Caribbean Journal of Science, Vol. 41, No. 2, 283-295, 2005

Shell Properties, Water Vapor Loss, and Hatching Success of Eggs from a Rain Forest Population of the Pearly-eyed Thrasher (*Margarops fuscatus*)

WAYNE J. ARENDT

USDA Forest Service, International Institute of Tropical Forestry, Sabana Research Station, HC 2 Box 6205, Luquillo, PR 00773, warendt@fs.fed.us

ABSTRACT.—I calculated various shell properties, water vapor loss, and hatching success of eggs of the Pearly-eyed Thrasher (*Margarops fuscatus*) using measurements obtained during a long-term study in the Luquillo Mountains, Puerto Rico. Empirical results were comparable to standard reference formulae, demonstrating that published formulae can be used with confidence by field biologists studying this and other passerine birds laying prolate spheroid shaped eggs. Shell mass averaged 0.66 g and shell thickness averaged 0.12 mm. Egg surface area averaged 19.31 cm^2 (range =18.4-20.34 cm^2) as derived from published allometric relationships. Observed and derived eggshell densities were 2.06 g/cm^3 and 2.05 g/cm^3, respectively. Average egg density was 1.32 g/cm^3. Water vapor flux resulted in an average egg-mass loss of 0.087 g each day, culminating in a 1.22-g reduction over the entire 14-d incubation period. Based on a fresh egg mass of 8.02 g, 3,009 fertile eggs lost 15.2% of their initial mass. Whereas the total loss of egg mass (in grams) was about the same for all eggs in the laying sequence, smaller (3^{rd}—and 4^{th}-laid) eggs lost a higher percentage of total mass than did the larger ones (1^{st}—and 2^{nd}-laid). There were inter-breeding season differences in mass (= water) loss. The rate of daily water loss increased significantly as the incubation period progressed. The pattern of increase was intermediate between that of small passerines and typical non-passerine species. Hatching success declined throughout the study due to environmental and biological factors.

KEYWORDS.—Allometry, density, incubation, mass, Puerto Rico, volume, water balance, water vapor.

INTRODUCTION

Hatchability of avian eggs fluctuates markedly among and within orders, families, species, populations, and even within individual clutches (Müeller and Scott 1940; Sotherland et al. 1979; Erikstad et al. 1998; Royle and Hamer 1998). Numerous factors may act together to lower hatchability. Key biological and environmental factors include infections caused by microorganisms (Cook et al. 2003, 2005), temperature (Arnold et al. 1987; Stoleson and Beissinger 1999; Conway and Martin 2000a,b; Beissinger et al. in press), and toxic effects caused by environmental contaminants such as selenium, mercury, and PCBs (McCarty and Secord 2000; Henny et al. 2002; Spallholz and Hoffman 2002). Also important are intrinsic factors including several external and internal parameters of the egg itself, which in turn respond to numerous genetic and environmental controls on a spatiotemporal scale. For example, shell thickness and mass per unit surface area are useful indicators of shell strength (Voisey and Hunt 1974; Hamilton 1978). Shell strength and structure play a major role in egg viability throughout incubation and, ultimately, hatchability (Richards et al. 2000). Egg and shell thickness, mass, and density are greatly influenced by genetic components (e.g., porosity—which is also partly environmentally controlled) and the health of the gravid female (Rahn et al. 1979; Whittow 1997). Moreover, with exceptions (e.g., Taliaferro et al. 2001), eggshell thickness and mass, as well as whole egg mass and density, are all highly correlated with the availability of egg-forming chemicals, nutrients, and minerals such as

ms. received September 22, 2004; accepted April 14, 2005

calcium found naturally in the soil or dispensed during experimental studies of captive birds (Simkiss 1975; Graveland 1996; Navarro et al. 2001; Reynolds 2001). Naturally acidic soils, and those made highly acidic as a consequence of heavy deposits of acid rain, often are calcium-poor; and calcium poor soils are known to affect egg-formation and reproductive success of resident bird populations (Tilgar et al. 1999).

In this study, several egg parameters (shell thickness, mass, and density, as well as whole egg surface area, mass, density, and water vapor conductance) were calculated by subjecting numerous field measurements of Pearly-eyed Thrasher (*Margarops fuscatus*) eggs to published reference formulae. Although several egg-related parameters were measured; two, namely water vapor flux and whole egg density (derived from a combination of egg mass, egg length, shell surface area, and shell mass), were prime measures sought because both reflect the effects of intrinsic (genetic and physiological) and extrinsic (environmental and ecological) variation. My main objective was to fill an information gap by creating a representative database for an insular, montane population of a tropical passerine mimid. A second objective was to investigate the possible relationship between the observed and predicted egg densities and poor hatching success in this population. The third and final objective was to compare and select published allometric relationships that can be used more widely by field biologists to investigate the egg-related factors influencing reproductive success in other mimids and passerine birds in general.

Materials and Methods

Study Area

I conducted the study at elevations between 600 and 900 m within the 11,330-ha Caribbean National Forest (also known as the Luquillo Experimental Forest, LEF) in the Sierra de Luquillo Mountains in northeastern 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 over 500 cm and 18.5°C on peaks higher than a 1,000 m (García-Martinó et al. 1996). The forest is comprised of four major vegetation associations that are altitudinally stratified and placed into separate life zones (see Wadsworth 1951; and Ewel and Whitmore 1973, for a complete description).

Egg monitoring was part of a broader, long-term life-history study of the Pearly-eyed Thrasher (Arendt 1993). Between January 1979 and July 2000, 3,867 eggs were measured and weighed shortly after laying using dial and digital calipers accurate to 0.02 and 0.01 mm, respectively, and 10-g and 50-g spring scales with increments of 0.2 and 0.5 g, respectively, to record fresh egg mass and water loss every 24-48 hours (details in Arendt 1993). To compare with the field measurements, 27 eggs were weighed using an electronic balance. The 27 eggs were then emptied of their contents and the remaining shells were dried in a silica-lined beaker and weighed on the same balance. Measurements on the 27 sampled eggs also included fresh egg mass and daily water loss throughout the 14-day incubation period prior to the laboratory measurements.

Shell mass, thickness, density, and surface area

Observed longitudinal and egg-mass data from a set of 3,581 fertile Pearly-eyed Thrasher eggs that hatched normally were included in several standard formulae to calculate four egg properties: shell mass, shell thickness, density, and surface area (Table 1). Digital calipers were used to measure shell thickness of each of the 27 eggs subjected to more rigorous laboratory measurements. The five surface-area formulae were then compared (Table 2). Entries in Table 2 under the last column (Gonzáles et al. 1982) are the averages obtained by entering the volumes of each egg calculated by the four volume formulae into the Gonzáles et al. (1982) formula.

Egg density

Density was calculated by substituting the observed initial egg mass, egg length,

TABLE 1. Standard reference formulae used in calculating shell mass, thickness, density, and surface area of 3,581 eggs of the Pearly-eyed Thrasher.

	Egg shell			
Source	Mass[1/]	Thickness	Density[2/]	Surface area[3/]
Rahn & Paganelli (1989a,b)	$0.0547 \cdot M^{0.102}$	$0.055 \cdot M^{0.358}$	$(SM/ST \cdot SA)$	
Müeller and Scott (1940)				$4.670 \cdot M^{0.666}$
Carter (1975) (a) in Table 2				$0.911 \cdot L^{0.289} \cdot B^{0.316} \cdot M^{0.488}$
Carter (1975) (b) in Table 2				$3.978 \cdot M^{0.705}$
Gonzáles et al. (1982)				$4.689 \cdot V^{0.673}$
Rahn & Paganelli (1989b)				$4.835 \cdot M^{0.662}$

[1/]M = fresh egg mass.
[2/]SM = shell mass; ST = shell thickness; and SA = shell surface area.
[3/]L = egg length, and B = egg breadth; V = volume, which was calculated using standard reference formulae (Arendt 2004).

TABLE 2. Comparison of five surface-area formulae using longitudinal measures and fresh-egg masses from 3,581 eggs of the Pearly-eyed Thrasher. Tabular entries are in square centimeters.

	Carter (a) (1975)	Carter (b) (1975)	Müeller & Scott 1940	Rahn & Paganelli (1989b)	Gonzáles et al. 1982
Mean	19.23	18.4	19.85	20.34	18.73
SD	1.13	1.11	1.14	1.16	1.11
Minimum	13.70	11.13	12.35	12.70	12.47
Maximum	23.82	22.70	24.21	24.77	24.97

shell surface area, and shell mass of 3,581 eggs of the Pearly-eyed Thrasher into two standard equations (Paganelli et al. 1974; and Rahn and Paganelli 1989a). Egg density was also measured by dividing initial egg mass by egg volume (Rahn and Paganelli 1989a).

Water vapor flux

Water vapor flux (W_{H20}), which is equivalent to daily egg-mass loss, was obtained from 18,121 multiple weighings of 3,009 fertile eggs between 1979 and 1999. Total reduction in egg mass was obtained by subtracting the last measurement (taken on day 14) from the initial (fresh) egg mass on day 0 (< 24 h following laying). Then, to test the accuracy of a widely used standard formula in calculating water vapor loss in the Pearly-eyed Thrasher, I substituted observed fresh egg masses from 3,009 fertile eggs into Ar and Rahn's (1980) published formula: $W_{H20} = 130.4 * M^{0.977} / I^{0.937}$), where M is fresh egg mass and "I" is the length (in days) of the incubation period; "I" is 14 days for *M. fuscatus* when the day of oviposition is designated "0" and 15 days when the day of deposition is designated as "1." Dead (deceased embryos) or infertile eggs were not included in the analyses.

Hatching Success

The fate of each of the 3,867 eggs laid between 1979 and 2000 was recorded by assigning a numerical code to each outcome. There were 27 fate categories—see Arendt (1993) for a list of specific fates. In analyses of hatching success, I excluded all eggs lost by causes other than hatching failure (e.g., predation, egg damage, and female desertion).

Statistical analyses

SigmaStat® Version 3 (Fox et al. 2003) was used. During exploratory analyses, all variables used in the statistical analyses were checked for normality (Kolmogorov-Smirnov test with Lilliefors' Correction) and/or equal variance (Levene Median Test). First Order Linear Regression was used to investigate the apparent decline in egg hatching success with each subsequent breeding season. Because the assumptions of normality and equal variance were violated in all remaining statistical analyses, nonparametric Kruskal-Wallis One-Way ANOVA on Ranks was used to compare published surface-area formulae, as well as water vapor loss among years. Spearman Rank Order Correlation was used to evaluate the potential relationship between the number of eggs laid and percentage hatched. Dunn's Method was used in post-hoc inter-year comparisons testing because of unequal sample sizes. Spearman Rank Order Correlation was used to test the relationship between total egg-mass loss, precipitation, and ambient temperature. Precipitation and ambient temperature data constitute 7-mo averages (Jan.-July) recorded at three weather stations from within the LEF at elevations above (Pico del Este) and below the study area, and from both the eastern (Bisley) and western (El Verde) sectors of the forest. A 95% level of confidence ($\alpha = 0.05$) was maintained in all of the analyses.

RESULTS

Shell mass, thickness, density, and surface area

Four eggshell parameters were calculated to obtain a representative estimate of the Pearly-eyed Thrasher's average whole egg density, which is the product of shell mass/shell thickness*shell surface area. Shell mass of 27 eggs weighed on an electronic balance averaged 0.66 g (SD = 0.35, range = 0.43-1.70 g). This observed shell mass (0.66 g) was comparable to both mean and median estimates of shell mass (0.51 g; SD = 0.04, range = 0.24-0.68) derived from a standard reference formula (Rahn and Paganelli 1989a). Mean and median shell thicknesses were 0.12 mm (SD = 0.003, range = 0.09-0.13 mm) as derived from the observed egg mass and longitudinal data. After converting shell thickness to centimeters for use in the density equation, both mean and median eggshell density estimates were 2.06 g/cm^3 (SD = 0.01, range = 2.05-2.07 g/cm^3). Applying the fresh egg masses to the four surface-area formulae (see Methods), the eggs' surface area averaged about 19.3 cm^2 (Table 2).

Egg density

Mean and median egg densities resulting from two standard reference formulae were: 1.31 g/cm^3 (range = 1.22-1.39 g/cm^3) (Paganelli et al. 1974), and 1.34 g/cm^3 (range = 1.01-1.51 g/cm^3) (Rahn and Paganelli 1989a); standard errors were all < 0.001. Using Rahn and Paganelli's (1989a) formula, the density of egg contents was 0.85 g/cm^3.

Water vapor flux

Water vapor flux (W_{H20}) resulted in an observed average egg-mass (= water) loss of 0.087 g/day (SD = 0.056, range = 0.074-0.106). Daily water loss predicted by Ar and Rahn's equation also averaged 0.087 g (SD = 0.063, range = 0.061-0.109). Separating by lay order, total egg-mass loss (Fig. 1A) was not significantly different among

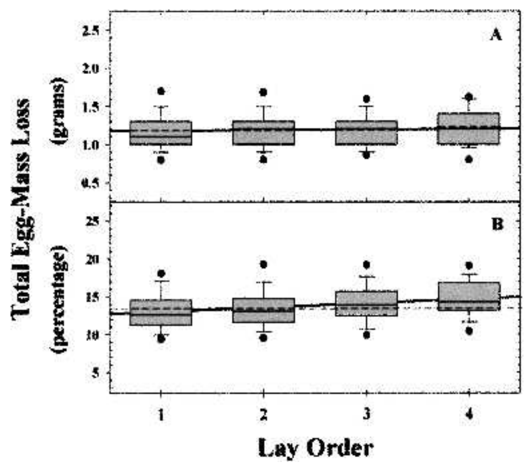

FIG. 1. Total egg-mass loss by lay order in 3,009 fertile eggs of the Pearly-eyed Thrasher inhabiting the Luquillo Experimental Forest, Puerto Rico (1979-1999). The boundary of each box closest to zero indicates the 25th percentile, solid lines within each box mark the median, and the boundary of the box farthest from zero specifies the 75th percentile. Whiskers above and below each box designate the 90th and 10th percentiles, respectively. Plot-wide dashed lines are overall means, whereas solid lines are regression lines.

the four eggs in the laying sequence (H = 0.66, P = 0.88). Average mass losses in 1st—4th-laid eggs were 1.17, 1.18, 1.24, and 1.28 g, respectively. Each of the eggs—in the Pearly-eyed Thrasher's (maximum) 4-egg clutch—lost an average of 1.22 g during incubation (Fig. 1A). The observed fractional water loss (F_{H20}) was 0.145 g (SD = 0.01; range = 0.107-0.171 g). Total water loss predicted by Ar and Rahn's equation was 1.32 g, and the fractional water loss (F_{H20}) was 0.151 g (SD = 0.003; range = 0.115-0.158 g).

There were significant differences (Fig. 1B) among the percentages of mass loss among the four eggs in the laying sequence (H = 38.56, P < 0.001). The smaller, 3rd– and 4th–laid eggs lost a higher percentage of total mass than did the larger, 1st– and 2nd–laid eggs (median percentages for 1st– to 4th –laid eggs were 14.5, 14.7, 15.7, and 16.8, respectively).

The rate of daily water vapor loss increased significantly at different stages of incubation (Fig. 2A). To eliminate possible clutch effects, e.g., variability among eggs, the pattern of daily water vapor loss in 1st –laid eggs only is shown Figure 2B. Egg-mass loss is half (0.03 vs. 0.06 mg*egg $^{-1}$*day $^{-1}$) in 1$^{st.}$-laid eggs (Fig. 2B) than that when all eggs in the laying sequence (range: 1-4) are combined (Fig. 2A).

Between 1979 and 1999, inter-year differences were noted in total egg-mass loss among fertile eggs, but were not closely related to either precipitation (Fig. 3A) or ambient temperature (Fig. 3B). There was no correlation between egg-mass loss and precipitation (r_s^2 = –0.10; P = 0.68), a somewhat marginal association between egg-mass loss and ambient temperature (r_s^2 = 0.45; P = 0.06), and no apparent relationship between precipitation and ambient temperature (r_s^2 = –0.08; P = 0.72). However, an ANOVA on Ranks resulted in 21 sigificantly different (H = 135.2; df = 17; P < 0.001) inter-year comparisons of total egg-mass loss, with three years (1990, 1991, and 1997) demonstrating the least amount of mass loss (≤1.10 g) during incubation.

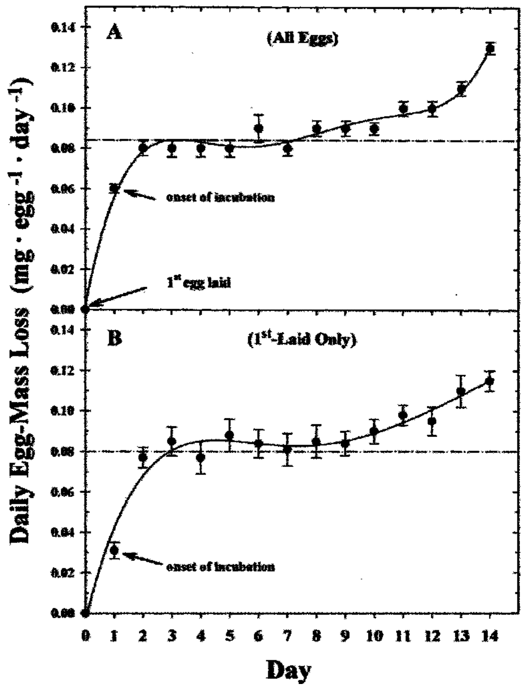

FIG. 2. Daily mass loss (± SE) in eggs of the Pearly-eyed Thrasher in the Luquillo Experimental Forest, Puerto Rico (1979-1999). All eggs were lumped for analysis in Graph A, whereas Graph B represents 1st-laid eggs only. On the x-axis, "0 percent" marks the day the egg was laid and thus was in the nest less than 24 hours.

Hatching success

A summary of egg hatching success during 18 breeding seasons between 1979 and 1999 is given in Table 3. The overall average hatch success was 71.2 percent, but seasonal hatching success varied greatly (min. = 47.7% in 1998; max. = 82.7% in 1981). There was a general decline in hatching success throughout the study (Fig. 4A). There was also a marginal association between the number of eggs laid and the percentage of eggs hatched (Fig. 4B).

DISCUSSION

Shell mass, thickness, and surface area

In studies treating physiological, nutrient, and energy based questions relating to birds' eggs, a measure of density is often valuable. Three separate egg densities are

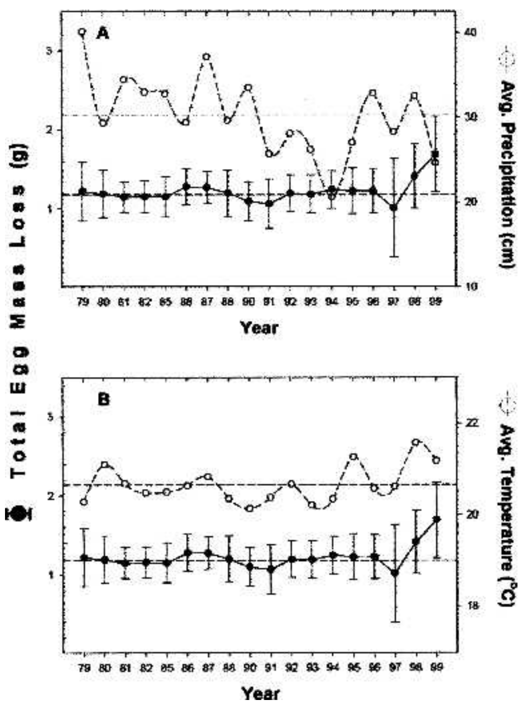

FIG. 3. Inter-seasonal comparisons of total egg-mass loss (± SD) throughout the 14-day incubation period and in relation to precipitation and ambient temperature.

usually calculated—total egg density (shell plus contents), shell density, and density of the egg's contents. Before density measures can be obtained, however, shell mass, thickness, and the egg's surface area must be determined. Empirical data from *Margarops'* eggs as well as published formulae were used to calculate these parameters. Both the mean and median estimates of shell mass (0.51 g) predicted by the published formulae were slightly, but not significantly ($T = 235$, $P = 0.28$), lower than the observed (0.66 g), thus substantiating their utility for use in species such as Pearly-eyed Thrasher and undoubtedly other passerines with similarly shaped eggs. From an ecological perspective, even though as with most forests, the LEF's soils are acidic, calcium levels are high as a result of elevated humidity and, consequently, lower rates of calcium carbonate accretions, which commonly occur in arid areas (McDowell and Asbury 1994; Zarin and Johnson 1995a,b; Cox et al. 2002), which could in part account for the elevated shell density in this thrasher population.

Gonzáles et al. (1982) maintained that, regardless of the different mathematical approaches used to determine surface area (see Carter 1975 and Hughes 1984 for examples), the reason there is such parity among the results is due to the practically linear relationship between surface area and egg volume.

After comparing all five surface-area formulae using *Margarops'* fresh egg masses and volume, I too found that, for the Pearly-eyed Thrasher, not only did they accurately estimate the surface area of the eggs, they also compared favorably with Carter's (1975) formula based on a combination of length, breadth, and mass measurements, consequently obviating the need to obtain longitudinal measures in calculating the surface area of eggs.

Egg density

Rahn and Paganelli (1989b) found an average eggshell density of 2.05 g/cm^3 for 3,931 passerine species included in Schönwetter's Tables (in Rahn and Paganelli 1989b). Thus, the eggshell density calculated for the sample of 3,581 eggs of the Pearly-eyed Thrasher (2.06 g/cm^3) was effectively the same as Rahn and Paganelli's standard value for more than three thousand passerine species. Knowing total egg and shell densities, one can calculate the density of an egg's contents. For several species, Rahn and Paganelli (1989a) found that the density of egg contents is virtually the same (1.03 g/cm^3). The density of Pearly-eyed Thrasher egg contents (0.85 g/cm^3) was within 0.18 g of the average for other species. Although seemingly nil, this additional (*ca*. 20%) reduction in egg-content density might very well be biologically significant by further contributing to the lower hatching success of this mid-elevation population (Cook et al. 2003, Cook et al. 2005).

In comparison to other avian taxa amongst which egg mass ranges from 300 mg in small hummingbirds to 9 kg in the recently extinct elephant bird of Madagascar (Diamond 1982), eggs of passerine birds

TABLE 3. History of hatching success of Pearly-eyed Thrasher eggs in the Luquillo Experimental Forest, Puerto Rico, during 18 breeding seasons between 1979 and 1999.

	Total number of					
YEAR	Breeding females	Available boxes	Nestings	Eggs laid	Eggs hatched	Percent hatched
1979	17	13	27	78	58	74.36
1980	29	26	68	203	154	75.86
1981	29	27	72	214	177	82.71
1982	44	37	103	304	245	80.59
1985	35	31	66	179	137	76.54
1986	29	28	63	186	139	74.73
1987	38	35	103	297	209	70.37
1988	35	35	85	241	182	75.52
1990	42	41	57	167	138	82.63
1991	44	41	134	367	284	77.38
1992	45	42	100	292	231	79.11
1993	45	41	115	352	284	80.68
1994	47	39	94	272	163	59.93
1995	37	37	96	267	154	57.68
1996	38	24	54	152	95	62.50
1997	32	29	53	146	104	71.23
1998	21	21	37	107	51	47.66
1999	8	17	8	23	12	52.17
Total:	—	—	1,335	3,847	2,817	—
Average:	34.17	31.33	74.17	213.72	156.50	71.20
Minimum:	8	13	8	23	12	47.66
Maximum:	47	42	134	367	284	82.71

vary relatively little (0.6-37 g) in total mass (Rahn et al. 1985). Consequently, a total egg density value (shell and contents) of 1.06 g/cm^3 has been calculated for passerines in general (Rahn and Paganelli 1989a). The Pearly-eyed Thrasher's average egg density of 1.32 g/cm^3 was somewhat higher than that of the average passerine. However, it falls within both minimum and maximum density values derived by Rahn and Paganelli for all passerines. It is counter intuitive that the Pearly-eyed Thrasher's average overall egg density would be higher than that of the average passerine's, especially when considering the additional 20% reduction in the density of egg contents derived for this population. However, this is easily explained owing to the fact that egg density (shell and contents) was calculated by substituting the observed initial egg mass, egg length, and shell surface area data into two standard equations (Paganelli et al. 1974; and Rahn and Paganelli 1989a), as well as the fact that egg density was also measured by dividing initial egg mass by egg volume (Rahn and Paganelli 1989a). Consequently, the Pearly-eyed Thrasher's average egg density is higher than that of the average passerine as a result of its larger egg size, and thus larger longitudinal and mass measurements.

Water vapor flux and conductance in avian eggs

Eggs begin losing mass immediately after laying (Hanna 1924; Rahn and Ar 1974; Booth and Rahn 1990) and lose about 15% (± 2.5%) over the entire incubation period (Manning 1981; Diamond 1982; Booth and Rahn 1990). Most egg-mass loss is due to the evaporation of water through pores in the eggshell up to the external pipping stage of incubation (Ar and Rahn 1980). Generally, however, in the eggs of small passerines, the rate of mass loss rapidly increases over the first half of incubation and

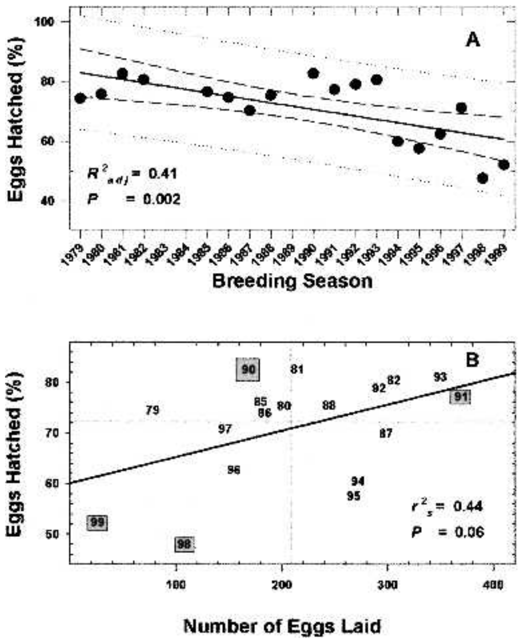

FIG. 4. Linear Regression of the percentage of eggs hatching during 18 breeding seasons between 1979 and 1999 (Graph A), and the correlation between the number of eggs laid and percentage hatched (Graph B). The points in Graph A represent the data-dependent variable (hatching success) plotted against the independent variable (breeding season). The solid line running through the points represents the regression line. The dashed lines represent 95% confidence intervals, and the dotted lines the prediction intervals. The double-numbered symbols in Graph B represent years. Years emphasized in the text have been encapsulated in boxes with gray shading.

remains relatively constant thereafter (Booth and Rahn 1990). There are also inter-year differences (see for example Manning 1981) that are most likely due, at least in part, to environmental and biological factors.

Water vapor flux in eggs of the Pearly-eyed Thrasher

The empirical data established that the average Pearly-eyed Thrasher egg loses about 0.087 g each day. Therefore, based on the average 14-day incubation period for the species, each egg should lose on average about 1.22 g of its initial mass as water. Thus, both the observed water loss, and that derived from Rahn et al.'s (1975) equation, confirmed that eggs of the Pearly-eyed Thrasher lose about 15% of their initial mass, as do several other species.

In comparative analyses, percent egg-mass loss is preferred to that of mass loss in grams due to spurious variation resulting simply from substantial differences in egg size. Though not investigated, two factors may have contributed to the higher percentage of mass loss in the smaller eggs; higher surface-to-volume ratios of the smaller eggs (conducive to greater rates of water loss) and the fact that most females have begun more constant incubation by the time the 3rd and 4th eggs are laid (Cook et al. 2005), thus affording higher temperatures throughout their development. In the field, there is often no noticeable loss in egg mass until the female begins more constant incubation, which is normally on the penultimate egg. Thus, at daily nest visits the first-laid egg of a 3-egg clutch often does not show a noticeable reduction in mass for the first 1-2 days, whereas 3rd—and 4th-laid eggs will begin losing mass the same day they are laid.

Within the first day of incubation, egg-mass loss is half in 1st-laid eggs than that when all eggs in the laying sequence are combined, which may be due to lower ambient and internal temperatures and higher moisture surrounding the generally unincubated 1st-laid eggs. When all eggs are combined, however, the inverse effect is observed, i.e., egg-mass loss doubles from deposition to day 1, possibly owing to higher internal and surface egg temperatures and lower surface moisture produced by females incubating—and 2-egg clutches as early as the day of deposition of the first egg. Consequently, an elevated increase in mass loss occurs as early as the first day after laying. It is noteworthy that it was once thought water vapor loss (W_{H20} = $mg \cdot d^{-1}$) remains constant throughout incubation (Groebbels and Möbert 1927; Drent 1973; Ar et al. 1974; Ar 1990). However, as in my research (with the occasional exception, e.g., Kern and Cowie 1995), several other studies have shown that there is an increase in the rate of water loss in many species through incubation, especially in passerines (Carey 1979; Hanka et al. 1979;

Kern 1986; Rahn and Paganelli 1990; Carey et al. 1994).

The patterns of daily mass loss in eggs of the Pearly-eyed Thrasher are similar to, and intermediate between, those of eggs typical of small passerines (rate of mass loss increases over the first half of incubation and then remains relatively constant) and those of non-passerines (rate of mass loss increases steadily, especially late in incubation). As in other passerines, for the first 8-9 days the rate of mass loss in *Margarops'* eggs increases rapidly and then levels off, whereas during the last 5-6 days of incubation, as observed in many non-passerines, there is a definite second increase in daily mass loss, even prior to the external pipping stage (days 12-14). Why should the Pearly-eyed Thrasher reflect patterns of egg-mass loss characteristic of both passerines and non-passerines? There are extrinsic factors (environmental, e.g., rainfall, temperature, and humidity) and intrinsic factors (physical, e.g., egg size and volume, and physiological properties such as embryo development and respiration) influencing such patterns and variation. Eggs of the Pearly-eyed Thrasher are intermediate in size between the small eggs of typical passerines reported in the literature and those of the customary non-passerine species often selected for analyses (e.g., Procellariiformes, Anseriformes, Charadriiformes, and Galliformes). Because moisture and temperature often play major roles in the rate of evaporation, the slow rate of egg-mass loss in 1st-laid eggs from deposition to day 1 in figure 2B is most likely due to lower ambient and internal temperatures and higher ambient and surface moisture because the female generally doesn't constantly incubate the first egg. In this rainforest population, first-laid eggs of 3-egg clutches are usually cold and moist to the touch until the laying of the second egg. Conversely, the rapid increase in egg-mass loss from oviposition (day 0) to day 1, when all eggs from clutches ranging from 1-4 are combined (Fig. 2A), is more likely a consequence of rapid moisture loss from incubated eggs with higher surface and internal temperatures produced by incubating females. From days 2-9 the increased constancy of incubation results in minimal variation in temperatures surrounding the eggs and consequently a more stable rate of water loss. From days 10-14 the embryo is well along in development and its increased metabolism raises the internal temperature of the egg (Cook et al. 2003), which results in an increase in water vapor conductance and evaporation (Badzinski et al. 2002). Water vapor conductance is also elevated when developed embryos begin to absorb calcium from the eggshell (Romanoff 1967) which, along with the piercing of the air sac and external pipping, may also contribute to the increase in egg-mass loss during the last days of the Pearly-eyed Thrasher's egg stage.

Fluctuations in ambient temperature (Hussell 1985; Veiga 1992; Stoleson and Beissinger 1999, Conway and Martin 2000a,b), rainfall and, thus, humidity (Wilson 1991; Fasenko et al. 1992; Walsberg and Schmidt 1992) are thought to be responsible, at least in part, for the observed and often significant differences in water loss among eggs laid in different years. Environmental factors may greatly influence water loss, and thus become primary causes of inter-seasonal differences, mainly because Pearly-eyed Thrasher females are 'lazy' incubators (Cook et al. 2005). Unlike most passerines, which incubate on average about 80% of daylight hours, Pearly-eyed Thrasher females incubate only about 50% of time during daylight hours, thus exposing eggs to the environment for prolonged periods. Even so, preliminary analyses correlating total egg-mass loss, precipitation, and ambient temperatures are less than conclusive. Although there was a slight direct relationship (P = 0.06) between total egg-mass loss and ambient temperature, of which the latter was well within the range (9° and 26°C) shown by Conway and Martin (2000b) to be optimal for detecting such a correlation, only two ('90 and '91) of the three years responsible for the significant inter-year differences in egg-mass loss were at the lower end of the ambient temperature scale. The 1997 breeding season's average ambient temperature was the same as the overall average 7-mo ambient temperature for the 18 breeding seasons. The potential relationship between egg-mass loss and precipitation was even less obvious. Relative to other years, the 1990 breeding season was wet and cool, the 1991 season was dry and cool, whereas the 1997 season was very close to the precipitation mean for the 18 breeding seasons. The only common denominator among the three years is that of sharing the three lowest total egg-mass losses (≤1.10 g) over the entire 18 breeding-season period.

Hatching success

There was a gradual decline in hatching success throughout this study, a chief cause of which is believed to be a series of major cyclonic events beginning with Hurricane Hugo in 1989, followed by several lesser hurricanes during the 1990s, and culminating with a second major storm, Hurricane Georges, in 1998. The Pearly-eyed Thrasher rebounded well immediately following Hurricane Hugo, producing this study's second highest percentage of eggs hatched during the first (1990) breeding season following the storm. The thrasher then nested for 11 consecutive months and produced the most eggs (n = 367) during a single breeding season (Table 3, Fig. 4B). However, following a volley of major cyclonic events (major wind storms and lesser hurricanes) during the mid-90s, and subsequent food shortages in the forest during the 1990s (Arendt 1993; Wunderle 1999; Thompson-Baranello 2000; Arendt 2004), hatching success dropped off after 1993, especially just prior to, and following, Hurricane Georges. Except for the 1987 breeding season, the percentages of eggs hatched per eggs laid for the remainder of the breeding seasons during the 1980s remained clustered around the average for all 18 seasons (Fig. 4A), whereas, with the exception of the first three years following Hurricane Hugo, hatching success during the 1990s fell below the 18-season average (Fig. 4B). In short, between 1979 and 1993, the average seasonal hatching success rate was 78%, but dropped to only 59% between 1994 and 1999. It is quite plausible that the effects of the two, almost back-to-back, hurricanes resulted in the further depletion of minerals and other nutrients so vital to egg formation and hatching success from already acidic forest soils (Cox et al. 2002).

In addition to environmental factors, biological agents such as pathogenic microorganisms affect hatching success in the Pearly-eyed Thrasher. In a series of experimental studies, Cook et al. (2003, 2005) found that this mid-elevation population experiences a lower hatching success than populations at either lower or higher elevations because microbial infection is greater in eggs exposed to cool, humid conditions than at either colder and more humid, or warmer and drier conditions. In addition to high humidity, very low or high ambient temperatures cause a dramatic reduction in egg viability in this species. Unquestionably, these biological factors, when combined with the detrimental effects of poor soils on egg formation, will lower hatching success even more.

Summary and conclusions

Empirical data were gathered and subjected to published standard reference equations to create a representative database for several egg parameters of the Pearly-eyed Thrasher, a tropical insular mimid. Water vapor loss was governed by a combination of environmental factors shortly after egg deposition, embryo respiration and metabolism later in the incubation stage, and female behavior throughout the egg stage. Egg hatching success is low in this mid-elevation population due to a combination of environmental and biological factors. Information gained from this study can be used as comparative data by others studying the species on additional islands and in diverse habitats. It is hoped that the almost universal applicability of several published egg-parameter relationships exemplified in this study will encourage their wider recognition and use by regional ornithologists.

Acknowledgments.—For taking time out of his busy schedule during a brief visit to the Puerto Rican Parrot captive breeding facility, I thank Dr. George Bartholomew of the University of California at Los Angeles for versing me in the correct method of weighing birds' eggs using an electronic balance and drying the eggshells in silica gel-lined beakers for further analyses. For field assistance, I thank Giovanni Cabán Ruíz (1984); Carlos Ruíz and parrot project volunteers (1987); Oscar Díaz and Carlos Cianchini (1988). From 1990 to 1997, most egg data were collected by Roberto Díaz, and from 1997 to 2000 by Morris Ford, to both of whom I express my sincerest gratitude. Manuscript reviews by Mark I. Cook, Joseph M. Wunderle, Jr., and two anonymous reviewers enhanced earlier drafts. Since the study's inception, financial and logistical support have been provided by the USDA Forest Service and the International Institute of Tropical Forestry. This research was done in cooperation with the University of Puerto Rico.

LITERATURE CITED

Ar, A. 1990. Roles of water in avian eggs. In *Egg incubation: its effects on embryonic development in birds and reptiles*, eds. D. C. Deeming and M. W. J. Ferguson, 229-243. United Kingdom: Cambridge University Press.

Ar, A., and H. Rahn. 1980. Water in the avian egg: overall budget of incubation. *Am. Zool*. 20:373-384.

Ar, A., C. V. Paganelli, R. B. Reeves, D. G. Greene, and H. Rahn. 1974. The avian egg: water vapor conductance, shell thickness and functional pore area. *Condor* 76:153-158.

Arendt, W. J. 1993. *The Pearly-eyed Thrasher: Distribution, Ecology and Life-History Strategy of an Avian Supertramp*. Ph.D. dissertation. Madison: University of Wisconsin.

Arendt, W. J. 2004. A Quarter Century of Variation in Color and Allometric Characteristics of Eggs from a Rain Forest Population of the Pearly-eyed Thrasher (*Margarops fuscatus*). *Caribb. J. Sci*. 40:204-217.

Arnold, T. W., F. C. Roher, and T. Armstrong. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *Am. Nat*. 130:643-653.

Badzinski, S., C. D. Ankney, J. O. Leafloor, and K. F. Abraham. 2002. Egg size as a predictor of nutrient composition of eggs and neonates of Canada Geese (*Branta Canadensis interior*) and Lesser Snow Geese (*Chen caerulescens caerulescens*). *Can. J. Zool.* 80:333-341.

Beissinger, S. R., M. I. Cook, and W.J. Arendt. (in press). The "shelf life" of bird eggs: experimental analysis of egg viability using a tropical climate gradient.

Booth, D. T., and H. Rahn. 1990. Factors modifying rate of water loss from birds' eggs during incubation. *Physiol. Zool*. 63:697-709.

Carey, C. 1979. Increase in conductance to water vapor during incubation in eggs of two avian species. *J. Exp. Zool*. 209:181-186.

Carey C., O. Dunin-Borkowski, F. León-Velarde, D. Espinoza, and C. Monge. 1994. Gas exchange and blood gases of Puna Teal (*Anas versicolor puna*). *J. Comp. Physiol*. 163:649-656.

Carter, T. C. 1975. The hen's egg: estimation of shell superficial area and egg volume, using measurements of fresh egg weight and shell length and breadth alone or in combination. *Br. Poult. Sci.* 16: 541-543.

Conway, C. J., and T. E. Martin. 2000a. Evolution of passerine incubation behavior: influences of food, temperature, and nest predation. Evolution 54:670-685.

Conway, C. J., and T. E. Martin. 2000b. Effects of ambient temperature on avian incubation behavior. Behav. Ecol. 11:178-188.

Cook, M. I., S. R. Beissinger, G. A. Toranzos, R. A. Rodríguez, and W. J. Arendt. 2003. Trans-shell infection by pathogenic micro-organisms reduces the shelf life of non-incubated birds' eggs: a constraint on the onset of incubation? *Proc. R. Soc. Lond. Ser. B: Biol. Sci*. 270:2233-2240.

Cook, M. I., S. R. Beissinger, G. A. Toranzos, R. A. Rodríguez, and W. J. Arendt. 2005. Microbial infection affects egg viability and incubation behavior in a tropical passerine. Behavioral Ecology 16: 30-36.

Cox, S. B., M. R. Willig, and F. N. Scatena. 2002. Variation in nutrient characteristics of surface soils from the Luquillo Experimental Forest of Puerto Rico-A multivariate perspective. *Plant and Soil* 247:189-198.

Diamond, J. M. 1982. How eggs breathe while avoiding desiccation and drowning. *Nature* 295:10-11.

Drent, R. H. 1973. The Natural History of Incubation. In *The Breeding Biology of Birds*, ed. D. S. Farner, 262-311. Washington, DC: National Academy of Sciences.

Erikstad, K. E., T. Tveraa, and J. O. Bustnes. 1998. Significance of intra-clutch egg size variation in Common Eider. *J. Avian Biol*. 29:3-9.

Ewel, J. J., and J. L. Whitmore. 1973. *The Ecological Life Zones of Puerto Rico and the U.S. Virgin Islands*. USDA-For. Serv. Res. Pap. ITF-18, Río Piedras, Puerto Rico: Institute of Tropical Forestry.

Fasenko, G. M., R. T. Hardin, F. E. Robinson and J. L. Wilson. 1992. Relationship of hen age and egg sequence position with fertility, hatchability, viability and preincubation embryonic development in broiler breeders. *Poult. Sci.* 71:1374-1383.

Fox, E., K. Shotton, and C. Ulrich. 2003. *SigmaStat User's Manual*. Chicago, Illinois: SPSS, Inc.

García-Martinó, A. R., G. S. Warner, F. N. Scatena, and D. L. Civco. 1996. Rainfall, runoff, and elevation relationships in the Luquillo Mountains of Puerto Rico. *Caribb. J. Sci*. 32:413-424.

Gonzáles, M., P. Roca, F. Sáinz, and M. Alemany. 1982. A comparison between egg surface areas and volume of several avian species. *Comp. Biochem. Physiol*. 73A:301-302.

Graveland, J. 1996. Avian eggshell formation in calcium-rich and calcium-poor habitats: importance of snail shells and anthropogenic calcium sources. *Can. J. Zool*. 74:1035-1044.

Groebbels, F., and F. Möbert. 1927. Oölogische Studien 2. Ueber die künstliiche bestimmung der brutdauer einiger vogelarten mit besonderer berücksichtigung des eigewichts. *Verhandl. Ornithol. Gesells. Bay*. 17:198-204.

Hamilton, R. M. G. 1978. Observations on the changes in physical characteristics that influence egg shell quality in ten strains of White Leghorns. *Poult. Sci.* 57:1192-1197.

Hanka, L. R., et al. 1979. Ontogenetic changes in water vapor conductance of eggs of Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). *J. Exp. Zool*. 210:183-188.

Hanna, W. C. 1924. Weights of about three thousand eggs. *Condor* 26:146-153.

Henny, C. J., E. F. Hill, D. J. Hoffman, M. G. Spalding, and R. A. Grove. 2002. Nineteenth Century mercury: hazard to wading birds and cormorants of the Carson River, Nevada. *Ecotoxicol*. 11:213-231.

Hughes, R. J. 1984. Estimation of shell surface area from measurements of length, breadth, and weight of hen eggs. *Poult. Sci.* 63:2471-2474.

Hussell, D. J. T. 1985. On the adaptive basis for hatching asynchrony: brood reduction, nest failure and asynchronous hatching in snow buntings. *Ornis Scand.* 16:205-212.

Kern, M. D. 1986. Changes in water-vapor conductance of Common Canary eggs during the incubation period. *Condor* 88:390-393.

Kern, M. D., and R. J. Cowie. 1995. Humidity levels in Pied Flycatcher nests measured using capsule hygrometers. *Auk* 112:564-570.

Manning, T. H. 1981. Analysis of weight lost by eggs of eleven species of birds during incubation. *Can. Field-Nat*. 95:63-68.

McCarty, J. P., and A. L. Secord. 2000. Possible effects of PCB contamination on female plumage color and reproductive success in Hudson River Tree Swallows. *Auk* 117:987-995.

McDowell, W. H., and C. E. Asbury. 1994. Export of carbon, nitrogen, and major ions from three tropical montane watersheds. *Limnol. Ocean.* 39:111-125.

Müeller, C. D., and H. M. Scott. 1940. The porosity of the egg-shell in relation to hatchability. *Poult. Sci.* 19:163-166.

Navarro, J. L., M. L. López, D. M. Maestri, and D. O. Labuckas. 2001. Physical characteristics and chemical composition of Greater Rhea (*Rhea americana*) eggs from wild and captive populations. *Br. Poult. Sci.* 42:658-662.

Paganelli, C. V., A. Olszowka, and A. Ar. 1974. The avian egg: surface area, volume, and density. *Condor* 76:319-325.

Rahn, H., and A. Ar. 1974. The avian egg: incubation time and water loss. *Condor* 76:147-152.

Rahn, H., and C. V. Paganelli. 1989a. Shell mass, thickness and density of avian eggs derived from the tables of Schönwetter. *J. Ornithol*. 130:59-68.

Rahn, H., and C. V. Paganelli. 1989b. The initial density of avian eggs derived from the tables of Schönwetter. *J. Ornithol*. 130:207-216.

Rahn, H., and C. V. Paganelli. 1990. Gas fluxes in avian eggs: driving forces and the pathway for exchange. *Comp. Biochem. Physiol*. 95:1-15.

Rahn, H., A. Ar, and C. V. Paganelli. 1979. Bird embryos take up oxygen and discharge carbon dioxide by simple diffusion through microscopic pores in the eggshell. *Sci. Am*. 240:46-55.

Rahn, H., C.V. Paganelli, and A. Ar. 1975. Relation of avian egg weight to body weight. *Auk* 92:750-765.

Rahn, H., C. V. Paganelli, and P. R. Sotherland. 1985. Initial mass of avian eggs: comparison between measured and calculated values. *J. Ornithol*. 126: 210-212.

Reynolds, S. J. 2001. The effects of low dietary calcium during egg-laying on eggshell formation and skeletal calcium reserves in the Zebra Finch *Taeniopygia guttata*. *Ibis* 143:205-215.

Richards, P. D. G., P. A. Richards, and M. E. Lee. 2000. Ultrastructural characteristics of ostrich eggshell: outer shell membrane and the calcified layers. *J. S. Afr. Vet. Assoc*. 71:97-102.

Royle, N. J., and K. C. Hamer. 1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. *J. Avian Biol.* 29:266-272.

Romanoff, A. L. 1967. *Biochemistry of the Avian Embryo*. New York: Wiley.

Simkiss, K. 1975. Calcium and avian reproduction. *Symp. Zool. Soc. Lond*. 35:307-337.

Sotherland, P. R., G. C. Packard, and T. L. Taigen. 1979. Permeability of magpie and blackbird eggshells to water vapor: variation among and within nests of a single population. *Auk* 96:192-195.

Spallholz, J. E., and D. J. Hoffman. 2002. Selenium toxicity: cause and effect in aquatic birds. *Aquat. Toxicol*. 57:27-37.

Stoleson, S. H., and S. R. Beissinger. 1999. Egg viability as a constraint on hatching synchrony at high ambient temperatures. *J. Anim. Ecol*. 68:951-962.

Taliaferro, E. H., R. T. Holmes, and J. D. Blum. 2001. Eggshell characteristics and calcium demands of a migratory songbird breeding in two New England forests. *Wilson Bull*. 113:94-100.

Thompson-Baranello, J. J. 2000. *Resource and population modeling of the Puerto Rican Parrot* (Amazona vittata). Master's thesis, University of Puerto Rico.

Tilgar, V., R. Mänd, and A. Leivits. 1999. Effect of calcium availability and habitat quality on reproduction in Pied Flycatcher *Ficedula hypoleuca* and Great Tit *Parus major*. *J. Avian Biol.* 30:383-391.

Veiga, J. P. 1992. Hatching asynchrony in the House Sparrow: a test of the egg-viability hypothesis. *Am. Nat.* 139:669-675.

Voisey, P. W., and J. R. Hunt. 1974. Measurement of egg shell strength. *J. Text. Stud*. 5:135-182.

Wadsworth, F. H. 1951. Forest management in the Luquillo Mountains. I. The setting. *Caribb. For*. 12:93-114.

Walsberg, G. E., and C. A. Schmidt. 1992. Effects of variable humidity on embryonic development and hatching success of Mourning Doves. *Auk* 109:309-314.

Wilson, H. R. 1991. Physiological requirements of the developing embryo: temperature and turning. In *Poult. Sci. Symp. 22: Avian Incub.*, ed. S. G. Tullett, 145-156. London: Butterworth-Heineman.

Whittow, G. C. 1997. Factors affecting egg mass loss in the Phoenix Petrel on Christmas Island. *J. Field Ornithol*. 68:376-381.

Wunderle, J. M., Jr. 1999. Pre—and Post-hurricane fruit availability: implications for Puerto Rican Parrots in the Luquillo Mountains. *Caribb. J. Sci*. 35:249-264.

Zarin, D. J., and A. H. Johnson. 1995a. Base saturation, nutrient cation, and organic matter increases during early pedogenesis on landslide scars in the Luquillo Experimental Forest, Puerto Rico. *Geoderma* 65:317-330.

Zarin, D. J., and A. H. Johnson. 1995b. Nutrient accumulation during primary succession in a montane tropical forest, Puerto Rico. *Soil Sci. Soc. Am. J*. 59: 1444-1452.