Journal of the American Mosquito Control Association, 13(4):361–367, 1997

THE RELATIONSHIP BETWEEN THE DENSITY OF *AEDES VIGILAX* (DIPTERA: CULICIDAE) EGGSHELLS AND ENVIRONMENTAL FACTORS ON KOORAGANG ISLAND, NEW SOUTH WALES, AUSTRALIA

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ABSTRACT. Knowledge of oviposition sites selected by wetland mosquitoes could improve mosquito control and guide wetland rehabilitation practices to avoid creating or exacerbating a mosquito problem. Two studies that enumerated *Aedes vigilax* eggshells found in salt marsh soil on the western portion of Kooragang Island in New South Wales, Australia, allowed an evaluation of oviposition sites. In one study, the density of eggshells found in samples collected from a large area was related to environmental factors, including distance from nearby drainage channels, vegetation cover, elevation, and terrain characteristics. Multiple-regression analysis suggested eggshell densities were positively correlated with the presence of depressions and ponds, vegetation cover, and distance from culverts, but negatively related to elevation. In another study, eggshell density was related to relative elevation and vegetation species within each of two 400-m^2 plots on Kooragang Island. In all but one instance, samples from bare soil contained fewer eggshells than samples with vegetation cover at both plots. Eggshell density did not differ between the two dominant vegetation species, *Sarcocornia quinqueflora* and *Sporobolus virginicus,* although bare soil of one plot had a mean eggshell density similar to that of soil with *S. quinqueflora* cover. Eggshells were at highest density at intermediate elevations at one plot but at low elevations at the other.

INTRODUCTION

One of the most important mosquito pests in coastal Australia is *Aedes vigilax* (Skuse), which is distributed among salt marsh and mangrove zones of the coastline and in saline regions of the Murray river (Russell 1993). Because *Ae. vigilax* may disperse far from the larval habitat, and because it is an established vector of Ross River virus and dog heartworm, it has become a focus of control efforts in urban coastal regions. Source reduction methods such as runneling and open marsh water management are appropriate for this species; their application can obviously benefit from the identification of mosquito oviposition sites. Knowledge of oviposition sites may also improve salt marsh rehabilitation practices by providing ecosystem managers with guidelines that reduce the potential for creating or exacerbating a mosquito problem.

Sampling of eggshells is a useful tool for identifying oviposition habitats of mosquitoes in coastal wetlands (Kay and Jorgensen 1986, Ritchie et al. 1992, Ritchie and Jennings 1994). Because the spatial distribution of eggshells is thought to be temporally stable, sites suitable for oviposition may bear large numbers of eggshells (Lopp 1957, Ritchie et al. 1992, Ritchie 1994). Eggshell sampling indicates potential mosquito productivity because egg and eggshell densities are generally correlated (Scotton and Axtell 1979, Kay and Jorgensen 1986, Ritchie and Johnson 1991).

The density of *Ae. vigilax* eggs, as estimated directly or through induced hatching of larvae from soil, has previously been related to environmental factors such as vegetation, elevation, and position relative to larval habitat (Kerridge 1971, Dale et al. 1986, Kay and Jorgensen 1986). Although these relationships have been characterized in southeast Queensland salt marshes (Kay and Jorgensen 1986, Ritchie 1994, Ritchie and Jennings 1994), there has been no similar study in temperate regions of Australia, and no studies have considered the influence of multiple environmental factors on egg or eggshell density.

Here, we used multiple-regression analysis to examine the relationships between environmental factors and variations in the density of *Ae. vigilax* eggshells at macro- and mesoscales on Kooragang Island, New South Wales, Australia.

MATERIALS AND METHODS

Kooragang Island (32°51′S, 151°43′E) is a 2,560-ha deltaic feature bordered by the north and south arms of the Hunter River, Newcastle, Australia (Fig. 1). The island is divided into 3 zones: an industrial zone to the southeast, the Kooragang Island Nature Reserve to the northeast, and an area designated for wetland rehabilitation to the west. The study described here was done in the rehabilitation zone. Much of this zone is characterized by grazed pasture, salt marsh, large semipermanent bodies of water, depressions, and mangrove-lined creeks. Livestock and vehicle disturbances are common. The vegetation is dominated by *Sarcocornia quinqueflora* (Bunge ex Ungen-Sternberg) (Chenopodiaceae) and *Sporobolus virginicus* (Linn.) Kunth (Poaceae), with *Triglochin striata* Ruiz and Pavon (Juncaginaceae) and *Suaeda australis* (R. Br.) Moq. (Chenopodiaceae) occurring as subdominants. The dominant species varies with location, and the vegetation lacks typical zonation

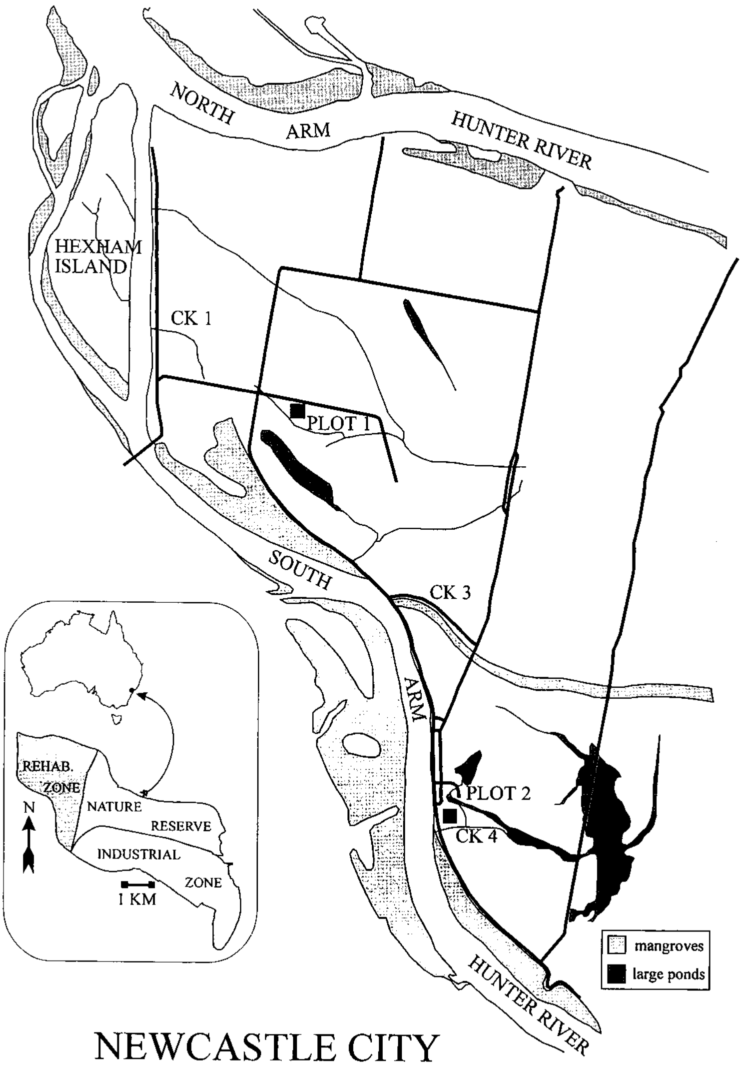

Fig. 1. Sampling locations for *Aedes vigilax* eggshells within the rehabilitation zone (shaded portion of inset) on Kooragang Island, New South Wales, Australia. The macroscale study was conducted near creeks 1, 3, and 4. Plots 1 and 2 mark the mesoscale study.

(Zedler et al. 1995). *Juncus acutus* Linn. (Juncaceae) and *J. kraussii* Hochst occur along some pasture–salt marsh interfaces.

The macroscale study site was an *S. quinqueflora*- and *S. virginicus*-dominated salt marsh bordering 3 creeks, hereafter referred to as creeks 1, 3, and 4 (Fig. 1). *Avicennia marina* (Fusk) occurred along the creek banks in some areas. Concrete culverts of various diameters restrict tidal flushing of each creek, though the culvert of creek 1 was replaced with a bridge shortly after sampling was completed (Streever et al. 1996). In June 1995, 40 1-m^2 sampling stations were established at each creek using randomly generated compass bearings (0–360°) and distances (1–50 m). An initial starting point was haphazardly chosen, and all other sampling stations were located relative to this point. At all creeks, 2 or 3 starting points were chosen to ensure dispersion of sampling stations. Each sampling station was subdivided into 16 subquadrats. A 15-cm^3 soil core was extracted from each subquadrat. The 16 soil cores of each sampling station were combined. Percent cover of vegetation was visually estimated in the subdivided quadrat. Distances (m) of each sampling station from the creek and culvert were measured. Elevation of each sampling station was determined to the nearest cm, related to known elevations on the island, and expressed in meters relative to the Australian Height Datum (AHD). Each sampling station was classified into a terrain category as follows: 1) plain, 2) hoofprinted plain, 3) depression, 4) hoofprinted de-

Table 1. Summary statistics for the eggs and eggshells of *Aedes vigilax* collected from the 120 samples of the macroscale study.

Variable	Total	Mean (1 SE)	variance/mean	Range	% of total
Eggs	168	1.40 (0.58)	28.77	0–65	1.2
Hatched eggshells	11,411	95.09 (29.61)	1,106.09	0–2,715	81.8
Unhatched eggshells	2,400	20.00 (4.56)	124.83	0–385	17.0
Total	13,979	116.49 (34.19)	1,204.49	0–3,115	100.0

pression, 5) pond, or 6) hoofprinted pond. Ponds either formed parts of creek systems or were joined to them via channels, whereas depressions were defined as isolated.

For the mesoscale study, eggshell sampling was done in April 1996 within 2 square 400-m^2 plots, hereafter referred to as plots 1 and 2 (Fig. 1). Plot 1 bordered a large body of semipermanent saline water that forms part of an extensive network that produces large broods of *Ae. vigilax* from spring to early autumn (Cooper, personal communication 1996). Plot 2 consisted of undulating salt marsh situated near creek 4. Small ephemeral pools formed within this plot after spring tides or heavy rainfall. Relative relief at both sites was *ca.* 16 cm. The two sites differed considerably in their topography; plot 1 gradually decreased in grade toward the pond, whereas plot 2 had an irregular surface.

Each plot was divided into a grid at 1-m intervals. One hundred random sampling points were selected from the grid. Individual 15-cm^3 soil cores were taken from each sampling point at both plots. Elevation was recorded to the nearest cm at each sampling point and expressed relative to the lowest sampling point. *Sarcocornia quinqueflora, S. virginicus, S. quinqueflora–S. virginicus* (mixed), and bare soil were scored as present or absent within a 15-cm-diam area at each sampling point.

Soil samples from each study were placed into plastic bags and refrigerated for at least 3 wk at 3°C to reduce the likelihood of hatching during processing. Approximately one fifth of each soil sample was processed for eggs and eggshells using water flotation (Ritchie and Jennings 1994, Turner and Streever 1997). Mesoscale samples were similarly processed but without subsampling. Whole eggs were identified as intact, cylindrical, and black or deep brown in color. Hatched eggshells were characterized by the presence of a line of eclosion. Unhatched eggshells resembled whole eggs but were flattened, usually discolored, and lacked evidence of eclosion. Egg caps were not recorded.

Multiple-regression analysis was used to assess the importance of environmental factors in explaining variation in eggshell density. All factors chosen for study were thought to play some role in influencing eggshell density, so all factors were retained in the models regardless of their significance. Terrain categories used in the macroscale study were treated as indicator variables for regression analysis, but categories were reduced from 6 to 3 after *t*-tests determined that mean eggshell density did not differ significantly between depressions and hoofprinted depressions ($t = -0.93$, df $= 23$, $P = 0.36$), ponds and hoofprinted ponds ($t = 1.09$, df $= 9$, $P = 0.30$), or plains and hoofprinted plains ($t = 0.38$, df $= 82$, $P = 0.70$). Thus, the categories used were plains, ponds, and depressions. Sites (i.e., creeks 1, 3, and 4) were also treated as indicator variables. The reference group was "plain" for terrain category, and "creek 4" for site. Ground cover categories were used as indicator variables for the mesoscale study, with bare soil as the reference group. The importance of indicator variables to each model was determined relative to the reference group. Single-factor analysis of variance (ANOVA) and Tukey's multiple-comparison test were used to test for differences in eggshell density among terrain categories in the macroscale study and among ground cover categories in the mesoscale study. The response variable used for all analyses was the total number of eggs and eggshells per sample, and counts were transformed with $\log_{10}(x + 1)$ for all analyses. Statistical analyses were carried out with Statistica® (Statsoft 1995).

Table 2. Summary statistics for each environmental factor based on the 120 samples of the macroscale study. Terrain categories are excluded.

Environmental factor	Mean (1 SE)	Range
Distance from culvert (m)	224.9 (11.7)	27–510
Distance from creek (m)	25.3 (1.6)	3–90
Sarcocornia quinqueflora cover (%)	24.2 (1.7)	0–70
Sporobolus virginicus cover (%)	15.4 (2.0)	0–91
Elevation (m AHD)	0.63 (0.01)	0.31–1.00

RESULTS AND DISCUSSION

Macroscale study: Soil samples were dominated by hatched eggshells, followed by unhatched eggshells and eggs. The distribution of eggs and eggshells was highly aggregated, with variance-to-mean ratios greatly exceeding 1 (Table 1). Fifteen percent of samples contained no eggs or eggshells, and 17.5% contained more than 100. Egg density was very low and variable; 77% of samples contained no eggs, and 5% contained between 10 and 65. Summary statistics for environmental factors are outlined in Table 2.

Table 3. The regression model developed by the macroscale study showing the relationship between the density of *Aedes vigilax* eggshells and environmental factors. The response variable was $\log_{10}$ (eggs and eggshells per sample + 1).

Environmental factor	Coefficient (1 SE)	Probability[1]
Intercept	0.747 (0.405)	ns
Distance from culvert (m)	0.002 (0.001)	**
Distance from creek (m)	0.006 (0.001)	ns
Sarcocornia quinqueflora cover (%)	0.009 (0.004)	*
Sporobolus virginicus cover (%)	0.007 (0.003)	*
Elevation (m AHD)	−1.306 (0.607)	*
Depression	1.080 (0.158)	***
Pond	0.439 (0.205)	*
Creek 1	0.473 (0.199)	*
Creek 3	−0.257 (0.180)	ns

Overall model: $F_{9,110}$ = 16.05, adjusted r^2 = 0.53, n = 120, P = ***

[1] Significance of each regression coefficient: ns, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

The environmental factors explained 53% of the variability in eggshell density (Table 3). All factors except "distance from creek" and the indicator variable, creek 3, contributed significantly to model fit. For the range of values used (Table 2), the model showed that eggshell density was greatest at creek 1, where moderate vegetation cover surrounded depressions at the low elevations distant from the culvert (i.e., the flooding source). Conversely, eggshell density was estimated to be least on poorly vegetated plains close to drainage lines at creeks 3 and 4. Combining percent cover for both species of vegetation also suggested that higher eggshell densities were related to higher vegetation cover. The importance of depressions was apparent when eggshell density was categorized by terrain. Mean eggshell density was lowest in plains, intermediate in pond habitats, and highest in depression habitats (Fig. 2).

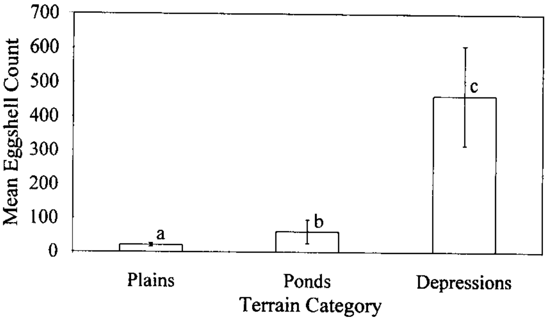

Fig. 2. Mean eggshell count categorized by terrain. Groups with different letters are significantly different at $P < 0.05$. Error bars are 1 SE.

Other studies have suggested that salt marsh mosquitoes lay eggs close to potential larval habitat such as depressions (Kerridge 1971, Sinclair 1976, Addison et al. 1992, Ritchie et al. 1992, Ritchie 1994). Ritchie et al. (1992) demonstrated that eggshells of *Ae. taeniorhynchus* occurred in highest densities in pond banks, with lower densities in pond bottoms, plains, and uplands in 3 out of 4 sites. Ritchie (1994) further demonstrated higher eggshell densities of *Ae. vigilax* in the banks of depressions than in plains. In our study, the low eggshell density of salt marsh plains may be offset by their large spatial extent, possibly making salt marsh plains important overall contributors to mosquito production. Higher frequency of flooding and flushing of ponds relative to depressions may make ponds suboptimal oviposition sites for *Ae. vigilax*. Flooding of many ponds on Kooragang Island is restricted by culverts. Removal of these culverts may decrease mosquito production by increasing flooding frequency and allowing access to predators. The presence of hoofprints appeared to play no significant role in increasing oviposition, possibly because of the presence of other more preferred habitats in the region. However, tidal dispersal of *Ae. vigilax* larvae may distribute new larvae from oviposition sites to hoofprint-disturbed habitats in some areas. Hoofprints cover extensive areas of marsh on the island; thus, their importance to larval entrapment, survival, and adult production warrants further investigation.

Percent cover of vegetation for both *S. virginicus* and *S. quinqueflora* was positively related to eggshell density. Dale et al. (1986) proposed that *Ae. vigilax* require moderate densities of vegetation so that gravid females can access the soil surface but

Table 4. Summary statistics for the eggs and eggshells of *Aedes vigilax* collected for the mesoscale study.

Site	Category	Mean (1 SE)	variance/mean	Range	% of total
Plot 1	Eggs	1.08 (0.27)	6.67	0–18	3.9
	Hatched eggshells	22.98 (4.85)	102.44	0–330	82.7
	Unhatched eggshells	3.73 (0.94)	23.92	0–58	13.4
	Total	27.79 (5.84)	122.60	0–369	100
Plot 2	Eggs	0.12 (0.08)	4.93	0–7	1.5
	Hatched eggshells	6.66 (1.21)	21.98	0–64	82.8
	Unhatched eggshells	1.26 (0.28)	6.18	0–19	15.7
	Total	8.08 (1.42)	25.01	0–83	100

Table 5. Regression equations describing the relationship between the density of *Aedes vigilax* eggshells, vegetation, and elevation for the mesoscale study. The response variable was $\log_{10}$(eggs and eggshells per core +1).

	Plot 1		Plot 2	
Environmental factor	Coefficient (1 SE)	Probability[1]	Coefficient (1 SE)	Probability[1]
Intercept	0.02 (0.18)	ns	1.16 (0.23)	***
Elevation	0.17 (0.06)	**	−0.23 (0.06)	***
$(\text{Elevation})^2$	−0.01 (0.003)	**	0.01 (0.003)	***
Sarcocornia quinqueflora	0.51 (0.19)	*	0.08 (0.14)	ns
Sporobolus virginicus	0.14 (0.35)	ns	0.70 (0.16)	***
S. quinqueflora + *S. virginicus*	0.46 (0.20)	*	0.58 (0.13)	***
Overall model	$F_{5,94} = 7.27$, $r^2 = 0.24$, $n = 100$	***	$F_{5,94} = 8.79$, $r^2 = 0.28$, $n = 100$	***

[1] Significance of each regression coefficient: ns, not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

also ensure that eggs are protected from desiccation immediately after oviposition. Due to the low to moderate coverage of both plant species in this study (Table 2), the effect of high vegetation cover on eggshell density is not known.

All of the environmental factors in our study may influence soil moisture in ways that affect egg conditioning and oviposition. Moderate to high substrate moisture is a prerequisite for oviposition by floodwater mosquitoes such as *Aedes* and *Psorophora* (Knight and Baker 1962, Strickman 1980, Novak 1981, Meek and Williams 1986, Welch and Olson 1987). However, *Ae. vigilax* avoid laying eggs in waterlogged soil (Sinclair 1976). Our study suggests that the requirements for oviposition and egg conditioning are met in association with moderately vegetated areas around the depressions that are most distant from the flooding source at the lowest elevations. Flooding frequency may be expected to be low in such habitats, but higher vegetation cover in combination with low elevations may maintain high soil moisture. The interaction of flooding frequency, soil moisture, and the environmental factors are complex because of the topographically heterogeneous nature of the island and the fact that flooding is restricted by culverts.

Mesoscale study: Similar to the macroscale study, hatched eggshells dominated samples in the mesoscale study; unhatched eggshells and eggs constituted smaller fractions of the total. The distribution of eggs and eggshells was also highly aggregated (Table 4). Twenty-four percent of the variation in eggshell numbers at plot 1 was accounted for with the regression model in Table 5. Eggshell density was estimated to be highest at 8.5 cm relative elevation with vegetation present. Analysis of variance suggested that mean eggshell density was significantly lower in bare soil than in both *S. quinqueflora* and mixed samples (*S. quinqueflora* and *S. virginicus*). There was no significant difference in eggshell density between *S. quinqueflora* and mixed samples (Fig. 3). Only three samples came from stands of *S. virginicus,* so no conclusions could be made regarding its effect on eggshell density. Twenty-eight percent of the variability in eggshell density at plot 2 was explained with the regression model in Table 5. Eggshell density was shown to be lowest at 11.5 cm relative elevation among bare soil and *S. quinqueflora* stands and highest among *S. virginicus* stands and mixed vegetation at the lowest elevations within the plot. In contrast to plot 1, analysis of variance showed significant differences in mean eggshell density among the dominant vegetation categories (Fig. 4).

This study has shown that the effects of vegetation species and elevation were site-specific. Past

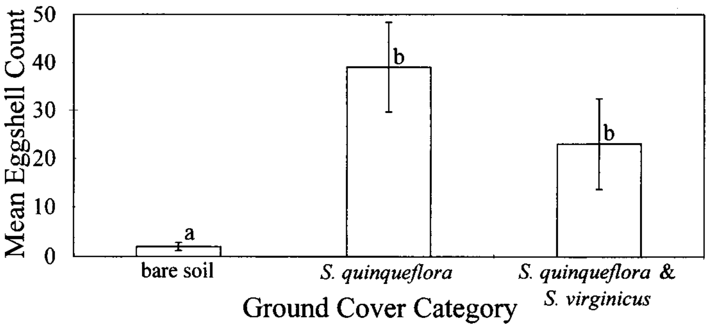

Fig. 3. Mean eggshell count categorized by ground cover for plot 1. Groups with different letters are significantly different at $P < 0.05$. Error bars are 1 SE.

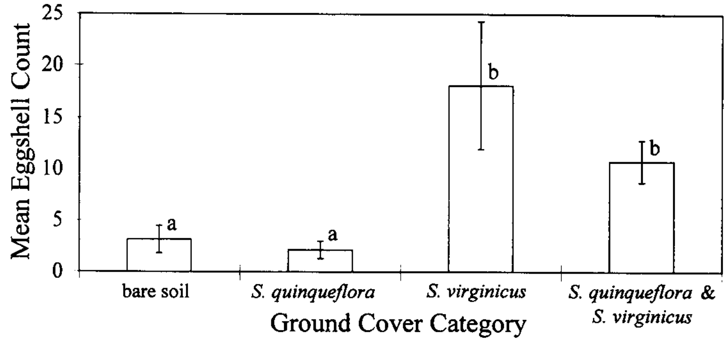

Fig. 4. Mean eggshell count categorized by ground cover for plot 2. Groups with different letters are significantly different at $P < 0.05$. Error bars are 1 SE.

research indicates that the eggs of *Ae. vigilax* are usually associated with the presence of vegetation (Reynolds 1961, Kerridge 1971, Sinclair 1976). A similar association with the presence of vegetation was described for the inland floodwater mosquito, *Ae. vexans* (Horsfall et al. 1975). In general, there was little difference in the effects of *S. quinqueflora, S. virginicus,* and a mixture of the 2 species on the density of *Ae. vigilax* eggshells. However, there were comparable eggshell densities between bare soil and *S. quinqueflora* at plot 2. Similarly, Ritchie (1994) did not find differences between ponds vegetated with either *S. quinqueflora, S. virginicus,* or the mangrove *A. marina.* In contrast, Kay and Jorgensen (1986) suggested that *Ae. vigilax* preferred to oviposit among *S. virginicus,* although egg densities were variable and eggs were also found among *S. quinqueflora.* In this study, the effect of vegetation density was not considered and, as suggested by the macroscale study, may account for some of the unexplained variation in eggshell density at the plots.

The zone of highest eggshell density within the plots may represent optimal soil moisture conditions for oviposition. Earlier studies have determined the presence of preferred elevations through egg and eggshell sampling (Kerridge 1971, Horsfall et al. 1975, Enfield and Pritchard 1977, Novak 1981, Fallis and Snow 1983, Curtis 1985, Dale et al. 1986, Suggars et al. 1986, Ritchie and Johnson 1991). The width, definition, and position of the preferred horizon for oviposition around larval habitats vary with rainfall, local topography, vegetation density and species, accumulation of detritus, and drainage. In our study, the relative relief in both plots was only 16 cm; thus, the preferred zone of soil moisture was not well defined.

Management implications: The current study suggests that depression habitats are the main source and ponds are a secondary source of *Ae. vigilax* eggs. Mosquito production in depressions may therefore be reduced by converting the depressions into pondlike systems using runneling or open marsh water management techniques. Moreover, shallow depressions should not be created during wetland rehabilitation where mosquito production is an issue. Areas designated for wetland rehabilitation or creation in the upper intertidal zone should be graded evenly so that no pools form after flooding by spring tides. There is little effect of different plant species on eggshell density in the surrounding soil; thus, species of plant is not a major consideration during wetland rehabilitation. However, eggs are known to be oviposited onto the bases of *S. virginicus* (Kay and Jorgensen 1986). This is yet to be quantified for Kooragang Island but should be taken into consideration when selecting plant species for wetland rehabilitation.

ACKNOWLEDGMENTS

We acknowledge support provided by Pat Dale, Brian Conroy, Peggy Svoboda, and the Kooragang Wetland Rehabilitation Project. We thank Greg West for his assistance in map preparation. We thank undergraduate ecology students in the Department of Biological Sciences, University of Newcastle, for their participation in the mesoscale study. Financial assistance provided by BHP (Newcastle Steelworks) is appreciated.

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