggest that an individual female Cliff or Barn swallow can lay eggs that look more alike than do the eggs of different females. If a sample size on the order of 26–30 nests is obtained, one

TABLE 2. Comparison of variance within clutches vs. between clutches for variables measuring egg appearance in Cliff Swallows and Barn Swallows, based on photographs with large egg images (see text). Significant differences denoted by \*.

Variable	A. Cliff Swallow ( <i>n</i> = 5 clutches)				B. Barn Swallow ( <i>n</i> = 26 clutches)			
	Within-clutch variance	Between-clutch variance	<i>F</i> <sup>a</sup>	<i>P</i>	Within-clutch variance	Between-clutch variance	<i>F</i> <sup>b</sup>	<i>P</i>
Length	0.00560	0.00583	1.040	0.417	0.00396	0.0241	6.086	<0.001*
Breadth	0.00100	0.00700	7.000	0.002*	0.00119	0.0132	11.092	<0.001*
Shape	8.988	3.098	0.345	0.843	5.613	15.662	2.790	<0.001*
Total spots/mm <sup>2</sup>	0.0168	0.0271	1.613	0.219	0.0157	0.0339	2.159	0.004*
Upper left spots/mm <sup>2</sup>	0.0360	0.0384	1.067	0.405	0.0380	0.0621	1.634	0.048*
Lower left spots/mm <sup>2</sup>	0.0252	0.0612	2.429	0.090	0.0318	0.0635	1.997	0.009*
Upper right spots/mm <sup>2</sup>	0.0250	0.0296	1.184	0.355	0.0255	0.0207	0.812	0.718
Lower right spots/mm <sup>2</sup>	0.0212	0.0117	0.552	0.700	0.0215	0.0303	1.409	0.121

<sup>a</sup> *df* = 4, 16 for each.

<sup>b</sup> *df* = 25, 94 for each.

TABLE 3. Comparison of average within-clutch variances for variables measuring egg appearance in Cliff Swallow nests known to have been parasitized by a conspecific ( $n = 5$ ) and nests not known to have been parasitized ( $n = 30$ ). Significant differences denoted by \*.

Variable	Mean within-clutch variance			
	Nonparasitized nests	Parasitized nests	$F^a$	$P$
Length	0.00710	0.00360	0.507	0.924
Breadth	0.00207	0.00160	0.773	0.695
Shape	8.916	7.357	0.825	0.641
Total spots/mm <sup>2</sup>	0.00680	0.00940	1.382	0.177
Upper left spots/mm <sup>2</sup>	0.0152	0.0278	1.829	0.045*
Lower left spots/mm <sup>2</sup>	0.0142	0.0186	1.310	0.216
Upper right spots/mm <sup>2</sup>	0.0171	0.0168	0.982	0.477
Lower right spots/mm <sup>2</sup>	0.0136	0.0120	0.882	0.577

<sup>a</sup>  $df = 14, 95$  for each.

can demonstrate a statistical likelihood that eggs within a clutch are more similar in appearance than eggs from different clutches.

We urge caution for three reasons, however, in using these results to infer parasitic egg laying in Cliff and Barn swallows. First, although the within- and between-clutch variances differed significantly (Tables 1A, 2B), the relative magnitudes of these variances were small. Egg dimensions and degree of spotting often differed almost imperceptibly among eggs and clutches, making us uncomfortable in subjectively assigning parentage of eggs within a clutch based on these small differences. Shape differed the most among eggs and of the variables we measured was probably the most reliable indicator of parentage. Given the small degree of differences among eggs, assigning presumed parasitic eggs as being laid by specific neighboring females seems potentially inaccurate (cf. Møller 1987).

Second, statistically significant differences resulted only when the number of clutches compared was on the order of 26–30. When a smaller sample of clutches (five for Cliff Swallows and seven for Barn Swallows; Tables 1B, 2A) was analyzed, only one variable in one species exhibited a within-clutch variance that was statistically significantly different from the respective between-clutch variance. If one compares only a few nests (e.g., a presumably parasitized nest vs. that nest's three or four closest neighbors), one cannot conclude for that small sample that eggs within a clutch look more alike than eggs from different clutches. Our results suggest that greater within- than between-clutch similarity in egg appearance is probably only a statistical effect that occurs when a relatively large number of clutches are compared to each other. For these swallows

within-clutch variance in a given nest is not low enough on average to reliably know that a nest has suffered parasitism if an odd egg is present.

Third, there was no consistent pattern of greater within-clutch variance for Cliff Swallow nests known to have been brood-parasitized (Table 3). This suggests that within-clutch variance in non-parasitized nests is high enough to mask any effect parasitic eggs might have on within-clutch variance. Thus, detection of these parasitic eggs based solely on egg appearance would be unlikely in this sample. The fact that we were unable to detect greater within-clutch variance for parasitized nests with this relatively small sample of nests known to have been parasitized (five) underscores the importance of sample size on the probability of detecting differences in variances.

These results are consistent with the observation that Cliff and Barn swallows do not recognize their own eggs based on appearance (Brown 1984, Møller 1987). If within-clutch variance for a given nest is not low enough for humans to reliably distinguish, with exact measurements, cases of potential multiple parentage in a nest, perhaps neither can the birds themselves. Eggs from different females may look so similar that the odds may be great of removing one's own egg if a nest owner responded to parasitism of its nest.

In one of the few other studies with relevant data, Nolan (1978, p. 182) presented measures of variation in egg length, breadth, volume, and elongation for clutches from six different female Prairie Warblers (*Dendroica discolor*). Nolan did not present explicit measures of within- and between-clutch variance, but the data he presented allowed calculation of these. We determined within- vs. between-clutch variance for each of

his variables and analyzed them in the same way as our swallow data (Tables 1, 2). Variance within clutches was not significantly different from variance between clutches for egg length ( $F = 1.783$ ,  $P = 0.131$ ,  $df = 5$ , 58 on all tests) or egg volume ( $F = 1.630$ ,  $P = 0.166$ ), but within-clutch variance was significantly less than between-clutch variance for egg breadth ( $F = 2.757$ ,  $P = 0.026$ ) and egg elongation ( $F = 3.902$ ,  $P = 0.004$ ). Thus these data suggest that egg characteristics may be only partly useful in discriminating parentage among eggs in Prairie Warbler clutches.

We conclude that researchers should not assume that parasitic eggs within a clutch can be safely inferred based on differences in dimensions or degree of spotting. Even though statistically significant differences existed among variances when a large sample of swallow clutches was considered, for reasons discussed above egg appearance is probably unreliable and unsuitable for inferring intraspecific brood parasitism in Barn and Cliff swallows. For Cliff Swallows especially, the unreliability of this method does not justify the increased time necessary to cut through nests, remove and measure eggs, and subsequently repair nests.

If egg characteristics are to be used in other species to infer intraspecific brood parasitism or to assign parasitic eggs to specific individuals, a quantitative analysis of within- vs. between-clutch variance in egg appearance should be undertaken as a prelude to any such study. Within-clutch variation must be so low that any given nest will differ significantly from any potential group of nests (e.g., its neighbors). The variability within and between clutches must be measurably large enough for visual discrimination by humans. Studies of intraspecific brood parasitism that do not present quantitative measures of variance (e.g., Gibbons 1986, Møller 1987) must be viewed with caution. Furthermore, not considered in our study is the fact that some species lay a terminal egg very different in appearance from the others and that a female's age may affect how her eggs look (e.g., Preston and Preston 1953, Gemperle and Preston 1955, Richdale 1955, Koskimies 1957, Coulson 1963, Nolan 1978, Lowther 1988). Timing of laying is a confounding factor which could potentially lead to high within-clutch variation and thus to inaccuracies in inferring parasitism based solely on egg appearance, a point also made by Lowther (1988). Whether individuals lay odd-looking terminal

eggs must be known before an investigator can safely assign parentage in a clutch by simply looking at the eggs present.

#### ACKNOWLEDGMENTS

We thank Mary Bomberger Brown, Jerri Hoskyn, and Martin Shaffer for field assistance; Anthony Joern for allowing us to use the facilities of the Cedar Point Biological Station; the National Science Foundation (grant BSR-8600608), the National Geographic Society, and Yale University for financial support; and Steve Beissinger and Peter Walsh for helpful comments on the manuscript.

#### LITERATURE CITED

- ANDERSSON, M. 1984. Brood parasitism within species, p. 195–228. In C. J. Barnard [ed.], Producers and scroungers: strategies of exploitation and parasitism. Croom Helm, London.
- ANDERSSON, M., AND M. O. G. ERIKSSON. 1982. Nest parasitism in Goldeneyes *Bucephala clangula*: some evolutionary aspects. *Am. Nat.* 120:1–16.
- BAERENDS, G. P., AND A. J. HOGAN-WARBURG. 1982. The external morphology of the egg and its variability. *Behaviour* 82:1–32.
- BROWN, C. R. 1984. Laying eggs in a neighbor's nest: benefit and cost of colonial nesting in swallows. *Science* 224:518–519.
- BROWN, C. R., AND M. B. BROWN. 1988. A new form of reproductive parasitism in Cliff Swallows. *Nature* 331:66–68.
- BROWN, C. R., AND M. B. BROWN. 1989. Behavioural dynamics of intraspecific brood parasitism in colonial Cliff Swallows. *Anim. Behav.* 37:777–796.
- COLWELL, M. A. 1986. Intraspecific brood parasitism in three species of prairie-breeding shorebirds. *Wilson Bull.* 98:473–475.
- COULSON, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proc. Zool. Soc. Lond.* 140:211–227.
- EARLE, R. A. 1986. The breeding biology of the South African Cliff Swallow. *Ostrich* 57:138–156.
- EMLEN, S. T., AND P. H. WREGE. 1986. Forced copulations and intra-specific parasitism: two costs of social living in the White-fronted Bee-eater. *Ethology* 71:2–29.
- FETTEROLF, P. M., AND H. BLOKPOEL. 1984. An assessment of possible intraspecific brood parasitism in Ring-billed Gulls. *Can. J. Zool.* 62:1680–1684.
- GEMPERLE, M. E., AND F. W. PRESTON. 1955. Variation of shape in the eggs of the Common Tern in the clutch-sequence. *Auk* 72:184–198.
- GIBBONS, D. W. 1986. Brood parasitism and cooperative nesting in the Moorhen, *Gallinula chloropus*. *Behav. Ecol. Sociobiol.* 19:221–232.
- GOCHFELD, M. 1977. Intra-clutch egg variation, the uniqueness of the Common Tern 3rd egg. *Bird-Banding* 48:325–332.
- GOWATY, P. A., AND A. A. KARLIN. 1984. Multiple maternity and paternity in single broods of apparently monogamous Eastern Bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol.* 15:91–95.

- HOOGLAND, J. L., AND P. W. SHERMAN. 1976. Advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.* 46:33-58.
- KENDEIGH, S. C., T. C. KRAMER, AND F. HAMERSTROM. 1956. Variations in egg characteristics of the House Wren. *Auk* 73:42-65.
- KENDRA, P. E., R. R. ROTH, AND D. W. TALLAMY. 1988. Conspecific brood parasitism in the House Sparrow. *Wilson Bull.* 100:80-90.
- KOSKIMIES, J. 1957. Variations in size and shape of eggs of the Velvet Scoter, *Melanitta fusca* (L.). *Arch. Soc. Zool. Bot. Fenn. 'Vanamo'* 12:58-69.
- LANIER, G. A., JR. 1982. A test for conspecific egg discrimination in three species of colonial passerine birds. *Auk* 99:519-525.
- LITTLEFIELD, C. D. 1981. A probable record of intraspecific egg dumping for Sandhill Cranes. *Auk* 98:631.
- LOWTHER, P. E. 1988. Spotting pattern of the last laid egg of the House Sparrow. *J. Field Ornithol.* 59:51-54.
- MAND, R., A. NIGUL, AND E. SEIN. 1986. Oomorphology: a new method. *Auk* 103:613-617.
- MARBLE, D. R. 1943. Genetics of egg shape. *Poult. Sci.* 22:61-71.
- MØLLER, A. P. 1987. Intraspecific nest parasitism and anti-parasite behaviour in Swallows, *Hirundo rustica*. *Anim. Behav.* 35:247-254.
- NOLAN, V., JR. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. *Ornithol. Monogr. No. 26*. American Ornithologists' Union, Washington, DC.
- PEARL, R., AND F. M. SURFACE. 1914. A biometrical study of egg production in the fowl. III. Variation and correlation in the physical characters of the egg. *U.S. Dep. Agric. Bur. Anim. Ind. Bull.* 110, Part 3.
- PEARSON, T. G., [ED.] 1917. *Birds of America*. Vol. 3. University Society, New York.
- POWER, H. W., E. LITOVICH, AND M. P. LOMBARDO. 1981. Male Starlings delay incubation to avoid being cuckolded. *Auk* 98:386-389.
- PRESTON, F. W., AND E. J. PRESTON. 1953. Variation of the shapes of birds' eggs within the clutch. *Ann. Carnegie Mus.* 33:129-139.
- RICHDALE, L. E. 1955. Influence of age on the size of eggs in Yellow-eyed Penguins. *Ibis* 97:266-275.
- ROMANOFF, A. L., AND A. J. ROMANOFF. 1949. *The avian egg*. John Wiley and Sons, New York.
- ROSENE, W. 1969. *The Bobwhite Quail, its life and management*. Rutgers Univ. Press, New Brunswick, NJ.
- SHIELDS, W. M., AND J. R. CROOK. 1987. Barn Swallow coloniality: a net cost for group breeding in the Adirondacks? *Ecology* 68:1373-1386.
- SOKAL, R. R., AND F. J. ROHLF. 1969. *Biometry*. W. H. Freeman, San Francisco, CA.
- VAN BREE, P.J.H. 1957. Variations in length and breadth of eggs from a colony of Black-headed Gulls (*Larus r. ridibundus* Linnaeus) on the island of Texel. *Beaufortia* 5:245-255.
- WELLER, M. W. 1959. Parasitic egg laying in the Red-head (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.* 29:333-365.
- WILKINSON, L. 1987. SYSTAT: the system for statistics. SYSTAT, Evanston, IL.
- WOOD, N. A. 1974. The breeding behaviour and biology of the Moorhen. *Br. Birds* 67:104-115, 137-158.
- YOM-TOV, Y. 1980a. Intraspecific nest parasitism in birds. *Biol. Rev. Camb. Philos. Soc.* 55:93-108.
- YOM-TOV, Y. 1980b. Intraspecific nest parasitism in the Dead Sea Sparrow, *Passer moabiticus*. *Ibis* 122:234-237.