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THE EFFECT OF INTRASPECIFIC EGG DESTRUCTION ON THE STRENGTH OF MARSH WREN EGGS

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ABSTRACT.—Marsh Wrens (*Cistothorus palustris*) regularly peck and break eggs of conspecifics, presumably to drive conspecifics away and thereby reduce the potential for intraspecific competition. We hypothesized that egg-pecking behavior represents a strong selective force that should favor adaptations, such as structurally stronger eggs, that lower the effect of conspecific attacks on Marsh Wren reproductive success. We tested this hypothesis by investigating whether Marsh Wren eggs are structurally stronger than would be expected for their size. We compared the strength of Marsh Wren eggs with that of eggs of 10 other passerine species and found that Marsh Wren eggs tolerated 2.9 times greater pressure than would be expected for their size. To identify the structural mechanisms responsible for greater strength of Marsh Wren eggs, we conducted two analyses. First, we related variation in the strength of Marsh Wren eggs to variation in their volume, shape, and eggshell thickness. Eggshell thickness was the only significant predictor of the strength, explaining 30% of the variation. Second, we selected 101 passerine species that lay eggs of similar size and compared eggshell thickness and shape of their eggs with those of Marsh Wren eggs. Marsh Wren eggs had significantly thicker eggshells and rounder eggs than eggs of the other species, indicating that both characteristics contributed to their unusual strength. Our results are consistent with the hypothesis that, in Marsh Wrens, conspecific egg destruction has led to the evolution of unusually strong eggs. *Received 21 March 1995, accepted 6 September 1995.*

THE MARSH WREN (*Cistothorus palustris*) is a polygynous passerine that breeds in marshes throughout temperate North America (Bent 1948). Males defend all-purpose territories within which they construct many domed nests (Verner 1965, Verner and Engelsen 1970). Females choose one of these nests for breeding, line the nest cup with a large amount of soft material, and lay a clutch of four to six eggs (Welter 1935, Bent 1948, Verner 1965). Only females incubate, but males frequently feed older nestlings and fledglings (Welter 1935, Verner 1965).

Marsh Wrens regularly peck and break eggs of other birds, including conspecifics (Allen 1914; Verner 1975; Picman 1977a, b). When small nestlings are present, Marsh Wrens often peck them and remove them from the attacked nests (Picman 1977a, b). Egg-pecking behavior is characteristic of adults of both sexes, and also of recently fledged young (Picman 1977b). The behavior presumably functions as a mechanism of interference competition through which Marsh Wrens exclude from their own nesting area potential competitors such as Red-winged Blackbirds (*Agelaius phoeniceus*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), and other Marsh Wrens (Picman 1980, 1984; Ritschel 1985; Leonard and Picman 1986). Egg-pecking by conspecifics is a frequent cause of Marsh Wren nesting failure. Leonard and Picman (1987) found that 9.6% of all Marsh Wren nests failed as a result of conspecific attacks. Of the successful nests, 14.3% suffered partial losses of either eggs or young owing to Marsh Wren attacks. Picman (1977b) offered experimental nests with eggs to breeding Marsh Wrens and found that the wrens destroyed 28.6% of the clutches. This evidence indicates that a substantial proportion of Marsh Wren reproductive effort is lost to conspecific attacks.

We hypothesized that these attacks represent a strong selective force favoring the evolution of adaptations that reduce the impact of conspecific attacks on Marsh Wren reproductive success. Increased egg strength may represent one such adaptation. The greater strength of wren eggs could be achieved through increased eggshell thickness (Romanoff and Romanoff 1949, Picman 1989b), more rounded shape of an egg (Picman 1989b), and possibly through a higher content of inorganic constituents (especially calcium) in eggshells (Picman 1989b). The first goal of our study was to test the hypothesis that, as a result of intraspecific egg destruction, Marsh Wren eggs are stronger than would be expected for their size. To evaluate this hypothesis, we compared the strength of Marsh Wren eggs with those of eggs of a sample of other passerines. Our second goal was to establish the importance of egg size, egg shape, and eggshell thickness in determining the strength of Marsh Wren eggs.

METHODS

Egg collections.—We collected 42 freshly laid eggs from 21 Marsh Wren nests (two eggs from each clutch) between 10 and 15 June 1989 in a brackish-water marsh on Westham Island, Delta, British Columbia, Canada (49°15′ N, 123° 10′ W). One egg was damaged during handling, reducing the sample to 41 eggs. For a comparative study of egg characteristics, we selected five small passerines: Tree Swallow (*Tachycineta bicolor*), Black-capped Chickadee (*Parus atricapillus*), Cedar Waxwing (*Bombycilla cedrorum*), Yellow Warbler (*Dendroica petechia*), and Purple Finch (*Carpodacus purpureus*). In May and June of 1989 and 1993, we collected two freshly laid eggs from each of 8 to 31 clutches of these species near Ottawa, Ontario, Canada (45° 23′ N, 75° 32′ W). One egg of the Yellow Warbler and one egg of the Cedar Waxwing were broken during handling. All eggs were stored in a refrigerator at 4°C and 100% humidity until the analyses.

Eggshell measurements.—To measure puncture resistance of an egg, we used the mechanical puncture-resistance tester described by Picman (1989a). The tester consists of an egg-support stand, metal bar, and spring-loaded Pesola balance. The metal bar moves around a centrally located hinge, has a small steel punch (1.2 mm diameter) at one end, and is attached to the Pesola balance at the other end. The egg-support stand has a small cup-shaped depression for holding the test egg in place. The Pesola balance generates pressure on the metal bar, which transmits the pressure to the egg through the steel punch. We measured the puncture resistance of an egg at three points that were uniformly spaced along the widest circumference of the egg. We used the mean puncture-resistance score obtained from the three (or two, if egg cracked during last test) tests done with each egg. The pressure (in grams) required to puncture the eggshell was used as an index of its strength.

The length (L) and breadth (B) of all eggs were measured with calipers to the nearest 0.05 mm. The ratio of L:B was used as an index of egg shape (egg roundness). We calculated egg volume (V) from the equation provided by Spaw and Rohwer (1987):

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

We used volume to examine the role of egg size in eggshell strength, and to establish whether egg size confounded analyses of the other predictor variables (eggshell thickness, egg shape). Thickness of eggshells (including egg membranes) was measured with a micrometer to the nearest 0.001 mm at three points where puncture-resistance tests were previously performed (see Picman 1989b). From the three measurements, we calculated the mean eggshell thickness for each egg.

Are Marsh Wren eggs stronger?—To obtain a more accurate estimate of the relative strength of Marsh Wren eggs, we regressed puncture resistance on volume for 10 passerine species. From this regression, we calculated the expected puncture resistance for eggs of the size of Marsh Wren eggs. To increase the range of egg volumes, we included data on eggs of several larger passerines: Bobolink (*Dolichonyx oryzivorus*), Red-winged Blackbird, and Yellow-headed Blackbird (see Picman 1989a). In addition, we included data on 13 eggs of the American Robin (*Turdus migratorius*) and 14 eggs of the Common Grackle (*Quiscalus quiscula*) that were analyzed as part of another study (J. Picman unpubl. data).

Mechanisms of increased puncture resistance.—To establish which eggshell characteristics are responsible for the increased strength of Marsh Wren eggs, we conducted the analyses at two levels. The within-species level of analysis determined which predictor variables were correlated with puncture resistance of eggs of a given species. This analysis was performed with the eggs of the Marsh Wren, as well as those of the other five control species to establish if the selected eggshell characteristics have consistent effects on egg strength. The among-species level of analysis established which eggshell characteristics that play a role in egg strength (as determined by within-species analysis) have been favored by natural selection to produce stronger eggs in the Marsh Wren. This was achieved by comparing the characteristics of Marsh Wren eggs with those of the eggs of the control species. A shift of Marsh Wren egg characteristics in a predicted direction (i.e. rounder eggs, thicker eggshells) would indicate the role of a given eggshell characteristic in the greater strength of the Marsh Wren eggs.

Within-species analyses.—Because assumptions of parametric statistics for the dependent variable (puncture resistance) were satisfied, we used linear regression and Pearson correlation to quantify the relationship between dependent variables and predictor variables for each species (i.e. the Marsh Wren and five control species). To establish the relative importance of egg shape, eggshell thickness, and egg volume in determining puncture resistance, and to estimate the combined effect of the three predictor variables on within-species variation in puncture resistance, we conducted a forward stepwise multiple regression (Zar 1984) for each species.

Among-species analyses.—To establish if Marsh Wren eggs differ from those of five other small passerines

TABLE 1. Mean (± SD) puncture resistance, volume, shape, and eggshell thickness of eggs of six passerine species. Marsh Wrens compared with other species using Dunn's multiple comparisons test; n = number of eggs measured.

Species	n	Puncture resistance (g)	Volume (cm^3)	Shape ($L:B$)	Eggshell thickness (mm)
Tree Swallow	62	92.5 ± 19.7*	1.747 ± 0.144*	1.421 ± 0.070*	0.080 ± 0.004*
Black-capped Chickadee	24	59.0 ± 21.5*	1.209 ± 0.290	1.266 ± 0.073	0.069 ± 0.007*
Marsh Wren	41	195.6 ± 40.6	1.366 ± 0.095	1.293 ± 0.054	0.107 ± 0.008
Cedar Waxwing	29	92.0 ± 14.6*	2.647 ± 0.263*	1.400 ± 0.044*	0.088 ± 0.005
Yellow Warbler	61	66.5 ± 16.2*	1.394 ± 0.178	1.295 ± 0.072	0.073 ± 0.005*
Purple Finch	16	70.3 ± 8.4*	1.962 ± 0.160*	1.342 ± 0.045	0.079 ± 0.004*

*, $P < 0.05$.

in volume, shape, eggshell thickness, and puncture resistance, we used Kruskal-Wallis ANOVA to test for differences among species and then compared Marsh Wren eggs with those of each of the other species using Dunn's multiple comparisons test for groups with unequal sample sizes. To provide a more powerful test on the relative importance of egg shape and eggshell thickness in strength of Marsh Wren eggs, we compared Marsh Wrens to all passerine species laying similar-sized eggs (n = 101; data provided by Schönwetter 1979, 1984). Because the average mass of the eggs of *Cistothorus p. palustris*, the subspecies that we examined, is 1.25 g (Schönwetter 1979), we selected only those species with a mean egg mass of 1.20 to 1.30 g. All 101 species were represented by one subspecies only. If, for a given species, data were available for several subspecies, we selected the nominate subspecies. If that was not possible, we selected the subspecies with the largest sample of eggs. We then compared eggshell thickness and shape of Marsh Wren eggs with those of the control species using a one-sample t-test. Because our measurements of thickness of Marsh Wren eggshells were higher than those provided by Schönwetter (1979), we compared the control passerines with both Schönwetter's data and our data on Marsh Wren eggs.

RESULTS

Are Marsh Wren eggs stronger?—Puncture resistance of Marsh Wren eggs was significantly higher than that of eggs of the other passerines (Table 1). Marsh Wren eggs withstood 2.1 to 3.3 times more pressure than was required to puncture eggs of the other species. This result is even more significant than these data suggest because eggs of the control species with the highest puncture resistance (Tree Swallow, Cedar Waxwing, and Purple Finch) were significantly larger than Marsh Wren eggs (Table 1). To obtain a more accurate estimate of the relative strength of Marsh Wren eggs, we regressed puncture resistance on volume for 10 passerine species. From the regression equation, we calculated the expected pressure needed to puncture an egg the size of a Marsh Wren's egg. The observed puncture resistance of Marsh Wren eggs was 2.9 times greater than expected for eggs of that size (i.e. 68 g; Fig. 1). To establish if this difference in strength of eggs of Marsh Wrens and control species is statistically significant, we conducted the following tests. First, we characterized the relationship between

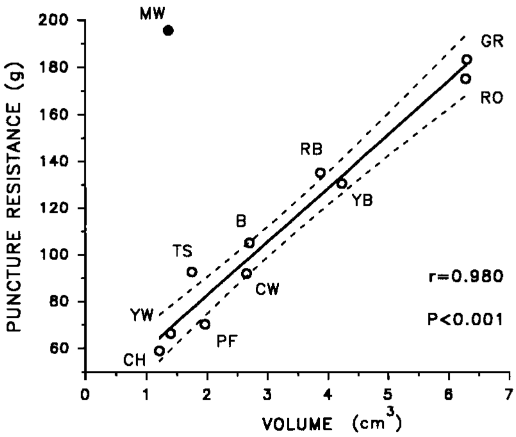

FIG. 1. Puncture resistance of Marsh Wren (MW) eggs compared with 10 other passerines (B, Bobolink; CH, Black-capped Chickadee; CW, Cedar Waxwing; PF, Purple Finch; GR, Common Grackle; RB, Red-winged Blackbird; RO, American Robin; YB, Yellow-headed Blackbird; YW, Yellow Warbler; TS, Tree Swallow). Confounding effects of egg volume on puncture resistance are controlled by regressing puncture resistance on volume of eggs. For the 10 control species, puncture resistance (R) is related to egg volume (V) as: $R = 36.892 + 22.922V$ (F = 214.3, df = 1 and 8, $P < 0.001$). Dashed lines indicate 95% confidence intervals.

TABLE 2. Pearson correlations between puncture resistance and volume, shape, and eggshell thickness; n = number of eggs measured.

Species	n	Volume	Shape	Eggshell thickness
Tree Swallow	62	−0.146	−0.416**	−0.068
Black-capped Chickadee	24	0.732**	0.231	0.373
Marsh Wren	41	0.017	−0.092	0.547**
Cedar Waxwing	29	−0.131	0.002	0.603**
Yellow Warbler	61	0.073	0.345*	0.402*
Purple Finch	16	0.101	0.428	0.236

*, $P < 0.01$; **, $P < 0.001$.

puncture resistance and egg volume for a group of control species (see Fig. 1). Second, using the regression equation, for all species we calculated the vertical deviation from the regression line (henceforth residual puncture resistance). Third, we compared the residual puncture resistance of Marsh Wren eggs with those of the control species. This comparison demonstrated that Marsh Wren eggs were significantly stronger ($t = -48.21$, $P < 0.001$).

Within-species analyses of mechanisms of increased puncture resistance.—Puncture resistance of Marsh Wren eggs was significantly correlated with eggshell thickness, but not with volume or shape (Table 2). Eggshell thickness was not correlated with egg shape or volume, but there was a significant negative correlation between egg volume and shape (Table 3), indicating that Marsh Wren eggs become rounder as they increase in volume. If puncture resistance increases with volume and decreases with shape, then small round eggs may be as strong as large oval eggs, and this may confound the predicted effects of shape and volume on puncture resistance. Therefore, we used stepwise multiple regression to examine the role of the predictor variables on puncture resistance. Eggshell thickness was the only significant predictor, explaining 30% of the variation in puncture resistance (Table 4). The lack of a significant effect of volume and shape confirmed the results of the simple correlations (Table 2).

In the control species, puncture resistance was significantly positively correlated with egg volume only in the Black-capped Chickadee (Table 2). Puncture resistance was significantly correlated with egg shape in two species (Table 2); in the Tree Swallow, puncture resistance increased as the eggs became rounder, whereas in the Yellow Warbler it decreased. Eggshell thickness was significantly positively correlated with puncture resistance in the Yellow Warbler and Cedar Waxwing but had no significant effect on puncture resistance in the remaining three species (Table 2). In the control species, only four out of 15 correlations among the predictor variables yielded a significant relationship: Egg shape was positively correlated with eggshell thickness in the Cedar Waxwing, whereas eggshell thickness was positively correlated with volume in the Yellow Warbler and Purple Finch, and negatively correlated with volume in the Tree Swallow (Table 3).

We examined the relative contribution of all three predictor variables to puncture resistance in a stepwise multiple regression analysis. Egg volume entered the regression equation only in the Black-capped Chickadee, explaining 54% of

TABLE 3. Pearson correlations between the independent egg variables (shape, thickness, volume) for eggs of Marsh Wrens and the other passerines.

Species	n	Shape vs. thickness	Shape vs. volume	Thickness vs. volume
Tree Swallow	62	0.174	0.037	−0.392**
Black-capped Chickadee	24	0.025	0.200	−0.194
Marsh Wren	41	0.037	−0.531***	0.092
Cedar Waxwing	29	0.453*	0.358	0.023
Yellow Warbler	61	−0.050	−0.057	0.540***
Purple Finch	16	0.139	0.262	0.514*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

TABLE 4. Stepwise multiple-regression analyses on effect of egg shape (S), egg volume (V), and eggshell thickness (T) on puncture resistance (R) of Marsh Wren eggs and a sample of small passerines. Only variables with significant effects on R ($P < 0.05$) included in equations. Sample sizes as in Table 1.

Species	Regression equation	r^2(%) S	V	T	Total	F[a]
Tree Swallow	$R = 259.41 - 117.41S$	17.3	—	—	17.3	12.53
Black-capped Chickadee	$R = -130.20 + 60.27V + 1{,}685.30T$	—	53.6	27.6	81.2	45.52
Marsh Wren	$R = -124.17 + 2{,}992.95T$	—	—	29.9	29.9	16.66
Cedar Waxwing	$R = 33.66 - 113.02S + 2{,}458.40T$	9.3	—	36.4	45.7	10.95
Yellow Warbler	$R = -140.61 + 82.83S + 1{,}371.20T$	13.3	—	16.1	29.4	12.11
Purple Finch	No variables entered	—	—	—	—	—

[a] All $P < 0.001$.

the variation in puncture resistance (Table 4). Shape entered three regression equations (Tree Swallow, Cedar Waxwing, Yellow Warbler), explaining 9 to 17% of the variation in puncture resistance (Table 4). Finally, eggshell thickness entered three equations (Black-capped Chickadee, Cedar Waxwing, Yellow Warbler), explaining 16 to 36% of the variation (Table 4). Overall, the combination of these three variables explained between 17 and 81% of the variation in puncture resistance (Table 4). The multiple regression analysis demonstrated that eggshell thickness and egg shape were related to puncture resistance in most species. However, eggshell thickness explained more variation and was more consistent in the direction of its effect than was egg shape (Table 4). These results support our previous conclusion that eggshell thickness is the most important factor determining the puncture resistance of Marsh Wren eggs.

Among-species analyses of mechanisms of increased puncture resistance.—If eggshell thickness is responsible for the increased strength of Marsh Wren eggs, then Marsh Wren eggs should have thicker eggshells than the eggs of other species. Marsh Wrens eggshells are 1.2 to 1.6 times thicker that the eggshells of five other species that we examined (Table 1). To estimate more accurately the relative eggshell thickness of Marsh Wren eggs, we regressed eggshell thickness on volume for 10 passerine species (Fig. 2). From the regression, we calculated that Marsh Wren eggshell thickness is 1.5 times greater than would be expected for eggs of the same volume (0.073 mm; Fig. 2). A comparison of the residual eggshell thickness of Marsh Wrens with the 10 control species demonstrated that Marsh Wren eggs are significantly thicker than eggs of the other species ($t = -32.36$, $P < 0.001$).

If eggshell thickness is the only characteristic responsible for the unusual strength of Marsh Wren eggs, then Marsh Wren eggs should have the same puncture resistance as eggs of other birds with eggshells of the same thickness. We regressed puncture resistance on eggshell thickness for 10 passerine species (Fig. 3) and found that Marsh Wren eggs have 1.4 times higher puncture resistance than would be expected from their eggshell thickness. A comparison of the residual puncture resistances between Marsh Wrens and the control species demonstrated that this difference is highly significant ($t = -32.36$, $P < 0.001$). Therefore, eggshell thickness alone cannot explain the unusual strength of Marsh Wren eggs, and some

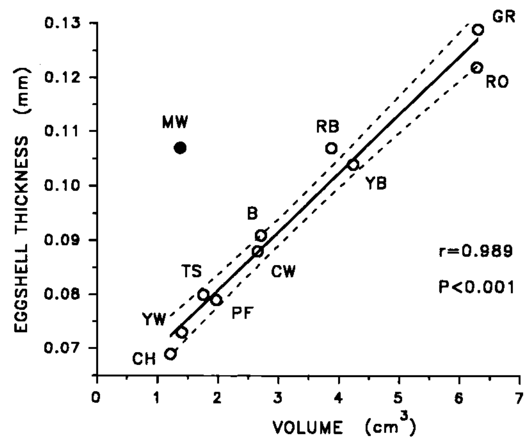

FIG. 2. Eggshell thickness in Marsh Wrens compared with 10 control species (species abbreviations as in Fig. 1). Confounding effects of egg volume in control species taken into consideration by regressing eggshell thickness on egg volume. For control species, eggshell thickness (T) is related to the egg volume (V) as: $T = 0.059 + 0.011V$ ($F = 322.1$, df = 1 and 8, $P < 0.001$). Dashed lines indicate 95% confidence intervals.

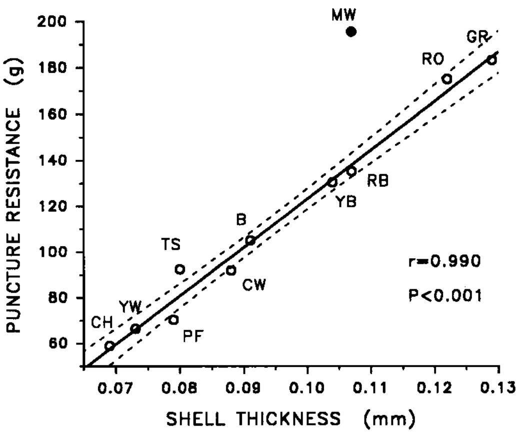

FIG. 3. Puncture resistance of Marsh Wren eggs compared with 10 control passerines (species abbreviations as in Fig. 1) when shell thickness taken into consideration. Confounding effects of shell thickness controlled by regressing puncture resistance on shell thickness (only control species included in regression). Puncture resistance (R) is related to shell thickness (T) as: $R = -88.654 + 2119.011T$ ($F = 481.66$, df $= 1$ and 8, $P < 0.001$). Dashed lines indicate 95% confidence intervals.

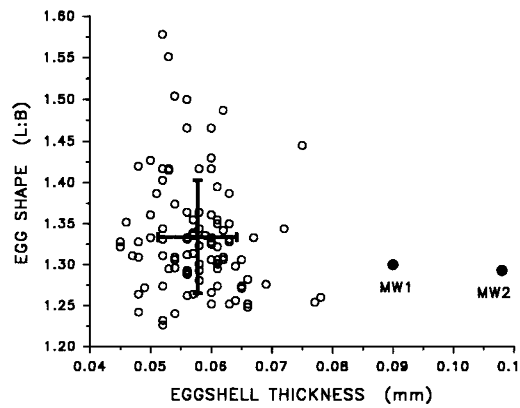

FIG. 4. Egg shape and shell thickness of Marsh Wren eggs and 101 other passerines, controlling for egg mass (only species with eggs of same mass included). Because of differences in shell thickness, both our study population (MW2) and Schönwetter's (1979; MW1) population are shown. The cross denotes mean and standard deviation for thickness and shape for eggs of 101 other species. Statistical comparisons summarized in Table 5.

other factors (such as egg shape) also must be important.

The preceding among-species analyses have two shortcomings. First, our sample of control species was small and possibly not representative of all passerines. Second, our regression analysis of puncture resistance on eggshell thickness may have been confounded by covariation in egg volume and egg shape. To control for this covariation, and to increase sample sizes, we compared Marsh Wren eggs with eggs of 101 passerine species whose eggs are about the same mass as Marsh Wren eggs ("control" species). Within the control group, eggshell thickness was not correlated with egg shape ($r = -0.16$, df $= 99$, $P = 0.107$), therefore allowing a direct comparison of Marsh Wren eggs with eggs of other passerines with respect to shell thickness and egg shape. Marsh Wren eggs were significantly rounder and their eggshells were thicker than those of the other passerines (Fig. 4, Table 5), indicating that both characteristics are responsible for the unusual strength of Marsh Wren eggs.

DISCUSSION

Are Marsh Wren eggs stronger?—We found that Marsh Wren eggs were 2.9 times stronger than similar-sized eggs of other passerines. This result is consistent with our hypothesis and indicates that the relative strength of Marsh Wren eggs is an adaptation to reduce the likelihood of egg breakage by conspecifics. However, there are at least two alternative explanations for unusually strong eggs in Marsh Wrens.

First, Mallory and Weatherhead (1990) proposed that in waterfowl, nesting inside dark cavities might increase chances of accidental egg breakage, thereby favoring stronger eggs. Marsh Wrens construct domed nests that resemble cavities. Consequently, the unusual strength of Marsh Wren eggs could be an adaptation to their cavity-nesting habit. However, two of our control species (Tree Swallow, Black-capped Chickadee) are cavity nesters that lay eggs with lower puncture resistance than Marsh Wren eggs (Table 1). In addition, the large-scale comparative study demonstrated that Marsh Wren eggs have thicker eggshells than eggs of 101 passerines, including all cavity-nesting species (Fig. 4). Thus, the cavity-nesting habit does not explain the greater strength of Marsh Wren eggs.

Second, unusual strength of Marsh Wren eggs could be an adaptation to intraspecific brood parasitism. Dumping an egg into a dark cavity will cause that egg to fall a short distance, increasing chances of its breakage. Intraspecific egg dumping should thus favor relatively stronger eggshells because this will reduce chances of egg breakage. Intraspecific brood parasitism in Marsh Wrens has recently been revealed through DNA fingerprinting, although its occurrence is relatively rare (Schriml, Ell, Picman, and Sabour unpubl. data). Therefore, egg dumping is unlikely to be an important selective force in the evolution of eggshell strength in Marsh Wrens.

Mechanisms of increased puncture resistance.—Within species, puncture resistance was influenced significantly by eggshell thickness but not by egg volume or egg shape. Among species, both eggshell thickness and egg shape were important, but not egg volume. Because the among-species analysis was based on a larger sample, it probably was more sensitive in detecting the influence of egg shape. Therefore, we conclude that the increased puncture resistance of Marsh Wren eggs is due to their thicker shells and rounder shape.

Only 30% of the variation in puncture resistance of Marsh Wren eggs was explained by the three predictor variables. Hence, 70% remains unexplained. This unexplained variation could be due to other eggshell characteristics such as the proportion of inorganic constituents (especially calcium) and the density and porosity of eggshells (Romanoff and Romanoff 1949, Burley and Vadehra 1989, Picman 1989b). In addition, several potential sources of error may have been introduced when measuring puncture resistance and eggshell thickness. First, puncture resistance may have been affected by the position of the steel punch on the egg. The punch was placed at the widest point of the egg, but a slight deviation from its position may have affected the measurement due to varying surface curvature of the eggshell. Second, measurements of eggshell thickness may have been influenced by variation in the size of eggshell fragments. Due to eggshell curvature, even small variations in fragment size may have affected the estimate of thickness. These sources of error could account for some of the unexplained variation in puncture resistance. However, these sources of error were similar for all species and therefore cannot explain the differences in puncture resistance and eggshell thickness among species.

The Marsh Wren eggs we measured were 19% thicker than those measured by Schönwetter (1979). This difference could have resulted from different methods used to measure eggshells or from differences in eggshell thickness between study populations. If the difference was due to

TABLE 5. Comparison of Marsh Wren eggs to similar-sized eggs of 101 passerine species with respect to egg shape and eggshell thickness. Residuals for control species compared with that for Marsh Wrens by a one-sample t-test. MW1 refers to published data on eggs of *Cistothorus palustris palustris* (Schönwetter 1979); MW2 refers to data obtained in our study.

Origin of data	t-value[a]
Shape	
MW1	4.9
MW2	5.9
Thickness	
MW1	−45.9
MW2	−71.8

[a] All $P < 0.001$.

a methodological bias, then Marsh Wren egg measurements should show the same degree of bias as the other species. If the difference was due to variation between populations, then some of our populations should have thicker and others thinner eggshells than Schönwetter's populations. As a result, the average difference in eggshell thicknesses should be zero. We tested these hypotheses by calculating the difference between Schönwetter's and our data for each species. The difference for Marsh Wrens was significantly higher than the mean difference for the other species ($t = -2.95$, df = 3, $P < 0.05$). Moreover, the mean difference for all species was significantly greater than zero ($t = 3.0$, df = 4, $P < 0.025$). This suggests that Schönwetter's method produced systematically lower estimates of eggshell thickness, and that there also were differences in eggshell thickness between our population and Schönwetter's populations.

Other mechanisms of increased puncture resistance.—Two additional mechanisms could increase puncture resistance of Marsh Wren eggs. First, females line the nest cup with a thick layer of soft material composed of dry strips of cattail (*Typha* sp.) and feathers of various birds (Welter 1935, Verner 1965). The lining is flexible and acts as a shock absorber, thereby reducing the chance of egg breakage (Picman 1977b). Future studies should consider the shock-absorbing qualities of the lining when estimating puncture resistance of Marsh Wren eggs.

Second, our results suggest a negative correlation between the volume and shape of Marsh Wren eggs (Table 3), implying that wren eggs become rounder as they increase in volume. We propose that this negative correlation represents a special adaptation by which strength is maintained as eggs increase in size. Consider an egg that increases in volume while maintaining the same $L{:}B$ ratio and shell thickness. As the volume increases, the egg surface becomes less curved relative to the size of a Marsh Wren beak. The flat surface reduces the load-bearing capacity of the egg, making it more fragile (Bernadou and Boisserie 1982). We suggest that in Marsh Wrens, the fragility of large eggs due to their greater volume is compensated for by their rounder shape. Our hypothesis is corroborated by data on the Brown-headed Cowbird (*Molothrus ater*). Cowbirds also lay eggs with unusually strong shells, and the volume of cowbird eggs is also negatively correlated with their shape (Picman 1989b). However, in eight other species with eggs of normal strength, the correlation between shape and volume is not significant, or is significant and positive (Table 3; Picman 1989b). These species with normal eggs differ from those with unusually strong eggs in the direction of the correlation (significantly negative vs. significantly positive or not correlated; Fisher exact test, $P = 0.022$).

The greater thickness of Marsh Wren eggshells is adaptive because it reduces the chances of egg breakage during conspecific attacks. However, thicker eggshells are more costly to females and their young for the following reasons. First, laying female Marsh Wrens must accumulate greater calcium reserves for the formation of their eggshells than females of other birds. If calcium is limited, then females must spend extra time and energy to obtain it. Second, thicker eggshells make hatching more difficult for young. We suspect that this cost may have led to additional adaptations allowing the embryo to hatch successfully. Future research should examine the consequences of thicker eggshells on the hatching process.

Based on our study, we can make several predictions on the occurrence of stronger eggs in other species. First, stronger eggs should be favored in other passerines where conspecific egg destruction is a major cause of nesting failure. For example, the House Wren (*Troglodytes aedon*) is well known for its tendency to destroy eggs of other birds, including those of conspecifics. Intraspecific egg destruction is an important source of House Wren nesting failure, being responsible for 5 to 19% of all egg losses (Kendeigh 1941, Belles-Isles 1987, Finch 1990, Pribil and Picman 1991). Therefore, we predict that the House Wren also should have relatively strong eggs. Second, stronger eggs should be favored in species that are often victimized by other egg-destroying species. The two most obvious examples are: (1) species regularly parasitized by cowbirds and other brood parasites that remove some of the host eggs; and (2) species whose nest attempts frequently fail as a result of attacks by other egg-destroying species. However, selection for strong shells may be effective only in situations where: (1) attackers puncture-eject vs. grasp-eject the host eggs; and (2) greater eggshell strength can effectively lower the chances of breakage (i.e. where attackers are not larger than victims).

To conclude, our results support the hypothesis that intraspecific egg destruction has led to the evolution of unusually strong eggs in Marsh Wrens. Future studies should examine eggshell strength in other species that are exposed to frequent egg destruction by conspecifics or heterospecifics.

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