

ESTIMATING CONSPECIFIC NEST PARASITISM IN THE NORTHERN MASKED WEAVER BASED ON WITHIN-FEMALE VARIABILITY IN EGG APPEARANCE

WENDY M. JACKSON¹

Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195, USA

ABSTRACT.—The Northern Masked Weaver (*Ploceus taeniopterus*), like many weavers, exhibits a dramatic degree of intraspecific variability in egg appearance. While the rule is that all eggs within a nest look alike, this rule frequently is violated. By observing marked females laying eggs, I determined that within-female variability in egg appearance is both significantly and substantially lower than the variability seen among eggs laid by different females. Because communal breeding does not occur in this species, and because I ruled out parasitism by heterospecifics, nests containing odd-looking eggs must have been victimized by conspecific nest parasites. Based on the maximum variability in egg appearance observed in non-parasitized clutches, and by noting clutches with peculiar laying sequences that are indicative of parasitism (e.g. two eggs appearing on the same day), I determined the rate of conspecific nest parasitism in the Northern Masked Weaver to be between 22.8% and 34.7%. This is one of the highest rates of conspecific nest parasitism reported for passerines. My results support the conclusion that conspecific nest parasitism is a widespread and common behavior among *Ploceus* weaverbirds. Received 6 December 1990, accepted 13 January 1992.

THE Northern Masked Weaver (*Ploceus taeniopterus*), like many of its congeners, exhibits a dramatic degree of intraspecific egg-color variability (Mackworth-Praed and Grant 1955, Moreau 1960, Freeman 1988, pers. observ.). Eggs range from dark brown to tan to blue-green. They can be either speckled or immaculate and, if speckled, can have various patterns of speckling. Typically, as in other *Ploceus* species with variable eggs, all the eggs within a nest look alike, suggesting that eggs produced by individual females do not vary in appearance. Initial support for this conclusion comes from studies of a captive colony of Village Weavers (*P. cucullatus*; Victoria 1972, Collias 1984); eggs laid over a lifetime by individually marked females varied little in either color or speckling.

However, the rule that all eggs within a nest look alike is frequently violated in the Northern Masked Weaver, as well as in other weavers. In a study of *Ploceus* egg collections, Freeman (1988) found that among 16 species with variable eggs, between 2% and 29% of the nests of a species contained an odd-looking egg. If females produce only one egg type, these odd-looking eggs must have been laid by a brood parasite. Communal nesting is unknown among

Ploceus species and, in this study of the Northern Masked Weaver, I never observed two females tending to the same nest. Freeman (1988) concluded that the parasites were conspecifics, rather than *Chrysococcyx* cuckoos, common brood parasites of many tropical Old World passerines, because he found no correlation between the incidence of cuckoo parasitism reported in the literature and the incidence of odd-egg clutches. In addition, Jensen and Vernon (1970) incubated 12 oddly colored eggs they discovered in weaverbird nests, and all of them hatched into weavers of the species in whose nest they were found. Finally, *Chrysococcyx* cuckoos are relatively unimportant brood parasites of the Northern Masked Weaver (Jackson in press a). Thus, conspecific nest parasitism (CNP) appears to be a common occurrence among *Ploceus* weaverbirds.

Conspecific nest parasitism is now known to be widespread and common in birds. In an extensive review of the phenomenon, Rohwer and Freeman (1989) listed more than 140 species that engage in this behavior. The number known to exhibit this behavior has increased dramatically over the years and is likely to continue growing (see Jackson 1990). This growth is the result of improved detection rather than changes in the rates of CNP. Because in most species there is little variation in egg appearance, either within a nest or between nests, researchers rare-

¹ Present address: Burke Museum DB-10, University of Washington, Seattle, Washington 98195, USA.

ly can tell whether a nest has been parasitized by making a single visit. Rather, daily nest inspections and marking eggs are required to detect peculiar laying sequences indicative of parasitism. Even when this is done, if the parasite lays its eggs in sequence with those of the host, the parasitic eggs may go undetected. Biochemical analyses are sometimes used to exclude maternity, but in addition to being labor intensive, they are useless if suspected parasitic eggs are ejected by the host before the researchers analyze them. Indeed, most techniques probably result in underestimates of the frequency of CNP in a particular species. The various techniques used to detect CNP and their drawbacks have been reviewed by MacWhirter (1989).

In species with variable eggs a single visit to a nest may be sufficient to determine if it has been parasitized—if the extent of variability in appearance among eggs laid by individual females is known and this variability is known to be significantly less than between-female variability. That is, a nest of such a species can be considered parasitized if the variability in appearance of its eggs exceeds the amount of variability that can be accounted for by within-female variability. Within-clutch variance in egg appearance has been used to infer CNP in several studies (see Brown and Sherman [1989] and references therein). However, few of these investigators measured aspects of egg appearance, and in none of these studies were females actually seen laying eggs. Møller (1987), in a study of Barn Swallows (*Hirundo rustica*), and Gibbons (1986), in a study of Moorhens (*Gallinula chloropus*), went a step further and matched oddly colored eggs to those found in other nests to infer which females had laid the parasitic eggs. However, neither observed females laying eggs, nor did they quantify aspects of egg appearance. Although Møller's and Gibbons' conclusions that parasites are neighboring females are reasonable (corroborating evidence supports their conclusions), Brown and Sherman (1989) noted that unless within- versus between-clutch variability is quantified, inferring CNP based on the presence of an oddly colored egg remains problematic.

Two studies in which eggs were measured are those by Fetterolf and Blokpoel (1984) and Brown and Sherman (1989). Fetterolf and Blokpoel found that in Ring-billed Gulls (*Larus delawarensis*), variance in egg appearance between nests was greater than variance within nests. Although they did not observe females laying

eggs, they did measure eggs found in the nests of individually marked females in successive years. This reduced variance that might have resulted because one or both of the nests were parasitized.

Brown and Sherman (1989) measured the degree of variability in egg appearance both within and between randomly chosen clutches of Cliff Swallows (*Hirundo pyrrhonota*) and Barn Swallows. Although they found some aspects of egg appearance to be significantly more variable between clutches than within clutches, they concluded that the degree of difference was not sufficient to allow them to decide whether or not a nest had been parasitized. Furthermore, among Cliff Swallows, within-clutch variance in clutches known to be parasitized, based on peculiar laying sequences, was not significantly greater than within-clutch variance in clutches not known to be parasitized (i.e. did not have peculiar laying sequences), as would have been expected if between-clutch variability were sufficiently greater than within-clutch variability. It is possible that some of the clutches not known to be parasitized were, in fact, parasitized, which would mask the predicted difference.

If variance in egg appearance has the potential to allow researchers to infer conspecific nest parasitism in any species, *Ploceus* weaverbirds are prime candidates for such an analysis. The intraspecific variability in egg color seen among these weaverbirds is unrivaled by that seen in any other species, even those noted for their egg variability (e.g. the Common Murre, *Uria aalge*). My purpose was to use variation in egg appearance to determine the incidence of CNP in the Northern Masked Weaver. I first document the degree of variability among eggs I observed being laid by individually marked females (nonparasitized clutches). I then show that this variability is both significantly and substantially lower than the variability among eggs laid by different females. Based on the maximum variability in egg appearance seen in nonparasitized clutches, and by noting clutches with peculiar laying sequences, I determined the rate of CNP in the Northern Masked Weaver to be between 22.8% and 34.7%, one of the highest rates reported for passerines.

METHODS

STUDY ORGANISM AND STUDY SITE

For three seasons, from 1986 through 1988, I studied a population of Northern Masked Weavers breeding

at Lake Baringo, Rift Valley Province, Kenya (0°35'N, 36°5'E). The nests of this species are built primarily in marsh grass (*Echinochloa haploclada*) and reeds (*Typha* sp.), and occasionally in small acacia trees (*Acacia* sp.), making them very accessible. In addition, the nests lack entrance tubes, making it easy to remove eggs for inspection.

Although males build the nests, they essentially never enter a nest after they have finished weaving it. All incubation and care of the young is performed by females. Males are polygynous and, although they may have more than one mate at a time, the mates are acquired sequentially, so that two females mated to the same male are rarely in the same stage in their nesting cycles. Females usually commit to a nest one day prior to when they begin laying, and males build more nests than are ultimately used.

WITHIN- VS. BETWEEN-FEMALE VARIABILITY IN NONPARASITIZED CLUTCHES

Egg-laying observations.—To document within-female variability in egg appearance, in 1987 and 1988, 32 individually marked females were observed laying more than one egg. Females were marked in one of two ways: some were color banded, either having been mist netted or having been caught in their nests. Because the latter technique frequently caused females to abandon their nests, most females were marked as follows: I placed a dab of solid cooking grease mixed with nontoxic paint in the bottom of a female's nest, so that when she entered it some of the paint would stain her belly and breast feathers. By noting the pattern of these stains, I could recognize females throughout their laying periods.

I used the following technique for observing marked females laying eggs: I checked the nest before my observations began to make certain the egg had not already been laid that morning (all 74 eggs observed being laid were laid before noon). I then sat on a stool approximately 3 m from the nest and waited for a female to arrive. If it was the first day of observation at a nest, either I observed the bands of the female as she entered, or I noted the paint pattern on her feathers as she left. If it was a subsequent day of observation, I compared the band combination or paint pattern of the female entering the nest with that of the female who laid the egg on the previous day. After the female left, I immediately marked the egg with indelible ink, and assessed three aspects of appearance: background color, speckling pattern and egg volume (a measure of egg size). I never observed more than one female laying in a single nest.

Because females of some species are thought to lay a terminal egg that differs from their previous eggs (e.g. see Lowther 1988), I made special attempts to observe the final egg. I observed all the eggs of a female's clutch being laid in 16 cases (10 females laid three eggs and 6 females laid two eggs); I refer to these 16 clutches as "nonparasitized clutches." I also observed the first and third egg being laid in 5 clutch-

es, and the first two of three eggs being laid in 11 clutches; I refer to these 16 cases as "nonparasitized partial clutches."

Assessing egg appearance.—In 1986, egg color was assigned to one of 24 subjective categories, ranging from blue-green to dark brown. In 1987 and 1988, egg color was quantified by matching eggs to the closest "color chip" from the matte finish version of the *Munsell Book of Color* (Munsell Color, Inc. 1976). When the color of the egg fell between two color chips, the values for the two chips were averaged. Because each color chip represents a point in three-dimensional space, there are three values assigned to each chip (hue, value and chroma). So that the experiments in 1986 could be combined with the others, I converted categories to Munsell values as follows: I plotted a frequency distribution for the categories in 1986 and for the Munsell values in 1987–1988; I matched the distributions by inspection. Although the frequency distribution for the Munsell values had a greater number of divisions than did the distribution for the categories, so that within a category there might be some slight variation in color, the technique does not result in any systematic bias in assessing egg color.

Although the Munsell variable for hue has a circular distribution, the eggs of the Northern Masked Weaver span only 135° of the circle (i.e. less than one-half of the circle), from 5 Yellow-Red (Hue #15) to 2.5 Blue-Green (Hue #52.5), and do not straddle the arbitrary beginning point of the circle. Therefore, I can treat hue as a linear variable without overestimating differences between two eggs (e.g. when two eggs fall on opposite sides of the beginning point, yet in reality are quite similar in hue).

Hue, value and chroma are highly intercorrelated in this species; bivariate correlations calculated from 1,790 eggs in this study ranged from 0.81 to 0.88. Therefore, I combined these three variables with a principal-components analysis to derive a single variable I term "color." The first component accounted for 90.4% of the variance in these three variables, and the scores calculated using this factor were entered as the values for color.

Speckling pattern was determined by noting the amount of speckling and the distribution of the speckling over the egg. Amount of speckling was categorized as none (no speckling), sparse ($\leq 25\%$ of the egg speckled), medium (26–50% of the egg speckled) and heavy ($\geq 50\%$ of the egg speckled). Distribution of the speckling, if the egg was speckled, was categorized as even (speckling evenly distributed over the egg), slightly graded (speckling slightly more concentrated at the blunt end), and graded (speckling concentrated at blunt end). Because amount of speckling and distribution of speckling are correlated ($r = 0.77$), I performed a principal-components analysis to combine these variables into one variable termed "speckling pattern." The first component extracted accounted for 88.7% of the variance in these variables, and the component scores calculated in this analysis were entered as speckling pattern.

Egg volume (V) was calculated using the formula given in Spaw and Rohwer (1987):

$$V = 0.498LB^2, \quad (1)$$

where L is length and B is breadth, which were measured to the nearest 0.1 mm with calipers in 1986 and usually to the nearest 0.05 mm in 1987–1988.

Statistical analysis.—To determine if between-female variance in egg appearance was greater than within-female variance, I performed a one-tailed F -test, examining the ratio of between-group variance to within-group variance. As the within-group variance, I used the average within-female variance for each of the three variables. As the between-group variance, I used the variance among clutch means for each variable rather than the overall variance among all eggs because the former statistic is a more accurate measure of the degree of variation between nests (see Baerends and Hogan-Warburg 1982, Brown and Sherman 1989).

VARIABILITY IN PARASITIZED CLUTCHES

Nest inspections.—In 1987 and 1988 my study spanned the entire breeding season from mid-May to mid-September, whereas in 1986 it spanned all but the end of the season (observations stopped in late August). I monitored all nests that I found, and inspected the contents of all accessible nests. Only a handful of nests were inaccessible. I followed the majority of nests from the day the males began building them until the fate of the nest was determined. I found that males tore down the unused nests, the young fledged, or the active nests failed due to predation or some other reason (Jackson in press b). Some nests were not discovered until females had either started laying or completed their clutches. More than 700 nests ultimately were used by females (i.e. received at least one egg).

Most nests were inspected daily, usually in the afternoon and at 24-h intervals. Upon inspection, I marked each egg with indelible ink, and assessed color, speckling pattern, and (in most cases) length and breadth. When I knew the laying sequence within a nest, I marked each egg accordingly. Otherwise, I marked eggs with numbers in a random order. By keeping track of individual eggs, I could detect peculiarities in the laying sequences indicative of parasitism. Once a clutch was completed, I continued to monitor the number of eggs in each nest by touch: if an egg disappeared, I noted which one. I also removed all the eggs from a nest every few days to see if any new eggs had appeared while previously marked eggs had disappeared.

Inferring CNP from peculiar laying sequences or clutch size.—Forty-eight of the 645 nests that received at least two eggs were considered parasitized based on one or more of the following four criteria, all of which are independent of egg appearance:

(1) In seven nests, two eggs appeared on the same

day. No species is known to lay more than one egg per day (Lack 1968), and the average laying interval for the 27 females I observed laying eggs on two consecutive days was approximately 25 h. Thus, when two eggs appear in a nest on the same day, they must have been laid by two different females. This criterion is used frequently for determining if a nest has been parasitized (Yom-Tov 1980, Møller 1987, Kendra et al. 1988, Brown and Brown 1989).

(2) In 21 nests, an egg appeared following at least one day on which no egg appeared. The maximum gap between eggs in these nests was nine days. The vast majority of passerines whose laying interval is known lay at the rate of one egg per day (Lack 1968). In addition, none of the 16 females whose entire clutch I observed being laid skipped a day in their laying cycles, and the remaining 16 females had the “missing” egg appear on the day expected if females lay one egg per day. Thus, a gap in the laying cycle probably results when a host has completed her clutch and at least a day passes before a parasite places her egg in the nest. This criterion has also been used by other researchers to infer parasitism (Yom-Tov et al. 1974, Brown and Brown 1988).

(3) In two of the cases in which I detected a gap in the laying sequence, and in one additional case, I have evidence that an egg had been physically transferred from one nest to another. In the first two cases, an unmarked egg appeared four and nine days following clutch completion, which then hatched in eight and four days, respectively. Almost invariably, eggs of this species hatch 12 days after the day they were laid (hatching is asynchronous in this species, with one egg hatching each day), so these two eggs must have been laid elsewhere, incubated for a while, and then transferred to these nests. In the third case, a marked egg appeared in a nest that already contained one marked egg—the former egg must have been laid elsewhere and then moved. Although the egg did not have a nest number (it was marked only according to the laying sequence in its own nest), evidence points to a nest a few meters away as the source. Egg transferring is a frequently employed parasitic tactic among Cliff Swallows (Brown and Brown 1988), and has also been documented in Black-billed Magpies (*Pica pica*) and Pinyon Jays (*Gymnorhinus cyanocephalus*; Trost and Webb 1986).

(4) I considered an additional 17 nests parasitized because they contained four eggs. The mean clutch size is 2.57 ± 0.63 ($n = 678$), excluding one-egg nests that were destroyed or that disappeared before a second egg could appear, but including one-egg clutches that were tended by females. Because a four-egg clutch exceeds the mean clutch size plus two standard deviations, and because only 3.8% of the nests contained four eggs, it is reasonable to assume such nests have been parasitized. In addition, 11 clutches with peculiar laying sequences also contained four eggs, supporting my assumption that four-egg clutches result

from conspecific nest parasitism. Thus, while some of the four-egg clutches may not have been parasitized, evidence suggests that many have been parasitized, and I included them in this category. Enlarged clutches have been considered by many researchers to be parasitized (see Yom-Tov et al. 1974, Freeman 1988).

Indices of variability in egg appearance.—As an index of variability, I used within-nest standard deviations in color, speckling pattern, and volume. For the entire sample of 645 nests that received at least two eggs, standard deviations in color ranged from 0.000 to 1.830 (mean = 0.096), in speckling pattern from 0.000 to 1.741 (mean = 0.120), and in volume from 0.000 to 1.174 (mean = 0.092).

INCIDENCE OF CONSPECIFIC NEST PARASITISM

Determining the minimum estimate of CNP rate.—I established the following criteria based on variability in egg appearance for deciding which of the remaining 581 clutches that received at least two eggs were parasitized (48 clutches were already known to be parasitized, and the 16 complete clutches that I observed being laid were already known not to be parasitized; however, the 16 partial clutches that I observed being laid could still have been parasitized). I considered a clutch parasitized if it had a standard deviation in any one of the variables that exceeded the corresponding maximum standard deviation of the 32 nonparasitized clutches or partial clutches. Clutches could meet this criterion for more than one of the three aspects of egg appearance.

Because standard deviation is inversely proportional to clutch size, standard deviations were adjusted as follows: the maximum standard deviation in color of the nonparasitized clutches was 0.260 for a two-egg clutch. In this clutch, the two eggs differed by one step in hue. A clutch of three eggs, in which two eggs are identical and the third differs by one step in hue, would have a standard deviation of 0.212, while a clutch of four eggs fitting the scenario would have a standard deviation of 0.196. Thus, standard deviations in color for clutches of three eggs were multiplied by 1.226 (i.e. $0.260/0.212$) and those of four eggs were multiplied by 1.327.

The maximum standard deviation in speckling pattern of the nonparasitized clutches was 0.318 for a clutch of three eggs. In this clutch one egg was one step less speckled than the other two eggs. A clutch of two eggs fitting this scenario would have a standard deviation of 0.390, while a clutch of four eggs would have a standard deviation of 0.294. Thus, standard deviations for two-egg clutches were divided by 1.226, while those for four-egg clutches were multiplied by 1.082. The maximum standard deviation in volume for the nonparasitized clutches was 0.212 for a clutch of three eggs. Standard deviations in volume of two-egg and four-egg clutches were adjusted as for speckling pattern.

Finally, none of the nonparasitized clutches had an egg that differed in both color and speckling pattern from the other egg(s), yet 11 of the 581 clutches in question contained such eggs and were considered parasitized.

The frequency distributions of the adjusted standard deviations in color, speckling pattern and volume for the 597 clutches without peculiar laying sequences or containing four eggs (this number includes the 16 complete clutches that I observed being laid) are found in Figure 1. Note that the distributions for color and speckling pattern do not include the 417 clutches and 502 clutches, respectively, with no variability at all. In these figures, the arrows correspond to the maximum standard deviation observed in the nonparasitized clutches or partial clutches, and any clutch to the right of these arrows was considered parasitized. The distribution for variability in speckling pattern appears discontinuous because of the categorical nature of these data.

Determining maximum estimate of CNP rate.—The above method for calculating the rate of parasitism results in an underestimate because at least some of the clutches with low indices of variability in egg appearance, yet without peculiar laying sequences, are likely to be parasitized. Support for this conclusion comes from a more detailed inspection of the variability seen in the 48 clutches known to be parasitized. If I had ignored the fact that these clutches had peculiar laying sequences or contained four eggs, and relied only on my indices of variability to decide whether they had been parasitized, I would have detected only 27 (or 56.2%) of these 48 cases of CNP. The proportion of nests with peculiar laying sequences or containing four eggs that would have escaped my indices was not different among years (numbers in left two columns of Table 1; $G = 0.149$, $df = 2$, $P > 0.05$). Thus, I consider 56.2% to represent the "efficiency" of my variability indices for all years.

If I assume that the distribution of variability seen in the 48 clutches with peculiar laying sequences or containing four eggs is the same as the distribution I would see in the clutches that are parasitized but do not have peculiar laying sequences, then I can use the information about the efficiency of my variability indices to estimate the maximum rate of CNP. In other words, I can calculate how many of the clutches with little or no variability in egg appearance, but with normal or unknown laying sequences, are likely to be parasitized.

I calculated this number for the three years combined as follows: the number of nests considered to be parasitized based only on my variability indices (i.e. not on the basis of laying sequence) is 99 (see bottom row, Table 1). This number should represent only 56.2% of the cases of parasitism in nests without peculiar laying sequences. Thus, another 77 nests are likely to be parasitized, but which thus far have gone undetected because their indices of variability fall

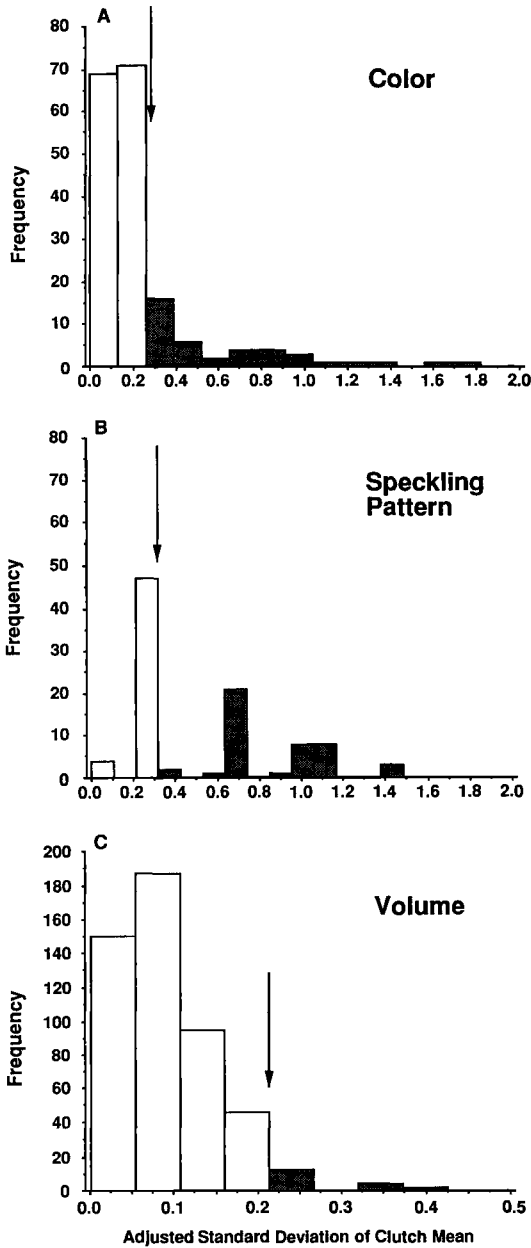


Fig. 1. Frequency distribution of adjusted standard deviations in egg appearance for the 597 clutches without peculiar laying sequences or containing four eggs. Arrow corresponds to maximum standard deviation in nonparasitized clutches; clutches to the right of this arrow are considered parasitized (speckled bars), while those to the left (white bars) are considered not to be parasitized. (A) Distribution for color, excluding 417 clutches with zero variability. (B) Distribution for speckling pattern, excluding 502 clutches with zero variability. (C) Distribution for volume.

TABLE 1. Number of parasitized clutches with peculiar laying sequences or containing four eggs not detected with variability indices, and estimated number of clutches with regular or unknown laying sequences not detected with variability indices. Corresponding total percentages given.

Year	Clutches with peculiar laying sequences or containing four eggs		Clutches with regular or unknown laying sequences	
	No. detected	No. not detected	No. detected	Estimated no. not detected
1986	4	3	20	16
1987	14	12	43	34
1988	9	6	36	28
Total	27 (56.2%)	21 (43.8%)	99	77

below the cutoffs I established, and because they have regular or unknown laying sequences. The total number of parasitized nests for all years combined using this method is 224 (i.e. 27 + 21 + 99 + 77; refer to bottom row of Table 1).

RESULTS

Within- vs. between-female variability in nonparasitized clutches.—There was little variance in any of the three variables among the eggs produced by an individual female, but this was especially true for color and speckling pattern (Table 2). In only one instance did a female produce eggs that differed by as much as one step in hue, and in 28 cases there was no variability in color. In only one instance did a female produce eggs that varied in speckling pattern; one egg was one step less speckled than the other eggs. The eggs that differed were always the last eggs to be laid in the nest.

In contrast, there was tremendous variability among eggs produced by different females. The results of the *F*-tests are found in Table 2. Be-

TABLE 2. Within-female variance in egg color, speckling pattern, and volume vs. between-female variance for 32 nonparasitized clutches or partial clutches.

Variable	Within-female variance	Between-female variance	<i>F</i> _{31,72}	<i>P</i>
Color	0.003	0.905	301.667	<0.0001
Speckling pattern	0.003	0.852	284.000	<0.0001
Volume	0.009	0.052	5.778	<0.0001

TABLE 3. Mean (and minimum-maximum) standard deviations in color, speckling pattern and volume of nonparasitized and parasitized clutches (i.e. clutches with peculiar laying sequences or containing four eggs). Mann-Whitney *U*-tests are two-tailed, corrected for ties.

Variable	Nonparasitized clutches or partial clutches ^a	Parasitized clutches ^b	Mann-Whitney <i>U</i>	<i>P</i>
Color	0.017 (0.000-0.260)	0.294 (0.000-1.830)	234	<0.001
Speckling pattern	0.010 (0.000-0.318)	0.477 (0.000-1.511)	300	<0.001
Volume	0.075 (0.000-0.213)	0.131 (0.030-0.313)	319	<0.001

^a Sample size is 32.

^b Sample size is 48 for color and speckling pattern, and 42 for volume.

tween-female variance was significantly greater than within-female variance for all three aspects of egg appearance, and for egg color and speckling pattern, this ratio was extremely large.

Variability in parasitized clutches.—The 48 clutches considered parasitized based on their peculiar laying sequences or because they contained four eggs were significantly more variable than the 32 nonparasitized clutches or partial clutches in all three variables (Table 3), but especially in color and speckling pattern. These results are expected based on my earlier finding that between-female variance in egg appearance is greater than within-female variance in egg appearance, and they lend further justification to my using variability in egg appearance to decide if a clutch has been parasitized. In the clutches where an egg was laid out of sequence, the egg out of sequence was typically the odd egg.

Incidence of conspecific nest parasitism.—The total numbers of clutches (all years combined) considered to be parasitized on the basis of either laying sequence, clutch size or the indices of variability in egg appearance (or combination of indices) are found in Table 4. The re-

TABLE 4. Number of clutches determined to be parasitized on the basis of laying sequence and clutch size or indices of variability in egg appearance (all years combined).

Peculiar laying sequences and four-egg clutches	48
Color	
No other criteria	30
In addition to speckling pattern	20
In addition to speckling pattern and volume	1
Speckling pattern	
No other criteria	33
In addition to volume	1
Volume (no other criteria)	14
Total	147

sulting minimum estimates of the rates of CNP by year are found in the left side of Table 5. The minimum average rate of parasitism using this method is 22.8%.

Table 1 contains a breakdown of the analysis by year. The maximum estimates of the rates of parasitism using this method are found in the right side of Table 5 for comparison with the minimum estimates of CNP. The maximum average rate of parasitism using this method is 34.7%.

DISCUSSION

Between-female variance in egg appearance is significantly greater than within-female variance in the Northern Masked Weaver and, in the case of color and speckling pattern, the variance is at least two orders of magnitude greater. These results, coupled with the observation that clutches determined to be parasitized based on independent criteria are more variable than are nonparasitized clutches, lend strong justification to my using variability in egg appearance to infer cases of conspecific nest parasitism. Additional justification comes from the observation that female weaverbirds appear to do the same. In egg-recognition experiments, I found

TABLE 5. Minimum and maximum estimates of number of parasitized nests and rate of conspecific nest parasitism by year and on average.

	Minimum estimates			Maximum estimates	
	Total no. nests	No. parasitized nests	CPN rate	No. parasitized nests	CPN rate
1986	127	27	21.3	43	33.9
1987	238	69	29.0	103	43.3
1988	280	51	18.2	79	28.2
Average	645	147	22.8	224	34.7

that a female's response to "parasitic" eggs is strongly dependent on the degree of difference in color between her own eggs and the parasitic egg(s): the greater the difference the more likely she is to reject the egg or eggs (Jackson 1990).

The rates of CNP reported here are among the highest reported for any species (Jackson 1990). Because CNP is so common, at first it is surprising that I never observed parasitism during egg-laying observations. However, there are two reasons why that is not unexpected. First, my observations were made without the use of a blind—logistical problems of working in a marsh where water levels fluctuated daily and sizably made using one impossible. Therefore, birds were aware of my presence, and probably were relatively alert when I was in the marsh. If males were more wary of intruders during this time, females may have been thwarted in their parasitic attempts. Second, the majority of my observations were made in the first month of the 1988 breeding season. The rate of parasitism in nests not under direct observation during this period was also relatively low (approximately 15%). Thus, I would not have expected to observe very many cases even if my presence did not have an effect.

Two potential sources of error in my methods that would result in underestimates of the rate of CNP are as follows. First, my method of determining parasitism based on variability in egg appearance ignores all one-egg clutches. Forty nests that received one egg disappeared or were destroyed before a second egg could appear. In at least some of these instances, the first egg probably was parasitic. As noted earlier, males of this species build many more nests than are ultimately used by females, and tear down almost every unused, complete nest. If a parasite lays her egg in a nest that appears to be in use by a host female, but in fact is not, the male may tear it down despite (or perhaps because of) the fact that it contains an egg. I have no way of knowing how many of the 40 nests fit this scenario.

Second, my assumption that the distribution of variability in egg appearance among nests determined to be parasitized based on peculiar laying sequences or clutch size is the same as the distribution in the clutches that are parasitized, but which do not have peculiar laying sequences, could be a source of bias. For example, clutches with peculiar laying sequences might result from poor attempts at parasitism.

If so, and if potential parasites attempt to match their eggs to their hosts' eggs, then the variability in the clutches known to be parasitized might be greater than the variability in clutches without peculiar laying sequences.

However, there is no compelling reason to consider eggs added in a peculiar fashion poor attempts at parasitism. Hosts do not count eggs to detect parasitism, but rather show true recognition of their own eggs (Jackson 1990), so a second egg appearing on a given day or a fourth egg appearing in a nest are not providing additional information to the host. Eggs added after the host has finished laying her clutch have the potential for being less successful than eggs added during the host's laying period, so these might represent "last ditch" efforts at parasitism. However, as noted earlier, at least two such cases resulted from an egg having been physically transferred from one nest to another, and these eggs were successful. Thus, I believe that my assumptions about the distributions of variability in clutches with and without peculiar laying sequences is justified. Note that if the assumption were not true, the rates of parasitism reported here again would be underestimates.

Once I determined the degree of variability among eggs produced by individual females, determining the rate of CNP in the Northern Masked Weaver became an easy task. The same should prove true for other *Ploceus* species as well, especially because several species show variability that exceeds the variability seen among Northern Masked Weaver eggs (Freeman 1988, pers. observ.). That is, in weaver species with variable eggs, a researcher should be able to tell with a high degree of certainty whether or not a nest has been parasitized by simply looking at it. Thus, the results reported here support Freeman's (1988) conclusion, based on the appearance of odd-looking eggs in clutches of eggs found in museums, that CNP is a widespread and common occurrence in *Ploceus* weaverbirds.

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