Wind Exposure and Distribution of Pitcherplant Mosquito (Diptera: Culicidae)

STEPHEN B. HEARD[1]

Department of Biology, Leidy Labs, University of Pennsylvania, Philadelphia, PA 19104–6018

ABSTRACT In western Newfoundland the pitcherplant mosquito, *Wyeomyia smithii* (Coquillett), is absent from many potential habitat patches (bogs with populations of the purple pitcher plant, *Sarracenia purpurea*) Bog size, pitcher-plant density, and wind exposure in bogs were estimated and ranked Rank ordered variables were intercorrelated and any single variable had significant predictive power for mosquito occurrence, but only wind exposure was significant in a multiple regression. Bogs exposed to wind harbored smaller or no mosquito populations A likely explanation for this pattern is that reduced winter snow cover induces high overwinter mortality of diapausing mosquito larvae

KEY WORDS *Wyeomyia smithii*, distribution, overwintering

Wyeomyia smithii (Coquillett) is a small mosquito whose larvae are obligate inhabitants of water-filled purple pitcher plant (*Sarracenia purpurea* L.) leaves W smithii has been widely used as a model organism; for instance, to address hypotheses about keystone predation (Addicott 1974), population genetics and natural selection (e.g., Bradshaw & Holzapfel 1986), life history theory (e.g., Bradshaw & Holzapfel 1983, Istock 1981), behavioral ecology (Heard 1994a), physiological ecology (e.g., Kingsolver 1979), toxicology (Fairchild et al. 1987), and resource processing (Heard 1994b). Although the autecology of *W. smithii* and its interactions with other pitcher-plant inquilines have been studied extensively (Heard 1994b and references therein), little has been written about factors controlling the distribution of the species

At the broadest geographic scale, the distribution of *W. smithii* appears to be more or less concordant with that of its host *S. purpurea* (Bradshaw & Holzapfel 1986, Istock & Weisburg 1987). *S. purpurea* occurs in *Sphagnum* bogs and on other wet, infertile soils over much of eastern and north central North America. Istock & Weisburg (1987) noted the existence of 'a few' sites with pitcher plants but without *W. smithii*, attributing these to local extinctions during past droughts. However, in western Newfoundland (and also in northern Saskatchewan; Burgess & Rempel 1971) mosquitoes are very patchily distributed, with many bogs harboring healthy populations of pitcher plants, but few or no mosquitoes. I conducted an observational study to identify physical factors influencing the distribution of *W. smithii* among bogs.

I focused on three attributes of bogs (patches of potential mosquito habitat) potentially important to larval or adult mosquitoes. First, I examined effects of wind exposure. Wind exposure could act through effects on winter snow cover and, hence, conditions for overwintering larvae or through an influence on dispersal of the poorly flying adults. Second, I tested for an effect of bog size, which might be important for island biogeographic reasons (e.g., MacArthur & Wilson 1967) Third, I tested for an effect of pitcher-plant density within bogs.

Materials and Methods

In 1990 and 1991, I examined pitcher plants in 36 bogs in and around Gros Morne National Park, Newfoundland, Canada (49° 30' N, 57° 50' W; Fig. 1). Thirty-four of the 36 bogs were visited twice; one bog was visited only in 1990 and one only in 1991.

In each bog, and independently in each year, I recorded rank indices of wind exposure (scale 0–3), bog size (scale 0–4), and pitcher-plant density (scale 0–3). Wind exposure of a bog was assessed considering shelter offered by surrounding vegetation and topography with respect to prevailing winds (from the southwest; Caines & Deichmann 1990). I then checked one leaf from each of 50 pitcher plants for the presence of *W. smithii* larvae. All leaves were healthy 2nd-yr leaves potentially harboring late-instar mosquito larvae. I refer to the number of leaves containing larvae as *W. smithii* frequency
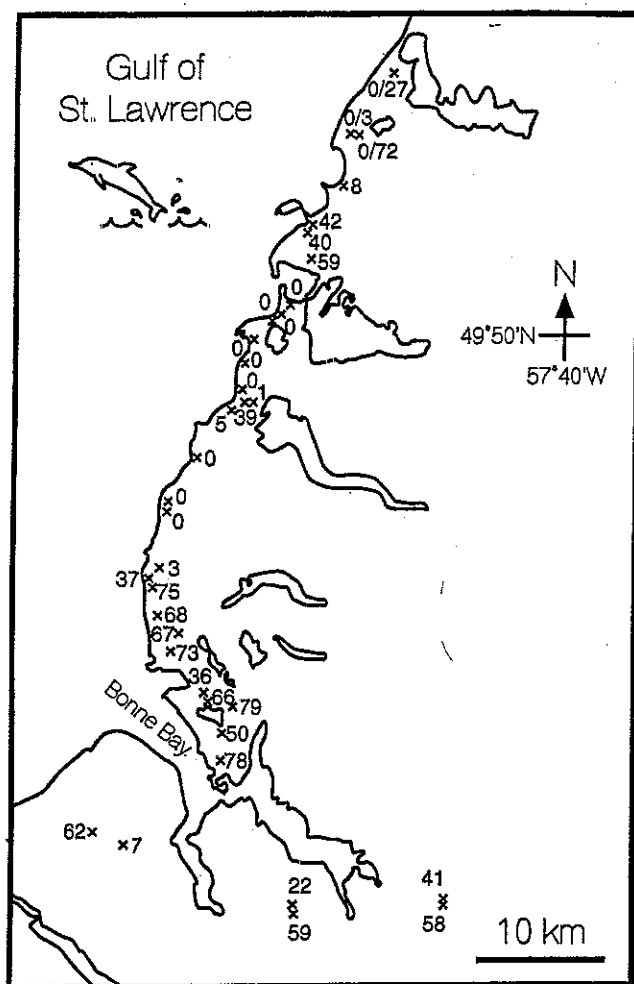
Fig. 1. Map of the study area, showing locations of bogs (X) where mosquito frequency was assessed. Associated numbers are *W. smithii* frequencies: numbers of leaves containing larvae, out of 100 leaves examined (50 in 1990 and 50 in 1991). Bogs with two numbers separated by slashes are those for which two frequencies were determined: for the exposed central area (first number) and for a sheltered edge in lee of trees or shrubs (second number).

In three large bogs (the northernmost three in Fig. 1), I assessed *W. smithii* frequency separately for the sheltered, western edge and for a more exposed central location. I used both measures in analyses, giving a total of 39 frequencies. Other sites were separated by habitat unsuitable for *W. smithii*.

Although indices of wind exposure, bog size, and pitcher-plant density were subjective, they were also reliable as ordinal variables. In each year, data were recorded on a single day (27 June 1990 and 26 June 1991, just before *W. smithii* pupation). Indices for bogs visited twice were highly repeatable between years (wind exposure: Pearson's $r = 0.96$; bog size: $r = 0.95$; pitcher-plant density: $r = 0.83$; all $n = 37$, $P < 0.0001$). The use of rank indices allowed the capture of rank-level information about a large number of bogs; quantitative measurements would have required prohibitive levels of effort. Wind

Table 1. Pearson correlation coefficients and associated probabilities for all combinations of the three explanatory variables

	Wind exposure	Bog size
Pitcher-plant density	-0.61	-0.38
	$P < 0.0001$	$P = 0.0168$
Bog size	$+0.60$	—
	$P < 0.0001$	

exposure, in particular, could be quantified only with simultaneous and long-term wind-speed measurements from several microhabitats within each bog.

Because *W. smithii* frequency was highly correlated between years ($r = 0.95$, $n = 37$, $P < 0.0001$), I combined the 1990 and 1991 data for further analyses. I used the average of the two values for wind exposure, bog size, and pitcher-plant density, and I used the sum of the two *W. smithii* frequencies (giving a number of leaves out of 100 harboring *W. smithii*). For the two bogs that were visited only once, I proceeded as if a second visit had produced identical data. Given the high correlation between years, the error introduced by this procedure is negligible.

I used a multiple regression analysis conducted with SAS PROC GLM (SAS Institute 1988), using type III sums of squares, to examine the dependence of mosquito frequency on bog attributes. I used a backward elimination procedure, beginning with an analysis including all three explanatory variables as well as all possible two- and three-way interactions. I then dropped nonsignificant interactions and finally main effects, pooling any variance associated with these factors with the error variance. All factors so pooled were clearly nonsignificant (all $F < 1.14$; df = 1, 31–35; $P > 0.29$). I also examined patterns of association among the possible explanatory variables by calculating pairwise Pearson's correlation coefficients, and because there were significant correlations, I examined regressions with each explanatory variable entered alone. In these single-factor regressions I tested for nonlinearity according to Zar (1984).

The use of frequency data and discrete independent variables prevented the use of standard F tables to evaluate significance (Zar 1984). Instead, I evaluated significance of regression F statistics by comparing actual F values to distributions obtained from 1,000 random permutations of the data (Manly 1991). Departures of randomization probabilities from tabulated values were negligible.

Results

The three bog attributes were significantly intercorrelated (Table 1); larger bogs tended to have lower pitcher-plant densities and, as might be expected, to be more exposed to wind. Any of

Table 2. Test statistics and associated probabilities for single-variable regressions

Explanatory variable	Slope	F	df	P	r^2
Wind exposure	−17.9	31.7	1, 37	<0.0001	0.46
Bog size	−13.9	13.2	1, 37	0.0009	0.26
Pitcher-plant density	+20.8	12.2	1, 37	0.0013	0.25

Dependent variable in each case is mosquito frequency

the three attributes had significant explanatory power when used alone in a regression of mosquito frequency (Table 2). Wind exposure, however, explained a much larger fraction of the variance in mosquito frequency than did either of the other two bog attributes (46 versus 25–26%).

In the multiple regression analysis, no interaction terms were significant (all $F < 0.64$; df = 1, 31–32; $P > 0.43$). With wind exposure also in the model, neither bog size nor pitcher-plant density was significant, even after pooling the interaction sums of squares to improve power (both $F < 1.14$; df = 1, 35; $P > 0.29$). Therefore, the final model included only wind exposure as a factor. Mosquito frequency declined significantly (randomization $P < 0.001$) with wind exposure (Fig. 2). The regression did not depart significantly from linearity ($F = 0.47$; df = 5, 32; $P = 0.47$).

Discussion

Because the three bog attributes measured were intercorrelated, it is difficult to partition variance in mosquito frequency unambiguously
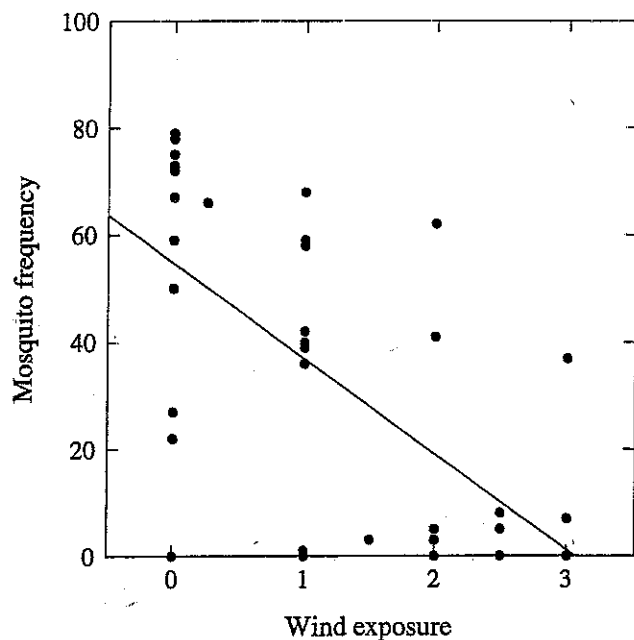

Fig. 2 Mosquito frequency as a function of wind exposure. Line is the least squares regression equation: (frequency) = 54.7 − 17.9 · (wind); $r^2 = 0.46$ ($F = 31.7$; df = 1, 37; randomization $P < 0.001$).

among them. However, for three reasons, it is probable that wind exposure most directly influences mosquito frequency.

First, the multiple regression, based on type III sums of squares, indicated that wind exposure has predictive power for mosquito frequency even after bog size and pitcher-plant density have been considered. However, the converse is not true: after wind exposure is considered, neither of the other variables contributes any further to the model.

Second, in three bogs (the northernmost three in Fig. 1), I found mosquitoes present in pitchers growing along the sheltered western edges, but not in the more exposed central portions. In these contrasts, bog size and pitcher-plant density do not differ and cannot be driving the pattern.

Finally, for island biogeographical reasons mosquito frequency should, if anything, increase with bog size. Larger bogs might be expected to have higher population densities, lower population extinction rates, and higher immigration rates (MacArthur & Wilson 1967). Instead, mosquito frequency declines with bog size (Table 2), suggesting that the bog size effect is indirect. Of the measured bog attributes, only wind exposure is plausible as a strong influence on mosquito frequency.

A likely mechanism for the wind exposure hypothesis is to be found in the overwintering biology of W. smithii, which spends the winter in a third-instar diapause (Smith & Brust 1971) in the frozen pitcher fluid. Evans & Brust (1972, in Manitoba) and Paterson (1971, in New Brunswick) found that overwintering W. smithii showed substantial mortality at temperatures below about −3°C, with 100% mortality within 3 wk at −10°C. As winter air temperatures for both areas are often below −10°C (as they are at Gros Morne; Caines & Deichmann 1990), Evans & Brust (1972) and Paterson (1971) argued that W. smithii populations are dependent on an insulating snow cover to protect larvae from freezing mortality. More sheltered bogs in the study area have more complete snow cover (A. Marceau, Gros Morne National Park, personal communication) and, therefore, variation in wind exposure could produce variation in W. smithii winter survival and control the inter-bog distribution of the species. Wind exposure under this scenario should be most important near the northern limit of W. smithii, and it is suggestive that W. smithii is apparently sporadic in northern Saskatchewan (Burgess & Rempel 1971) and is not yet known from pitcher-plant populations in northeastern British Columbia (P. Belton, personal communication). Wyeomyia smithii has also been reported from several sites in Labrador (Evans 1971, Haufe 1953), although no information is available on local distributional patterns.

In contrast to *W. smithii*, the pitcher-plant midge, *Metriocnemus knabi* (Coquillett), is present in high frequencies in both sheltered and exposed western Newfoundland bogs (personal observation). *M. knabi*, however, is much more cold tolerant and should not depend as strongly on snow cover: Paterson (1971) found only moderate mortality of New Brunswick *M. knabi* larvae stored at −16.5°C for 26 d. The omnipresence of *M. knabi* also weighs against two alternative mechanisms for the association between wind exposure and mosquito frequency. Because adult *W. smithii* are poor fliers, wind exposure might conceivably limit adult dispersal, but *M. knabi* adults fly just as weakly. Similarly, if lower prey capture rates made pitcher-plant leaves in exposed bogs less hospitable, both species should be affected as both are strongly resource-limited in western Newfoundland (Heard 1994b).

In the northern part of its range, *W. smithii* is restricted to a subset of potential habitat patches (bogs). Although historical factors (Istock & Weisburg 1987) may play some role in this restriction, there appears to be a strong effect of at least one present-day physical factor: mosquitoes are uncommon or absent in northern bogs exposed to wind. In this feature of its natural history, *W. smithii* is unlike the syntopic midge *M. knabi*, which despite having a rather similar life cycle, is a virtually omnipresent inhabitant of pitcher-plant leaves.

Acknowledgments

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