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A Quarter Century of Variation in Color and Allometric Characteristics of Eggs from a Rain Forest Population of the Pearly-eyed Thrasher (*Margarops fuscatus*)

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ABSTRACT.—Egg color, size, and shape vary considerably within and among female Pearly-eyed Thrashers (*Margarops fuscatus*). Results of a 25-yr study (1979-2004) are presented to provide comparative data. In a sample of 4,128 eggs, typical shape was prolate spheroid; but several variations were observed, depending on the age, stature, and physiological condition of the female, as well as environmental influences such as the availability of essential nutrients. From a subset of 3,867 eggs measured between 1979 and 2000, a species-specific egg shape, or elongation index of 1.44 was derived (mean = 1.44; SD = 0.07; range = 0.93-1.85). Pooling eggs from among completed clutches of 1-4 eggs in each (mode = 3), the average egg measured 32.40 mm in length (SE = 0.02; range = 18.13-38.97 mm) and 22.50 mm in breadth (SE = 0.01; range = 16.81-33.61 mm). Observed average fresh egg mass for a set of 3,581 eggs was 8.8 g. Of three standard formulae used to predict average fresh egg mass, Rahn et al. (1985) was the most accurate (8.7 g). Averaging five standard formulae resulted in an egg volume of *ca.* 7.0 cm^3. In the Pearly-eyed Thrasher, egg size and mass tended to decrease just as it does in several non-passerine species. Light clutch mass relative to body mass is a preadaptation that increases *Margarops'* potential of laying more clutches throughout its reproductive life, thus enhancing its lifetime reproductive success and ensuring its continual survival in the region.

KEYWORDS.—**allometric, egg, Margarops fuscatus,** ***morphology, Pearly-eyed Thrasher, Puerto Rico, passerines.***

INTRODUCTION

To investigate the causative factors influencing the observed variation in birds' eggs, field biologists are often in need of conspecific comparative data from studies conducted in other geographical areas and habitats. However, even for the most common and wide-ranging species, comparative data on various parameters, especially egg mass, are lacking. For example, in most field studies egg mass is not recorded as often as are longitudinal measurements (egg length and breadth). Or, when egg mass is measured in the field, often times neither the hour, nor sometimes even the day, of egg deposition is known. Therefore, one is obligated to rely on standard published formulae; never knowing for sure which, if any, will adequately predict the egg size, fresh egg mass, or volume of the species under study.

As part of a long-term, life-history study of a Caribbean mimid, the Pearly-eyed Thrasher *Margarops fuscatus* (Arendt 1993), data on several physical and physiological properties of its eggs were collected over a 25-yr period. In this study I compared the variation in *Margarops'* egg color, size, mass, and volume, as well as potential causative factors. My goal is to offer comparative, empirical data for those studying the Pearly-eyed Thrasher in other areas of its range. Additionally, some standard, published formulae are discussed and recommended for use by field ornithologists in estimating the volume and fresh egg mass of *Margarops'* eggs, and other species as well, when only linear measurements are available or when egg mass is recorded but the time between egg deposition and measurement is not known.

MATERIALS AND METHODS

Study area

I conducted the study in the 11,330-ha Caribbean National Forest (also known as the Luquillo Experimental Forest, hereafter LEF) in eastern Puerto Rico (18°19′N, 65°45′W). Average annual rainfall and temperatures range (respectively) from 300 cm and 25.5 °C in the foothills to more than 500 cm and 18.5 °C on peaks higher than a 1,000 m. The forest is comprised of four major vegetation associations that are altitudinally stratified and placed into separate life zones (see Ewel and Whitmore 1973 for a complete description). Located between roughly 600 and 900 m and encompassing 3,318 ha (*ca*. 30% of the LEF) is the *palo colorado* forest type in the lower montane wet forest zone. It is named for the *palo colorado* or swamp cyrilla (*Cyrilla racemiflora*) which, although rarely exceeding heights of 18 m, may reach almost 3 m in diameter and can survive more than a thousand years (Weaver 1986). The cyrilla's propensity for producing natural cavities makes it a preferred nest-tree for cavity-nesting birds such as the Pearly-eyed Thrasher.

Fieldwork commenced in 1978 with the monitoring of about 40 modified Wood Duck (*Aix sponsa*) nest boxes (Arendt 1993). Each thrasher box was placed about 0.1 km apart at elevations ranging from about 600 to 900 m primarily in *palo colorado* forest. Thrasher boxes were closely monitored throughout the nesting period. They were inspected every two days, or daily during critical periods, e.g., egg laying, hatching, and the fledging of young. With few exceptions, females laid one egg each day; each was marked with a felt-tip pen to confirm order in the laying sequence. During nonbreeding seasons, each box was checked for signs of activity every two weeks, or weekly, just after or prior to breeding.

Eggs were measured and weighed using digital and dial calipers accurate to 0.01 and 0.02 mm, respectively, and 10 to 50-g spring scales with increments of 0.2 to 0.5 g. Egg data included in the analyses were collected between January 1979 and March 2004. Eggs were considered infertile if found addled after the normal 14-15 day incubation period; thus, some addled eggs may have contained deceased minuscule embryos not discernable to the naked eye. See Arendt (1993) for methods of capturing, sexing, and ageing Pearly-eyed Thrashers.

Egg color.—Egg color codes follow Smithe (1975). In the text, "dark bluish green" refers to Munsell Color Code 93, or Robin's Egg Blue, 3.5 B 7.9/5.5; "turquoise green" = Munsell Color Code 64, or Turquoise Green, 10.0 BG 6.0/8.0; "dull, pale sky blue" = Munsell Color Code 66, or Sky Blue, 2.5 PB 7.0/7.0.

Egg size.—Sample sizes of pale (n = 113) and albinistic (n = 90) eggs were substantially smaller than that of normally pigmented eggs (n = 3,664). Consequently, when comparing the three groups, comparable sample sizes were obtained by assigning fifty random numbers, produced by a random-numbers generator, to the corresponding row number of the dataset of normally pigmented eggs. Size parameters included were minima, maxima, averages, medians, modes, and 25-75 percentiles.

Egg and clutch mass.—Following Chardine's (1986) recommendation, I use the term egg "mass" in lieu of egg "weight." To avoid pseudo-replication because eggs within a clutch are not independent (Smith et al. 1993), an average clutch mass was calculated by tallying egg masses and dividing by the number of eggs ($n = 1 - 4$; mode = 3) within complete clutches.

Volume.—One of the most accurate and direct ways to measure egg volume is by water displacement using a volumeter (Loftin and Bowman 1978; Thomas and Lumsden 1981; Morris and Chardine 1986). For the field biologist such direct measures may be impractical. Fortunately, accurate measurements of egg volume may be obtained using the allometric relationship between egg dimensions and mass (Olsen et al. 1994). Egg volume is measured in cubed centimeters when derived from longitudinal and mass measurements taken in the field.

To ascertain a reliable measure of egg volume for the Pearly-eyed Thrasher, five standard allometric formulae were averaged. Three were based on longitudinal measures: (a) Tatum (1975): $V = 3.14*L*B^2/6$; (b) Hoyt (1979): $V = 0.51*L*B^2$; and (c) Ojanen et al. (1978): $V = 0.042 + 0.467*L*B^2$; where V = volume, numeric values = species-specific (or group) coefficients, L = egg length, and B = egg breadth. One equation was based on egg length, shell surface area, fresh egg and shell mass: Rahn and Paganelli (1989): $V = (L*A) + (FEM*M_{shell}/1.03)$, where A = surface area in cm^2 ($4.83*FEM^{0.662}$) and M_{shell} = shell mass in grams ($0.054*\text{Egg Mass}^{1.024}$). The fifth and final method was based on fresh egg mass: Paganelli et al. (1974): $V = 0.982*FEM^{0.874}$, where the numeric values are coefficients for a large number of species combined.

Longitudinal egg measures.—Since the length and breadth of Pearly-eyed Thrasher eggs were measured throughout this study, an ample database was created that can be used to compare the accuracy of standard formulae in estimating actual egg dimensions. In total, 7,734 longitudinal measurements (length and breadth) were taken on 3,867 eggs laid between 1979 and 2000, and were compared with a standard published formula (Rahn and Paganelli 1988), which uses fresh egg mass (FEM) to calculate the length ($L = 15.1*FEM^{0.345}$) and breadth ($B = 11.3*FEM^{0.325}$) of birds' eggs. Numeric values are species-specific mass coefficients. Mass coefficients specifically for the Pearly-eyed Thrasher were calculated and substituted into Rahn and Paganelli's (1988) formula ($L = 15.3*FEM^{0.346}$ and $B = 8.18*FEM^{0.325}$).

Fresh egg mass.—Three standard formulae, two using only longitudinal measurements to derive a measure of cubage ($L*B^2$, which is roughly proportional to the volume), and one based on egg mass, were most accurate in predicting the Pearly-eyed Thrasher's fresh egg mass: (1) Hoyt (1979): $FEM = 0.54*L*B^2$; (2) Ankney and Johnson (1985): $FEM = 0.111 + 0.526*L*B^2$; and (3) Rahn et al.'s (1985) equation, which included Schönwetter's (1960-1984) empirical measurements (*n* = 7,246 eggs; 3,931 from passerines): $FEM = 0.991*M_t^{0.999}$. In the first two formulae, 0.54, 0.111, and 0.526 are mass coefficients calculated for individual species or groups (e.g., passerines) from the relationship: $K_m = M/L*B^2$. Here, M is equivalent to fresh egg mass, L = egg length, B = egg breadth, and M_t = egg mass at some time "t" (measured in days) after oviposition.

Statistical analyses.—SigmaStat® Version 3 (Fox et al. 2003) was used. During exploratory analyses, all variables were checked for normality (Kolmogorov-Smirnov test with Lilliefors' Correction) and equal variance (Levene Median Test). In all cases, normality and/or equal variance assumptions were violated. Consequently, nonparametric tests were used for all analyses, e.g., Spearman Rank Order Correlation in comparisons of residuals; Mann-Whitney Rank Sum (2 groups) and Kruskal-Wallis ANOVA on Ranks (< 2 groups). The Student-Newman-Keuls (SNK) test was used in post-hoc comparisons testing when sample sizes were equal and no data were missing. Dunns test was used whenever sample sizes were unequal or there were missing data. A 95% level of confidence ($\alpha = 0.05$) was maintained in all of the analyses.

RESULTS

Egg color.—Normally, the modal hue of eggs of the Pearly-eyed Thrasher ranges from robin blue to turquoise green (see Methods for codified descriptions). In general terms, luster and hue range from shiny, dark bluish-green to a very dull, pale sky blue with a chalky appearance. Of 3,867 eggs sampled from 1979 to 2000, 113 pale sky blue eggs were recorded. Although pale blue eggs are often either the first or last eggs laid within a clutch at any given time during the breeding season, over the entire study, the number of pale blue eggs was about evenly distributed among the first- to third-laid eggs in the laying sequence (38, 37, 32, respectively). Only six fourth-laid pale blue eggs were recorded. Whereas on average 1 - 4 pale blue eggs were observed in most years, there were more of them in three years, 19 eggs in 1982 and 15 eggs each in 1987 and 1991, the latter of which was two years after a major habitat disturbance (Hurricane Hugo) and a period when food resources were scarce (Arendt 1993; Wunderle 1999). Similar post-disturbance food shortages were documented following Hurricane Georges in 1998 (Thompson-Baranello 2000). It is also noteworthy that during the two primary egg-laying months of March and April in 1982, average rainfall was 12.64 and 17.27 cm, respectively; well below a 25-yr monthly average of 32.7 cm. Reduced rainfall undoubtedly resulted in less fruit production and diminished food resources, thereby explaining at least in part why most pale eggs were recorded in that year.

Seasonally, lackluster eggs were laid over a nine-month period (October to June of each breeding season), but most lackluster eggs were observed either early (29 eggs from October to February) or late (43 eggs from late May to June) in any given season. Pale blue eggs were significantly (Mann-Whitney Rank Sum Test: T = 4,622.5, P = 0.031) smaller (lumped average volume = 6.54 cm^3; SE = 0.06; median 6.47 cm^3; range = 5.02-8.49 cm^3) than normally pigmented eggs (lumped average volume = 6.69 cm^3; see Appendix for remaining parameters); and weighed significantly (T = 12,331, P < 0.001) less (lumped average fresh egg mass = 8.7 g; SE = 0.08; median 8.6 g; range = 6.9-10.8 g) than normally pigmented eggs (average mass = 8.8 g, range = 4.3-11.8 g; see Appendix).

By comparing eggs seasonally, it appears that most pale blue eggs were laid in third or later clutches, which was not the case. Although the number of normally pigmented eggs remained about the same in all clutches, more than half of the pale blue eggs (n = 59) were found in first and second clutches. This apparent discrepancy is easily explained by considering the substantial temporal variation in the onset and ample (7-9 month) duration of the Pearly-eyed Thrasher's breeding seasons (Arendt 1993). Fates of the 113 pale blue eggs were as follows: 86 (76%) hatched normally; 11 (10%) failed to hatch because of brittle shells, 9 (8%) were addled, and 7 (6%) were "missing from nest" and were presumed depredated.

Albinistic eggs.—Of 3,867 eggs sampled between 1979 and 2000, 90 eggs (*ca.* 2%) were unpigmented: 31 first-laid, 30 second-laid, 28 third-laid, and 1 fourth-laid egg (Fig. 1). With very few exceptions (e.g., Fig. 2), egg dimensions (lengths, breadths, masses, and volumes) and fertility of unpigmented eggs were similar to those of pigmented eggs (Appendix). Moreover, of the 33 clutches comprised of unpigmented eggs, 26 (79%) were successful (at least one egg hatched in each clutch). Fates of the 90 unpigmented eggs were as follows: 70 (78%) hatched normally; 9 (10%) were addled; 6 (7%) were lost to nest predation—thrashers (n = 3 eggs), rats (2), and unknown predators (1); a clutch of three unpigmented eggs was lost when the female abandoned her nest as a result of human interference (nearby construction of a weather monitoring station); one unpigmented egg was lost through the death of a developed embryo; and one failed to hatch as a result of a soft shell.

FIG 1. Three-egg clutch of albinistic (unpigmented) eggs. Despite their lack of pigmentation, albinistic eggs were generally undistinguishable in size from normally pigmented eggs.

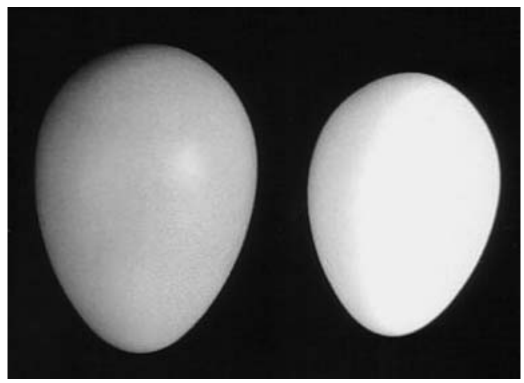

FIG 2. Comparison of a normally pigmented egg to an albinistic egg, one of very few instances in which there was a discernable size difference between the two classes of eggs.

Five female thrashers were involved in

the laying of 33 clutches of unpigmented eggs over a span of 14 years (some years were shared by two females, and no unpigmented eggs were observed in 1988 or 1989). Years in which each of the five females laid unpigmented clutches were: 1981-1982, 1981-1987, 1982, 1990-1991, and 1991-1993 (range = 2-7 breeding seasons per female). In descending order, the number of clutches comprised of unpigmented eggs produced by each female was 15, 9, 6, 3, and 1 clutch, averaging 6.6 clutches per female. The number of unpigmented eggs produced by each female was 40, 20, 18, 9, and 3 eggs, averaging 18 eggs per female. Every clutch laid by the five females contained unpigmented eggs. That is, none of the five females was observed laying pigmented eggs at any time during her reproductive years.

Egg shapes and sizes.—As in most passerines, the Pearly-eyed Thrasher's egg dimensions and mass vary significantly within and among clutches. Descriptive statistics for the longitudinal dimensions, masses, and volumes of 4,128 eggs of 194 females are presented in the Appendix. Eggs were typically prolate spheroid, although several variations (Fig. 3) were documented (long and short ovate, often with bulbous tips, round, elliptic, and even almost solid block-shaped-virtually no tapering at either end). From a set of 3,867 eggs, an elongation (or sphericity) index (length/breadth) was used to obtain an overall measure of egg shape. The resultant median of the sphericity index is 1.44 (SD = 0.07; range = 0.93-1.85). Eggs with smaller elongation values (< 1.44) were most rounded, whereas those with the larger values (> 1.44) were most pointed.

In general, females in their prime (2-6 yr) laid the typical prolate spheroid shaped eggs, whereas abnormally shaped eggs were laid by either young (≥ 1 yr) or old (> 6 yr) females. Young females typically laid small and rounded (pullet) eggs, whereas older females generally laid eggs that were long or short ovate with bulbous tips (Fig. 3). Broad eggs with bulbous tips are associated with the loss of elasticity in the oviducts of older females.

Egg size varied significantly among lay order (Table 1). The largest eggs were 2-3 three times larger than the smallest. Length and breadth, and thus mass, decreased with the laying of each successive egg within a clutch, with final eggs (usually third- and fourth-laid) being noticeably smaller than first- and second-laid eggs (Appendix).

Although there were exceptions, most large eggs (length > 34 mm, breadth > 23 mm) were laid by older females. For first-laid eggs with lengths ranging from 27.97 to 33.98 mm, average female age was 3.3 yr.

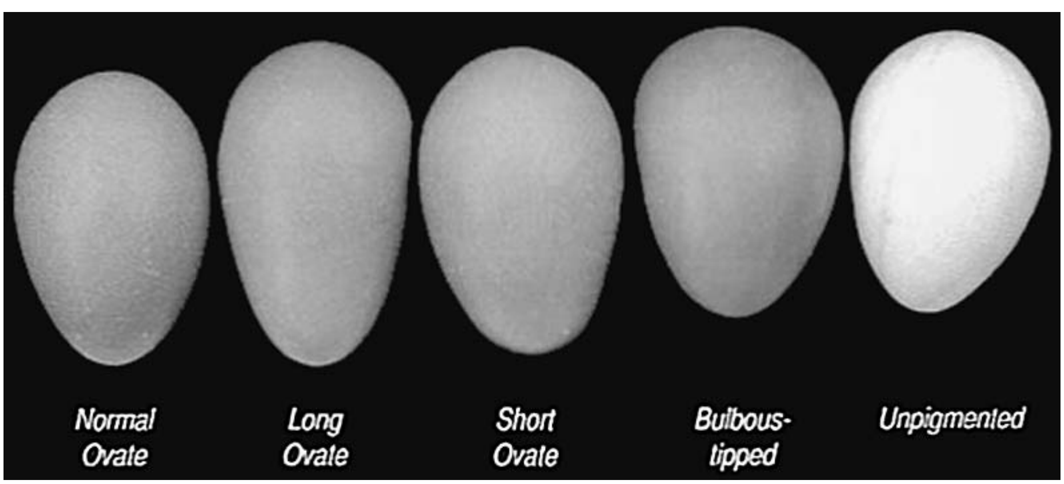

FIG 3. Variation in Pearly-eyed Thrasher egg shape, size, and color, all of which are traits governed by a host of endogenous and exogenous factors.

TABLE 1. Comparison of fresh egg mass (g) by lay order among 2,600 Pearly-eyed Thrasher eggs. Only category 1 (successful hatch) eggs were included.

	Lay order			
	First	Second	Third	Fourth
Sample size	840	893	793	74
Mean	9.1	8.9	8.4	8.1
SD	0.72	0.68	0.61	0.57
Median	9.0*	8.9*	8.4*	8.2*
25th percentile	8.5	8.4	8.1	7.7
75th percentile	9.5	9.3	8.9	8.5
Minnimum	6.5	6.7	6.2	6.8
Maximum	11.2	11.2	10.2	9.3

*Kruskal-Wallis One Way ANOVA on Ranks; $P <$ 0.05 in all six pair-wise comparisons (Dunn's Method).

Average length steadily increased to 34 mm in females between 3.4 and 5.4 years old. Conversely, females past their prime (2-6 yr), and especially very old females ($\geq$ 10 yr), reverted to laying smaller eggs. Using linear regression, Arendt (1993) compared body mass, length, breadth, and fresh egg mass of 20 females $\geq$ 8 yr old (range = 8-14 yr). In general, female stature and egg size were small when females were young (see also Kendeigh 1975; Nolan and Blank 1980; and Smith et al. 1993), body mass and egg size increased during the females' prime (variable, ranging from 2-6 yr), then decreased thereafter (Arendt 1993).

Empirical longitudinal egg measures compared to standard formulae.—Rahn and Paganelli's (1988) formula accurately predicted the actual lengths (Mann-Whitney Rank Sum Test: 25-75 percentiles = 31.46-33.38 for observed versus 31.82-33.09 for estimated lengths; $P = 0.36$) and breadths (25-75 percentiles = 22.04-22.98 for observed versus 22.37-22.65 for estimated breadths; $P = 0.73$) (Table 2). There was a significant correlation between observed and estimated egg lengths ($R^2_{adj.} = 0.40$; SE = 0.75; $P < 0.001$) and breadths ($R^2_{adj.} = 0.96$; SE = 0.04; $P < 0.001$). In wild populations in general, variability is greater in egg lengths than in egg breadths.

Fresh egg mass from empirical data and standard formulae.—Pooling lay order (1st – 4th-laid eggs combined), the average observed fresh egg mass of a set of 3,581 apparently "normal" eggs (excluding addled eggs, and those with discernibly deceased embryos, etc.) was 8.8 g (SE = 1.1; range = 4.3-11.8 g). These empirical results were compared to three standard, published formulae (described in "Methods"). The formula based on egg mass (Rahn et al. 1985), which uses either fresh egg mass or a mass taken from any day during the incubation period, was more precise in predicting fresh egg mass when compared to empirical data than either of the two formulae using longitudinal measures. This relationship held even after a species-specific mass coefficient for the Pearly-eyed Thrasher ($K_m = 0.528$) was substituted for those originally used in the formulae of Hoyt ($K_m = 0.54$) or Ankney and Johnson ($K_m = 0.526$). Using Rahn et al.'s (1985) formula, the predicted average fresh egg mass was 8.7 g (SE = 0.9; range = 2.8-11.7 g). Observed and derived fresh egg

TABLE 2. Comparison of observed longitudinal measures of eggs of the Pearly-eyed Thrasher with those derived from a standard formula.

	Egg length[1/]		Egg breadth[1/]	
	Empirical (this study)	Rahn and Paganelli (1988)	Empirical (this study)	Rahn and Paganelli (1988)
Mean	32.46	32.45	22.51	22.50
SD	1.49	0.99	0.70	0.23
SE	0.03	0.02	0.01	< 0.01
Median	32.40	32.48	22.50	22.50
Mode	32.04	32.09	22.60	22.53
Minimum	27.97	27.60	19.72	19.16
Maximum	38.97	35.95	25.16	23.33

[1/] n = 3,867 each for length and breadth; measurements are in mm.

masses were significantly correlated ($R^2_{adj.}$ = 0.99; SE = 0.001, $P < 0.001$). The two linear measurement-dependent formulae were about equal in predicting fresh egg mass. Furthermore, although not as precise as Rahn et al.'s (1985) equation, the egg masses and associated parameters resulting from both linear-based formulae were very similar to the empirical results: (mean = 8.7 g; SE = 1.0; range = 2.7-11.7 g), each with coefficients of determination $R^2_{adj.}$ = 0.80 (SE = 0.33, $P < 0.001$).

Egg and clutch mass in relation to adult body mass.—Rahn et al. (1975) derived an allometric equation for determining egg mass. Egg mass is equal to a*body mass^b, where "a" is the proportionality constant and is characteristic for each group, and the power function "b" is 0.67 and is common to all avian Orders and Families. To test the accuracy of this equation in predicting the average mass of eggs of the Pearly-eyed Thrasher, a value of 0.34 (the mean for 14 passerine species) was used for the proportionality constant. Thus, the Pearly-eyed Thrasher's average egg mass would be $0.34*112^{0.67}$, or 8.02 grams. This result is similar to the empirical average of 8.8 g obtained from the set of 3,581 eggs masses represented in the Appendix.

In addition to the taxon-specific allometric equation for determining egg mass, Rahn et al. (1975) also derived a common egg mass regression equation for all birds: $FEM = 0.277*B^{0.77}$, where FEM is fresh egg mass and "B" is body mass. To calculate the mass of Pearly-eyed Thrasher eggs, an observed average female body mass of 112 g was substituted for "B." This resulted in an average egg mass of 10.5 g, which is somewhat larger than most observed field values. In the LEF between 600-800 m, only the largest eggs, those generally laid by older females, were so heavy.

The average mass of 1073 clutches was 34.3 g (median = 34.2 g), or about 31% of the average 112-g adult female's body mass (n = 215 females, median body mass = 111 g, mode = 110 g).

Egg volume.—The volume of an average Pearly-eyed Thrasher egg is about 7.0 cm^3 (range = 6.56-8.62 cm^3) as derived by averaging the five standard formulae presented in Table 3.

DISCUSSION

Egg color.—Egg color varies considerably within, and especially among, species as a result of genetic, physiological, and environmental factors (Collias 1984, 1993; Clutton-Brock 1991; Kim et al. 1995). Several of these factors influence the variation observed in eggs of the Pearly-eyed Thrasher.

Sky Blue eggs.—All pale blue eggs appeared to be lacking in minerals. They were often the first or last eggs laid in a clutch and generally appeared at the extremes of the breeding seasons. This suggests that pale blue eggs are produced when the necessary minerals and other nutrients needed in shell formation are in short supply (see also Rickard and Fitzner 1985; Graveland 1996), either within ovipositing females (single eggs of a clutch), or the environment in general (complete clutches). This, how-

TABLE 3. Standard equations used to predict the average volume (cm^3) of 3,581 Pearly-eyed Thrasher eggs.

	Tatum[1/] (1975)	Hoyt[1/] (1979)	Ojanen et al.[1/] (1978)	Rahn and Paganelli[2/] (1989)	Paganelli et al.[2/] (1974)
Mean	8.62	8.40	7.69	6.69	6.56
Median	8.59	8.37	7.67	6.66	6.59
SD	0.75	0.73	0.67	0.63	0.49
95% CI	0.03	0.03	0.05	0.02	0.02
Minimum	6.10	5.95	5.45	4.28	3.52
Maximum	12.01	11.70	10.72	9.60	8.51

[1/] *Egg volumes derived from linear measures:* (a) Tatum (1975); (b) Hoyt (1979); (c) Ojanen et al. (1978).
[2/] *Egg volumes derived from linear, area, and mass measures:* (a) Rahn and Paganelli (1989); (b) Paganelli et al. (1974).

ever, was not investigated in the LEF thrasher population.

Albinistic eggs.—Albinistic eggs are unusual in passerines (Power 1966; Gross 1968; Fiedler 1974; Munro et al. 1981; Hayes 1985; Kattan 1993). The percentage of albinistic clutches observed in the current study (2%) is similar to the 2.9% (25 unpigmented eggs out of a sample of 837) observed in the Mountain Bluebird (*Sialia currucoides*) in Manitoba, Canada (Munro et al. 1981). For comparison, 2.4-7.5% of the nests of the Eastern Bluebird (*Sialia sialis*) in Central Minnesota contained unpigmented eggs (Fiedler 1974). Thus, the 2.4 percent of clutches comprised of unpigmented eggs as well as the 2.0 percent of albinistic eggs within each clutch observed in this study both fall within published ranges, albeit at the lower extremes.

Unlike the pale blue eggs observed throughout this study, which could be products of environmental stress, e.g., lack of calcium and other minerals in the shell, the production of unpigmented eggs in this population is most plausibly attributed to genetic factors (Sadjadi et al. 1983; Collias 1993; Kim et al. 1995). The most convincing evidence that the production of albinistic eggs by Pearly-eyed Thrashers is congenital rather than environmentally induced is that two of the five females were mother and daughter. Moreover, these females laid albinistic clutches invariably. This pattern is in agreement with Hayes (1985); in his study of the Western Bluebird (*Sialia mexicana*), he documented one female that laid 16 albinistic eggs in three separate clutches. More recently, Collias (1993) presented data based on 815 eggs produced over a 14-yr period by 37 female Village Weavers (*Ploceus cucullatus*). She found color and extent of egg spotting within individual females were constant throughout life. The results from these two studies, as well as those from my study, are, however, contrary to those reported by Fiedler (1974). She noted the production of albinistic eggs in the Eastern Bluebird was not consistent within the same female. Nor were female offspring necessarily genetically predisposed to lay unpigmented eggs. Of seven female bluebirds that laid unpigmented eggs, only three did so consistently. One female that hatched from an unpigmented egg was observed incubating a clutch of five blue eggs two years later, an event not as yet observed in the present study.

Egg shapes and sizes.—Although there may be an optimal size and shape for avian eggs (Barta and Szekely 1997), avian egg size varies considerably. In this study of the Pearly-eyed Thrasher, egg size varied significantly within the laying sequence, within and among seasons and females, and especially throughout the females' reproductive lives (Arendt 1993). Empirical data as well as standard formulae demonstrated that egg breadth was less variable than length. The largest eggs were 2-3 three times larger than the smallest, which is uncommon among many species (Christians 2002). This trend, in which egg size and mass decrease with the laying sequence, is found in many non-passerines such as gulls (Preston and Preston 1953; Meathrel and Ryder 1987), but is opposite of that found in several other species of passerine birds, among which there is often a linear increase in egg size and mass with each additional egg laid (Rydén 1978; Weatherhead 1985; Briskie and Sealy 1990). Conversely, however, in many passerines, especially those with large clutch sizes, there is no apparent trend of either an increase or decrease in egg size and mass with laying sequence. Oftentimes, intermediate eggs are larger than either initial or final eggs of a clutch as a result of factors such as fluctuating food supplies, ambient temperatures, and differences between precocial and altricial species (Ojanen et al. 1981; Slagsvold et al. 1984; Järvinen and Ylimaunu 1986; Greig-Smith et al. 1988). Slagsvold et al. (1984) proposed that birds adopting the "brood reduction strategy" have a small final egg (e.g., the Pearly-eyed Thrasher), whereas those adopting the "brood survival strategy" have a relatively large final egg (e.g., Cichon 1997).

As in all birds, the variability among Pearly-eyed Thrasher eggs was caused by endogenous factors (Williams 1996 Christians 2002; Ricklefs and Wikelski 2002; Styrski et al. 2002) and exogenous factors (Ojanen et al. 1981; Horak et al. 1995;

Graveland 1996; Hipfner et al. 2001a), of which some are not mutually exclusive (Järvinen and Ylimaunu 1986: Moore et al. 2000). Whereas the general trend for decreasing egg size in the laying sequence and egg variation in general throughout a female's reproductive life is mostly endogenous, stemming from physiological and physical properties of the female, several exogenous factors, e.g., food supply and weather conditions, alter egg size on a spatiotemporal scale. In comparative studies, several authors have shown egg size varies in the same females within and among clutches and seasons (Ojanen 1979; Nilsson and Svensson 1993; Horak et al. 1995; Flint et al. 2001; Johnson et al. 2001; Pinowski et al. 2001; Christians 2002), especially throughout a female's reproductive life (Coulson et al. 1969; Nolan and Blank 1980; Collias 1984; Redmond 1986; Jager et al. 2000). Egg breadth is also known to be constrained by the width of the female oviduct (Järvinen and Väisänen 1983; Hendricks 1991; Encabo et al. 2002). Older females tend to lay longer and broader eggs than do younger breeders (Preston 1958; Birkhead and Goodburn 1989; Arendt 1993) as the oviducts of older females lose elasticity as part of the ageing process (Kendeigh 1975; Potti 1993).

Empirical longitudinal and mass measures compared to standard formulae.—Egg dimensions are important for estimating several size, strength, and volumetric measures used in various physiological and ecological studies of avian eggs. However, if longitudinal measures are lacking, researchers must rely on published formulae to estimate them. Rahn and Paganelli's (1988) formula, which uses egg mass, accurately predicted the length and breadth of Pearly-eyed Thrasher eggs. Therefore, field biologists can confidently use their formula to estimate longitudinal measures (length and breadth) of the eggs of Pearly-eyed Thrashers, as well as other passerine species, based solely on fresh egg mass. Conversely, having instead only longitudinal data, field biologists can use with assurance any of the longitudinal formulae discussed above to accurately determine fresh egg mass for the thrasher and other passerines.

Egg and clutch mass in relation to adult body mass.—Using allometric relationships, Rahn et al. (1975) derived a general formula based on an inverse function of egg mass as a percentage of body mass for more than 800 species of birds in 16 Orders and more than 40 Families. Application of Rahn et al.'s formula revealed that *Margarops'* clutch mass was lighter in relation to its body size than was predicted for a typical 100-g bird. Current standard allometric formulae similar to that of Rahn et al. (1975) stem from research conducted more than 80 years ago. After analyzing Heinroth's (1922) egg mass data from 432 species of birds, Huxley (1929) was one of the first to recognize the inverse correlation between egg mass and body size—see also Saunders et al. 1984 (birds of prey) and Järvinen and Pryl 1989 (passerines).

A consequence of light egg and clutch mass is a short incubation period (Lack 1968; Grant 1982) which, in turn, increases the potential of laying more clutches each season. This is one of several preadaptations that increases the thrasher's potential of laying more clutches throughout its reproductive life, thus enhancing its lifetime reproductive success and ensuring its continual survival (Arendt 2004).

Egg volume.—Why is it important for field ornithologists to report egg volumes? The best single measure of an egg's size is its volume (Preston 1974). Egg volume is also often used as a predictor of hatchling weight (Nolan and Thompson 1978). Historically, volume was also used as an accurate measure of egg quality (Paganelli et al. 1974; Tatum 1975; Hoyt 1979; Smart 1991; Williams 1994; Flint and Grand 1999; Pelayo and Clark 2002). However, Ricklefs (1984) cautioned using egg size or mass as a measure of egg quality since actual composition, e.g., the amount and quality of yolk, is usually independent of linear or volumetric measures. More recently, Badzinski et al. (2002) suggested that variation in metabolic rates of embryos also limits the utility of egg size as an accurate predictor of nutrient constituents. Therefore, volume may be used best by field ornithologists solely as a measure of an egg's size.

Care also must be taken when using volume formulae based on longitudinal measurements. Kern and Cowie (1996) reported Hoyt's equation (based on longitudinal measures) tended to significantly overestimate egg volume by *ca*. 2% in the Pied Flycatcher (*Ficedula hypoleuca*), a medium-sized passerine. Thus, as anticipated, values from the three equations based solely on longitudinal measures were invariably greater than those based on fresh egg mass or longitudinal, area, and mass measures in estimating the volume of *Margarops*' eggs. Consequently, the use of mass-based formulae is encouraged.

Summary and conclusions.—Several measurements using empirical data and published formulae were used to describe the eggs of the Pearly-eyed Thrasher. These measures and formulae are intended for use not only by those interested in the avian egg in general, but more importantly as a database to be used for comparative purposes by others working specifically with the Pearly-eyed Thrasher and other passerines, most of which also have prolate spheroid shaped eggs. Comparative studies are encouraged since it is well known that egg size varies geographically and even among closely related taxa (Dresser 1905-1910; Heinroth 1922; Romanoff and Romanoff 1949; Schönwetter 1960-1984; Murphy 1983), as well as among habitats (Báldi and Csörgő 1993; Horak et al. 1995), sometimes related to nest-site safety in different habitats (Hipfner et al. 2001b). I hope that others will broaden the scope of the current study by investigating and comparing the egg parameters discussed herein, as well as additional ones in their respective geographical areas, particularly among several subspecific thrasher populations along altitudinal and latitudinal gradients since egg size tends to increase along altitudinal (Koenig 1982; Hamann et al. 1989) and, to a lesser extent, latitudinal gradients (Svensson 1978; Olsen and Marples 1993; Chylarecki et al. 1997).

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APPENDIX. Descriptive statistics for the longitudinal dimensions, volumes, and masses of 3,867* eggs laid by 182 female Pearly-eyed Thrashers between January 1979 and July 2000 in the Luquillo Experimental Forest, Puerto Rico. Linear measurements are in millimeters, volumes are in cubic centimeters, and masses are in grams.

Parameters	Average	SE	Median	Mode	95% CI	Minimum	Maximum
Eggs combined (n = 3,867)							
Length	32.43	1.76	32.37	32.90	4.87	18.13	38.97
Breadth	22.52	2.15	22.53	22.60	5.97	16.81	25.08
Volume**	6.69	0.01	6.66	6.62	0.02	4.28	9.6
Lay mass	8.8	1.1	8.8	9.0	3.1	4.3	11.8
Hatch mass	7.6	1.2	7.6	7.6	3.3	3.1	10.5
Egg 1 (n = 1,386)							
Length	33.01	1.66	32.98	33.40	4.61	18.13	38.97
Breadth	22.66	1.09	22.68	22.90	3.04	20.28	25.08
Volume	6.92	0.02	6.88	6.81	0.04	4.28	9.60
Lay mass	9.0	1.1	8.9	8.9	3.1	4.3	11.8
Hatch mass	7.8	1.0	7.8	8.0	2.9	4.0	10.5
Egg 2 (n = 1,252)							
Length	32.51	1.49	32.45	32.30	4.14	27.97	37.38
Breadth	22.65	2.11	22.64	22.50	5.86	20.27	24.68
Volume	6.76	0.02	6.73	6.62	0.03	4.83	8.96
Lay mass	8.9	0.7	8.9	8.8	2.0	6.7	11.2
Hatch mass	7.7	0.7	7.7	7.4	2.0	5.4	9.9
Egg 3 (n = 1,102)							
Length	31.82	1.27	31.80	32.20	3.54	28.78	36.73
Breadth	22.27	0.73	22.26	22.00	2.04	16.87	24.50
Volume	6.40	0.02	6.40	6.08	0.03	4.83	7.97
Lay mass	8.5	0.7	8.4	8.5	1.8	6.2	10.4
Hatch mass	7.3	1.0	7.3	7.0	2.8	3.1	9.2
Egg 4 (n = 127)							
Length	31.11	1.27	30.78	29.68	3.53	28.12	35.72
Breadth	22.03	0.52	22.05	22.00	1.44	20.24	23.50
Volume	6.09	0.05	6.06	6.79	0.10	4.91	7.70
Lay mass	8.0	0.4	8.0	8.2	1.1	6.7	9.3
Hatch mass	6.9	0.4	6.9	6.9	1.1	5.8	8.2
Unpigmented eggs combined (n = 90)							
Length	32.38	0.11	32.32	32.38	0.22	28.50	36.52
Breadth	22.32	0.06	22.29	22.30	0.13	20.42	24.24
Volume	6.57	0.05	6.52	6.64	0.10	5.11	7.96

APPENDIX. Continued.

Parameters	Average	SE	Median	Mode	95% CI	Minimum	Maximum
Lay mass	8.6	0.1	8.5	8.4	0.1	7.1	10.2
Hatch mass	7.5	0.1	7.5	7.6	0.1	6.2	8.8
Unpigmented egg 1 (n = 31)							
Length	33.06	0.21	33.18	32.38	0.43	30.36	36.52
Breadth	22.44	0.12	22.30	22.30	0.25	21.21	24.24
Volume	6.81	0.10	6.81	6.73	0.20	5.59	7.96
Lay mass	8.8	0.1	7.6	8.3	0.2	7.4	10.2
Hatch mass	7.7	01	8.4	8.2	02	6.3	8.8
Unpigmented egg 2 (n = 30)							
Length	32.44	0.11	32.31	31.62	0.23	31.25	33.60
Breadth	22.44	0.11	22.37	22.30	0.22	21.28	23.84
Volume	6.62	0.07	6.58	6.52	0.15	5.77	7.43
Lay mass	8.6	0.1	7.7	7.9	0.2	7.8	9.8
Hatch mass	7.67	0.1	8.27	7.8	0.2	6.3	8.7
Unpigmented egg 3 (n = 28)							
Length	31.56	0.20	31.52	31.51	0.40	28.50	33.18
Breadth	22.12	0.10	22.08	22.04	0.22	20.42	23.30
Volume	6.28	0.07	6.31	6.31	0.15	5.11	6.93
Lay mass	8.3	0.0	7.4	7.6	0.1	7.2	9.0
Hatch mass	7.3	0.1	8.0	7.5	0.2	6.3	8.0
Unpigmented egg 4 (n = 1)							
Length	31.28						
Breadth	22.26						
Volume	6.22						
Lay mass	8.3						
Hatch mass	7.3						

*Sample size for linear measurements of pigmented eggs is 3,867; for lay and hatch egg masses, the sample size of pigmented eggs was reduced to 3,156 following the elimination of egg categories that could affect egg mass, e.g., addling, embryo deaths, abandoned eggs, etc.

**Volumes were derived using Rahn and Paganelli's (1989) formula (see Table 2).