Adv. Odonatol. 6 : 59-77 April, 1994

MATING HABITAT CHOICE AND REPRODUCTIVE SUCCESS OF *PACHYDIPLAX LONGIPENNIS* (BURMEISTER) (ANISOPTERA : LIBELLULIDAE)

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Male *P. longipennis* defend shoreline territories, usually at ponds, where most mating and oviposition occur. Relationships between some shoreline characteristics and *P. longipennis* activity were investigated in New Jersey, USA. Males and females preferred similar, but not identical, regions of the pond edge and avoided others. Preference was positively correlated with vegetation height and with sunlight. Females were more selective than males in use of favored areas, and males were more selective at low than at high populations. Addition of perches and floating vegetation to unattractive areas markedly increased the use of those areas by both sexes. Males guarded their mates as the latter oviposited. Guarded females usually oviposited longer than unguarded females except at very high male densities. Females mated and initiated oviposition at frequencies approximately proportional to their frequency of occurrence but oviposited much less persistently in areas where they rarely occurred. Although a male's expectation of encountering females and mating was lower in regions of lowest density than in those of intermediate or high density, mated females tended to oviposit more persistently in the lowest density zones. Consequently, males apparently had lowest expectations of fertilizing eggs in regions of intermediate density, despite the fact that energetic costs of territory maintenance probably were higher than at low density. This situation might result from imperfect congruence of male and female perceptions of territory quality. Also, males in regions of higher mating probability might benefit if their mates return to oviposit without remating after leaving the pond. Both males and females could obtain benefits from areas where they occur most abundantly as a consequence of increased larval survival.

INTRODUCTION

A fundamental tasks of behavioral ecology is to explain, in adaptive as well as mechanistic terms, the spatial and temporal distribution of organisms. Furthermore, dispersion patterns and local population density are important determinants, as well as consequences, of species-specific mating strategies (EMLEN & ORING, 1977 ; THORNHILL & ALCOCK, 1983) and the reproductive tactics of individuals (CAMPANELLA, 1975 ; UEDA, 1979). The reproductive interests of males and females of a species may sometimes be in opposition (e.g., PARKER, 1979), and this divergence of interests, too, may be reflected in differing patterns of dispersion. Dragonflies often are good subjects for investigation of interactions between dispersion and reproductive behavior because many species are readily observable at sexual rendezvous sites, and their distribution is easy to assess.

Pachydiplax longipennis is a medium-sized libellulid that often is abundant at ponds and along sheltered lake shores. Various aspects of its reproductive behavior have been described (e.g. JOHNSON, 1962 ; ROBEY, 1975 ; FRIED & MAY, 1983), and its mating system was studied in detail by SHERMAN (1983a, b), who considered, among other things, factors that determine the spatial and temporal distribution of both males and females at breeding sites in South Carolina.

Our purpose here is to investigate further some characteristics and their effect on distribution of *P. longipennis* at a different breeding site, plus the effects of male and female distributions on one another and the effects of variation in local abundance of males and females on some aspects of apparent reproductive success of each sex.

MATERIAL AND METHODS

STUDY SITE

Pachydiplax longipennis was studied at a small, artificial pond (0.12 ha ; Fig. 1) on Rutgers University Horticultural Farm # 1 in New Brunswick, NJ, U.S.A. (40°28'N, 74°26'W). Vegetation of various heights, including overhanging trees (*Salix babylonica*), occurs at the immediate edge of the pond. Beyond the pond's edge are lawns and mature trees. The only perch sites available for dragonflies were either along the pond bank or in a small area of emergent vegetation near the outlet. A sandspit, with little vegetation and no perch sites, had developed as indicated (Fig. 1), due to outwash from the inlet stream.

To aid quantitative recording of dragonfly location and distribution, the pond margin was divided into 54 rectangular zones, each 10 ft (3.0 m) long and 60 ft^2 (5.6 m^2) in area (30 ft^2 on shore and 30 ft^2 over water) subdivided into 20 areas 2 × 1.5 ft each. Zone borders were marked by colored stakes.

Land vegetation height was estimated by placing a ruler at the center of each subdivision in each zone and measuring from the ground to the top of the tallest adjacent plant (BROWN, 1954). Values were averaged for the entire zone. Water surface vegetation was not quantified owing to its sparse, patchy nature and its extremely variable distribution as a result of wind drift.

GENERAL OBSERVATION AND CENSUS METHODS

We surveyed the pond by walking clockwise around it and observing each zone in turn for 30 s, using binoculars as necessary. The following data were recorded: the number of each sex of *P. longipennis* in the zone, whether the zone was shaded,

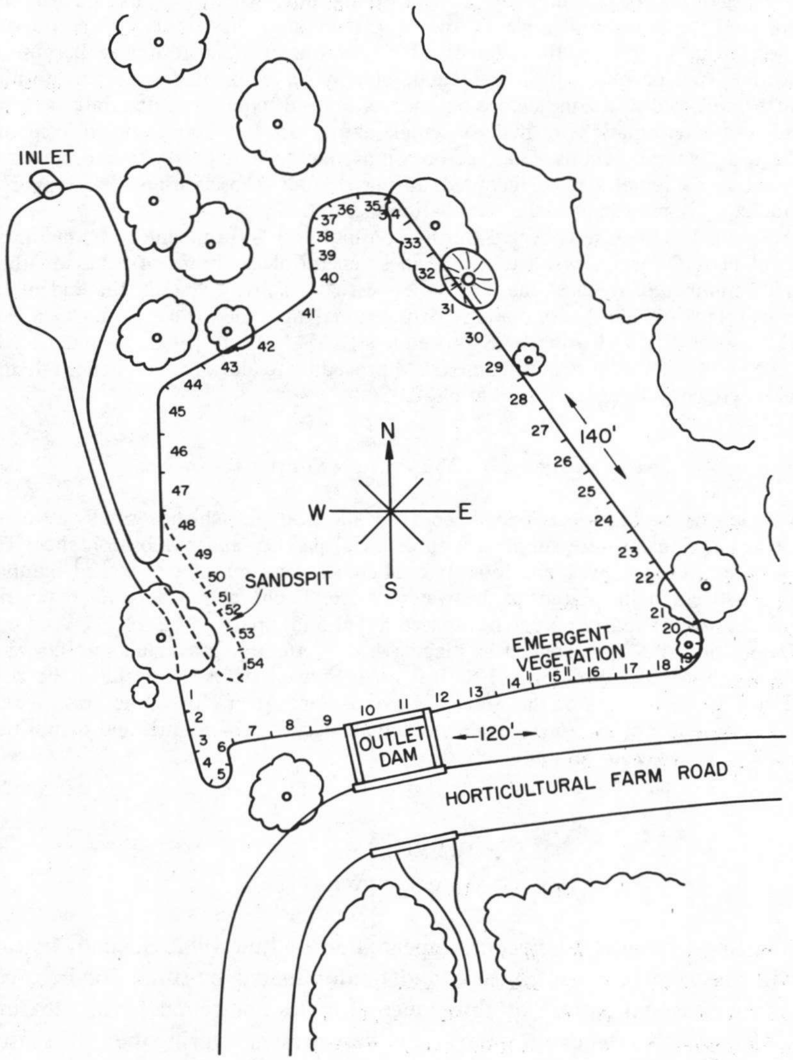

Fig. 1. Map of study site, New Brunswick, NJ, U.S.A. Numerals around pond border indicate position of each zone.

whether mating and/or oviposition occurred and, in the latter case, how many ovipositional dips were made by the female. All individuals initially present in or entering the zone during the 30 s observation were counted. Not all data were collected during every pond survey; males and females were counted during 47 complete surveys, but only during 39 was full information on mating and oviposition obtained.

Females appeared relatively infrequently and stayed only briefly, so they were observed closely whenever encountered, and other observations were suspended during these periods. Female activity recorded included time seen, zone, perch height, time mating began and ended, number of ovipositional dips, whether a male guarded her or not, and the number of males in the area. Only after the female left the pond or was lost from sight were the interrupted survey observations resumed. Because of these opportunistic observations of female activity, data on mating and oviposition might be collected in a zone before or after its normal sequence. Such data were not included in determinations of male or female abundance but were included in mating and oviposition tabulations. On rare occasions mating and oviposition occurred in a zone but no females were recorded during the 30 s observation. This apparent contradiction is an artifact of the observation method.

Additional data were collected during continuous 10-30 min intervals, mainly at zones of high *P. longipennis* activity. Besides general observations of behavior, these included number of females entering the zones, 30 s activity level at the end of the observation period, number of matings, ovipositional dips, and male guarding behavior.

Data were analyzed using SAS procedures (SAS Institute, 1983) as noted in the text. ANOVA was performed using the GLM procedure to allow for unbalanced design. Results were considered significant at $p < 0.05$

PERCH AND SURFACE VEGETATION SUPPLEMENTATION

For part of the summer zones 50 and 51 on the sandspit (which normally attracted very few individuals) were supplied with artificial perches and oviposition sites. The zones were separated by a one foot space. Perches were multiple-branched bamboo stems 30-40 cm high, placed at the water's edge. Each zone had either 6 perches spaced 2 ft (0.6 m) apart or 3 perches spaced 5 ft (1.5 m) apart.

Oviposition sites were created by placing 4, 8, or 16 large grass stalks in the water within bamboo poles oulining a 3 × 10 ft area. Sixteen stems nearly filled the zone while still allowing areas of the water for oviposition. At any one time grasses were placed in only one of the zones. Male and female occurrence, mating, and oviposition were noted as above for 30 s intervals.

RESULTS

TEMPORAL ACTIVITY PATTERNS

The first teneral *P. longipennis* appeared on 14 June 1982. Sexually mature individuals were seen on 22 June and predominated by June 26. Figure 2 shows the seasonal pattern of abundance of males and females from 26 June until 24 September, when no more adults were present. During the 1982 season an average of 58.9 ± 57.7 males and 4.0 ± 4.9 females were seen at the pond during a survey ($n = 44$). There was a strong correlation between the

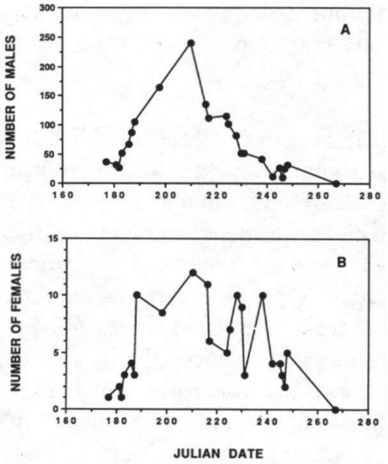

Fig. 2. Seasonal variation in number of male (A) and female (B) *P. longipennis* at the study site in 1982. Points represent means of all censuses taken between 10:00 and 17:00 on each day. Julian day 200 is 19 July.

total number of males and females present during a survey ($r = 0.77$, $p. < 0.001$).

Reproductively active individuals typically began arriving at the pond between 08:00 and 09:00. Timing of male occurrence was weakly bimodal, with a peak at noon, a slight reduction in early afternoon, and a second peak at 16:00-17:00. Afterwards the number of males declined sharply, and usually all had left the pond by 18:00. The female population rose to a plateau at noon, stayed nearly constant until about 15:00, then peaked sharply at 16:00 hours and dropped thereafter (Fig. 3). Although *P. longipennis* were less abundant in 1981 than 1982, activity patterns were generally similar. In 1981 males showed a much less pronounced second activity peak than in 1982. The female activity pattern was nearly identical both years.

SPATIAL DISTRIBUTION

Average male residence time at a given location on the pond was fairly long relative to each census, so results depict approximately the distribution of males in the various zones during the census interval and are expressed as a density (no. per zone). Individual females, on the other hand, usually were present only briefly at a given spot, relative to either the duration of a census

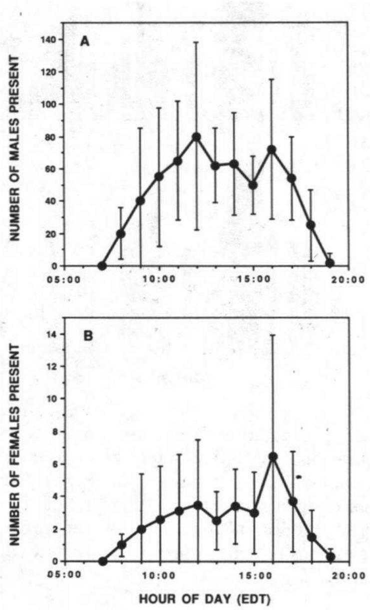

Fig. 3. Daily variation in number of male (A) and female (B) *P. longipennis* at the study site in 1981 and 1982. Points represent the mean for all censuses taken during that hour, error bars are S.D. Time is Eastern Daylight Savings Time ; at New Brunswick sunrise varies from about 05:30 on 21 June to 06:45 on 21 September and sunset from about 20:30 to 19:00 over the same period.

or to male residence time, so female distribution is expressed as frequency (no. per observation ; an observation is one 30 s scan of one zone).

Males

Mean densities ranged from 0.13-2.96 male/zone (grand means ± S.D. = 1.21 ± 0.70), and the distribution departed significantly ($p < 0.001$) from a uniform one (Fig. 4). Two lengths of shoreline were notable for extreme densities : the densest region of the pond included zones 14-18, where emergent vegetation grew, while 8 of the 9 least populated zones (47-54) were along the sandspit. The rest of the zones did not form any readily identified areas of closely similar densities. During surveys in which the overall population of males on the pond was less than the mean value, male distribution was less uniform (coefficient of variation significantly higher, $F = 1.55$, $p = 0.05$; ZAR, 1974) than at higher population levels.

It was convenient for some analyses to group the zones on the basis of density into 3 categories, comprising the 18 zones of lowest, intermediate, and highest density (Table IV, below). DUNCAN's multiple range test showed significant differences ($p < 0.05$) among all three groups.

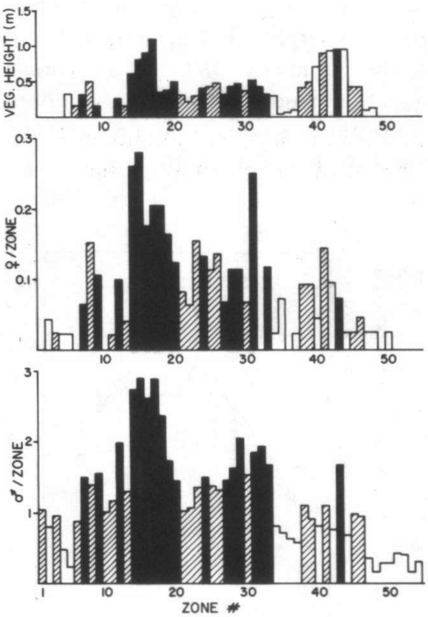

Fig. 4. Distribution of male and female *P. longipennis* and vegetation height by zone number around the pond perimeter (cf. Fig. 1). Solid bars designate zones categorized as high male density zones, hatched bars as intermediate male density, and open bars as low male density.

Females

Although female *P. longipennis* were much less abundant than males (grand mean frequency 0.084 ± 0.074, range of means 0.00-0.29 ; Fig. 4), female frequency also departed very significantly from uniformity (ANOVA, $p < 0.001$). Areas of extreme frequency occurred in pattern similar to male density (Fig. 4), and in general male and female abundance covaried rather closely, although by no means exactly (Fig. 5). Female distribution, however, was more uneven than that of males ; the coefficient of variation of mean female frequency per zone was significantly higher than that of male density

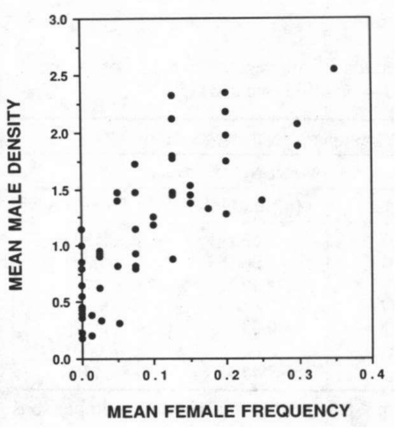

Fig. 5. Relation between male density and female frequency of occurence. Each point is the mean per zone for all censuses. Correlation coefficient, $r = 0.724$.

($F = 1.97$, $p < 0.01$; ZAR, 1974 ; zero values for female frequency were arbitrarily assigned a value of 0.01, approximately half the minimum possible non-zero frequency). Consequently, the ratio of females to males tended to be highest in zones of highest male density.

As with the males, female frequencies were combined into larger groupings of 18 zones each (Table V, below). DUNCAN's multiple range test showed significant differences ($p < 0.05$) among all groups.

RESPONSE TO VEGETATION HEIGHT AND SUNLIGHT

Both male and female distribution were correlated with mean vegetation height within a zone (Fig. 4). Zones 41-43 had unusually low apparent density for their vegetation height. These were the only zones that had to be approached through underbrush behind them ; subsequent observation with binoculars from across the pond showed that the disturbance markedly reduced male density, so these three zones were eliminated from further analyses of spatial distribution, although the overall effect of this correction was minor. Zones 1-4 were also omitted because the steep bank and dense undergrowth prevented measurement of vegetation height.

In the remaining zones a highly significant, positive, linear correlation existed between male or female occurence and vegetation height (Table I). Analyses of mean densities, which eliminate much of the day-to-day variation due to weather, seasonal changes in population, etc. suggest that vegetation height may explain 40-45% of spatial variation.

Zones exposed to sun at the time of census were greatly preferred to shaded ones by males and females (Tab. II). The correlation of mean male density and female frequency with vegetation height is almost equally strong in direct sunlight and shade, however (Tab. I). Thus it is unlikely that the apparent response of *P. longipennis* to vegetation height is an artifact of any correlation of vegetation characteristics with sunlight.

Table I

Correlation statistics for male density and female frequency with vegetation height of a zone. No data are included from zone 1-4 or 41-43 (see text)

	Correlation P. longipennis with vegetation			
	Individual Census	Mean No./Zone		
		All Data	In Sun Only	In Shade Only
Male	$r = 0.2717$* $p < 0.0001$ $n = 2106$	0.6737 0.0001 47	0.6305 0.0001 47	0.5935 0.0001 47
Female	$r = 0.1662$* $p < 0.0001$ $n = 2106$	0.6288 0.0001 47	0.5316 0.0001 47	0.5796 0.0001 47

* Difference between males and females significant, $p < 0.01$; other male/female comparisons not significant.

Table II

Effect of sunlight on male density/female frequency of *Pachydiplax longipennis* (mean ± S.D.). Statistical tests are two-tailed Student's t-tests ; $n = 47$

	Direct Sunlight	Shade	Statistical Significance
Male	1.65 ± 1.79	0.63 ± 1.26	$p < 0.001$
Female	0.11 ± 0.34	0.05 ± 0.22	$p < 0.05$

PERCH AND VEGETATION SUPPLEMENTATION

Prior to supplementing zones 50 and 51 on the sandspit with perches and floating vegetation male density was low and females were entirely absent. *P. longipennis* briefly flew through unaltered sandspit zones, rarely perching or interacting with each other. When these zone were supplemented with perches and water surface vegetation, males perched, patrolled, defended against intruders, mated and guarded females. Females mated, oviposited, and perched when harassed. Numbers of *P. longipennis* rose the same day the zones were supplemented. Table III shows the effects of adding either 6 perches and 16 floating grass stems or 6 perches only. Increases over the unsupplemented situation all were significant except for females in the zone with perches only ; also, both male density and female frequency were significantly higher in the zone with floating grasses than in that with perches only. Abudance of both males and females was also significantly elevated when only 8 or 4 floating grass stems or only 3 perches were added, but relative effects of different levels of supplementation could not be tested owing to large variation in the population of *P. longipennis* on the pond as a whole during the experimental period. However, the effect of perch number with 8 floating grasses present was tested during a period of nearly constant overall population; female frequency was significantly lower with only 3 perches available (0.11 ± 0.31, n = 74) than with 6 perches (0.45 ± 0.56, n = 208; t = 4.38, $p < 0.01$).

On 26 August perches alone were added, without floating vegetation. The resulting male density (0.26 ± 0.51 males/zone) was not significantly different from when the sandspit was bare (0.60 ± 1.03 males/zone; the latter was measured earlier in the season, when the total population was higher), but male behavior was distinctly altered. When perches were present one or two males often held territories, while without perches all males were transient rather than resident.

Table III

Occurrence and frequency of reproductive activity of *P. longipennis* at sandspit zones 50 and 51 before and during addition of 6 perches and 16 floating grass stems (oviposition sites), with comparable data for the remainder of the pond during the same time period. Data are given as mean ± S.D.

Condition	N[1]	Male Density	Female Frequency	Mating[2] Frequency	Oviposition[2] Frequency	Dips[3]
Before addition	30	0.60 ± 1.03	0.0	0.0	0.0	---
Perches only added	83	1.41 ± 1.02	0.036 ± 0.19	0.0	0.0	---
Perches and grasses added	82	3.45 ± 1.55	0.71 ± 0.78	0.098 ± 0.337	0.32 ± 0.49	28.5 ± 27.0
Pond mean[4]	230	1.64 ± 1.47	0.17 ± 0.46	0.035 ± 0.184	0.035 ± 0.184	26.4 ± 32.0

[1] Number of 30 s observations.
[2] Number of matings and ovipositing females per observation.
[3] Number of oviposition dips per ovipositing female.
[4] Data from 12-19 Aug. 1982, 11:00-12:00, excluding sandspit (zones 47-54).

MATING AND OVIPOSITION BEHAVIOR

General Behavior

During 179 observations in which females were sighted before oviposition began, only 55.3% of females mated. Of those that mated, 52% apparently began ovipositing before mating (mean 3.45 ± 2.30 dips, n = 11); after mating 77% oviposited immediately but 23% were lost from sight without ovipositing, almost always as a result of being chased by males. Females that did not mate were significantly more likely (94%; $\chi^2 = 9.77$, $p < 0.05$) to oviposit at least briefly.

Males apparently did not respond to perched females but usually tried to clasp and mate with any nearby female that hovered and/or began ovipositing or that was already mating or being chased by other males. Immediately after mating, the male hovered near his mate as she oviposited, attempting to drive off conspecific males that approached her. All mated females were guarded initially. If male density was low in the area and no conspecifics challenged the guarding male, he sometimes perched near the oviposition site but flew to meet any conspecific that neared the ovipositing female. Recently mated females guarded in such a manner apparently laid more eggs (43.1 ± 28.5 dips/ovipositional bout, $n = 60$) than unmated and thus unguarded females (18.0 ± 23.7, $n = 49$); the difference is highly significant ($t = 4.87$, $p < 0.01$).

Table IV

The occurence during 39 complete surveys of males, females, matings and ovipositional dips seen during 30 second surveys grouped into three categories of 18 zones each as determined by mean male density; $n = 720$ observations for each category. Most data are given as mean ± S.D.; if no error expression is given, figures were calculated from mean data as indicated. Numbers in brackets are total positive observations for each category

	Zone Category		
	Low	Med	High
male/zone	0.51 ± 0.98 [364]	1.13 ± 1.54 [815]	1.85 ± 2.10 [1335]
female/zone	0.018 ± 0.131 [13]	0.085 ± 0.320 [61]	0.168 ± 0.416 [121]
females/zone	0.035	0.075	0.091
matings/zone	0.0042 ± 0.084 [3]	0.012 ± 0.111 [9]	0.022 ± 0.157 [16]
mates/male	0.0082	0.011	0.012
dips/mated female	44.3 ± 38.6	23.9 ± 34.8	26.9 ± 39.0
dips/male	0.365 [133]	0.263 [215]	0.322 [430]

Mating and Oviposition in Relation to Dispersion

The rank correlation of mean number of matings observed in each zone with the mean number of males in that zone during complete pond censuses was significant and positive ($r_s = 0.29$, $n = 54$, $p < 0.03$). The number of matings per male was nearly equal for high and intermediate density zones and about 50% higher than in low density zones (Tab. IV). A more striking increase in male mating success occurred in zone categories of increasing female frequency (Tab. V). On the other hand, the number of ovipositional dips made by mated females tended to decline from low to intermediate or high density zones, perhaps due to increasing interference from non-mate males (see below). Thus a male's expectation of fertilizing eggs that were immediately oviposited apparently was lowest in the intermediate male density categories (Tab. IV). Nearly the opposite pattern of male fertilization success occurred among categories of differing female frequency; no eggs were deposited by mated females in low frequency zones, maximal eggs per male were deposited at intermediate frequency, and a moderately lower number in the highest frequency zones (Tab. V).

Table V

Variation in female mating and oviposition activity and of male density and reproduction during complete pond surveys, in relation to frequency of female occurence; zones are equally apportioned into categories of low, medium, or high frequency as explained in the text. Frequencies or densities of occurence are given as mean ± S.D.; other data for females are given as total numbers observed per zone category, those for males as ratios of total mates or dips to total males per category. Expected frequencies for calculation of log-liklihood (G) are based on the assumption that events were distributed in proportion to mean frequency of female occurrence or, for oviposition and ovipositional dips by mated females, the mean frequency of mating. Numbers in parentheses are means per female

Behavior	Total Observations	Zone Category			G	p
		Low	Medium	High		
Frequency of Occurence		0.015 ± 0.012	0.063 ± 0.025	0.17 ± 0.042	--	--
Mating						
Total	28	0	9	19	2.82	>0.02
Followed by oviposition	16	0	6	10	0.04	>0.09
Oviposition						
All bouts	56	2	18	36	0.44	>0.8
All females	38	3	14	21	1.25	>0.5
Mated females	16	0	6	10	1.45	>0.4
Oviposition dips						
All females that oviposited	195	12 (6.0)	427 (32.8)	540 (27.8)	102.7	<0.001
Mated females that oviposited	28	0 (0)	368 (61.3)	410 (41.0)	77.1	<0.001
Male density		0.61 ± 1.11	1.08 ± 1.52	1.81 ± 2.10	--	--
Mates/male		0	0.0116	0.0145	--	--
Dips/male		0	0.0476	0.314	--	--

If differences in frequency of female visits to different zones reflect differential effects of various pond regions on female fitness, then females might preferentially mate or oviposit in the most frequented zones. On the other hand, males were generally more abundant in the same zones, and they often interfered with mating or oviposition. We attempted to examine these effects.

Oviposition persistence (the number of dips per oviposition bout) was negatively correlated with the number of males in a zone at the time a female was ovipositing in that zone. This relation was true for females as a whole and even more strongly for mated females (Fig. 6). Unmated, and thus unguarded, females typically made relatively few dips, independent of the number of males present. At very high male density, guarding became ineffective and mated females lost their advantage in terms of the number of dips accomplished. Note that the highest male densities are well above the average density recorded in even the most populous zones.

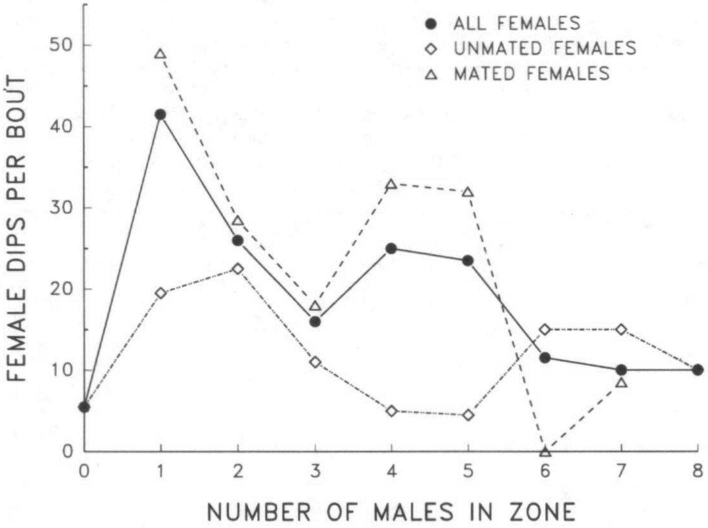

Fig. 6. Effect of local male density on the number of ovipositional dips performed by female *P. longipennis*. Circles indicate means at each male density for all females, squares are means for females that had mated at least once and therefore were guarded, and triangles are means for unmated and therefore unguarded females.

Females tended to dip very few times in zones of low average female frequency but to perform more dips in intermediate than high frequency zones. There was no difference among zone categories in the probability that an ovipositing female would mate within a zone or in the proportion of females that initiated oviposition (Tab. V).

DISCUSSION

We assume that location and frequency of mating and oviposition are related, in part, to behavioral strategies (*sensu* MAYNARD SMITH, 1982) evolved to maximize individual reproductive success. Thus a description of spatial and temporal distribution of individuals and behaviors is likely to provide insight into factors determining fitness. We further assume, in the absence of repeated observations of marked indivuals, that short-term mating and oviposition rates are postively correlated with and contribute to lifetime reproductive success. These assumptions are supported by other data for territorial libellulids (McVEY, 1981 ; SHERMAN, 1983b ; KOENIG & ALBANO, 1987), although they may not be true for all Odonata (BANKS & THOMPSON, 1985) ; other attributes, especially lifespan, may also be important determinants of lifetims success (BANKS & THOMPSON, 1985 ; KOENIG & ALBANO, 1987).

TEMPORAL DISTRIBUTION

Seasonal patterns of occurence of males and females are similar, but, in general, short-term fluctutions were more marked in females (Fig. 3). While this is certainly due in part to our sampling error, male *P. longipennis* may be affected similarly in their own "sampling program" and so have difficulty in predicting day-to-day variation in female availability (WOLF & WALTZ, 1988). However, SHERMAN (1983b) found that individual males return repeatedly over a number of days to mating sites, and our unpublished observations of marked individuals suggest a fairly long lifespan (up to 30 days), which would tend to buffer males against unpredictable variation in access to females.

Within a day, the pattern of variation in mean frequency of females was similar to that observed by SHERMAN (1983b) in SC, in that maximum numbers occurred rather late in the day. In our population, however, the peak at 16:00 hours was much more pronounced. CAMPANELLA & WOLF (1974) observed a distinct, late, secondary peak of visitation in *Plathemis lydia* and suggested that it may have included of females returning after earlier mating or oviposition attempts were interrupted. Possibly the late daily peak of *P. longipennis* females consisted in part of individuals returning after interrupted oviposition, although observations of marked females were too infrequent to test this. Alternatively, conditions such as temperature (cf. McVEY, 1984, for *Erythemis simplicicollis*) or calm wind may have been optimum at this time. Air and water temperatures may be maximal near 16:00 hours in summer, even though solar radiation intensity is reduced by then.

Males may be under considerable selective pressure to predict accurately the time of maximal net reproductive benefit (CAMPANELLA & WOLF, 1974), since costs of territory maintenance can be high (FRIED & MAY, 1983). Several studies (CAMPANELLA & WOLF, 1974 ; CAMPANELLA, 1975 ; PEZALLA, 1979 ; SHERMAN, 1983b) indicate that in territorial species male breeding activity is temporally more dispersed than that of females, as was true of our population (Fig. 2). This could occur because it is advantageous for males to arrive early to establish and hold a territory for the maximum possible duration (PEZALLA, 1979) or because some males are unable to establish territories at the optimum time (e.g., CAMPANELLA & WOLF, 1974). The latter is more likely in *P. longipennis* since individual males usually remain on territories for relatively short periods (SHERMAN, 1983b, and personal observations). We also noted, however, that maximum male density, at midday, did not coincide with maximum female frequency, although a secondary peak of male activity did. This pattern held through both years of our study as well as during that of FRIED & MAY (1983) for 1980. The midday maximum might reflect lower costs of territoriality at that time, as suggested, e.g., for *Micrathyria* spp. (MAY, 1977, 1980), or a greater readiness of females to mate then than later (ALCOCK, 1989 ; KAISER, 1985) ; the latter might occur if the late peak of female activity consisted of individuals returning to complete interrupted oviposition. Our data show no clear relationship, however, between time of day and the probability or persistance of oviposition or mating.

SPATIAL DISTRIBUTION

A successful male reproductive strategy depends also on prediction of female spatial distribution at the pond. Several previous studies have demonstrated the overriding importance of oviposition sites and/or females in determining the dispersion of males at breeding aggregations (ALCOCK, 1982, 1987 ; CAMPANELLA & WOLF, 1974 ; PEZALLA, 1979 ; SHERMAN, 1983b ; VAN BUSKIRK, 1986 ; WAAGE, 1973), although other factors such as perch availability (SHERMAN, 1983b ; WOLF & WALTZ, 1988) or exposure to predation may modify distribution. Female distribution, while probably influenced by the distribution and behavior of males (see below), is likely to be most strongly affected by presence or absence of advantageous oviposition sites (BUSKIRK & SHERMAN, 1985). SHERMAN (1983b) found that females oviposit only in areas of emergent, floating, or very slightly submerged vegetation. Our census data confirm that zones where emergent vegetation occurred were consistently the most attractive to females and the bare sandspit zones least attractive. Other potential oviposition sites included floating duckweed and algal mats and masses of leaves or sticks. We did not quantify their position or extent because these varied daily and even hourly with wind and runoff driven currents, but females clearly oviposited frequently in such areas and almost never did so in open water, In addition, supplementation of the previously unattractive sandspit area with floating grasses (but not with perches alone) resulted in a rapid upsurge in female visitation. Males, too, preferred zones of natural emergent vegetation and the supplemented sandspit zones. In the sandspit zones, no mating or oviposition occurred in the absence of added perches and floating vegetation whereas both were relatively frequent in their prensence. Thus males benefited by their attraction to oviposition sites ; it is unlikely that they were responding directly to the presence of females, since even in supplemented or naturally very attractive zones occurence of females was infrequent and sporadic.

Two other environmental variables were strongly correlated with both male and female abundance : the presence of sunlight, and shoreline vegetation height. *Pachydiplax longipennis* is a highly heliothermic species (MAY, 1976), and both oviposition (SHERMAN, 1983b) and territorial defense by males (FRIED & MAY, 1983) are energetically demanding activities that probably require maintenance of high body temperature. SHERMAN (1983b) found that females were most abundant at high light intensities except at air temperature > 32 C, a temperature rarely exceeded at our study site. Thus it is hardly surprising that both sexes prefer sunlit sites.

The explanation for the correlation of abundance with vegetation height is less obvious. The highest shoreline vegetation occurred in the same zones as the emergent vegetation, and the sandspit area had no or very low shoreline vegetation and only rarely any accumulation of debris or algae suitable for oviposition. If these areas (i.e., zones 14-18 and 47-54) are excluded, however, the correlation of mean frequency or density with vegetation height is still highly significant for females ($r = 0.467$, $p < 0.01$) and marginally significant for males ($r = 0.307$, $0.05 < p < 0.1$). We believe, therefore, that the correlation is due to attraction to some feature of the vegetation itself, although perhaps not only height *per se* (natural vegetation density, e.g., appeared roughly correlated with vegetation height), probably because it provides perches and shelter. This conclusion is supported by the fact that density in sandspit zones increased when perches were provided, even when these were not immediately adjacent to oviposition areas, and a few males maintained territories when perches were added even in the complete absence of oviposition sites. SHERMAN (1983b) also observed that males set up territories in previously unused areas of her pond when perches were supplied. Males clearly require perches for territory maintenance, probably both to watch for females and intruding males and as basking sites ; they never perched on the ground and seldom within 10 cm of the ground or water, and they very rarely flew continuously for extended periods. We have the impression, too, that in the presence of reasonably tall perches, males may partition territories vertically, although this needs confirmation.

Females also use shoreline vegetation, where they perch rather low among the foliage before and sometimes after ovipositing. This may provide concealment from predators and conspecific males and perhaps a vantage point for assessment of oviposition sites. It is noteworthy that during sandspit supplementation female, but not male, abundance was enhanced by adding more perches at a constant density of floating grasses.

REPRODUCTIVE SUCCESS

What are the reproductive consequences of heterogeneity of zone characteristics and of male and female zone preferences ? The principal requirements of a female probably are to oviposit in a site favorable for egg and larval development, rapid egg deposition, and avoidance of predation (McVEY, 1984 ; KOENIG & ALBANO, 1985), and to avoid harrassment by conspecific males. The strong preference for floating or emergent vegetation, found both by us and by SHERMAN (1983b), probably occurs because these situations minimize predation of eggs or larvae and/or provide warm microhabitats that promote rapid embryonic development. WOLF & WALTZ (1988) demonstrated that in *Leucorrhinia intacta* eggs develop much more rapidly at the warm temperatures associated with shallow water. Similar conditions are likely to occur at *P. longipennis* oviposition sites. Early larval development may likewise be facilitated by warm water (LEGGOT & PRITCHARD, 1985), and vegetation may reduce predation on eggs and larvae (WELLBORN & ROBINSON, 1987). Fish predation on ovipositing females might also be reduced in such areas (WOLF & WALTZ, 1988), although no fish occur in our study pond. The very low number of ovipositional dips made in areas of low frequency is consistent with the suggestion that females are assessing the relative suitability of oviposition sites.

On the other hand, harrassment by males was probably higher in areas of emergent, and possibly also floating, vegetation. The area of emergent vegetation corresponded to highest unmanipulated male density, and the sandspit experiment indicates that males respond to favorable oviposition sites. Although not known for *P. longipennis*, in most Odonata species females apparently arrive at rendezvous sites with ample sperm to fertilize a clutch of eggs (WAAGE, 1979, 1986 ; see SIVA-JOTHY, 1984, for exceptions). Thus mating is not essential, although it may be beneficial for a variety of reasons (THORNHILL & ALCOCK, 1983). Be that as it may, the presence of numerous males clearly can be detrimental to a female's ability to deposit a full clutch, as indicated in Fig. 6 (and see SHERMAN, 1983a). Our data provide no direct evidence of spatial avoidance of males by females (but see below), although the late peak of female activity might represent a temporal avoidance strategy. The inferred attraction of females to tall and/or dense vegetation might reflect, in part, an adaptation to avoid excessive interference from males.

For males, obtaining a mate is an additional, and probably overriding, consideration in site selection, and indeed the probability of mating is lowest in low density areas and highest, by a small margin, in the high density category (Table IV). If frequency of female occurrence indicates the quality of an area for *P. longipennis* reproduction, then the advantage in mating expectation is even more marked for males with increasing territory quality (cf. KOENIG, 1990).

Sperm displacement is evidently the rule among Odonata, however, and the vigorous mate-guarding behavior of male *P. longipennis* suggestes that this species is no exception. Therefore it is also probably highly advantageous for a male if his mate oviposits a full clutch before remating (SHERMAN, 1983a), so males also might gain from selecting territory sites with few other males nearby. Our data suggest, in fact, that a males's expectation of fertilizing eggs that are deposited immediately after mating is at least as high in low density zones as in others. The distribution among zone categories of total ovipositional dips immediately after mating was significantly different from that predicted if total dips were proportional to male density ($G = 5.08$, $p < 0.05$) ; a deficiency of dips apparently occurred at intermediate densities.

Why, then, do males not distribute themselves more evenly and equalize reproductive benefits ? Males are, in fact, more evenly distributed than females and more evenly distributed at high than at low density. They are also certainly territorial (SHERMAN, 1983b ; personal observations), so the most successful males might force others to occupy less favorable sites. Since the data on ovipositional dips are based on a small sample of mating females, especially in low density zones, we have some doubt that the apparently greater success of males in the low vs. the intermediate zones is real. If it is, however, it demands explanation because maintenance of territories in areas of intermediate to high male density incurs substantially greater energy costs that at low density (FRIED & MAY, 1983), and this may limit territory holding duration and territory size at high density (SHERMAN, 1983b ; KOENIG, 1990). Unless the situation at this pond is atypical of the species in general, an excess of benefits at least commensurate with this extra cost should be associated with these sites.

Possibly males cannot assess territory quality with great accuracy, because of inherent limitations (e.g., rapid shifts of small areas of floating vegetation) and/or countervailing female strategy. Females may be most likely and best able to oviposit persistently in area of at least moderately high quality *and* low male density. If they occasionally find such areas and deposit large clutches there, this could explain the rare matings followed by long ovipositions in low male density areas and possibly also the apparently greater number of dips among mated females in areas of intermediate female frequency. Alternatively, or in addition, two benefits might accrue in high or intermediate density areas that are not reflected by the number of eggs deposited immediately after mating. First, females may deposit eggs fertilized by a male after leaving his territory, and probably the pond as a whole, then returning to oviposit elsewhere; females often do oviposit without remating during a pond visit, although they typically dip less than mated females. Second, to the extent that intermediate and high density male sites correspond to regions more favorable to offspring success than those of low density, males at these sites may derive the same benefits as outlined above for females.

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