Choice and utilization of oviposition sites
by female *Calopteryx maculata* (Odonata: Calopterygidae)

I. Influence of site size and the presence of other females

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Summary. Females of the damselfly *Calopteryx maculata* (de Beauvois) initially choose the larger of a pair of adjacent oviposition sites, about 70% of the time (Table 1), or whichever of two equal sized sites had other ovipositing females on it (about 88% of the time – Table 2). These criteria for initial choice between a pair of sites also interact. Incoming females generally (57 to 74% of the time – Table 3) joined others on the small site rather than ovipositing alone at the adjacent, bigger site. When pairs of large and small sites were replicated across eight locations, there were nonsignificant trends towards greater utilization (eggs laid) of the larger of a pair of oviposition sites within locations (Table 4). The lack of agreement between initial choice and utilization shows that other factors besides size are important in the choice and use of oviposition sites. These include disturbance by males, the presence of other females and choice criteria that can only be assessed during oviposition. When all sites at the eight locations were equal in size, there was considerable day to day and location to location variation in eggs laid (Fig. 1). Viewed over periods of several days, some sites are obviously less attractive than others in terms of cumulative numbers of eggs laid at them. When the amount of vegetation was varied among locations, those with the bigger oviposition sites were used more often, sometimes significantly so, but there were also significant reversals (small sites used more often) (Table 5, Fig. 1). Thus, there is no simple effect of size on the utilization of oviposition sites by *Calopteryx maculata* females, despite a clear tendency for females to make initial choices based on this criterion. The considerable among and within location variation in number of eggs laid may reflect additional choice criteria or the interaction of size, the presence of other females, disturbance, and location.

Introduction

The oviposition site is a fundamental resource for both male and female reproduction in many damselflies and dragonflies (e.g. Waage 1979b, 1984; Corbet 1980; Sherman 1983; Fincke 1984; Koenig and Albano 1985). As such it is important to determine what factors influence the choice and utilization of oviposition sites by males and females and how variations among oviposition sites relate to reproductive success. This paper presents results of a study of the choice and use for oviposition sites by females of the damselfly, *Calopteryx maculata*. This is a large, stream dwelling, polygamous species with well developed territorial, pair-forming, courtship and post copulatory behavior centered around emergent aquatic vegetation into which females oviposit (Waage 1972, 1974, 1979b, 1983).

Oviposition sites used by *C. maculata* vary in size, type of vegetation, and location. Considerable variation occurs in the use of natural and artificial oviposition sites by females as well as mating and fighting frequency of resident males (Waage 1979b; unpublished, Alcock unpublished). It is reasonable to expect that much of this variation in oviposition site use reflects female and male responses to differences among oviposition sites. Besides the nature and location of the sites, the presence of males and females may also affect their attractiveness and utilization. During mating a male removes 80–100% of the sperm of previous males from the female's storage organs and then replaces it with his own (Waage 1979a). Therefore, guarding ovipositing mates ensures a male of fertilization of eggs being laid and allows the female a period of undisturbed oviposition (Waage 1978, 1979b). For females, the presence of males provides information on site location and the likelihood of protection and/or disturbance during ovi-

position. The presence of females may also indicate site location and likelihood of protection. Females may benefit from joining others already being guarded; they can often gain protection without the cost of mating (Waage 1978, 1979b; Alcock 1979, 1983).

Here, I address two questions about oviposition site choice and utilization by females of these damselflies: (1) Does oviposition site size and the presence of other females influence differential attractiveness to oviposition sites, and (2) Does site size also explain differences in utilization among oviposition site locations? I first present the results of paired-choice experiments that reveal *initial preferences* by females for larger sites and sites with ovipositing females already present. I then discuss experiments that show considerable variation in the *utilization* of equal and unequal sized oviposition sites within and among various locations. Finally, I discuss how variation in utilization may reflect a combination of choice criteria including the location and size of sites as well as the presence of other females at them.

Methods

Initial preferences were determined in 1984 and 1985 using pairs of oviposition sites, vegetation attached to stakes driven into the stream bottom, at two locations on the Palmer River in Rehoboth, Massachusetts. Each oviposition site consisted of one, two or three 22 cm leaves of commonly used oviposition material (*Sparganium* sp.). A pair of sites, 0.5 m apart, formed the nucleus of a single male's territory. Pairs of sites were placed in the stream at locations where females tended to aggregate on an adjacent bank. Males and females were marked with unique numbers on their wings.

An experiment consisted of recording female arrivals at and choice between a pair of alternative sites (e.g. big vs small) at each location. A positive choice was made when a female landed and began to probe the vegetation with her ovipositor. After two choices by the same female the positions of the alternatives were switched and the female removed from the area. Switching alternatives controlled for position effects during female approaches. The data below are for unbiased (equal approach to both sites), first choices by females (1985 data) or all choices by females (1984 data).

Statistical analysis of the data in Tables 1, 2 and 3A involved comparing the observed distribution of choices between sites and that expected for random choice between them. The log likelihood ratio test (G statistic) with the correction for continuity was used for sample sizes greater than 25. For smaller samples an exact probability of the binomial distribution was used in place of the G statistic to obtain a significance (P) value. For Table 3B a chi-square test for the homogeneity of two observed distributions of choices between sites was used.

The relationship between oviposition site size and location and their actual utilization by females was tested by establishing fresh oviposition sites at various locations and counting eggs laid in them during a fixed time period. Female visitation rates at natural oviposition sites were low enough that this indirect approach was more efficient than continual observation of sites.

However, there was no control on female presence and it was not possible to tell how many females were involved in ovipositing the eggs counted at each site.

During July 1985, four pairs of fresh oviposition sites were set up along a 20 m section (Area 1) of the Palmer River (Rehoboth, Massachusetts) in locations where natural sites would usually occur. Two of the Area 1 locations (I and II, Table 4) were the ones used in the oviposition site choice experiments discussed above. Another eight pairs of oviposition sites were set up about a mile downstream (Area 2, Fig. 1) along 20 m of stream where no other natural sites occurred. At each site fresh vegetation (no eggs in it) was put out, collected and then replaced at 2–3 day intervals. Eggs found in the collected vegetation were identified to species and counted under a dissecting microscope. Site utilization, then, is the number of *Calopteryx maculata* eggs per site (or mean number per leaf) per two days exposed to females.

In Area 1, all locations always had equal amounts and sizes of vegetation, but within a location the two sites either had the same number of leaves (2), or different numbers (1 vs 3). The manipulations were more complex in Area 2 (see Fig. 1). During the first 2 samples (two 2-day periods) each location had 2 leaves at each of the two sites. During the next 3 samples each location had one big (3 leaves) and one small (1 leaf) oviposition site, paired as in the female choice experiments above. For each sample above, the vegetation at each pair of sites (up and downstream) was switched at each location after one day. This randomized the effect of position within a location. Egg counts for the first 2 samples tested both the effect of location along the stream and position within a location. Egg counts for the next 3 samples tested both the effect of location (all locations with 4 leaves) and of big vs small sites within and among locations. Together the five samples (10 days) tested effect of location and day to day variation in site utilization.

The third manipulation at Area 2 involved varying the size of oviposition sites among locations. In four samples (two 2-day and two 3-day periods, Fig. 1, samples 6–9), half of the location had two leaves (one at each site) and half had six leaves (three at each site). Locations A, C, E and H were small (two leaves) on July 18–19 and 20–21 and then were big for July 23–25 and 26–28. Locations B, D, F and G were big followed by small for the same days. This tested the effect of big vs small oviposition sites among locations – big sites having 3 times as many leaves. Egg means and totals for the 3-day sample periods were adjusted to a 2-day estimate in the Tables and Fig. 1.

Results

I. Female choice between pairs of oviposition sites

Big vs small site. In this experiment the paired alternatives were three leaves vs one leaf of oviposition vegetation. Table 1 shows a significant preference for the bigger site at both locations in both years. Between 68 and 76% of initial choices were for the larger site. In all cases there were no other females present when a choice was recorded.

Female vs no female. The presence of ovipositing females was simulated by pinning dead females on the oviposition site. Males would either guard or

Table 1. Female choices between big (3 leaves) and small (1 leaf) sites. Gadj is the log likelihood ratio test corrected for continuity. Each test is a goodness of fit to an expected equal distribution of choices

Location	Choice			Difference from 1:1	
	Big	Small	Total	Gadj	P<
1984					
I	25	12	37	5.43	0.025
II	48	22	70	10.69	0.005
1985					
I	16	5	21	**	0.027
II	26	11	37	7.15	0.010

** P-value is an exact probability of the binomial – see Methods

Table 2. Female choices between equal sized oviposition sites with and without pinned females on them. Gadj statistic is for difference between the observed choices and an expected equal choice of both sites. The lack of significance for location Ia is due to the position of the pair of sites relative to the shore (see text) and Ib is a repeat of the experiment with the sites moved further from shore (IIa and IIb are replicates in the same position at a second location)

Location	Choice			Difference from 1:1	
	Female	None	Total	Gadj	P
1984					
IA	15	14	29	0.14	>0.5
IIA	36	5	41	28.47	<0.001
IB	14	0	14	**	<0.001
IIB	20	2	22	**	<0.001
1985					
I	14	3	17	**	<0.02
II	15	4	19	**	<0.02

** P-value is an exact probability of the binomial – see Methods

Table 3. Female choice combining oviposition site size and the presence of an ovipositing female. A. Gadj as in Tables 1 and 2. B. Gadj tests for homogeneity of choices between big vs small sites with and without a female present on the small site. All data are from 1985

A Choices between small site plus female and big site

Location	Choice			Difference from 1:1	
	Small + Female	Big	Total	Gadj	P
I	17	6	23	**	<0.04
II	21	13	44	2.41	>0.10
Pooled	38	19	57	7.17	<0.01

B Big vs small choices with and without a female present on the small site

	Location I Female present		Location II Female present	
	Yes	No	Yes	No
Big	6	16	13	26
Small	17	5	21	11
Total	23	21	34	38
Gadj	9.46		6.19	
P	<0.005		<0.025	

attempt to mate with them depending on how recently they themselves have mated (Waage 1979b). Otherwise, the sites were equal (two leaves each). When females had a choice between joining an "ovipositing female" or landing on an equal sized, unoccupied site; they usually joined the pinned female (Table 2). The single exception (1984, location IA) is discussed below. The attraction of females to sites with other females was greater (81–91% of choices) than to the larger of two sites in the previous experiment.

This experiment also clearly shows how oviposition site location can influence choices. In 1984, the sites at location I (IA in Table 2) were originally 1.5 m from shore. In this position there was no discrimination between the "female" and "no fe-

male" alternatives, even though at an identical pair of sites 4 m away (location IIA) females clearly chose the site with the pinned females. A second trial was run with the sites at location I now 2.5 m away from shore. The results (IB and IIB in Table 2) were now similar. At each location there was a significant preference for the site with the pinned females. These results suggest the original position of the sites at location I prevented approaching females, most of which flew down from perches on shore above the sites, from seeing the pinned females. Thus the location of an oviposition site relative to where females approach from may be an important factor in their initial choice of sites.

Big site vs small site + female. A third experiment tested whether or not the attraction to big sites would be lessened or reversed by putting a pinned female on the smaller of a pair of sites. This was expected from the greater response shown by females to the presence of other females than to the larger of two sites. Table 3A shows that at location I there was a significant reversal with females chosing the one leaf site with a female on it 74% of the time. At location II females chose small site

Table 4. Utilization of big vs small oviposition sites within locations. "Total" is the number of eggs deposited at each size site in 4 samples (Area 1) or 3 samples (Area 2). n is the number of leaves counted. "Mean" is the mean number of eggs deposited in a two day period per leaf at each size site. See Fig. 1 for the Area 2 locations. P is the probability value from Anova tests between mean number of eggs per leaf for big and small sites

Location	Small site (1 leaf)				Big site (3 leaves)				P
	Total	n	Mean	SE	Total	n	Mean	SE	
Area 1									
A	942	4	471.0	147.4	2385	12	397.4	86.8	0.54
B	561	4	280.6	161.2	774	11	129.0	29.8	0.21
C	163	4	81.6	40.6	870	12	145.0	32.6	0.59
D	344	3	172.0	91.8	1285	12	214.2	56.8	0.75
Area 2									
A	627	3	313.7	130.8	2507	9	417.8	125.6	0.46
B	549	3	274.3	117.1	326	9	54.3	21.3	0.12
C	491	3	245.7	200.9	1414	9	235.7	76.7	0.94
D	0	3	0.0	–	4	9	0.6	0.6	0.99
E	240	3	120.0	76.0	432	9	72.0	31.0	0.73
F	79	3	39.7	19.6	747	9	124.4	45.8	0.54
G	340	3	170.0	86.5	1954	9	325.7	81.4	0.27
H	585	3	292.3	52.1	1159	9	193.2	96.6	0.48

plus female 57% of the time, but this was not significantly different from equal choice. Another way of looking at these results is to compare the 1985 results at the same locations for big and small sites when a pinned female was or was not present on the smaller sites. Table 3B shows the expected reversal, which is significant at both locations. Thus the tendency to join other females might enhance the attractiveness of a big site or reverse the size effect for a small site under natural conditions comparable to these experimental ones.

These results demonstrate that females can discriminate between sites that vary in size and the presence of other females, and that attraction to other females over-rides attraction to the bigger of two sites. These results do not distinguish between proximate and ultimate criteria for choices by females. For example, large sites or ones with females on them may be chosen merely because they are more easily perceived by females and not because of any additional value to an ovipositing female or her offspring. In the next section I add the effect of oviposition site location, but the focus switches from initial choice to actual utilization of different oviposition sites within and between locations.

2. Size and location of oviposition sites and utilization by females

Utilization of big and small sites within locations. Table 4 shows the results for the big vs small sites within locations for Area 1 and 2. At all locations

in Area 1 there were more total eggs laid across samples (Table 4, total) at the big sites than at the small ones. This was also true for 6 of the 8 locations in Area 2. However, there was considerable variation among samples and at each area there was no significant difference between big and small sites in the total eggs laid at each location across samples (Anova). In fact there were samples in which 3–5 times as many eggs were were laid in the single leaf of the small site than in the three leaves at the big site it was paired with. The mean number of eggs per leaf also did not differ significantly between big and small sites (Table 4), and it was greater for the small sites at 6 of the 12 locations.

The ratio of the total number of eggs at the big site (3 leaves) to the total number at both sites (4 leaves) (Table 4) averaged 73% (58% to 84%) for Area 1 and 75% (37% to 90%) for Area 2. All of these ratios were significantly different (Chi square, $P < 0.01$) from 50% (equal utilization) suggesting a bias towards the larger of each pair of sites. However, all ratios except that for Area 1-A differed significantly from 70%, the expected ratio from initial choices (Table 1), and all but that for Area 2-C also differed from 75%, the expected ratio given the percentage of leaves at each location at the big site. Location D in Area 2 was excluded from this analysis. Thus across all days there is a clear trend towards preference for the bigger sites (except Area 2-B) but this preference does not reflect that expected based on initial choice experiments or proportion of leaves at each site.

Table 5. Small size (2 leaves) versus big size (6 leaves) oviposition sites at the same locations at different times in Area 2. See text and Fig. 1. n is the number of leaves counted. "Total" is the total number of eggs deposited at each location over four days when the location was either a small size or a big size oviposition site. Because some samples were out for 3 days, totals are adjusted to a two day period as in Table 4. "Mean" is the number of eggs deposited per two days at each location when it was either a big or small oviposition site. P is the significance level for an ANOVA comparison of the means for big and small replicates at each location

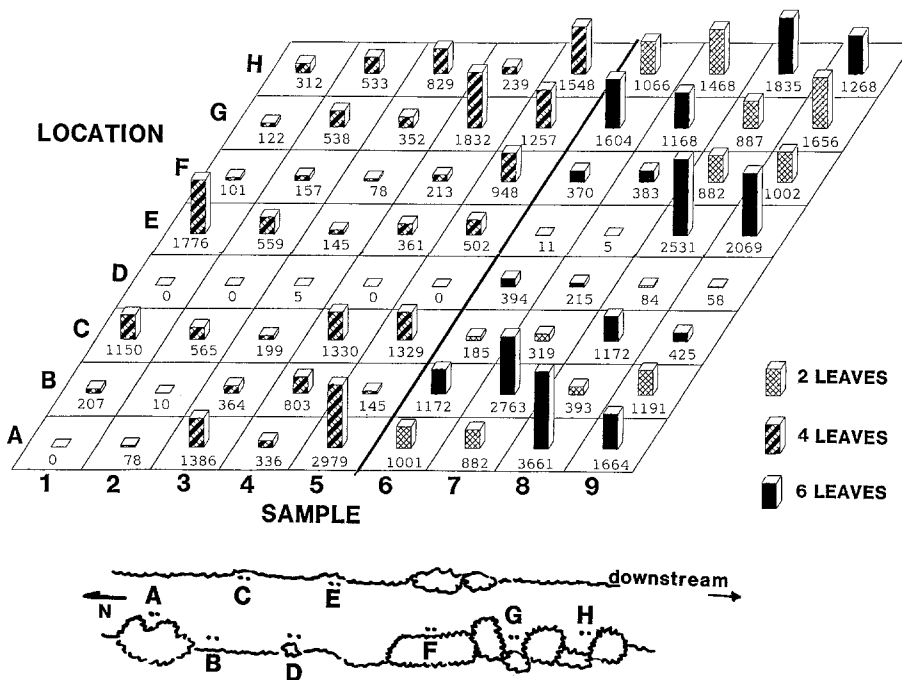| Location	Small size (2 leaves)				Big size (6 leaves)				
	Total	n	Mean	SE	Total	n	Mean	SE	P
A	1883	4	470.8	102.1	3550	12	295.8	64.8	0.07
B	1056	4	264.0	110.9	3935	12	372.9	77.0	0.51
C	504	4	126.0	21.2	1065	12	88.7	25.3	0.69
D	95	4	23.7	11.2	609	12	50.8	16.4	0.78
E	16	4	4.0	2.6	3067	12	255.6	41.0	0.009
F	1256	4	314.0	100.5	753	12	62.7	10.7	0.010
G	1695	4	423.8	143.1	2772	12	231.0	47.1	0.047
H	2534	4	633.5	151.6	2069	12	172.4	36.9	0.0001

Fig. 1. *Top:* Total number of eggs oviposited per two days into oviposition sites at each of 8 locations for 9 consecutive samples. For the first 5 samples all locations had the same amount of vegetation (four 22 cm leaves per location). For the next 4 samples, each location was alternated between two 22 cm leaves and six 22 cm leaves such that half of the locations were larger (*striped bars*) for two samples and then smaller (*checkered bars*) for two samples *Bottom:* Positions of the 8 oviposition site locations along a 20 m segment of the Palmer River

Utilization of locations varying in amount of vegetation. When each location in Area 2 was switched between having 2 or 6 leaves each (Fig. 1, samples 6–9), there was a tendency for greater utilization of the bigger sites. This was most pronounced for locations A–E and G (Fig. 1 and Table 5). However, the mean number of eggs per two days was significantly greater only at locations E, F and G and it was reversed at F where the smaller site received more eggs than the bigger one (Table 5). Thus changing the size of oviposition sites among locations had a variable effect, despite the expected initial preference of females for the bigger of two sites shown in the choice experiments.

Total eggs laid per location over time. Figure 1 shows the total number of eggs laid per 2 days per location for each of the 9 samples (20 days). Samples 1–5 have equal sized sites at all locations. The total number of eggs deposited at all locations during each sample increased during the 20 days (Spearmans $r = 0.883$, $H = 4.99$, $P < 0.001$). This probably reflected generally increasing population size and gradual discovery of Area 2 by males and females. The major pattern that emerges from Fig. 1 is that of considerable variation among locations for the same sampling date and among sampling dates for the same location. No one site consistently ranked first. For example, location A

ranked first on dates 3, 4 and 8, while E was first on dates 1 and 9. Site D was seldom used, while G and H were consistently used. There was a significant effect of site location on mean number of eggs laid there per sample (Anova, $F_{7,64} = 2.40$, $P < 0.03$) but that was due largely to the small number of eggs deposited at location D.

There were, however, some general trends reflecting the influence of site location along the stream. Locations H, G and A had the highest cumulative egg totals and they shared two characteristics. First, they were the first sites that females moving up- or downstream would encounter. The stream above and below the study area was nearly devoid of oviposition sites for about 15 m in each direction. Second, each of these sites was adjacent to bushes in which females often perched. Site D, in contrast, was out in the open with just a small plant nearby for the males or females to perch on.

Discussion

Agreement between initial choice and utilization experiments

When given the opportunity, C. maculata females choose the larger of two adjacent oviposition sites or the one at which there are other ovipositing females. These simple criteria for initial choice between a pair of sites become more complicated when they interact. Females generally join others on a small site rather than ovipositing alone at an adjacent bigger site. When the focus is shifted to actual utilization of oviposition sites, the results are not as clear. Part of the utilization experiment focused on paired big and small sites identical to those used for the initial choice experiments. At the 12 locations used (Table 4) there tended to be more eggs deposited in the bigger sites (73–75% of all eggs laid) which is consistent with the preference for the bigger of two sites in the initial choice tests (Table 1). However, the results for the utilization of big versus small sites were not statistically significant unless total eggs were pooled across all replicates. It is interesting that there were equal mean numbers of eggs per leaf between the big and small sites at each location (Table 4). One interpretation of these results is consistent with the initial choice tests. If females initially pick the bigger site 70% of the time (Table 1) then there should be roughly the same number of eggs per leaf at the three leaf site- 2 to 3 times as many females arriving and 3 times as many leaves to use. In contrast, equal choice of big and small sites should

have resulted in a lower mean number of eggs per leaf at the big sites. The results of the big versus small site utilization experiment are consistent with but do not unequivocally support the preference of females for the bigger of two adjacent sites. Thus my results serve primarily to show that there is no simple relationship between the relative size of sites and their use by ovipositing females.

Several factors could explain the lack of agreement between choice and utilization. First, the presence of other ovipositing females may also have influenced the utilization results. It seems likely that the choice of oviposition site by the first female to arrive may determine choices by subsequent females. If the first or 'seed' female usually chooses the big site then the use of bigger sites should be more pronounced. However, if the seed female had initially landed on the small site or had moved to it as a result of secondary criteria or disturbance, then subsequent females might join her on a smaller site. This could result in considerable variation in the actual utilization of sites, as seen in my results. Given my approach (counting eggs at unobserved sites) I was not able to control for presence or absence of ovipositing females.

Second, other criteria could be involved in the transition between initial attraction to a site and its use. This might include information gained about the plant substrate during oviposition or about the suitability of the leaves as perch sites while ovipositing. I attempted to control for both by using similar vegetation for all sites. Third, the results in Table 4 (similar numbers of eggs per leaf) might mean that females treat the 4 leaves at each location as a single unit for oviposition. In other words, a female is equally likely to oviposit into any for the four leaves or to distribute her eggs among them. A fourth factor is disturbance by males or other females that causes females to shift from one site to another at the same location. Such shifts after initial choice were observed during the paired choice experiments and in other observations of oviposition sites (Waage, unpublished).

The effect of location and size differences among locations

The initial design of the 8 location utilization experiments in Area 2 (Fig. 1) was to see if both location along the stream and size differences among locations would affect the use of oviposition sites by females. First, all locations were given the same amount of vegetation to see if position along the stream affected utilization of otherwise equal sites. Second, each location was alternated between be-

ing a big oviposition site (6 leaves) or a small one (two leaves) to see if females responded to size differences among oviposition sites meters apart rather than centimeters apart.

The results revealed general trends amidst considerable spatial and temporal variation in oviposition site utilization. There was a definite lack of oviposition at one site (D), low usage of two others (B and F) and relatively similar usage of the rest. The rank for both mean eggs per sample and total eggs across the five samples when locations were equal in size was $A > C > G > H = E > B = F > D$. However, only D was significantly different from the others given the large day to day variation in utilization of each site. It is important to note, however, that if each location was occupied by a male for the duration of the study and if each male fertilized all eggs at each site, then there would clearly be differential reproduction of these males despite equality of territory size and vegetation.

Several factors seemed responsible for the differential use of the 8 locations. Sites A, C, G and H were the first encountered by females moving up or downstream. Locations A, G, and H were adjacent to bushes on the west bank used by females as perching and feeding sites prior to oviposition. This suggests that females may tend to use the nearest oviposition site rather than examining several and choosing one. This interpretation is supported by preliminary data from long term observation of identical sites near and far from perching areas (Waage, unpublished). Finally, location D was an exposed site with only one small bush nearby and area E, while bushy, tended to be shaded early in the day and attracted relatively few females. Thus location seems to have an effect, though variable, on oviposition site utilization by females.

Alcock (personal communication) has found that males and females of Calopteryx maculata preferentially use oviposition sites with more vegetation at them when these sites are arranged in a linear array along a section of stream. He set up 4 sites with 1, 2, 4 and 8 leaves each. There were more matings, ovipositions and eggs laid at the bigger sites than at the smaller ones. The distance among sites was 1.5 m which is 3 times the distance between my paired sites and considerably less than that between the 8 locations in Area 2. In addition, his sites were in a row at midstream along a uniform section of stream. Thus his design is somewhat intermediate between that in my paired choice tests and my utilization within and among locations tests. Alcock also found a bias toward the first site encountered by females moving up

or down stream. Thus actual choices among sites by females may operate only at certain scales (sites within a meter or two of each other). When territories vary more in location and are further apart, as in my utilization design, the effect of size is less clear.

Conspicuousness of quality

At present it is not possible to distinguish between apparentness and quality as the cause of choice and utilization of oviposition sites. For example, the reversal of size preference by the presence of other females (Table 3) could mean that joining females is more advantageous than using a bigger site (see Waage 1979 b) or that it is easier to find a site when there are ovipositing females on it. The results presented here and those of Alcock (pers. comm.) are clearly initial investigations into complex questions of proximate and ultimate causality.

Oviposition site differences and reproductive success

It is not at all clear how female choice of oviposition sites relates to the reproductive success of males guarding different oviposition sites or of females using them. The interaction of size and female presence identified above can complicate the picture. For example, my observations of C. maculata reproductive behavior over 10 years agree with the pattern seen in Fig. 1. On any given day most activity is at one or a few sites but popular sites change from day to day. The results presented in this paper suggest that at least some of this day to day variation among locations (territories) may be due to 'seed' females and subsequent attraction to them. The attraction of additional females may or may not benefit resident males (Waage 1979 b; Alcock 1979, 1983). These does seem to be a benefit to females of joining others when they can be guarded without having to mate with the resident (Waage 1979 b).

Altogether, there is no simple effect of size on the utilization of oviposition sites by Calopteryx maculata females, despite a clear ability to make initial choices of where to begin oviposition based on discrimination between sites of different size. If females did show distinct and predictable preferences and males could mimic them, then territory quality might be clearly reflected in male choice and defense of territories and in their reproductive success. However, it is also possible that too many factors interact under natural conditions for either observers or damselflies to easily determine the

best places to obtain mates or oviposit. If so, then it may be that the way to successfully play damselfly lotteries is to stay in the game as long as possible. My results and those of Alcock (personal communication) suggest that how long a male remains at an oviposition site may be as important as which one he is at in terms of long term reproductive success. Despite lack of statistical significance in the daily use of alternative sites, had males remained in some areas (e.g. D, F or C in Area 2) they would have lower success than males remaining at others (A, G or H for example). Studies of lifetime reproductive success of damselflies and dragonflies have revealed the importance of longevity of both males and females (e.g. Fincke 1982, 1986; Banks and Thompson 1985; Hafernik and Garrison 1986; Koenig and Albano 1986).

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