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Factors influencing the seasonal life history of the pitcher-plant mosquito, *Wyeomyia smithii*

ALAN O. BERGLAND, MARCI AGOTSCH, DERRICK MATHIAS, WILLIAM E. BRADSHAW and CHRISTINA M. HOLZAPFEL Center for Ecology and Evolutionary Biology, University of Oregon, Eugene, U.S.A.

Abstract. 1. The effects of resource levels, thermal microclimate, and seasonal oviposition patterns on fecundity and survivorship in the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), were examined at a northern Wisconsin bog over the course of 2 years. *Wyeomyia smithii* are bivoltine at this locality, thereby enabling the study of summer and overwintering generations separately.

2. Nutrient resources of *W. smithii* were not limiting and there was no indication of density-dependent survivorship or fecundity.

3. Oviposition rates were highest in young, large pitchers and individual mosquitoes appeared to allocate only a few eggs to any one leaf.

4. Winter was the harsh season, and the principal manifestation of seasonal harshness was reduced survivorship.

5. Overwintering *W. smithii* that had been oviposited later in the summer had a higher odds of survival than those oviposited earlier in the summer.

6. It was concluded that dispersal of eggs among many pitchers serves to spread the risk of encountering lethal winter temperatures among spatially unpredictable patches.

Key words. Fecundity, keystone species, life history, oviposition, prey capture, resource levels, seasonality, survivorship, thermal microclimate, *Wyeomyia smithii*.

Introduction

Understanding the environmental sources of phenotypic variation in fitness traits within a local population is important for interpreting the forces of selection acting on that population. Herein, the environmental variation across local spatial and seasonal scales is examined, along with the effect of that variation on the survival and fecundity of the mosquito, *Wyeomyia smithii*. *Wyeomyia smithii* lives its entire pre-adult life inside the water-filled leaves of its host, the carnivorous pitcher plant, *Sarracenia purpurea*. Pitchers represent highly circumscribed, replicate habitats, thereby providing an unusual opportunity to observe natural variability and conduct manipulative field experiments across spatial and seasonal scales.

The nutritional resources of fauna developing within the leaves consist of prey captured by the host leaf. Prey capture generally increases with leaf size and decreases with leaf age (Fish & Hall, 1978; Wolfe, 1981; Bradshaw, 1983; Cresswell, 1991; Heard, 1998), but at least in Newfoundland (50°N) does not vary over the summer (Heard, 1998). Nutrient levels within pitchers can affect both pre-adult survivorship and adult reproductive capacity (Istock *et al.*, 1975; Farkas & Brust, 1985; Bradshaw & Holzapfel, 1986, 1992).

Sarracenia purpurea are found in different microhabitats within particular localities and are thus subject to varying degrees of environmental exposure leading to different thermal regimes within their leaves (Kingsolver, 1979). Thermal regimes within pitchers affect larval survivorship, particularly when they exceed *W. smithii*'s upper and lower lethal limits (Kingsolver, 1979; Farkas & Brust, 1985; Bradshaw *et al.*, 2004).

The timing of oviposition may also play a role in affecting the survival and reproductive capacity of *W. smithii*. For the

Correspondence: Alan O. Bergland, Department of Ecology and Evolutionary Biology, Box G-W, 80 Waterman Street, Brown University, Providence, RI 02912, U.S.A. E-mail: Alan_Bergland@Brown.edu

overwintering generation, there should be an optimal time to enter diapause (Taylor, 1980). Individuals that continue developing too late in the season may fail to reproduce successfully (Bradshaw *et al*., 2004) and those that enter diapause too early may experience reduced fitness due to a prolonged, warm-season diapause as has been shown both in the laboratory (Bradshaw *et al*., 1998, 2004; Tatar *et al*., 2001) and in the field (Leather *et al*., 1993).

This study will determine how the local nutrient levels, thermal environment, and oviposition date affect survival and reproductive capacity, and how these factors differentially affect summer and overwintering generations. Survivorship, fecundity, and patterns of oviposition of *W. smithii* were determined for both summer and winter generations in a bivoltine population where prey capture of the host leaves was concurrently manipulated. Specifically, the following predictions were tested: (1) Supplementing prey capture should increase survivorship and fecundity whereas reducing prey capture should decrease survivorship and fecundity. (2) Per-leaf oviposition patterns should be positively correlated with larval resources, i.e. with prey capture by the host leaf. (3) Temperatures in pitchers vary according to the degree of shading or with southern or northern aspect, thus larval *W. smithii* living in areas with more extreme temperatures should have lower survivorship than those in more moderate areas. (4) Oviposition dates closer to winter should result in higher overwintering survivorship.

Materials and methods

Life-history and biology of *Wyeomyia smithii* and its host, *Sarracenia purpurea*

Wyeomyia smithii, the pitcher-plant mosquito, completes its pre-adult development in the water-filled pitchers of *Sarracenia purpurea*, the purple pitcher-plant. Larval *W. smithii* feed on prey captured by its host plant as well as microbial communities living in the pitcher water (Addicott, 1974). Northern *W. smithii* diapause and overwinter as third-instar larvae, metamorphose to pupae in the spring and early summer, and eclose as adults shortly thereafter (Lounibos & Bradshaw, 1975; Bradshaw & Lounibos, 1977).

The pitcher-plant midge, *Metriocnemus knabi*, also inhabits *S. purpurea* during its larval stage at this locality. Competitive effects of *W. smithii* on *M. knabi* occur primarily at high densities of both species and are less than the effect of *M. knabi* on itself; effects of *M. knabi* on *W. smithii* are significant only at high densities where the effect of *M. knabi* on *W. smithii* is facilitative, not competitive (Bradshaw, 1983). Both the mean crowding of *W. smithii* and the mean interspecific crowding of *W. smithii* on *M. knabi* decline with latitude (Bradshaw, 1983) and Heard (1994b) did not find significant competitive interaction between *M. knabi* and *W. smithii* at another northern bog. Consequently, it was assumed that interspecific competition between *M. knabi* and *W. smithii* was negligible at the study area, Why Not Bog, and did not warrant the additional flushing of leaves necessary to extract *M. knabi* from the narrow base of the leaves.

Sarracenia purpurea is a carnivorous pitcher plant that lives throughout the eastern U.S.A. and Canada (30–54°N) in bogs, cedar swamps, and wet pine savannahs. Leaves of *S. purpurea* open from early spring to early autumn. Initially, the leaves are soft and flaccid but harden within approximately a week of opening, during which time they begin to fill with rainwater and dew. The leaves remain green throughout the winter and generally senesce their second summer. Leaves develop in a sequential whorl and can be rank aged from the overlap of their successive petioles (Fish & Hall, 1978).

The study area: Why Not Bog

Why Not Bog (locality ML in Lair *et al*., 1997; Bradshaw *et al*., 2000, 2003a, 2003b, 2004; Bradshaw & Holzapfel, 2000, 2001a, 2001b) is an elliptical, kettle hole bog in northern Wisconsin, U.S.A. (46°N, 89°W). Surrounding the open water of Why Not Bog is a floating sphagnum moss mat, lined on its periphery primarily by small *Picea mariana* (black spruce), *Larix laricina* (tamarack), clusters of *Chamaedaphne calyculata* (leatherleaf), and *Ledum groenlandicum* (Labrador tea). Conifer forests line the exterior of the bog mat. Two distinct areas were distinguished in which *S. purpurea* live: the open bog mat exposed to the full sun and the ecotone where pitcher plants are shaded by the surrounding trees and shrubs. Plants along the northern edge of the bog have a southern aspect and experience greater sunlight throughout the day than plants along the southern edge of the bog (Bradshaw *et al*., 2000; 2004). Plants at the western edge of the bog experience an intermediate level of insolation.

Experimental design and methods

Survivorship and fecundity: the rob Peter to pay Paul (RPPP) experiment. In the autumn of 2001, seven sites were identified across Why Not Bog. These sites were distributed across the bog with two sites in the northern quadrant, two sites in the southern quadrant, and three sites in the western quadrant. In the northern and southern quadrants, one site of each was located in the open bog mat and one site was located in the ecotone. In the western quadrant, two sites were located in the open bog mat and one site was located in the ecotone.

In each site, ten plants were selected by their presumed success the previous summer, i.e. plants with many healthy leaves. An attempt was made to select plants with varying leaf sizes. Leaves of each plant were marked with plant and leaf numbers using a black Sharpie© pen. Leaf numbers corresponded to the rank age of the leaf. Leaf rank 1 was the first leaf opened on the plant the previous summer.

Populations of *W. smithii* in each leaf were censused with replacement during the autumn of 2001 and 2002. The number of *W. smithii* were recorded along with the width at its widest point perpendicular to the keel (in millimetres) of the leaf in which they resided.

During the spring of 2002 and 2003, *W. smithii* were censused once with replacement in each leaf of the identified plants. From mid-June to mid-September during the summers of 2002 and 2003 all marked leaves on the 70 plants were censused for pupae every 2–4 days. Pupae were removed and sexed. Female pupae were weighed using a Cahn C-31 microbalance accurate to 1 µg. Occasionally, adult eclosion occurred before the census. In that case, pupal sex was determined from the exuviae and female mass was estimated from regression of known female pupal mass on the area of the anal paddles of its respective exuvia. Anal pupal paddle area (PPA) was defined as: $\mathrm{PPA} = (\mathrm{LW} \times \mathrm{LH}) + (\mathrm{RW} \times \mathrm{RH})$, where LW is left paddle width, LH is left paddle height, RW is right paddle width, and RH is right paddle height in millimetres. Female pupal mass (FPM) increased with the area of the anal pupal paddles ($r^2 = 0.63$, $P < 0.001$):

$$\mathrm{FPM(mg)} = -0.623 + 1543.24 \pm 149.02\,\mathrm{PPA}\,(\mathrm{mm}^2), \quad (1)$$

where the regression coefficient is provided ± SE.

From mid-June to mid-September, 2002 and 2003, resource levels were manipulated in leaves opening during that summer by removing prey, adding prey, or leaving prey in place (control leaves). At each site, the ten plants were assigned treatments that were applied to all of their leaves by turning cards. Three plants had prey removed from their leaves (*reduced* resources); these prey were added to leaves on three other plants (*augmented* resources), and four plants served as unmanipulated controls. During the summer of 2002 only prey floating on the water's surface were removed from the starved plants. During the summer of 2003 both floating and sunken prey were removed. Prey manipulations occurred on the same day as censusing and prey were transferred to leaves closest in age to the source leaf and only to plants within the same site. New leaves opening through the summer were labelled according to plant and age. Each time a plant was visited, new leaves were given a designation of *new bud*, *leaf about to open*, *open but flaccid*, or *open and hard*. Leaves were marked only when they were open and hard, so as to avoid leaf damage. On the day a leaf was marked, its width at the widest point, perpendicular to the keel, was measured.

Survivorship and fecundity: larval resources

At the beginning of the summer of 2002, ten plants with abundant, well-formed leaves were selected in the northern quadrants and ten similar plants in the southern quadrants of Why Not Bog. In each quadrant, five plants were located in the exposed bog mat and five were located in the protected ecotonal areas of the bog. As new leaves emerged they were marked in the same fashion as leaves of the RPPP plants. Leaves were censused every 2–4 days without replacement for prey capture. Prey were preserved in vials of 95% ethanol and measured at a later date. The same plants and procedures were used during the summer of 2003.

In order to quantify larval resources, the length of each preserved prey was measured and converted into prey biomass using the following methodology. During the spring of 1999, whole prey were collected from pitcher-plant leaves at eight northern (Maryland, U.S.A. to Newfoundland, Canada and west to Ontario, Canada) and two mountain (North Carolina, U.S.A.) localities. Their anterior–posterior length was measured and they were dried over desiccant to constant mass and weighed on a Mettler microbalance accurate to within 1 µg. Since ants were the predominant prey, the prey were grouped into ant and non-ant arthropods. Prey dry mass for each group was regressed on body length to obtain estimates of prey capture rate ($\mathrm{mg\,day^{-1}}$) and total accumulative prey capture (mg) from prey censuses of pitchers at Why Not Bog.

Dry body mass (mg) of prey was closely correlated with body length (mm) both for ants ($r^2 = 0.801$, $n = 383$, $P < 0.001$):

$$\log_{10}(\mathrm{drymass}) = -2.28 + 2.92 \pm 0.075 \log_{10}(\mathrm{bodylength}), \quad (2)$$

and for non-ant arthropods ($r^2 = 0.757$, $n = 143$, $P < 0.001$):

$$\log_{10}(\mathrm{drymass}) = -1.84 + 2.31 \pm 0.11 \log_{10}(\mathrm{bodylength}), \quad (3)$$

where the regression coefficients are provided with ± SE.

Temperature

In the autumn of 2001, Spectrum Watchdog 100 series data loggers were placed in the leaves of pitcher plants located centrally to the ten plants in each of the seven sites of the RPPP experiment. Two healthy (non-experimental) plants were chosen at each site to house a data logger. Each data logger was set to record temperature every 2 h and had the capacity to record temperatures for up to 6 months each. Data loggers were retrieved, data were downloaded, and the loggers were reset and placed back in their respective plants in the spring of 2002, autumn of 2002, spring of 2003, and autumn of 2003.

Oviposition and overwintering

Oviposition was monitored by counting eggs at each census in plants described above in which (a) prey were manipulated (RPPP) and (b) from which prey were removed without replacement. In the former case, eggs were censused with replacement in leaves opened during that summer; in the latter case, eggs were removed without replacement. Oviposition data from (b) were used to calculate oviposition patterns; data from (a) were used to calculate survival statistics. For both procedures, during the summer of

2002, only eggs floating on the surface were counted; those that had sunk to the bottom were not counted. During the summer of 2003, both floating and sunken eggs were counted. The relative embryonation or embryonic survivorship of floating vs. sunken eggs was not determined.

Statistical methods

Data were analysed in R 1.9.1 using the *stats* and *gee* packages (R Development Core Team, 2004). Female fecundity was defined as ($r^2 = 0.551$, $P < 0.001$)

$$\text{Fecundity} = a\log_{10}(1.05 + 0.345\,\text{FPM}), \qquad (4)$$

where FPM is female pupal wet mass in milligrams (Bradshaw & Holzapfel, 1992). Survivorship data were transformed using the arcsine square-root transformation, in order to correct for proportional data (Sokal & Rohlf, 1995), for ANOVAS and ANCOVAS. Overwintering survivorship per leaf was defined as

$$S_O = \frac{P_{SS}}{L_F}, \qquad (5)$$

and summer survivorship per leaf is defined as

$$S_S = \frac{P_{SS} + L_D}{E_{SS}}, \qquad (6)$$

where P_{SS} was the number of pupae collected during the spring and summer, L_F was the number of overwintering larvae in leaves the previous year, L_D was the number of larvae entering into diapause during the autumn, and E_{SS} was the number of eggs laid during the spring and summer. Individual survival was used for logistic regression, and the generalised estimation equation model was used in order to correct for leaf effect (Venables & Ripley, 2002). Significance values were calculated from the robust Z-score using the Wald test (Hosmer & Lemeshow, 2000).

Results

Survivorship and fecundity

Survivorship to pupation was higher in the summer than in the winter generation but did not vary significantly according to year, region of the bog, ecotone/mat, or prey treatment (Fig. 1, Table 1). Fecundity did not vary with year, season, region of the bog, ecotone/mat, or prey treatment (Fig. 2, Table 1).

Larval resources and oviposition

The rate of prey capture declined exponentially with leaf age (Fig. 3a; $r^2 = 0.24$, $P < 0.001$) and, using the relationship between prey body length and biomass, the total biomass of prey captured increased exponentially with leaf width (Fig. 3b; $r^2 = 0.18$, $P < 0.001$).

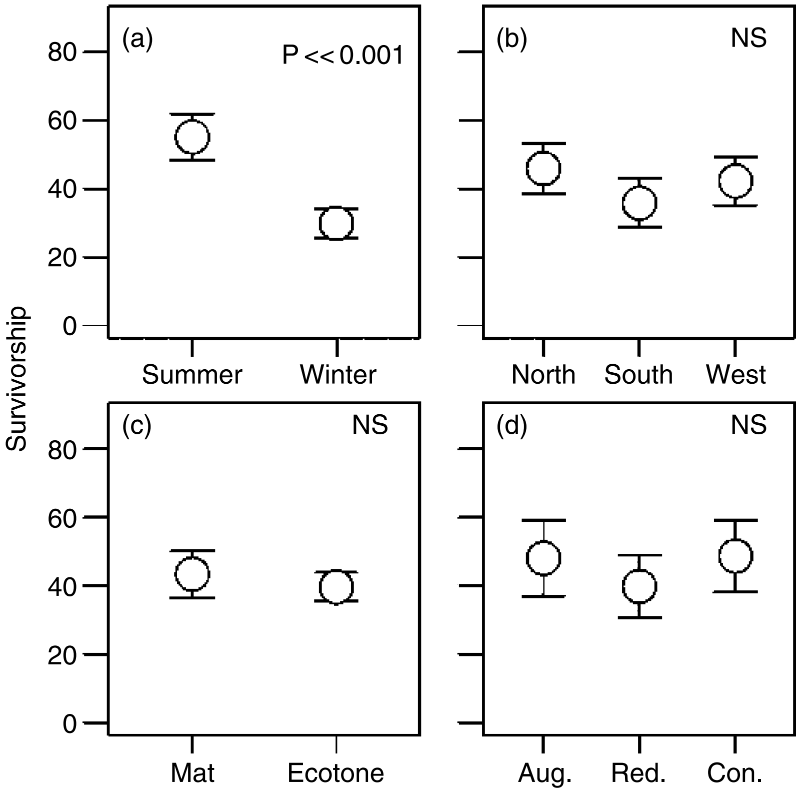

Fig. 1. Survivorship, arcsine square-root transformed, of *Wyeomyia smithii* partitioned between (a) generation, (b) location in the bog, (c) degree of exposure, and (d) relative resource level (Aug., augmented; Red., reduced; Con., control). Differences in survivorship were only found between summer and overwintering generations (a). Error bars show ±2 SE.

Table 1. Effect of season, location, exposure, and resource levels on survivorship and fecundity of *Wyeomyia smithii* from nested ANOVA. Season refers to either summer or winter generation, Loc. refers to quadrant (north, south, west), M/E refers to mat or ecotonal plants, and ARC refers to relative resource level (augmented, reduced, or control).

	Survivorship					Fecundity				
Source of variation	d.f.	SS	MS	*F*	*P*	d.f.	SS	MS	*F*	*P*
Year	1	1.651	1.651	0.079	0.82	1	21	21	0.036	0.88
Season(Year)	1	20.91	20.91	402.1	<0.001	1	585	585	0.080	0.79
Loc.(Season)	4	0.209	0.052	0.62	0.68	4	7307	1827	1.90	0.31
M/E(Loc.)	3	0.252	0.084	0.19	0.90	3	2885	962	1.73	0.30
ARC(M/E)	4	1.752	0.438	1.61	0.18	4	2222	556	0.53	0.71
Leaves	142	38.69	0.272			46	47999	1043		

Oviposition rates declined exponentially with leaf age (Fig. 3c; $r^2 = 0.76$, $P < 0.001$). Total eggs that accumulated in a leaf over the summer increased exponentially with leaf width (Fig. 3d; $r^2 = 0.33$, $P < 0.001$) and did not differ between the mat and ecotonal areas (Table 2).

Temperature

Summer (mid June to mid September) temperatures were divided into two categories: survivable temperatures, in which leaf temperature never rose above 41 °C (lethal to pupae; survivable by larvae: Zani *et al.*, 2005) for more than three consecutive days; and lethal temperatures, in which leaf temperature rose above 41 °C for four or more consecutive days. Lethal summer temperatures occurred in two of 19 leaves, one each in an exposed leaf and in a protected leaf (Table 3).

Late autumn, winter, and early spring (November, December, January, February, and March) temperatures were divided into two categories: survivable temperatures, in which leaf temperature never fell below −3 °C for more than three consecutive days; and lethal temperatures, in which leaf temperature fell below −3 °C for four or more consecutive days during the 5-month period (Bradshaw *et al.*, 2004). Survivable temperatures (Table 3) were more frequent in open mat than in the ecotonal areas of the bog (Fisher's Exact Test: $P = 0.040$). Within leaves in which lethal temperatures occurred, the number of lethal days did not differ between the mat (mean $\log_{10} \pm \mathrm{SE} = 1.65 \pm 0.18$) and ecotonal ($1.85 \pm 0.07$) areas of the bog (ANOVA: $F_{1,2} = 1.20$ $P = 0.296$).

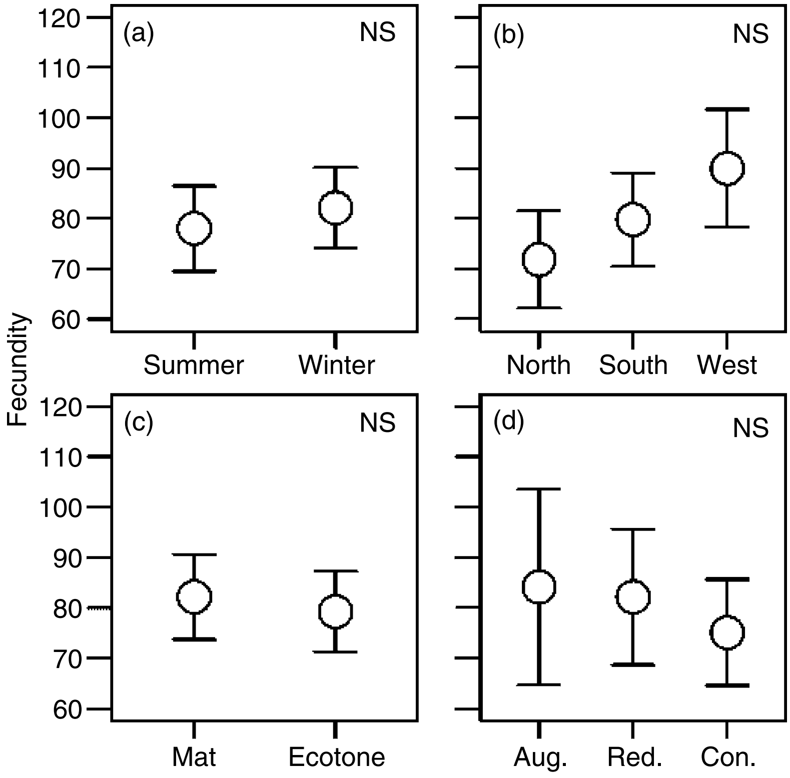

Fig. 2. Fecundity of female *Wyeomyia smithii* partitioned between (a) generation, (b) location in the bog, (c) degree of exposure, and (d) relative resource level (Aug., augmented; Red., reduced; Con., control). Error bars are ± 2 SE.

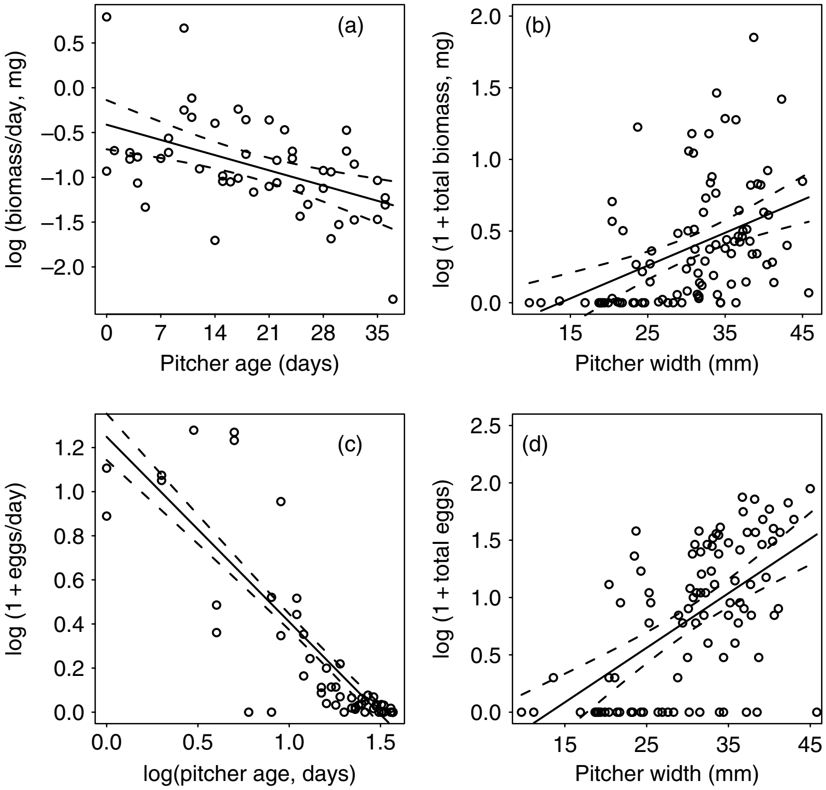

Fig. 3. Prey capture of *Sarracenia purpurea* and oviposition by *Wyeomyia smithii* with respect to pitcher age and pitcher size. (a) The rate of biomass captured, dry mass (mg)/day, by pitchers decreases exponentially with age. (b) The total biomass of prey captured, dry mass (mg), increases exponentially with pitcher width. (c) The rate of oviposition, eggs/day, decreases exponentially with pitcher age. (d) The total number of eggs oviposited in a pitcher increases exponentially with pitcher width. Solid lines represent the regression lines; dashed lines represent the 95% confidence intervals.

Oviposition dates, survivorship, and fecundity

The Julian opening date (JOD, days after 1 January) of pitchers increased with increasing rank age and decreased with the total number of pitchers developing on the plant during that year ($r^2 = 0.752$, $P < 0.001$):

$$\begin{aligned} \text{JOD} &= 232 + 76.22 \pm 1.82 \log_{10}(\text{Rank Age}) \\ &\quad - 68.30 \pm 2.94 \log_{10}(\text{Number of leaves}), \end{aligned} \tag{7}$$

where regression coefficients are provided ±SE. Because daily oviposition rate declines exponentially with leaf age (Fig. 3c), leaf opening date is used as a proxy for oviposition date.

Using this equation to assign an opening date for individual pitchers from 2001 *a posteriori* and using actual pitcher opening dates from 2002 and 2003, odds of survival increased 2.5% per day for the winter generation, and decreased less than 1% per day for the summer generation (Table 4). Fecundity did not vary with season, leaf opening date, or their interaction (Table 5).

Table 2. ANCOVA of total eggs oviposited by *Wyeomyia smithii* in a *Sarracenia purpurea* leaf with pitcher width as a covariate and degree of exposure (M/E, mat or ecotone) as the treatment.

Source of variation	d.f.	SS	MS	*F*	*P*
Width	1	12.40	12.40	40.36	<0.001
M/E	1	0.047	0.047	0.15	0.69
Width × M/E	1	0.14	0.14	0.45	0.50
Leaves	89	27.34	0.31		

Discussion

Wyeomyia smithii at Why Not Bog experience an environment wherein resources are abundant, summers are thermally benign, and winters are unpredictably harsh. Thus, contrary to the first prediction, survivorship and fecundity are independent of resource-level manipulation indicating a general excess of resources. However, in accord with the second prediction, per leaf oviposition patterns were positively correlated with larval resources. Contrary to the third prediction, survivorship in individual leaves does not depend upon location in the bog, despite a higher occurrence of lethal temperatures in the open bog. Finally, in accord with the fourth prediction, oviposition dates closer to winter increase the odds of survival over that winter. Odds of survival increases 2.5% per day, thereby imposing selective pressure in excess of drift for later oviposition of the overwintering generation at Why Not Bog where the population numbers of *W. smithii* are in the thousands.

However, larvae that survive winter at this locality have as high an expected fecundity as those developing in the summer (Table 1). This result differs from laboratory studies using New Jersey, U.S.A. (40°N, 74°W) populations of *W. smithii* (Bradshaw *et al.*, 1998) as well as other insects (e.g. various lepidopteran species and the bird cherry-oat

Table 3. Spatial distribution of lethal temperatures at Why Not Bog. Lethal temperatures are defined as number of times pitcher temperature exceeded 41 °C during four or more consecutive days during the summer or fell below −3 °C for four or more consecutive days during the winter.

		North		South		West	
Season	Coverage	Rep. 1*	Rep. 2	Rep. 1	Rep. 2	Rep. 1	Rep. 2
Summer 2002	Mat	0 (5)†	0 (4)	0 (0)	0 (0)	0 (0)	3 (37)
	Ecotone	0 (0)	NA‡	0 (0)	0 (0)	3 (24)	0 (0)
Summer 2003	Mat	NA	NA	0 (0)	0 (0)	0 (3)	0 (0)
	Ecotone	0 (0)	0 (0)	NA	0 (0)	NA	0 (0)
Winter 2001/2	Mat	0 (11)	2 (92)	0 (0)	NA	4 (51)	0 (0)
	Ecotone	3 (33)	NA	NA	1 (98)	2 (73)	NA
Winter 2002/3	Mat	6 (58)	4 (35)	0 (8)	1 (7)	0 (1)	2 (126)
	Ecotone	4 (51)	7 (82)	4 (50)	10 (158)	NA	7 (76)

*Each site had two replicate data loggers (Rep. 1 and Rep. 2).

†Number of times lethal temperatures occurred; numbers in parentheses show the total number of days that lethal temperatures occurred that season.

‡NA indicates data logger failure, and thus an incomplete temperature record.

aphid, *Rhodalosiphum padi*; see Leather *et al.*, 1993) in which overwintering incurred latent costs of reduced fecundity. At Why Not Bog, the principal manifestation of seasonal harshness is reduced winter survivorship (Fig. 1a).

The absence of a latent effect on fecundity may be due to the abundant resources at Why Not Bog. Larger leaves capture a greater biomass of prey (Fig. 3b) and accumulate a greater number of mosquito eggs than smaller leaves (Fig. 3d). This pattern has been used to imply adaptive oviposition behaviour in *W. smithii* that oviposit preferentially in the youngest leaves that have the greatest potential for future resources (Bradshaw, 1983; Bradshaw & Holzapfel, 1986). When larval resources are limiting and transient, pre-emptive competition can be an important component of fitness in mosquitoes (Livdahl, 1982; Broadie & Bradshaw, 1991; Maciá & Bradshaw, 2000). In southern populations along the Gulf Coast of Florida, U.S.A. (30°N, 85–87°W), larvae encounter density-dependent effects year-round, active prey capture declines with leaf age, and southern females oviposit in the very youngest leaves, relatively independently of size (Bradshaw, 1983; Bradshaw & Holzapfel, 1986).

Density-dependent development of *W. smithii* declines with increasing latitude or altitude of origin (Bradshaw & Holzapfel, 1986) and, concomitantly, leaf size becomes an increasingly important determinant of female oviposition behaviour (Bradshaw, 1983). At Why Not Bog, resources appear to be saturating as neither augmentation nor reduction of prey alter expected female fecundity (Fig. 2d), a highly sensitive measure of larval resource levels for *W. smithii* (Moeur & Istock, 1980; Bradshaw & Holzapfel, 1992) as well as other mosquitoes (Hawley, 1985). While competition for limiting resources cannot be invoked to explain oviposition behaviour of *W. smithii* at Why Not Bog, one cannot exclude the possibility that resource-dependent fitness has occurred at Why Not Bog in the recent past or that this oviposition behaviour reflects a broader, regional pattern or phylogenetic history of resource-dependent survivorship or reproductive success.

Table 4. Logistic regression, using generalised estimation equations, for larval *Wyeomyia smithii* survival as a function of leaf-opening date (JOD). *P*-values were calculated from the robust *Z*-score.

	n	Coefficient	Estimate	Robust SE	Robust Z	*P*
Summer	8255	Intercept	1.45	1.023	1.42	<<0.001
		JOD	−0.006	0.0048	−1.26	<<0.001
Winter	2637	Intercept	−6.95	1.80	−3.87	<<0.001
		JOD	0.025	0.0080	3.13	<<0.001

Along the Gulf Coast, individual *W. smithii* deposit only a few eggs in each leaf (Bradshaw, 1983). In far northern bogs (Heard, 1994a; Mogi & Mokry, 1980), only one or a few larvae are found in leaves, implying a similar allocation of only a few eggs per leaf. This individual oviposition behaviour was not observed at Why Not Bog, but the low rate of oviposition into leaves suggests that females are allocating only a fraction of their expected lifetime fecundity to each leaf, especially in older leaves (Fig. 3c). Southern populations encounter a mosaic of unpredictable resources and concomitant density-dependent development. Northern populations, released from much of this density-dependent constraint to fitness nonetheless encounter a

Table 5. ANCOVA of *Wyeomyia smithii* fecundity with leaf-opening date (JOD) as the covariate and season (summer or winter) as the treatment.

	Fecundity				
Source of variation	d.f.	SS	MS	*F*	*P*
Season	1	988	988	0.83	0.36
JOD	1	22	22	0.019	0.89
Season × JOD	1	1763	1763	1.48	0.23
Residuals	115	136643	118		

mosaic of unpredictable lethal winter temperatures leading to random survival. Parsimonious oviposition behaviour may therefore serve to spread the risk among spatially unpredictable patches in both southern and northern populations, but this behaviour may be maintained by different selective forces throughout the range of *W. smithii*.

Finally, the community composition within pitcher-plant leaves is largely determined by the abundance of *W. smithii* (predator), prey-capture by the host leaf, and their combined effect on species richness (Addicott, 1974; Cochran-Stafira & von Ende, 1998; Kneitel & Miller, 2002; Miller *et al.*, 2002). The food web in *S. purpurea* is unusual in exhibiting an increase in species richness with increasing latitude (Buckley *et al.*, 2003), contrasting with a latitudinal decline in density (Bradshaw, 1983; Bradshaw & Holzapfel, 1986). The present study found that even a reduction in prey in pitcher-plant leaves did not affect mosquito survivorship or pupal mass, indicating that at this northern bog, mosquitoes encounter an excess of resources, and suggesting that they should not be imposing limiting predation on populations of their invertebrate and microbial prey. Data from Why Not Bog therefore support the concept (Cochran-Stafira & von Ende, 1998; Miller *et al.*, 2002; Buckley *et al.*, 2003) of *W. smithii* as a keystone predator and the latitudinal decline in density of *W. smithii* as the reason for the unusual latitudinal increase in species richness in this community.

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