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Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*)

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Summary

Wyeomyia smithii mosquitoes distribute their eggs across available oviposition sites (water-holding pitcher plant leaves) of varying quality. I experimentally examined responses to three components of site quality: conspecific larval density, larval density of the pitcher plant midge, *Metriocnemus knabi*, and pitcher size. Responses to larval treatments were complex and apparently suboptimal. Although mosquito larval performance is better in leaves with fewer conspecific and more midge larvae, females did not lay more eggs in such pitchers. Instead, more eggs were laid in experimental pitchers containing either midge or mosquito larvae, but fewer eggs in pitchers with neither or both. More eggs were laid in larger pitchers, which tend to accumulate more resources and dry out less often. Therefore, although the oviposition decisions made were suboptimal, they were better than random.

Keywords: optimal offspring distribution; oviposition behaviour; pitcher plant; mosquitoes; *Wyeomyia smithii*

Introduction

In animals lacking either parental care or highly vagile juveniles, offspring survival, growth and fecundity may be strongly influenced by the quality of the microhabitats in which those offspring find themselves. Female behaviour governing the distribution of offspring among possible habitat patches can therefore be an important component of maternal fitness. Models of optimal offspring distribution (e.g. Parker and Courtney, 1984; Parker and Begon, 1986; Ives, 1989) are closely related to optimal foraging models, except that the decisions to be optimized involve the number of offspring left to feed and grow rather than the amount of time spent feeding in a patch. Aspects of site quality that may enter in such decisions include resource levels (e.g. Trimble, 1979), presence and density of intra- and interspecific competitors, predators and other potentially interacting species (e.g. McDaniel *et al.* 1979; Roitberg *et al.* 1982; McCrae, 1984; Messina *et al.*, 1992), physical and chemical suitability for offspring development (e.g. Trimble and Wellington, 1979), and probability of disturbance (e.g. Bradshaw and Holzapfel, 1988). A high quality site is one with a relatively high expected fitness return to a female per egg deposited there. However, perfect decisions in either foraging or offspring distribution may not be possible because animals cannot predict stochastic elements of future site quality, because they cannot always sense the relevant aspects of site quality (e.g. Sutherland *et al.*, 1988) or because individuals lack complete knowledge of the ecological landscape and must use imperfect rules to adjust their behaviour to perceived site quality distributions (e.g. Janetos and Cole, 1981; Cézilly and Boy, 1991). Because oviposition behaviour has such direct fitness consequences, the extent

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to which real organisms behave according to the predictions of optimal behaviour models has important implications for evolutionary and population ecology.

In this paper I examine the responses of pitcher plant mosquitoes (*Wyeomyia smithii* (Coq.) (Diptera: Culicidae)), in a natural field population, to oviposition sites of differing quality. *Wyeomyia smithii* larvae are obligate inhabitants of the water-filled leaves of the purple pitcher plant *Sarracenia purpurea*, which is widely distributed in bogs and other wet but infertile soils through much of eastern and central North America. The pitcher habitat is shared by the pitcher plant midge *Metriocnemus knabi* (Coq.) (Chironomidae), the pitcher plant sarcophagid *Blaesoxipha fletcheri* (Aldrich), the pitcher plant mite *Sarraceniopus gibsoni* (Nesbitt) and a variety of smaller organisms including rotifers, protozoa and bacteria.

The oviposition behaviour of mosquitoes has been widely studied and many species are capable of using tactile, chemotactile, olfactory or visual cues to assess such site characteristics as colour, reflectance, texture, moisture, salinity, surrounding vegetation, bacterial growth, conspecific population density and the presence of a wide variety of chemicals (for reviews, see Maire, (1983) and Bentley and Day, (1989)). However, at least some mosquitoes fail to make oviposition decisions that would provide demonstrable fitness advantages (e.g. Yap and Foo, 1984).

I examined the response of *W. smithii* females to three characteristics of possible oviposition sites (pitchers) which are components of site quality: pitcher size, conspecific larval density and *M. knabi* larval density. Pitcher size is a predictor of future resource levels (larger pitchers catch more prey; Cresswell, 1993) and also of the probability of desiccation (larger pitchers are less likely to dry out; Kingsolver, 1979). Conspecific larvae are important potential competitors, because mosquito populations at the study site are consistently and strongly food limited (Heard, 1994). *Metriocnemus knabi* larval density is relevant because in pitcher plant leaves, midge larvae facilitate mosquito larval growth (Bradshaw, 1983; Heard, 1994). If females select oviposition sites optimally, more eggs should be laid in larger pitchers, pitchers containing more midge larvae and pitchers containing fewer mosquito larvae. I compared this expectation with data from natural and otherwise unmanipulated pitcher plant leaves of various sizes and with known densities of midge and mosquito larvae, exposed to ovipositing females for several days.

Previous studies of *W. smithii* oviposition (Fish and Hall, 1978; Mogi and Mokry, 1980; Bradshaw, 1983; Istock *et al.*, 1983) have considered pitcher age (youngest pitchers preferred) and size (largest pitchers usually preferred) but have paid little attention to larval densities. Bradshaw (1983) suggested that *W. smithii* females avoid pitchers in which they have already oviposited for a short time, possibly implying a deterrent effect of mosquito density, but the suggestion appears to have been based on field observations of a single female and was not tested experimentally. Bradshaw (1983) also reported experimental evidence that even large numbers of eggs did not deter females from their preference for the youngest leaf in a rosette. However, in these experiments egg densities were neither controlled nor considered independently of pitcher age. Similarly, Istock *et al.* (1983) found that high egg densities did not deter females from their preference for cut pitcher plant leaves over jars of distilled water, but did not consider egg density independently.

Materials and methods

Study site and organisms

I studied *W. smithii* oviposition behaviour in Gros Morne National Park in western Newfoundland, Canada, in August 1991 and August 1992. The study site was a small bog near the park's Visitor Centre, known locally as 'Long Marsh' (49°34′35″N, 57°52′20″W, elevation 60 m). Pitcher plants were abundant. Larvae used to set up experimental treatments were collected from bogs within 10 km of the primary site. Most pitchers harboured both *W. smithii* and *M. knabi*, as well as populations of *S. gibsoni*, the rotifer *Habrotrocha rosa* Donner and protozoa. In August, many pitchers also contained larvae of *B. fletcheri*.

In Newfoundland, *W. smithii* is univoltine and oviposition by *M. knabi* and larviposition by *B. fletcheri* occur nearly simultaneously with *W. smithii* oviposition in late July and August (*contra* Fish and Hall, 1978). Northern populations of *W. smithii* are obligately autogenous (Bradshaw, 1980), making resource acquisition during the larval period of particular importance. Females are attracted to pitcher plant leaves for oviposition at least in part by a water-soluble chemical cue (Istock *et al.*, 1983). For an overview of the biology of *W. smithii* and pitcher plant inquiline communities, see, for example, Smith and Brust (1971), Bradshaw (1983), Farkas and Brust (1986), and Heard (1994).

Experimental methods

I prepared pitcher plant leaves with controlled numbers of inhabitants as follows. When pitchers are first produced, they are closed and sterile inside (Hepburn and St John, 1927). Approximately 2 weeks before beginning each year's experiment I selected healthy pitchers which had not yet opened. I covered each developing pitcher with a bag sewn from white bridal tulle (bridal veil fabric; mesh size ≈ 1 mm). Each bag was large enough to contain a fully expanded pitcher and was secured with a string tied around the petiole. Bridal tulle prevents access to pitcher interiors by ovipositing adult *W. smithii* and *M. knabi*, but blocks a minimum of light and allows normal leaf development. When all pitchers were fully expanded and open, I removed the tulle bags and immediately introduced larvae as required to make up the treatments. Each pitcher also received approximately 5 ml of distilled water. Because pitchers were not fully expanded when selected I could not control the distribution of pitcher sizes.

In 1991 I manipulated all three insect inquilines in a three-way, full factorial design. Treatments were *B. fletcheri* larvae 0 or 1, *M. knabi* larvae 0 or 25 and *W. smithii* larvae 0 or 20. *Metriocnemus knabi* and *W. smithii* larvae were a mixture of first, second and a few third instars (the first instars are of rather short duration). There were 10 replicates of each of the eight treatments. After removing the tulle bags I left the pitchers exposed to normal bog conditions, and to visits by ovipositing females, for 3 days. At the end of this period, I collected all the pitchers and dissected them. I recorded the number of *W. smithii* eggs in each pitcher, including hatched eggs (there were few of these). The laboratory incubation period for *W. smithii* eggs is approximately 3 days (Price, 1958), so hatched eggs were likely laid very early in the experimental period. For each pitcher, I also recorded a measure of pitcher size (width in mm of the hood at the widest point). Hood width is simple to measure and is highly correlated with other possible measures of pitcher size, including pitcher volume (Pearson's $r = 0.85, p < 0.0001, n = 318$) and pitcher mouth diameter ($r = 0.77, p < 0.0001, n = 329$; data from the same site in 1989).

In 1992 I used identical methods but different insect treatments. Other experiments had indicated no effect of *B. fletcheri* on *W. smithii* survival or growth (Heard, 1993) and preliminary analyses could detect no effect of *B. fletcheri* on *W. smithii* oviposition either. Therefore, I omitted the *B. fletcheri* treatment in 1992. I also used 20 *M. knabi* larvae instead of 25 and 10 *W. smithii* larvae instead of 20. These treatments required that fewer larvae be collected and were also closer to natural population densities (for *W. smithii*, 20 larvae exceeds the 95th percentile for 1989–1992 densities at the study site). In 1992 there were eight replicates of each of the four treatments, plus an extra 28 pitchers in the control group (no larvae) which were intended to allow a within-group estimate of the effect of pitcher size.

All leaves were the youngest open leaves in their rosettes when used in the experiments.

Leaves were assigned randomly to treatments, so that the remaining variation in leaf age and size would not produce spurious treatment effects.

Statistical analysis

All analyses were analyses of covariance (ANCOVA), conducted with SAS Version 6.03 (PROC GLM; SAS Institute Inc., 1988) using type III sums of squares. The statistical analysis proceeded in several steps. Because preliminary analyses showed no effect of *B. fletcheri* on *W. smithii* oviposition in 1991 ($F_{1,74} = 1.19$, $p = 0.28$ after pooling non-significant interactions), I ignored this treatment in all further analyses. Although different larval densities were used, I coded mosquito and midge treatments identically (+/−) in the 2 years of the study. Any differences in oviposition between 1991 and 1992 treatments that result from the different densities used would, as a result, appear in the year-by-midge and year-by-mosquito interaction terms.

The design I analysed was therefore a 2 × 2 × 2 fixed-effects factorial design (midge treatment, mosquito treatment and year) with a covariate (pitcher size). This design was unbalanced because I included the data for the extra 1992 control pitchers. I began by running a fully saturated model (including all possible interactions). I used a pooling procedure for non-significant interactions to improve estimates of error variance and increase error degrees of freedom. There is little agreement on pooling procedures for ANOVA interactions (cf. Bennett and Franklin, 1954; Zar, 1984), but in ANCOVA non-significant treatment-by-covariate interactions are routinely pooled. For consistency I chose to pool all non-significant ($p > 0.05$) interactions (both treatment-by-covariate and treatment-by-treatment). This was done in two steps. First, I reran the analysis omitting all three- and four-way interactions (all $F_{1,119} < 0.46, p > 0.50$) and pooled their sums of squares with the error. Of the six two-way interactions, five (including all treatment-by-covariate interactions) were still non-significant (all $F_{1,124} < 1.84$, $p > 0.17$), so I ran a third analysis omitting those five interactions as well. I report full results only for this final analysis.

The year effect might arguably be considered a random effect, but since interactions involving the year were omitted from the final analysis the distinction is unimportant here. Because egg number distributions are discrete and highly non-normal, for the final analysis I determined significance by randomization (Manly, 1991; 500 randomizations). The resulting probabilities differed only slightly from tabulated values, indicating that the ANCOVA procedure was robust to the violations of its assumptions.

Results

The pitchers I used ranged from 21 to 55 mm hood width when fully expanded (mean 37.7 ± 0.58 mm (SE), $n = 136$). This size range is typical of pitchers at the study site, except that it omits the very smallest pitchers. There was noticeable, but not unacceptable, mortality of introduced larvae, with approximately 80% of *W, smithii* larvae and 65% of *M. knabi* larvae surviving the introduction and 3 day experiment. Much of this mortality may have resulted from handling, although substantial mortality also occurs among undisturbed larvae (Fish and Hall, 1978; Bradshaw, 1983).

Wyeomyia smithii oviposition rates were low, with a mean of 0.99 (SE 0.18) eggs laid per pitcher across all treatments. Statistical tests for the final ANCOVA model are shown in Table 1 and estimated egg numbers for all treatment/year combinations are shown in Table 2. The final model included only one significant interaction (mosquito treatment by midge treatment). This interaction resulted from a pattern where more eggs were laid in pitchers receiving either the midge or the mosquito treatment, compared to pitchers receiving neither or both. Standard errors were relatively large, but so were maximum likelihood estimates of effects: treatments

Table 1. ANCOVA results for *W. smithii* oviposition preferences

Source[a]	df	MS	p[b]
Year	1	12.79	0.082
Pitcher size	1	17.59	0.050
Mosquito treatment	1	2.96	0.414
Midge treatment	1	3.17	0.384
Mosquito × midge	1	26.04	0.008
Error	129	2.01	

Pitcher size is a covariate. Interactions not shown were non-significant ($p > 0.05$).

[a] Total model MS = 13.46, $p = 0.007$, $r^2 = 0.11$.

[b] Probabilities determined by randomization.

Table 2. Estimated egg numbers for treatment groups from ANCOVA in Table 1

Midge treatment	Mosquito treatment	1991 egg number[a]	1992 egg number[a]
–	–	0.93 (0.37)	0.25 (0.31)
–	+	1.53 (0.40)	0.86 (0.47)
+	–	2.18 (0.41)	1.50 (0.47)
+	+	0.91 (0.40)	0.24 (0.47)

See text for larval treatments.

[a] Estimate (standard error), estimated for the overall mean pitcher size (37.7 mm hood width). Slope of pitcher size regression, 0.0549 ± 0.0267 (SE).

differ by factors of between 1.5 and 6 (Table 2). The mosquito treatment and midge treatment main effects were small and not significant (population means (adjusted for the covariate, estimated from the ANCOVA model, and pooling across all other factors) were +/– mosquito larvae, 1.01/0.98 eggs; +/– midge larvae, 0.92/0.75 eggs). The year effect was suggestive ($p = 0.082$), perhaps with more eggs in 1991. There was a just significant effect of the pitcher size covariate, with larger pitchers having more eggs laid (slope ± SE, 0.055 ± 0.027, $p = 0.050$). There was a very similar regression among control pitchers only (slope ± SE, 0.040 ± 0.019, $p = 0.042$). The overall model, while clearly significant ($F_{5,129} = 3.32$, $p = 0.007$), accounted for only 11% of the variance in egg numbers.

Discussion

Because I could not distinguish between sib and non-sib eggs, the oviposition rates I measured combine (as did those of Mogi and Mokry (1980) and Bradshaw (1983)) two sorts of information: a high quality pitcher might receive clutches from more females or a larger clutch from each female. Unambiguous discrimination between these would require following individual ovipositing females in the field and would make controlled experiments very difficult. Because relatively few eggs were found in my experimental pitchers, it would appear that clutch sizes (number of eggs laid by one female in one pitcher at one visit) are usually very small. Of 58 pitchers with at least one egg, 33 had only one, so many clutches must consist of a single egg (although female *W. smithii* may lay tens to over a hundred eggs over their lifetimes: Istock *et al.*, 1975; O'Meara *et al.*, 1981; Farkas and Brust, 1985). This is consistent with the results of Mogi and Mokry (1980), who found little evidence that clutch sizes exceeded one. However, Bradshaw (1983) reported observing a Florida female laying three eggs in one visit to a pitcher, so multiple-egg clutches are possible. In this respect *W. smithii* is intermediate between the other two insect inquilines of pitcher plants: *M. knabi* females appear to lay eggs in large numbers (S.B. Heard, unpublished data), while *B. fletcheri* females (which are ovoviviparous) deposit only a single larva into each pitcher (Forsyth and Robertson, 1975).

The overall response to the cues I examined was not strong: the total model r^2 was only 11%. However, this was not surprising, for two major reasons. The first is that the experiment had to be kept short, with relatively few eggs laid in the experimental pitchers. Most pitchers (90%) had zero, one or two *W. smithii* eggs. With a longer experiment, recruitment of mosquitoes and especially midges by oviposition would have seriously distorted the original treatments. Removal of recruited eggs from experimental pitchers was not an option: only by destroying the leaf can all material be removed (Natase *et al.* 1991) and chemicals leaching from the eggs could not be removed at all. With small and discrete values for the dependent variable, a large error variance is to be expected. The fact that the discreteness and non-normality of egg numbers violate ANOVA and regression assumptions is not important because I used randomization techniques to assess significance (Manly, 1991).

The second reason for the low model r^2 is that the experiments were conducted in a natural pitcher plant population, rather than in the laboratory. Although laboratory oviposition behaviour experiments afford greater control and therefore may give cleaner results, they are much more difficult to interpret and are prone to artefactual effects (e.g. Atkinson, 1983). Several uncontrolled factors seem likely to have contributed to error variance in my experiments. For instance, pitchers differed in their surrounding vegetation, the proximity of other pitchers and their microclimate, any of which might influence oviposition behaviour (Russell and Rao, 1942; Clements, 1963). Pitcher age, furthermore, is an important determinant of *W. smithii* oviposition, with the youngest pitchers apparently preferred (Fish and Hall, 1978; Bradshaw, 1983) based on chemical cues (Istock *et al.*, 1975, 1983). The pitchers used in these experiments were within a week in age, were the youngest in their rosettes when used and were randomized among treatments to prevent spurious effects due to pitcher age. However, remaining age variation may well have injected some noise into the results.

The (non-significant) trend toward lower egg numbers in 1992 is an expected result of lower *W. smithii* population densities that year. The mean per-pitcher larval density at the study site for the mosquito cohort emerging in 1991 was 5.35 (± 0.38 (SE), n = 249), compared to 2.85 (± 0.27, n = 196) for the cohort emerging in 1992. No two-way interactions involving the year effect were significant, indicating that responses to pitcher size and treatments were similar between the two years.

The significant positive regression of egg number on pitcher size is consistent with two previous reports (Mogi and Mokry, 1980; Bradshaw, 1983). The effect of pitcher size was independent of treatment and year (no significant two-way interactions involving pitcher size). Although I cannot exclude larger pitchers simply being more conspicuous, use of a quadratic term in pitcher hood width did not improve the model r^2 as it should have if conspicuousness is a function of pitcher area (visual cross-section). Therefore, it seems likely that the positive regression reflects active preference.

Larger pitchers are likely to prove superior larval habitats for three reasons. First, larger pitchers tend to catch more prey (Wolfe, 1981; Cresswell, 1993) and prey capture by pitchers strongly limits mosquito growth (Heard, 1994). Second, larger pitchers are less likely to dry out during the summer (Kingsolver, 1979), although at the Newfoundland study site this is probably unimportant because, except in extremely dry years, pitchers rarely dry out completely. Finally, larger pitchers generally contain more midge larvae (Paterson and Cameron, 1982), which facilitate mosquito growth (Bradshaw, 1983; Heard, 1994). Larger pitchers are not deterministically better, as there are substantial stochastic influences on all three of these factors, but pitcher size used as a cue can provide some predictive power. The apparent preference for larger pitchers should result in a larval distribution across pitchers that allows better mean larval growth, and hence a better fitness return to individual females, than would a random allocation of eggs to pitchers.

The effects of the larval density treatments were more complex (Tables 1 and 2). More *W. smithii* eggs were laid in pitchers that received one or the other, but not both, of the larval treatments (significant midge–mosquito interaction). There was no overall effect (main effect) of larvae of either species considered alone. This result was unexpected and is difficult to interpret. If it is real, it is possible that it indicates a non-linear response to increasing total larval density. The data are consistent with increased oviposition in pitchers with intermediate total densities (either treatment alone) but reduced oviposition in empty pitchers or pitchers with high total densities (two treatments together).

Many mosquito species do prefer to oviposit in water holding moderate densities of conspecific larvae, perhaps because this indicates a suitable habitat (Bentley and Day, 1989). Although effects of higher densities have not been as thoroughly examined, in some cases water with crowded larvae has proved repellent (e.g. Reisen and Siddiqui, 1978; Maire, 1985). Furthermore, females often seem unable to distinguish between conspecific and heterospecific larvae, at least within the Culicidae (e.g. Hudson and McLintock (1967) for *Aedes aegypti* but not for two *Culex*; Bruno and Laurence, 1979; McDaniel *et al.*, 1979). If the midge–mosquito interaction is to be explained in this way, *W. smithii* females must be capable of sensing larval densities but incapable of distinguishing between larvae belonging to different families of Diptera. This is unlikely if pheromones are involved, but possible with less specific cues such as fecal material or microbial metabolites (Bentley and Day, 1989). Experiments designed to manipulate total larval density and specific composition independently would be useful.

Whatever the interpretation of the midge–mosquito interaction, it seems clear that in terms of distributing larvae for maximal expected offspring fitness, female *W. smithii* do not respond optimally to larval densities. Although the best oviposition strategy is not precisely known, it is clear that (otherwise identical) pitchers with more midge larvae represent a better microhabitat for mosquito larval growth, while pitchers with more mosquito larvae are worse (Bradshaw, 1983; Heard, 1994) – and larval growth strongly influences adult fecundity (Istock *et al.*, 1975; Moeur and Istock, 1980; Farkas and Brust, 1985). If *W. smithii* females behaved optimally, therefore, we would expect a significant positive effect of midge density and a significant negative effect of mosquito density on oviposition. Instead, the mosquito density main effect was almost non-existent and the main effect of midge density was only slightly larger and not significant (Table 1) despite sample sizes sufficient to detect the pitcher size effect and the midge – mosquito interaction. Both main effects were swamped by the midge–mosquito interaction (Table 2).

Singer (1984) has pointed out that claims of suboptimality may err if choosing 'better' oviposition sites were to interfere with female survival or if females are limited by oviposition opportunities rather than eggs available for laying. Applied to my experiments, the first argument would require that ovipositing in a pitcher with no larvae or many larvae is in some way risky, which seems unlikely. The second argument is easy to counter, as *W. smithii* females can be seen in the field visiting and rejecting many pitchers before laying eggs (Bradshaw, 1983). While one can never refute all conceivable arguments of this type, it seems reasonable to conclude that *W. smithii* oviposition behavior is demonstrably suboptimal (although while it is imperfect, it is better than random due to the pitcher size response discussed above).

This imperfection in behaviour could be attributed to any number of causes, for instance, information processing constraints (Ward, 1992), weak selection against suboptimal alternatives (Janetos and Cole, 1981) or a lack of genetic variation for oviposition behaviour. Partly because the experiments reported here provide little information about the precise mechanisms of oviposition site selection, I cannot discriminate unambiguously between these possibilities.

The extent to which organisms in general achieve optimality in morphology and behaviour has been the subject of much recent discussion (Gould and Lewontin, 1979; Maynard Smith *et al.*, 1985; Ward, 1991; Ward, 1992), and imperfection in oviposition behaviour has been documented in other insect species (e.g. Singer, 1984; Yap and Foo, 1984). Pitcher plant mosquitoes appear to line up with organisms that are better than they might be, but not as good as we can imagine.

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