DISPERSAL OF ADULT FEMALE *CULEX ANNULIROSTRIS* IN GRIFFITH, NEW SOUTH WALES, AUSTRALIA: A FURTHER STUDY

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ABSTRACT. The dispersal of *Culex annulirostris* was studied during February 1986 in Griffith, N.S.W. using a mark-release-recapture technique. Parity was determined of recaptured females and a sample of the population at release. Parity rates of the 2 populations were comparable, and no significant differences were detected between the dispersal characteristics of the nulliparous and parous recaptured females. The maximum flight distance observed was 12 km, the limit of the trapping network. It was estimated that the mean distance traveled was 4.4 km and 36.6% (n = 377) of the population dispersed further than 5 km. The majority (81.2%, n = 377) of recaptures were taken within 2 days of release and the rate of dispersal of the population was estimated at 2.2 km/day.

Culex annulirostris Skuse is one of the most important vectors in Australia of Ross River virus, the causative agent of epidemic polyarthritis and Murray Valley encephalitis virus (Lee et al. 1989) and therefore the target of control measures. In New South Wales (NSW), Australia prior to 1985, larval control measures were restricted to a 5 km-wide zone surrounding urban centers. The effectiveness of this method is influenced by the dispersal powers of the adult mosquitoes and, where dispersal is significant, by the size of mosquito populations outside the treated area and efficiency of control measures.

Russell (1986a) studying dispersal of *Cx. annulirostris* from an isolated larval habitat, recorded flights of up to 7 km, the limit of the trapping grid employed. He postulated that flights greater than 7 km were likely and this was confirmed by O'Donnell et al. (1992) using mark-release-recapture methods; the maximum flight observed was 8.7 km.

These latter authors fitted Taylor's (1978) general dispersal equation to the observed decline in density of labeled adults with distance from the release points and estimated the average distance dispersed as 6.8 km (95% confidence limits: 4.1–40.9 km). Their analysis suggested that 50% of the marked *Cx. annulirostris* population dispersed 4.8 km or further; 10% dispersed 15 km or further. Taylor's (1978) model, in the same form, also fitted Russell's (1986a) data and yielded a comparable estimate of the average distance dispersed, 7.1 km.

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Following these studies, a further series of experiments was undertaken to examine the hypothesis that flights greater than 8.7 km are undertaken by *Cx. annulirostris* females.

MATERIALS AND METHODS

Capture, marking, release and recapture: The study area and the methods were similar to those of the previous study (O'Donnell et al. 1992). The study was undertaken at Griffith, N.S.W., from February 4 to 21, 1986. Mosquitoes for marking were captured nightly for 10 consecutive nights. Each night, mosquitoes were labeled using a different combination of Ciba-Geigy "Radglo" fluorescent powders with date-specific marks.

All releases took place on the night of capture and were made at the same location, at the center of the study area, corresponding to Release Point 1 in 1985 (O'Donnell et al. 1992). Trapping stations were located, as close as possible, at 0.1, 0.2, 0.4, 0.8, 1.5, 3.0, 5.0, 7.5, 10.0 and 12.0 km from the release point, along 4 axes. The trapping lines followed main roads for the inner stations and thereafter as close to the theoretical axis as possible; some of the outer traps were displaced from their theoretical position because of restricted access.

The daily distribution of recapture traps varied (Table 1). Initially, all stations were sampled with one or 2 Encephalitis Virus Surveillance (EVS) traps (Rohe and Fall 1979), but as the program continued, the inner stations were either sampled less intensively or excluded and more traps were placed at the outer stations with a maximum of 4 traps per station. The same daily pattern of traps was used on each axis, though minor differences resulted from occasional trap failures. Trapping was continued for 17 consecutive nights. Winds were light and variable during the nights of this study.

Collections from recapture traps were screened for labeled individuals with an ultraviolet lamp operating at 366 nm. The presence and color combination of the label and the spe-

Table 1. Allocation of traps on each axis during a study of dispersal of *Culex annulirostris* at Griffith, N.S.W.

	Trap position (km from release point)									
Date	0.1	0.2	0.4	0.8	1.5	3.0	5.0	7.5	10.0	12.0
February 4	1	1	1	1	2	1	2	1	2	1
5	1	1	1	1	2	1	2	1	2	1
6	1	1	1	1	2	1	2	1	2	1
7	1	1	1	1	2	1	2	1	2	1
8	1	1	1	1	2	1	2	1	2	1
9	1	1	1	1	2	1	2	1	2	1
10		2		2	2	2	2	1	2	
11		1		2	2	2	2	2	2	
12		1		2	2	2	2	2	2	
13				1	2	2	2	2	2	2
14					2	3	3	3	3	3
15					2	3	3	3	3	3
16					2	3	3	3	3	3
17					1	3	3	3	3	3
18						2	3	3	4	4
19		1				1	3	3	4	4
20		1				1	3	3	4	4
Total	6	12	6	13	27	30	47	34	44	32

cies of the recaptured individual were confirmed by microscopic examination (20–40×).

Determination of parity: Samples of 20–25 females, taken from each night's catch before labeling/release, and most recaptured specimens were classified as nulliparous or parous using the ovarian tracheole criteria of Detinova (1962).

Analysis of results: The numbers of nulliparous and parous females at release and recapture, the distribution of distances dispersed and times between release and recapture of the nulliparous and parous specimens were compared using chi-square statistic. As the numbers of recaptured females in some categories were very low, the data were grouped prior to analysis, in accordance with Cochran's (1954) criteria. Dispersal of the nulliparous and parous individuals was comparable, so they were pooled for all subsequent analyses.

Initially the recapture data were analyzed, as in the previous study (O'Donnell et al. 1992) using Taylor's (1978, 1980) general model of dispersal:

$$N = \exp\,(a + bX^c)$$

(where N is the density at distance X from the dispersal center and a, b and c are parameters) which was fitted to the observed relationship by maximum likelihood methods, using the computer program Genstat V (Payne 1987). The trap effect was assumed to be randomly distributed and was included as a component of the residual deviance. The direction effect, i.e., the 4 axes considered separately, was examined by inclusion as an extra parameter in the model.

Model-fitting was unsatisfactory and its application to this study was limited. However, further investigation was possible based on the observed recapture rates for each distance and time category.

The mean distance traveled (MDT) was determined using the method of Lillie et al. (1981). The study area was divided into a series of annuli, centered on the release point, the boundaries of which were derived from the point distances midway between adjacent trapping stations. The outer annulus was between 11 and 13 km. The density of labeled mosquitoes (Number of recaptured mosquitoes/Number of recapture nights) at each trapping station was calculated and assumed to be representative of the whole annulus, even though some trapping stations were not located at the mid-point of the annulus. The relative number of labeled *Cx. annulirostris* within the annulus was calculated as:

$$\text{Area of annulus} \times \text{density of labelled mosquitoes.}$$

The mean distance travelled was derived from the formula:

$$\text{MDT} = \frac{\Sigma\ (\text{Relative number of mosquitoes in annulus} \times \text{trap distance})}{\Sigma\ \text{Relative number of mosquitoes}}$$

The distribution of relative numbers by distance category was also used to determine the proportions of the recapture population dispersing more than 5 and 10 km from the release point. Total numbers dispersing less than and more than the distance limit were obtained by addition of the appropriate annulus values and the proportions were derived from these totals. As both specified distance limits fell within an annulus, the relative number in that annulus was divided between the 2 categories in direct proportion to the areas within and beyond the limit.

These methods do not permit the determination of confidence limits. However, approximate estimates of these parameters were obtained by regarding the axes values as replicates and calculating the means and 95% confidence limits by standard techniques.

The use of date-specific labels allowed the calculation, by standard methods, of the mean and 95% confidence limits of: 1) time between release and recapture, and 2) rate of dispersal. A second method of analysis took account of variations in trapping intensity between stations. The mean value and 95% confidence limits were calculated for each station, weighted by the relative number of mosquitoes recaptured at that distance (from the MDT analysis) and population values for the parameter obtained by a similar calculation to that used in the determination of the mean distance traveled.

RESULTS

Approximately 60,000 female *Cx. annulirostris* were marked and released between February 4 and 13, 1986. Of these, 377 were recaptured between February 4–21, a recapture frequency of approximately 0.6%.

The proportions of parous individuals at release, (29.1%, $n = 223$) and at recapture, (23.5%, $n = 366$) were not significantly different ($P > 0.1$); 11 recaptured specimens were not scored for parity. Distance dispersed (Table 2) and time from release to recapture (Table 3) of nulliparous and parous females were compared after grouping data as shown in the tables. The pattern of distance dispersed was similar for nulliparous and parous females (Table 2, $P > 0.25$). The evidence of a change in parity over time was marginally insignificant (Table 3, $P = 0.8$); after more than 4 days the proportion of captured females that was parous was 44% ($n = 18$) compared with 22% ($n = 348$) for captures within 4 days of release.

A total of 377 labeled *Cx. annulirostris* was recaptured, of which 16 had traveled 5 km or more and five, 10 km or more. The maximum flight recorded was 12 km, the limit of the recapture grid. A summary of the recaptures for each axis is given in Table 4.

Table 2. Comparison of the numbers of nulliparous and parous *Culex annulirostris* females recaptured at each trapping distance and as grouped for analysis. Expected values are shown in parentheses.

Distance (km)	Nulliparous No. recaps[1]	Nulliparous Gpd[2]	Parous No. recaps	Parous Gpd	Total No. recaps	Total Gpd
0.1	14	124	4	31	18	155
0.2	110	(118.6)	27	(36.4)	137	
0.4	11	79	2	24	13	103
0.8	68	(78.8)	22	(24.2)	90	
1.5	48	48 (50.5)	18	18 (15.5)	66	66
3.0	19	23	7	8	26	31
5.0	4	(23.7)	1	(7.3)	5	
7.5	3	6	3	5	6	
10.0	2	(8.4)	1	(2.6)	3	11
12.0	1		1		2	
Total	280	280	86	86	366*	366*

[1] Recaps = recaptures.
[2] Gpd = grouped data.
Chi-square at 4 d.f. = 4.622, $P = 0.25$–0.50.
* 11 recaptured mosquitoes were too damaged to be dissected.

Table 3. Comparison of the numbers of nulliparous and parous female *Culex annulirostris* recaptured on each day after release and as grouped for analysis. The expected values are shown in parentheses.

Time in field (days)	Nulliparous No. recaps[1]	Nulliparous Gpd[2]	Parous No. recaps	Parous Gpd	Total No. of recaps	Total Gpd
½	30	30 (33.7)	14	14 (10.3)	44	44
1	128	128 (125.5)	36	36 (38.5)	164	164
2	69	69 (67.3)	19	19 (20.7)	88	88
3	35	35 (30.6)	5	5 (9.4)	40	40
4	8		4		12	
5	8	18 (23.0)	4	12 (7.1)	12	30
6	1		2		3	
7	0		2		2	
8	1		0		1	
Total	280	280	86	86	366*	366*

[1] Recaps = recaptures.
[2] Gpd = grouped.
Chi-square at 4 d.f. = 9.326, $P = 0.05$–0.1.
* 11 recaptured mosquitoes were too damaged to be dissected.

The best fit of Taylor's (1978) model (Equation 1) to the observed recaptures was obtained with $c = 0.7$. However, the fit of the model was very poor, because of the large numbers captured at traps at 0.2 and 0.8 km from the release point compared with the much lower numbers captured at 0.1 and 0.4 km from the release point (Table 2). Therefore, the model fitting procedure was taken no further, and it was not possible to determine the average distance dispersed or the distance limits for specified proportions of the population as in the previous study (O'Donnell et al. 1992).

The values of mean distance traveled (MDT) and proportion of the population dispersing further than 5 and 10 km for each trapping axis and total recaptures, are shown in Table 5. The mean values and 95% confidence limits, derived from considering the axes results as replicates, were MDT, 4.5 ± 1.8 km; 5 km limit exceeded by 38.3 ± 26.6% and 10 km limit exceeded by 11.5 ± 9.4%. These values suggest that the 95% confidence limits (c.l.) on the total recapture values are of the order of ±40% of the MDT and ±75% of the proportional value.

Of the recaptured females, 30 (8.0%) were in the field for 4 days or longer and 5 (1.3%) for 6 days or longer. The maximum time between release and recapture was 8 days. The population estimates of time from release to recapture were 1.7 days (95% c.l. 1.6–1.8 days) for the unweighted mean and 2.4 days (95% c.l. 1.6–3.2 days) for the weighted mean.

The estimates of dispersal rate were: unweighted mean, 0.8 km/day (95% c.l. 0.6–0.9 km/day) and weighted mean, 2.2 km/day (95%

Table 4. Summary of *Culex annulirostris* females retrapped on each trapping axis during a study of dispersal at Griffith, N.S.W.

Distance from release point (km)	Axis 1		Axis 2		Axis 3		Axis 4		Total	
	R/N[1]	RR[2]	R/N	RR	R/N	RR	R/N	RR	R/N	RR
0.1	10/5	2.000	4/5	0.800	5/4	1.250	0/5	0.000	19/19	1.000
0.2	102/10	10.200	18/12	1.500	11/11	1.000	10/11	0.909	141/44	3.205
0.4	9/5	1.800	1/6	0.167	2/5	0.400	1/6	0.167	13/22	0.591
0.8	59/13	4.539	21/13	1.615	6/12	0.500	8/13	0.615	94/51	1.843
1.5	14/27	0.519	28/25	1.120	19/23	0.826	7/26	0.269	68/101	0.673
3.0	17/26	0.654	3/27	0.111	3/27	0.111	3/26	0.115	26/106	0.245
5.0	2/40	0.050	0/37	0.000	2/37	0.054	1/37	0.027	5/151	0.033
7.5	1/30	0.033	2/23	0.087	3/26	0.115	0/27	0.000	6/106	0.057
10.0	0/42	0.000	1/39	0.026	1/33	0.030	1/35	0.029	3/149	0.020
12.0	1/25	0.040	0/27	0.000	1/24	0.042	0/26	0.000	2/102	0.020
Total	215		78		53		31		377	

[1] R/N = no. of recaptured mosquitoes/no. of trapping nights.
[2] RR = no. of recaptured mosquitoes per trapping night.

Table 5. Mean distance traveled (MDT) and proportion of the *Culex annulirostris* population dispersing further than the specified distance for each trapping axis.

Trapping axis	MDT (km)	Proportion 5 km	(%) exceeding 10 km
1	3.5	20.4	10.1
2	4.1	38.2	4.7
3	6.1	60.6	19.0
4	4.4	34.0	12.4
Total	4.4	36.6	11.3

c.l. 1.2–3.2 km/day). The maximum observed rate was 10 km in 1 day (2 individuals).

DISCUSSION

The parity rate of the population at recapture (23.5%) was comparable to that at release (29.1%). The EVS traps attract only host seeking females, so that captured females are in the same state of their gonotrophic cycle. At Appin, near Sydney, N.S.W., the gonotrophic cycle of *Cx. annulirostris* was 4–6 days during the summer, under similar prevailing conditions to those in the present study (Russell 1986b). Of the recaptured females, 95.1% had been released 4 or fewer nights. Thus most specimens were recaptured before a gonotrophic cycle could have been completed since their initial capture and release. The parous rate increased ($P = 0.06$) in those captured more than 4 days after release (44.4%) compared with those recaptured more quickly (22.4%). This supports Russell's (1986b) finding that a gonotrophic cycle can be completed in 4 days. However, only small numbers (18 = 4.9%) were recaptured more than 4 days after release. Of the 3 specimens caught more than 6 days after release, one was still nulliparous showing that the gonotrophic cycle can exceed 6 days. It is possible that capture and subsequent release after labeling, which interrupted host seeking, may have unnaturally prolonged host seeking. However, it is also highly probable that with the high mosquito densities prevailing at Griffith, many individuals normally spend several nights host seeking, thus increasing the duration of their gonotrophic cycles.

By using EVS traps, only host seeking females were retrapped. Thus as individuals obtained a blood meal, they would not be available for trapping until they had oviposited. As most recaptures were within 4 days of release, this was a study of the dispersal of females that had been unsuccessful in feeding during the days between release and recapture.

The nulliparous and parous components of the recapture population did not differ significantly in their distributions of distances dispersed (Table 4, $P > 0.25$) or time intervals between release and recapture (Table 3, $P > 0.05$). Thus no aging effects on dispersal were detected, and in subsequent analyses the recaptured females were treated as a single population.

The maximum recorded flight was 12 km, the limit of the recapture grid. As the likelihood of capture at such distances from the release point is very low, flights of even greater magnitude may be postulated with confidence.

In our earlier study (O'Donnell et al. 1992), Taylor's (1978) dispersal model (Equation 1) gave a good fit to the recapture data with $c =$

0.55. In this study *c* was estimated as 0.7, suggesting that a value of this order is a reliable estimate of the exponent. However, the model did not provide a satisfactory fit overall, with unacceptably high deviances between the expected and observed recapture rates for those stations which were within 1 km of the release point.

The probable explanation of this discrepancy is the effect of local factors, for example shelter or hosts, which may have caused clustering of the population. More intensive trapping within 1 km of the release point may have elucidated this point. However, for logistic reasons adequate sampling at the greater distances from the release point was only possible if sampling close to the release point was reduced. The trapping strategy that was adopted resulted in detection of flights of 12 km, but reduced trapping near the release point.

Although the model fitting procedure was of limited value, it was possible to obtain a measure of the population's dispersal potential from the recapture rates. The relative numbers of recaptured mosquitoes were used to derive the mean distance traveled (Lillie et al. 1981) and proportions within specified distance limits.

The estimates of mean distance traveled in the 4 trapping axes, varied between 3.5–6.1 km, with a population value of 4.4 km. It was not possible to determine 95% confidence limits for this parameter, but by regarding the 4 axes as replicates, an approximate value of ±1.8 km is suggested. These findings, though not based on a model which reduces the effects of sampling errors, are nonetheless in close agreement with those recorded previously (MDT = 3.8 ± 0.3 km; O'Donnell et al. 1992).

The proportions of the population dispersing further than 5 km ranged from 20.4 to 60.6% over the 4 trapping axes, the population value being 36.6%. The range for the 10 km limit was 4.7–19.0% with a population estimate of 11.3%. The comparable figures for the best fit of the model in the earlier study are 48.3% dispersed further than 5 km and 21.4% further than 10 km (O'Donnell et al. 1992).

These earlier figures, especially the 10 km value, are higher than the findings of this study. This is the result of the different methods of calculation; the relative numbers per annulus approach is conservative and takes no account of dispersal beyond the maximum observed flight whereas the modeling approach, used previously, assumes that the observed relationship holds true over all distances and extrapolates beyond the maximum recorded flight distance. As seen here, this effect becomes more pronounced as the specified distance limit approaches the maximum observed flight.

Taking this qualification into account, the 2 values for the 5 km limit may be considered comparable. Of greater relevance, is that even when a conservative method of analysis is used, the proportions of the population dispersing further than the 5 and 10 km limits are relatively high. In areas such as Griffith with very large mosquito populations, the actual numbers dispersing over these distances must be considerable.

In the 1985 study, the rate of dispersal could only be measured by an approximate method, which yielded a range of 0.7–2.1 km/day for the whole population. The greatest flight observed in 1 day was 7.5 km. The use of date-specific labels in this study permitted a more precise determination of this parameter. The unweighted mean ($n = 377$) was 0.8 km/day (95% c.l. 0.6–0.9 km/day). The weighted mean was 2.2 km/day (95% c.l. 1.2–3.2 km/day). Two individuals dispersed 10 km in a single day. The findings of the 2 studies are in close agreement.

The total number of mosquitoes recaptured differed in the 4 trapping axes, equivalent to directional axes (Table 4), the order being axis $1 \gg 2 > 3 > 4$. This suggests that there was a directional bias toward axis 1 in the movement of labeled *Cx. annulirostris*. Much of the disparity, however, is due to differences in recapture numbers within 1 km of the release point. Relatively few traps were run in this area (Table 1), and clustering of labeled females close to the release point may have been a major cause of the observed inequalities. This suggestion is supported by the mean distance traveled and distance limit values (Table 5), axis 1 recording the lowest values of these parameters, despite its high recapture numbers. Overall, the pattern of dispersal was similar in all directions.

It is clear from this study, supported by the 2 earlier ones (Russell 1986a, O'Donnell et al. 1992), that *Cx. annulirostris* females can disperse at least 12 km and probably further. This is comparable to the dispersal distances recorded for *Cx. tritaeniorhynchus* Giles and *Cx. tarsalis* Coq., which have similar ecological requirements in Japan and the U.S.A., respectively (Service 1976). Wada et al. (1969) recorded flights of up to 8.4 m (13.4 km) for *Cx. tritaeniorhynchus*, and estimates of 9.6 m (15.4 km) (Dow et al. 1965) and up to 20 m (32 km) (Bailey et al. 1965) have been recorded for *Cx. tarsalis*.

Because of the dispersal powers of *Cx. annulirostris*, larval control in a 5 km barrier zone in an area with a high population of this mosquito will only provide partial protection for the community within. An extension of the barrier to at least 10 km is clearly indicated during an epidemic of viruses transmitted by this species.

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