EGGSHELLS AS AN INDEX OF AEDINE MOSQUITO PRODUCTION 1: DISTRIBUTION, MOVEMENT AND SAMPLING OF *AEDES TAENIORHYNCHUS* EGGSHELLS[1]

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ABSTRACT. The distribution of *Aedes taeniorhynchus* eggshells in Florida mangrove basin forests was determined and used to design a sampling plan. Eggshells were found in 10/11 sites (91%), with a mean ± SE density of 1.45 ± 0.75/cc; density did not change significantly year to year. Highest densities were located on the sloping banks of hummocks, ponds and potholes. Eggshells were less clumped in distribution than eggs and larvae and thus required a smaller sample size for a given precision level. While eggshells were flushed from compact soil that was subject to runoff during heavy rain, mangrove peat, the dominant soil of eggshell-bearing sites, was less dense and had little runoff or eggshell flushing. We suggest that eggshell surveys could be used to identify *Ae. taeniorhynchus* oviposition sites and oviposition patterns.

INTRODUCTION

Identification of oviposition sites and their potential mosquito production is critical to successful control of floodwater mosquito larvae. Egg and larval sampling are typically used to estimate larval hatch (Horsfall 1956, Horsfall et al. 1975) and adult emergence (Service 1976), respectively. Unfortunately, the high temporal and spatial variability of egg and larval populations necessitate repeated sampling and large sample sizes (Horsfall et al. 1975, Service 1976, Ritchie and Johnson 1991b). Additionally, prolonged flooding of oviposition sites can minimize the time that eggs (Strickman 1980, Ritchie and Johnson 1991a) and larvae (Clements and Rogers 1964) are available for sampling.

Eggshell density could be used to identify oviposition sites and estimate floodwater mosquito production under most circumstances. Aedine eggshells can accumulate in high densities in the soil (Lopp 1957, Scotton and Axtell 1979, Kay and Jorgensen 1986, Ritchie and Johnson 1989), and submerged soil can be readily sampled and processed for eggshells (Ritchie and Addison 1991). A preliminary study suggests that eggshells can depict oviposition patterns and thus potential mosquito production (Ritchie and Johnson 1991a). Oviposition sites elucidated by eggshell sampling could then be targeted for more intensive egg and larval sampling to justify mosquito control efforts.

In support of these arguments, we seek to demonstrate that *Aedes taeniorhynchus* (Wiedemann) eggshells, because of their lower spatial and temporal variability, are more efficient to sample than eggs and larvae. Also, we will quantify the dispersal of eggshells from the oviposition site. The relationship of eggshell density to larval production is discussed in a second paper (Addison et al. 1992).

MATERIALS AND METHODS

Eggshell distribution: Eggshells were sampled in 3 strata within 11 mangrove basin forests dominated by red mangrove (*Rhizophora mangle* Linn.; 4 sites), black mangrove (*Avicennia germinans* Linn.; 6 sites) or white mangrove (*Laguncularia racemosa* Gaertn. f.; 1 site). The pond stratum contained ponds and potholes commonly associated with *Aedes* production in salt marshes (LaSalle 1974, Balling and Resh 1983). The plains stratum encompassed flat areas surrounding ponds. The upland stratum was a transitional zone between mangrove and upland hammock that was identified as exposed soil when the mangrove forest was flooded to capacity.

Plains samples (n = 45 or 36) were collected randomly within a 31 × 37 m grid delineated by four 37-m long transects. Pond and upland strata samples were taken systematically in a grid transecting low to high elevations with 4–8 samples per row (total of 10–13 rows). Sample site elevation was measured by referencing water depth to a staff gauge of known elevation.

Modified 6 and 60-cc Monoject® plastic syringes were used, respectively, to take 3 and 15-cc soil cores. Eggshells were isolated by selective sieving with nested sieves (0.185 and 0.170-mm openings) (Ritchie and Addison 1991). Live eggs were also counted in 5 instances. Because *Aedes sollicitans* (Walker) has not been recovered in local mangrove forests (Ritchie and Johnson 1991b), all eggshells, eggs and larvae were presumed to be *Ae. taeniorhynchus.*

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The mean and variance were calculated for each sample set (n = 31 and 4 for the 3 and 15-cc soil cores, respectively) and the variance of systematic samples was calculated using the formula of Cochran (1977). Dispersion was measured by the mean to variance ratio and b of Taylor's Power Law (Taylor 1961). The number of eggshells/clump was estimated by regressing mean crowding (Lloyd 1967) on mean density (Iwao 1968, Kitron et al. 1989). Eggshell dispersion was compared with that for live eggs [n = 22, data from Ritchie and Johnson (1991b)] and larvae (43 populations estimated by stratified random sampling using a dipper and a minimum of 50 dips).

The relationship of eggshell density to soil depth was investigated at 4 sites. At each site, five 15-cc soil cores were collected and each core divided into three 0.85 cm sections of sequential soil depth. Each section was processed for eggshells by water flotation (Ritchie and Addison 1991). The proportion of eggshells/section was transformed by arcsine (Zar 1974) and compared by one way analysis of variance (Wilkinson 1988).

Temporal stability of eggshell density was studied by repeated sampling. Two sites were sampled in June 1988, 1989 and 1990. Five sites were sampled in June of 1989 and 1990. The mean eggshell density for 2 consecutive years for a site was compared with a paired t-test.

Eggshell sampling plan: The mean density of an eggshell population cannot be determined before samples are taken, so a fixed sample size plan was used. Ruesink's (1980) application of the coefficients of Taylor's power law to calculate the minimal density (X_m) of a population that can be estimated for a given sample size (n) and precision level (D) was used. Ruesink (1980) substituted Taylor's aX^b for s^2 in the sample size formula $n = s^2/(DX)^2$; the resulting formula is $X_m = (a/nD^2)^{1/(2-b)}$ where a and b are Taylor's intercept and slope coefficients, n is the sample size, and D the precision level expressed as the ratio of the standard error of the mean to the mean. In instances where negative values of Taylor's a prevent calculation of sample size, the following sample size formula (Southwood 1978) for a homogeneous habitat was used: $n = (S/EX)^2$ where n and X are as above and E is the predetermined standard error as a decimal of the mean. Standard errors ranging from 10 to 25% of the mean were chosen, reflecting values Southwood (1978) suggested for intensive and extensive sampling programs, respectively.

Movement of eggshells: Eggshells could disperse by flushing during heavy rain or by floating during flooding tides. We tested the hypothesis that compact soils would have lower water infiltration rates and higher rates of eggshell flushing than porous mangrove peat. Tests were conducted in plains and upland strata soils for both a *R. mangle* and *A. germinans* forest. Bulk density (Brady 1974) was used to quantify soil compactness. Ten 15-cc soil cores (2.5 cm deep) were collected randomly with the 60-cc syringe, oven dried at 105°C for 48 h, then weighed. Relative infiltration was measured with a cylinder infiltrometer (Bouwer 1986) on August 9, 1990. Test soil was cleared of detritus, then a plastic bucket (37 cm high × 26 cm diam.) with the bottom removed was driven into soil. After replacing the detritus, 1 liter of water was poured into the bucket. Infiltration was measured (n = 10) as the time from water introduction until no water was remaining. For trials with standing water after 20 min, infiltration times were set at 20 min. Flushed eggshells were collected in a modified polyvinylchloride (PVC) pipe (n = 8 and 7 in upland and plains strata, respectively, in the *R. mangle* forest; n = 10 for both strata in the *A. germinans* forest). A 2.5-cm diam. circle of stainless steel screen (150-μm openings) was glued with silicon caulk between two 5-cm sections of 2.5-cm diam. PVC pipe. The top of the pipe was buried flush with the soil surface; water entering the pipe passed through the screen, trapping any flushed eggshells. The density of eggshells in upstream soil was estimated from ten 15-cc soil cores. The number of flushed eggshells/core was standardized to an upstream eggshell density of 1/cc and a rainfall of 2.5 cm.

Bulk density, infiltration times, and the standardized number of flushed eggshells were analyzed by analysis of variance (Wilkinson 1988). Because of unequal n values, the Tukey-Kramer test (Kramer 1956), as recommended by Day and Quinn (1989), was used to compare group means.

Eggshell dispersion by floating was estimated for upland and plains strata at both forests. Five 15-cc soil cores (depth = 2.5 cm) were collected after a prolonged dry period (2+ wk with < 0.5 cm of rain) using a 60-cm plastic vial with the bottom cutoff. Floating of eggshells from the core sides was minimized by the tight fit between the core and the vial. The soil-bearing vial was submerged slowly in a 100-ml beaker containing 70 ml of water. After 1 min, the top 5 mm of soil was scored with forceps to simulate erosion due to flowing water. Floating material was collected and examined for eggshells. The number of eggshells remaining in each core was estimated by water flotation (Ritchie and Addison 1991). The proportion of eggshells that floated was transformed using arcsine (Zar 1974) and compared with a one way analysis of variance (Wilkinson 1988).

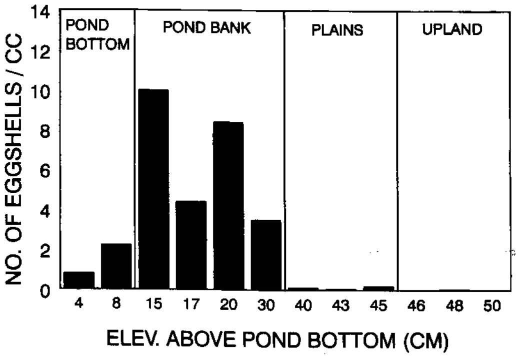

Fig. 1. Eggshell profile along a transect crossing a pond bottom, pond bank, mangrove plains, and transitional upland soil within a black mangrove basin forest. Eggshell density is the mean number of eggshells/cc.

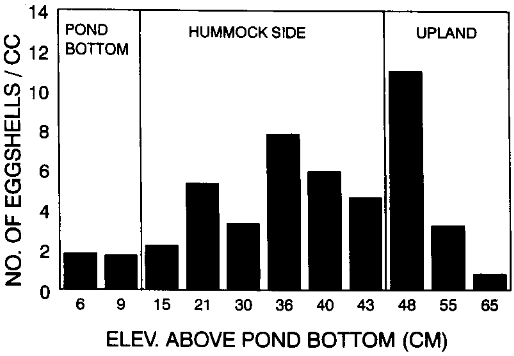

Fig. 2. Eggshell profile along a transect crossing a pond bottom, side of a hummock, and transitional uplands in a red mangrove forest. Eggshell density as in Fig. 1.

RESULTS

Eggshell distribution: Eggshells were found in 10/11 (90.9%) mangrove basin forests sampled. The number of eggshells/cc of soil ranged from 0 to 4.91, with a mean (± SE) of 1.45 ± 0.75 (n = 36). The number of eggshells/cc for pond, plains, and upland strata ranged from 1.00 to 4.78, 0.01 to 2.50, and 0.07 to 4.91, respectively. Eggshells were concentrated in ponds and potholes at 3 of the 4 sites with ponds; the mean ratio of pond:plains eggshell density for these sites was 16 : 1. High eggshell densities in pond banks could occur when optimal surface moisture is restricted to pond banks, thus concentrating oviposition to a small area. Winter and spring drought can prolong this situation, thus enhancing accumulation of eggs (Horsfall 1963). Eggshell density in the pond and plains strata was comparable (0.9:1) at the other site, perhaps due to the presence of sloping hummocks associated with high *Ae. taeniorhynchus* production (Travis and Bradley 1943, Ritchie and Johnson 1991b).

For the 5 sites where live eggs were tallied, 90 unhatched eggs and 1,273 eggshells were collected, with eggshells comprising 89.5 ± 3.4% of the total. Scotton and Axtell (1979) found that *Ae. taeniorhynchus* eggshells comprised only 44.8% of eggs and eggshells on dredged spoil. Perhaps the lower percentage of eggshells is the result of the limited age of the spoil sites (3 years) or inefficient recovery of eggshells (flotation in saturated salt solution used to isolate eggs).

Plots of eggshell density against elevation (termed an eggshell profile) revealed 2 general patterns. In a type I eggshell profile (Fig. 1), eggshells were concentrated within a narrow elevational range, such as the bank of ponds and pools. Type II eggshell profiles (Fig. 2) had multiple peaks. The only such site was subject to oviposition at nearly all elevations, even upland areas when the mangrove forest was submerged (Ritchie and Johnson 1991b). These eggs, seldom submerged by standing water, hatched when flooded by sheetflow runoff during heavy rain.[3] Horsfall (1963) also found that some woodland pools exhibited multiple peaks of oviposition extending above the maximum flood line.

For each dispersion index, aggregation decreased in order of eggs, larvae, then eggshells (Table 1). With time, the overlapping of oviposition events coupled with the movement, however slight, of eggshells would act to reduce eggshell clumping. Unfortunately, the large SE of clump size limited its value.

Eggshells were comparably distributed by depth in the top 2.5 cm of soil (F = 1.07, df = 59, P = 0.35). The mean (± SE) proportion of eggshells in the top, middle and bottom layer was 0.32 ± 0.05, 0.30 ± 0.04 and 0.38 ± 0.04, respectively.

No significant changes in eggshell density (t = 0.247, df = 8, P = 0.81) were found between paired annual samples, indicating that eggshell density is relatively stable. This contrasts sharply with the fluctuations of egg populations observed in mangrove forests (Ritchie and Johnson 1991b).

Eggshell sampling plan: Required sample sizes for estimating eggshell density were smaller than those for eggs and larvae (Fig. 3). The

[3] Ritchie, S. A. 1988. A simulation model of the population dynamics of the black salt marsh mosquito (*Aedes taeniorhynchus*) in a Florida mangrove forest. Ph.D. dissertation, University of Florida, Gainesville.

Table 1. Mean (± SE) dispersion indices for *Aedes taeniorhynchus* eggs (n = 22), larvae (n = 43) and eggshells (n = 35).

	Eggs	Larvae	Eggshells
Variance/mean	35.93 ± 8.46	25.54 ± 5.94	4.43 ± 0.64
Taylor's b	1.61 ± 0.11	1.52 ± 0.07	1.39 ± 0.08
Mean crowding	45.19 ± 10.81	37.75 ± 8.29	9.25 ± 1.83
Clump size	12.17 ± 27.17	10.00 ± 30.08	1.59 ± 2.94

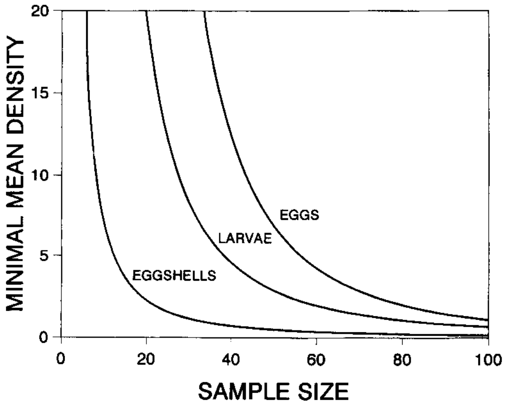

Fig. 3. Minimal mean density of *Ae. taeniorhynchus* eggs, eggshells, and larvae that can be estimated for a given sample size at a precision level (SEM/mean) of 0.10.

Table 2. Sample sizes for given x_m and precision levels (SE/mean) for *Aedes taeniorhynchus* eggshells in mangrove plains and upland strata.

	Precision level (SE/mean)		
x_m	0.10	0.15	0.25
0.25	78	34	14
0.50	52	23	9
1.00	34	15	7
2.00	23	10	3

divergence of eggshell density between pond and plains habitat dictated that these be used as sampling strata. Because Taylor's a was negative (−0.68) for eggshells from the pond stratum, x_m could not be determined. Using Southwood's formula, the respective sample size for $E = 0.10$, 0.15 and 0.25 was 56, 25 and 9 for pond eggshells. The number of samples for a given x_m and precision level needed to sample plains eggshells is shown in Table 2. Because the dispersion of eggshells collected from 3 and 15-cc soil cores was comparable (Fig. 4), common coefficients were used to calculate sample size. The 60-cc corer may be most effective in detecting low density eggshell populations. At 2 sites where a small larval brood was observed, eggshells were only collected from 15-cc soil cores, probably due to the larger overall amount of soil sampled.

Movement of eggshells: Eggshell flushing was greatest in dense soils featuring low infiltration rates (Table 3). In the red mangrove forest, flushed eggshells were collected following a rainfall of 4.8 cm (upland) and 2.9 cm (plains). In the black mangrove forest, flushed eggshells were collected from both strata after 3.3 cm of rain. Significant site and strata interactions were found for soil bulk density (F = 9.446, df = 36, P = 0.004) and infiltration time (F = 12.424, df = 36, P = 0.001). The standardized number of flushed eggshells was significantly related to strata only (F = 10.966, df = 31, P = 0.002).

Eggshell profiles also depicted differential eggshell flushing in plains and upland soils. Flushing may account for the concentration of eggshells at lowest elevations of the upland stratum in the red mangrove forest (Fig. 2). Eggshells were found at all elevations of sloping banks of ponds and hummocks, with the highest densities at intermediate elevations (Figs. 1, 2). Ritchie and Johnson (1991b) found that live eggs had a similar distribution, although the pond bottom was devoid of eggs. These data suggest that while some eggshells flush from pond banks, the general oviposition pattern depicted by the distribution of eggshells is accurate.

Few eggshells floated from submerged soil cores. For upland stratum soil cores, only 0.41 ± 0.27% and 2.00 ± 2.00% of the eggshells from red and black mangrove sites, respectively, floated. In the plains cores, only 3.87 ± 1.62% and 0% of eggshells from the red and black mangrove forest, respectively, floated. However, a significant interaction between site and stratum was found (F = 4.850, df = 16, P = 0.043). These data suggest that unless subject to erosion, eggshells disperse little from tidally flooded mangrove soil.

DISCUSSION

Sampling eggshells appears to be a valuable tool for the identification of *Ae. taeniorhynchus* oviposition sites. Eggshells are less laborious to sample than eggs and can be collected from flooded soil (Ritchie and Addison 1991). We are currently sampling eggshells to identify oviposition sites to be surveyed for larvae. The sloping banks of ponds, potholes and hummocks are especially targeted because they often contained higher eggshell densities than plains. By using eggshell sampling to map oviposition foci, larviciding can be pinpointed, minimizing the area of wetlands exposed to insecticide. Despite its utility, eggshell sampling cannot supplant egg and larval sampling, for only these can provide accurate estimates of larval hatch and adult emergence.

Eggshell density could also be used to identify gross ovipositional preferences. The concentration of *Ae. taeniorhynchus* eggshells in sloping hummocks, ponds and potholes is consistent with known distributions of salt marsh *Aedes* eggs (Travis and Bradley 1943, LaSalle 1974, Balling and Resh 1983, Ritchie and Johnson 1991b). This, coupled with our evidence that eggshell flushing and floating is minimal, suggests that eggshell density can be used to identify cumulative oviposition patterns within low density mangrove peat. However, such data must be interpreted with caution. Eggshell distribution might be dramatically altered by flushing, such as occurs during the tidal surge of a hurricane or during heavy rains in compact soil conducive to runoff.

Preliminary data suggest that eggshells might be useful in identifying oviposition sites of other aedine mosquitoes. We have collected significant number of eggshells from tires, pastures and woodland pools. Eggshells could be cleared (Craig 1955, Trpis 1970) and identified by size, shape and chorionic patterns using reference specimens and keys (Horsfall et al. 1952, Horsfall and Craig 1956, Craig and Horsfall 1960).

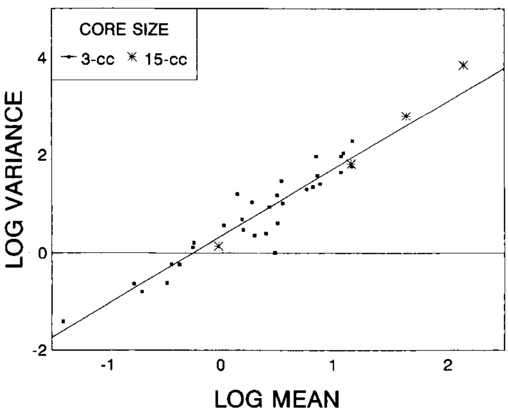

Fig. 4. Relationship of log mean and log variance for *Aedes taeniorhynchus* eggshells sampled ($n = 35$) from Florida mangrove basin forests, based on 3 and 15-cc soil cores. Line was drawn using the regression model $\log S^2 = 0.33 + 1.39(\log X)$.

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Table 3. Soil characteristics and associated eggshell flushing (mean ± SE) in lowland and upland strata of a red mangrove and a black mangrove basin forest.

	Soil characteristics		Number flushed eggshells	
Site	Compactness (g/cc)	Infiltration (min.)	Normal[1] (count)	Standardized[2]
Red mangrove				
Lowland	0.20[3]A ± 0.02	3.4A ± 1.9	5.9A ± 2.3	0.83AB ± 0.31
Upland	0.78B ± 0.03	19.9B ± 0.1	37.8B ± 9.5	7.85AB ± 1.98
Black mangrove				
Lowland	0.27A ± 0.03	1.2A ± 0.3	1.8A ± 1.4	0.13A ± 0.04
Upland	0.64C ± 0.05	8.6C ± 1.7	7.6A ± 9.5	9.02B ± 3.76

[1] Mean number of eggshell trapped within a 2.5-cm diam PVC pipe (see text).

[2] Flushed eggshells standardized to a 1 inch (2.54 cm) rainfall with an upstream eggshell density of 1/cc of soil.

[3] Column means followed by the same letter are not significantly different ($P \geq 0.05$) by a Tukey-Kramer test.

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