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Part II

A MARK-RECAPTURE STUDY OF IMAGINAL *ENALLAGMA CYATHIGERUM* (CHARPENTIER) AND *ARGIA VIVIDA* HAGEN (ZYGOPTERA: COENAGRIONIDAE)

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A mark-recapture study of the 2 spp. was performed at Del Puerto Cyn., 120 km SSE of San Francisco, Calif., USA, and analyzed by the Jolly and Manly and Parr methods. Movements for ♂♂ of both spp. tended to be local. Recapture data for ♀♀ were sparse, probably due to their greater movements. Morisita's dispersion index for both sexes of both spp. showed the following sequence, from most to least contagious distribution: *E. cyathigerum* ♀♀, *E. cyathigerum* ♂♂, *A. vivida* ♀♀, *A. vivida* ♂♂. These differences were due to the greater preference of *E. cyathigerum* for water sites. Female *E. cyathigerum* showed a 1:3 ratio of blue to brown-olive morphs, but there appeared to be no assortative mate selection by ♂♂. A significantly higher percentage of ♀♀ was taken in tandem or copula with unmarked ♂♂ than marked ones, suggesting that mated ♀♀ entered the water sites already in tandem or copula. Male *E. cyathigerum* and *A. vivida* lived an average of 4.68 and 3.02 days, respectively. The *Enallagma* life span estimate agrees well with reported estimates for other *Enallagma* spp.; but that of *A. vivida* is considerably shorter than for reported estimates for other *Argia* spp.

INTRODUCTION

Enallagma cyathigerum and *Argia vivida* are very common, predominantly blue and black damselflies widely distributed over the western United States. *E. cyathigerum* is circumboreal, occurring from Europe through northern Asia. In western North America, both species occur together along small streams, but *E. cyathigerum* also frequents ponds or lentic pools in streams (WALKER, 1953). PARR & PALMER (1971) and PARR (1976) recently studied a small population of *E. cyathigerum* in England, noting that its population properties may

differ from colder or more southerly continental populations. Because *E. cya-thigerum* is geographically variable (HEYMER, 1968; JURZITZA, 1975), I studied this species in California. *A. vivida*, also common at the same site, was also studied for comparative purposes.

At Del Puerto Canyon (37°27'N, 121°20'W), Stanislaus Co., California, these two species are the most abundant Odonata during late spring and early summer. The site is a small, spring-fed stream within a canyon in the Coast Range about 120 km SSE of San Francisco. The area is characterized by Oak-Pine Savannah Woodland, consisting primarily of *Quercus douglasii* Hooker and Arnolt, *Pinus sabiniana* Douglas, and *Juniperus californica* Carrière. Del Puerto Creek is ecologically varied with small narrow riffle zones interspersed with lentic pools. Within an area about 400 m long, 56 quadrats, each 8 m², were plotted into two sectors representing three still water and stream areas (Fig. 1). Sampling was done from 25 April to 4 May 1977, with 1 May not sampled because of inclement weather. *E. cyathigerum* was marked throughout the period and along the entire 400 m study area. The more abundant *A. vivida* was marked only between 25-29 April in the two sectors of designated quadrats. Movements for marked individuals for both species were recorded for 25 April - 4 May, 7 May and 15 May.

METHODS

Using a permanent "Pilot" felt-tipped pen, adults were marked with a number on the wing and released at the spot of capture. By this simple method, about 20 animals could be marked per hour — about 100 per day. The method produced little or no alteration of behavior, as probability of recapture did not deviate significantly from expected Poisson values. Tenerals were extremely difficult to mark and great care had to be taken not to damage their wings. Totals marked and recaptured were 614 and 165 (27%), respectively (Table I).

Table I

Numbers of individuals marked (N), number recaptured (RC),
and percent recaptured (% RC)

Species	Sex	N	RC	% RC
A. vivida	♂	162	39	24
	♀	102	5	5
E. cyathigerum	♂	297	118	40
	♀	53	3	6
Total		*614*	*165*	*27*

Females of both species had poor recapture rates, probably due to their greater vagility and behavior differences. The data are best for male *E. cyathigerum* (40%), because they were aggregated at the creek, while *A. vivida* occupied more diverse habitats. Individual movements (Figs. 1, 2) are minimum estimates, since they reflect the shortest distance between initial release (open circles) and subsequent recapture (closed circles).

JOLLY (1965) and MANLY & PARR (1968) stochastic mark-recapture methods were used to estimate population size and survival rates. They are the least deterministic techniques assuming variable daily survival and immigration rates. The Manly-Parr method, in addition, assumes differential mortality rates with respect to age and probably reflects the most realistic population parameters.

Average survival rates were calculated using the method of SCOTT (1973), who modified his formulae from JOLLY's (1965) estimation of the daily survival rate:

$$\varphi_{average} = \frac{C + \sum_{i=2}^{n-1} M_i}{\sum_{i=1}^{n-2} (M_i + S_i - m_i)} \quad \text{[symbols of JOLLY, 1965]}$$

C is a correction factor which must be added for each day missed and is determined by the formula[1]:

$$(C = [(\varphi_i)^{1/d} (M_i + S_i - m_i)] - M_{(i+1)},$$

where d is the number of days from the day just before the missed period, i, to the day just after the missed period, i + 1. Thus, if one day was missed, (as was the case for *E. cyathigerum*), then d = 3. A second method of estimation is accomplished by averaging the daily survival rates of JOLLY (1965). Survival rates based on an interval of more than one day were converted to daily one day rates, where d is defined as before by the formula (SCOTT, 1973):

$$\text{one day rate} = (\text{survival rate})^{1/d}.$$

According to Scott, the first method is the more precise, the second giving higher survival rates because individual survival rates can vary above 1.0 more than below 1.0. The average survival rate is converted to minimum expected life span estimates in days using the formula of COOK et al. (1967):

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[1]   The denominators given by SCOTT (1973: 664-665) should be $M_i + S_i - m_i$.

$$\text{expected life span} = \frac{-1}{\log_e \ (\text{average survival rate})}$$

which, if emigration occurred, must be increased. WATT et al. (1977) tested these formulae and found them to provide reliable population estimates of survival.

Indices of dispersion were calculated using the variance-mean ratio formula, $ID = \frac{s^2}{\overline{X}}$ (SOUTHWOOD, 1966), where $s^2 =$ variance of the number of samples and $\overline{X} =$ the mean. Unless the sample sizes are equal, these indices cannot be compared; however, MORISITA's (1959) formula allows for such comparisons:

$$I_\delta = q \ \frac{\sum\limits_{i=1}^{q} n_i(n_i - 1)}{N(N - 1)}$$

where $q =$ total samples, $n_i =$ numbers in the ith sample, $N =$ the number of individuals found in all the samples. In both indices, values < 1 indicate uniformity, values $= 1$ indicate randomness, and values > 1 indicate aggregation.

MOVEMENTS

Only movements for male *Enallagma* and *Argia* (Figs. 1, 2) are shown because recaptures of females were so sparse. The greatest movement for a male *Enallagma* was 288 m (Fig. 1) and 27% of the individuals moved more than 100 m. Most movements were around the lentic pool areas, though many *Enallagma* were seen in the riffle areas. Those movements to the hills occurred on overcast days or late afternoon hours when the insects left the water sites. Of the three *Enallagma* females recaptured, two had moved more than 80 m, indicating relatively high dispersal. Vagility is shown in Table II. Most males tended to remain within or near the same quadrat where marked, although 27% of the recaptures were at an adjacent or non-adjacent pond. However, two of the three females were taken at non-adjacent pools, indicating long movements. With increased time (> 10 days), movements of both sexes probably increase. Neither recaptures of stationary males nor movements upstream, downstream were significantly different from random 1:1:1 ratio, since about a third of the recaptures belonged to each category. Apparently stream flow or grade has little or no deterministic effect on the movements of this species.

The farthest movement for *A. vivida* (Fig. 2) was for a male (200 m), but the movements are not representative of the species, since only those marked in the sectors were sought. Many *Argia* were teneral or juvenile, which also explains their more random movements. Almost all *Enallagma*, on the other hand, were
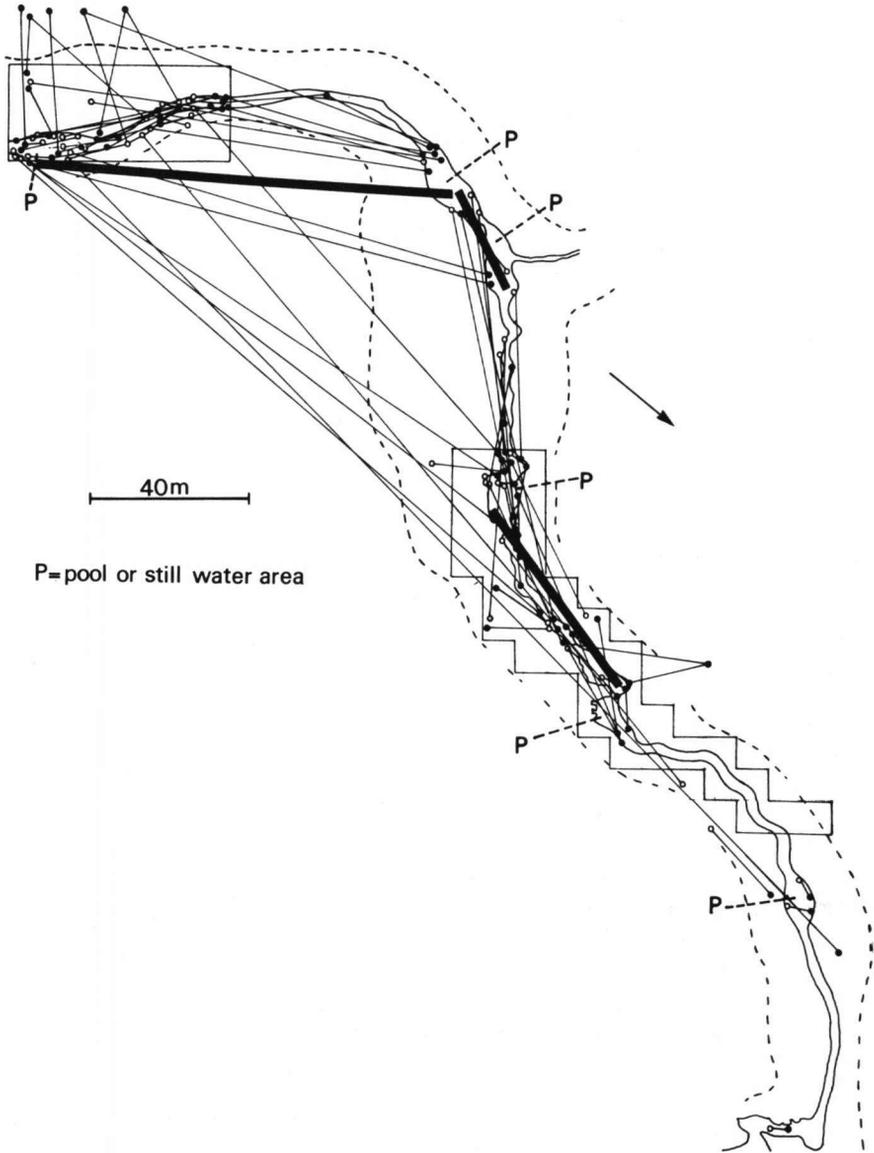
Fig. 1. Movements of *Enallagma cyathigerum* males 25 April - 4 May, 7 May, 15 May 1977. Open circles = initial captures, solid circles = recaptures. All linear movements are minimum distance estimates. Heavy black lines indicate movements of 10 or more individuals. The two sectors are outlined. Dashed lines along the creek represent valley line. Movements within the same quadrats or similar movements already shown are not included.

Table II

Number of recaptures per quadrat for *Enallagma cyathigerum*, 25 April-
7 May 1977. Maximum movement for each individual determines re-
capture parameter

Recapture parameter	Males		Females	
	N	(%)	N	(%)
always in same quadrat	27	(22.9)	–	–
adjacent or diagonal quadrat	18	(15.4)	1	(33.3)
in 2 non-adjacent quadrats	29	(24.7)	–	–
in 3 quadrats	11	(9.4)	–	–
in 4 quadrats	1	(0.1)	–	–
adjacent pool	26	(22.3)	–	–
non-adjacent pool	6	(5.2)	2	(66.7)
Total	*118*	*(100%)*	*3*	*(100%)*

mature and tended to restrict their movements to the water areas. The longest
movement of an *Argia* female was only 16 m, but as only 5% were recaptured,
their movements were undoubtedly much greater than this.

DISPERSION

Both indices of dispersion were calculated from the two sectors (Fig. 2) for
both sexes of both species (Table III). All groups were significantly aggregated
(P > 0.001), but Morisita's index shows *A. vivida* males to be the least aggre-
gated (2.72), followed by *Argia* females (2.90). The marked *Argia* were of a
more heterogeneous age structure, including tenerals, juveniles, and mature

Table III

Indices of dispersion for Del Puerto Cyn. *Argia vivida* and *Enallagma cyathigerum*

$$\left(ID = \frac{s^2}{X} ; \quad I_\delta = q \frac{\sum_{i=1}^{q} n_i (n_i-1)}{N (N-1)} \right)$$ estimated from 56 quadrats (448 m^2). All groups

are significantly aggregated (p > 0.001)

Species	Sex	X	s^2	ID	I$_\delta$
A. vivida	♂	3.75	28.32	7.55	2.72
	♀	1.91	8.89	4.66	2.90
E. cyathigerum	♂	5.95	98.60	16.57	3.58
	♀	0.74	2.56	3.46	4.60

adults. This, plus their occupation of more diverse habitats (rocks, boulders, bare ground), explains the low indices. The females, however, tended to aggregate more at the riffle areas, where many were engaged in oviposition.
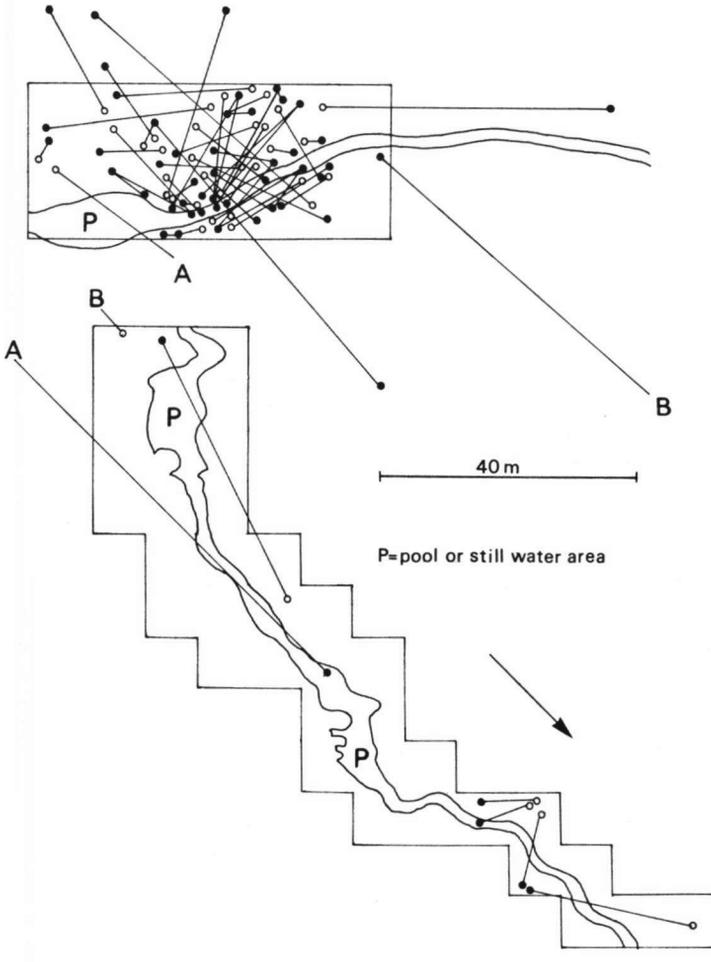

Fig. 2. Movements of *Argia vivida* males 25 April - 4 May, 7 May, 15 May 1977, within the two sectors shown in Fig. 1. Open circles = initial captures, solid circles = recaptures. A = long-range downstream movement (200 m); B = long-range upstream movement (112 m).

Both sexes of *E. cyathigerum* (Table III) were more aggregated than *Argia*, since the marked population sample was almost entirely mature, and since *E. cyathigerum* has a proclivity for water habitats. *Enallagma* strayed from the

water only during inclement weather, or when they left for the afternoon. Most individuals were at the water by 11.00 hours, while *Argia* appeared as early as 08.00 hours, when the sun first reached the valley floor. In general, *Enallagma* left the water at about 17.00 hours, while *Argia* remained at their diverse sites and probably roosted there as well. Female *Enallagma* showed greatest aggregation (ID = 4.60), probably because they were almost entirely confined to the oviposition sites at still water. Away from still water, a few were recovered from shrubbery in the hills; only one female was found at a riffle area. Selection for still vs. riffle water sites by ovipositing females of *Enallagma* and *Argia* respectively, was confirmed by the distribution of their respective nymphs: *Enallagma* occurred in the lentic pools, *Argia* primarily in the riffle areas.

FEMALE POLYMORPHISM

Female *E. cyathigerum* occur in three color forms: blue, brown, and olive. Color was recorded for 45 of the 51 mature females observed (Table IV). The brown and olive morphs were so similar in color that I treated the two as one morph. The genetic system controlling this color expression is unknown, but JOHNSON (1964, 1966) believes that a single allelic pair of autosomal genes is responsible for the dimorphic color expressions in the female coenagrionids *Ischnura damula* Calvert and *I. demorsa* (Hagen). The other possibility is that these colors are ontogenetic, with one color morph changing to the other through time. During my study, three fully mature, marked brown females remained brown after 4, 7, and 12 days, and one mature blue female was still blue the next day. Therefore, changes, if they do occur, probably go from blue to brown. However, I consider this a genetic dimorphism, and base my observations on this assumption. The frequency of blue (13) to brown (32) morphs does not significantly deviate from a simple 1:3 ratio ($x^2_{(1)} = 0.73$), indicating that a simple pair of alleles may control this expression.

Percentages of female morphs observed in tandem or in copula can be used as an indication of assortative mate selection by males. Table IV shows that 69%

Table IV
Frequency of polymorphic *Enallagma cyathigerum* ♀♀ – all sites.
Numbers in parentheses are percentages

Morph color	N (% total)	Single N (% morph)	In tandem or copula N (% morph)	In tandem or copula with unmarked ♂	In tandem or copula with marked ♂
blue	13 (29)	4 (31)	9 (69)	8	1
brown or olive	32 (71)	6[1] (19)	26 (81)	23	3
Total	45 (100)	10	35	31	4

[1] One ♀ was single but ovipositing, thus it had previously been in copula.

blue and 81% brown morphs were so engaged. A Chi-square test showed no significant difference ($\chi^2_{(i)} = 0.15$) from a non-assortative regime where 78% blue and 81% brown females would be mated. Thus, the adaptive value for this dimorphism remains unknown, but as my sample size (N = 45) was small, larger counts may show assortative mating to take place. Other common enallagmas (*E. boreale* Selys, *E. carunculatum* Morse, *E. civile* (Hagen), and *E. praevarum* (Hagen)) in central California also have dimorphic females. A frequency dependent mode of selection as recently proposed by JOHNSON (1975) for *Ischnura damula* and *I. demorsa* would not seem appropriate here, because the andromorphs (i.e., blue morphs) of all five species of *Enallagma* are very similar in appearance and also because the data did not show a preference of one over the other female morphs by the males. Later in the summer, four other *Enallagma* species occur at Del Puerto Canyon and a change in morph frequency might occur. Though females of *Argia vivida* are also blue or brown, the high percentage of juvenile specimens prevented a similar evaluation of their conditions.

Of the 35 females (Table IV) found in tandem or copula, 31 (88.6%) were with unmarked males, compared with 4 (11.4%) previously marked males. This difference indicates that most of the females entered the pond areas with males. Another possibility is that unmarked males had a selective advantage over marked ones in procuring single females at the water. However, the expected Poisson distribution for recapture of marked males (JOHNSON, 1962) showed no difference from the theoretical recapture frequency for unmarked males. Therefore, females probably accepted marked and unmarked males equally. If

Table V

Population parameters estimated from Jolly's multiple recapture data for *Enallagma cyathigerum* males. $\hat{\alpha}_i$ = proportion of marked animals, $\hat{M}_i$ = total marked population, Ni = total population estimates, $\hat{\phi}_i$ = daily survival rate, $\hat{B}_i$ = number of new animals joining population. Numbers in parentheses are calculations from MANLY & PARR (1968) method.

Date		$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i \pm 1.96$ SE	$\hat{\phi}_i$	$\hat{B}_i$
April	25	–	–	–	0.90 (0.84)	–
	26	0.40	19.7	49.3 ± 39.4 (46.7)	1.44 (1.60)	515.0 (346.6)
	27	0.06	37.1	586.1 ± 526.7 (421.3)	0.67 (0.70)	−99.0 (−33.3)
	28	0.25	74.4	293.4 ± 132.0 (262.7)	0.89 (1.08)	−27.5 (−39.9)
	29	0.49	113.2	233.2 ± 113.2 (245.0)	0.74 (0.99)	97.2 (34.5)
	30	0.36	98.0	271.4 ± 101.4 (276.0)	0.77 (0.96)	17.3 (−53.1)
May	1	–	–	–	[1.23] –	–
	2	0.49	110.2	225.1 ± 85.7 (211.1)	1.88 (1.68)	55.6 (84.6)
	3	0.53	254.7	479.5 ± – (440.0)	–	–
	4	0.60	–	–	–	–

Ave. Population Size: 305.4 ± 346.6 (271.8 ± 260.3)

all mated females first entered a site alone, they would presumably have an equal chance of encountering a marked or unmarked male. However, Jolly's recapture program estimates a marked proportion ($\hat{\alpha}_i$) average of 40% (± 34%; the high 1.96s is due to a one-day recapture percentage of only 6% (Table V); if ignored, the results are 45% (± 23%), compared with only 11.4% found in copula or tandem. These values are significantly different ($X^2_{(1)} = 18.34$).

POPULATION SIZE AND LONGEVITY

Population estimates were calculated only for the males of both species, because the low incidence of female recaptures precluded their analysis. Even so, the data reported here must be used with caution, since (1) the populations were not closed, thus giving rise to non-permanent emigration, an assumption not covered by JOLLY's (1965) or MANLY & PARR's (1968) model (SEBER, 1973); (2) sampling was weighted in quadrats of greater observed density; and (3) more individuals were present than could be marked, especially *Argia*. This resulted in a greater marking activity in some areas than in others.

Population parameters for *Enallagma* males are shown in Table V. Population size estimates of Jolly are largely concordant with those of Manly & Parr (Fig. 3), with the exception of 27 April. The Manly & Parr estimates tend to smooth out the population curve. From a low of about 45 individuals on 26 April, the population jumped to about 585 (Jolly) or 421 (Manly & Parr), then leveled off to about 250 for the next five days. May 3 was clear and windy, resulting in a large increase in numbers. The greater fluctuation of Jolly's estimates resulted in an overall average population of 305.4 ± 346.6 (Table V), but Manly & Parr's estimate was 271 ± 260.3, probably a more accurate figure due to the lower oscillations of daily population size, especially for 27 April (Fig. 3). As laboratory rearings of nymphs from Del Puerto Canyon have consistently shown about a 1:1 sex ratio, the total
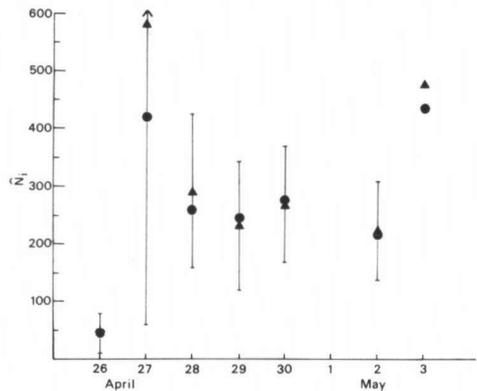

Fig. 3. Population (N_i) estimates of *Enallagma cyathigerum* males, 26 April - 3 May. No estimates were derived for 1 May. Triangles are estimates by Jolly method, circles are estimates by Manley-Parr method. Bars are 1.96 SE of Jolly estimates.

population size of adults at any given time within the 400 m stretch of canyon is probably about 600. Comparison of Jolly's and Manly & Parr's estimates

Table VI

Population parameters estimated from Jolly's multiple recapture data for *Argia vivida* males. $\hat{\alpha}_i$ = proportion of marked animals, $\hat{M}_i$ = total marked population, $\hat{N}_i$ = total population estimates, $\hat{\phi}_i$ = daily survival rate, $\hat{B}_i$ = number of new animals joining population. Numbers in parentheses are calculations from MANLY & PARR (1968) method.

Date	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i \pm 1.96$ SE	$\hat{\phi}_i$	$\hat{B}_i$
April 25	–	–	–	0.86 (0.59)	–
26	0.14	46.0	327.7 ± 320.4 (228)	0.64 (0.21)	24.8 (32.0)
27	0.26	61.0	235.3 ± 271.1 (81)	1.20 (0.44)	217.1 (180.0)
28	0.19	97.0	498.9 ± 801.6 (216)	–	–
29	0.41	–	–	–	–

Ave. Population Size: 354.0 ± 262.2 (175.0 ± 160.0)

(Table VI) of *Argia* for the two sectors shows wide discrepancies. The much smaller daily values of Manly & Parr result in an average population estimate about half the size of Jolly's. This is most likely due to the low number of intermediate recapture values ($10 > A_{1i}$, MANLY & PARR, 1968), so I consider Jolly's estimate of 354 ± 262.2 a more reliable figure. The average population estimates for both species are nearly equal, but the *Argia* numbers refer only to two sectors (about 200 m of canyon length) and *Argia* is, consequently, the more abundant species.

The overall survival rate using Scott's first method for *Enallagma* was 0.8077 or 4.68 days. This value is probably too conservative, because only fully adult individuals were marked and egress occurred on 27-28 April (Table V). Given a maturation of at least a week, male *Enallagma* probably live an average of 12-14 days. Two mature individuals lived at least 21 days following marking and therefore probably survived 28-30 days. The results are comparable with PARR's (1976) life table estimates of 6.5 days, but less than his estimate of 12.1 days using Fischer and Ford's method. I attribute lower overall survival rates in my study to the low incidence of recaptures, only 40% (Table I). Calculations of average survival rates using Scott's second method yielded results greater than unity.

Average survival rates for *Argia* were 0.718 (3.02 days) by Scott's first method and 0.8972 (9.22 days) by his second method. The first estimate may be a truer indication of survival because inclusion of tenerals and juveniles probably reflects higher daily mortality rates (Table VI) than for *Enallagma* (Table V). These lower rates, however, may also be the result of dispersal, since immature males wander from water to feed and mature, lessening their chances of subsequent recapture in that sector.

DISCUSSION

The average longevity of 4.68 days is shorter than PARR's (1976) 12.1 days for *Enallagma cyathigerum*, but it compares well with BICK & BICK's (1963) average of 3.3 days (Fischer and Ford method) and 3.5 days (life table method) for *E. civile*, with JOHNSON's (1964) estimate of 5.0 days (Fischer and Ford) for male *E. praevarum*, and with LOGAN's (1971) 4.2 days for *E. boreale* and 3.2 days for *E. carunculatum* (both Fischer and Ford). Using the life table, I calculate a mean age of 3.97 days (range 1-.9 days), an estimate slightly less than Jolly's average estimate. Since my estimates are minima, *E. cyathigerum* at Del Puerto Canyon probably has an actual average life span of 12-14 days.

The estimated average life span of *Argia vivida* (3.02 days, Scott's first method) is much less than that of *A. apicalis* (Say) (8.4 days males, 7.0 days females; BICK & BICK, 1965), *A. moesta* (Hagen) (about three weeks; BORROR, 1934), and *A. plana* Calvert (10.9 days males, 7.7 days females; BICK & BICK, 1968), except by estimate from Scott's second method (9.22 days). The low frequency of recapture (23%), plus the short duration of the study (five days), probably prevent a reliable estimate with the present data, and further studies will probably show an expected life span similar to other *Argia* species studied.

Movements of *Enallagma* (Table II) are difficult to compare with PARR's (1976) because his study site was a flatland area containing two small ponds, while my area was a small portion of a much larger water system dissecting rugged terrain. Consequently, the 27% movements to adjacent or non-adjacent ponds is not surprising. Besides daily movements up- and downstream, *Enallagma* probably flies over the surrounding hills and enters other nearby creeks. Parr observed almost 100% movement of tenerals away from water, but as I obtained no recapture information on tenerals or juveniles, I surmise that daily movements include *Enallagma* that fly across the surrounding hills and enter nearby creeks.

The other data coincide with PARR & PALMER's (1971) results for European *E. cyathigerum*. For example, they noted that nearly all females were in copula or tandem when seen at water. Thirty-seven of 51 females (73.6%) at Del Puerto were in tandem or copula. The low frequency of marked males found to be in tandem suggests that mating does not take place at the water, but I never observed any copulations along the canyon floor or walls. When I marked males and females in tandem, the marking procedure almost always caused them to separate, and the released, solitary females were almost at once seized by another male before they left the water. Parr calculated a mating frequency (number of matings observed in relation to the number of insects caught) of 6.5% for males, and 60.0% for females. Frequencies for the Del Puerto population were 9.1% for males, and 69.6% for females. Mating expectancies for each sex (observed number of matings divided by the number of individuals of that sex seen mating) were 1.0, the same as for PARR & PALMER's (1971) and BICK &

BICK's (1963) results for *E. cyathigerum* and *E. civile*, respectively. BICK & BICK (1963) suggest the low (3.5 days) longevity as the reason for the failure of 76% of the males of *E. civile* to mate, while PARR & PALMER (1971) suggest that the paucity of females at water and the "tendency for some males to be ineffectual sexually" are reasons for the high failure of *E. cyathigerum* to mate. However, JOHNSON's (1965) study of *E. praevarum* contained more imaginal females than males. His sampling of mated pairs showed that each male had mated an average of three times, while females had an average of two matings each. This situation is quite unlike my observations and those of others (PARR & PALMER, 1971; BICK & BICK, 1963), and illustrates the variability encountered in mark-recapture studies of dragonfly populations.

Mating frequencies for all *Argia* males and females were 16.2% and 48.15% respectively, but when only reproductively mature adults are counted, the values are 20.5% and 66.7% for males and females, respectively. The higher percentage for male *Argia* over that of male *E. cyathigerum* (9.1%) is probably due to the increased chance of encounter with a mature *Argia* female. Mating expectancies for both sexes were 1.0, nearly the same as for *A. apicalis* (BICK & BICK, 1965).

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