DISPERSAL OF ADULT FEMALES OF *CULEX ANNULIROSTRIS* IN GRIFFITH, NEW SOUTH WALES, AUSTRALIA

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ABSTRACT. The dispersal of *Culex annulirostris*, a major arbovirus vector in Australia, was studied in Griffith, N.S.W. using a mark-release-recapture technique. From an empirical model of dispersal, fitted to data on recaptured adults, the average distance dispersed was 6.8 km (95% c.l. 4.1–40.9 km), and 50% of the population dispersed 4.8 km or more. Maximum recorded dispersal was 8.7 km, and 2 individuals traveled more than 5 km in 1 day. The relevance of the findings to control strategy is discussed.

INTRODUCTION

In Australia, *Culex annulirostris* Skuse is the most important vector of Murray Valley encephalitis virus and a major vector of Ross River virus. It is also a serious biting nuisance, and in irrigated areas and during floods, may occur in very high densities (see Lee et al. 1989 for review). During an epidemic of Ross River virus at Griffith, New South Wales in 1984 (Hawkes et al. 1985), control measures were directed against the larvae of *Cx. annulirostris* in the urban area and a 5 km zone surrounding it. An initial decline in adult density was not sustained, and invasion from untreated areas was suspected. Therefore, dispersal of this species was investigated to provide information for planning effective control measures.

MATERIALS AND METHODS

Mosquito capture, marking, release and recapture: The study was undertaken from February 4 to 23, 1985 at Griffith (34° 17′ S, 146° 02′ E) and its environs, N.S.W., Australia. Adults for marking were captured between 1700 and 2100 h (Eastern Standard Time), from locations known to have large *Cx. annulirostris* populations, in 9 CDC light traps (Sudia and Chamberlain 1962) baited with dry ice and 4 EVS traps (Rohe and Fall 1979). Captured mosquitoes were taken to the laboratory, lightly anaesthetized with ether or chloroform and transferred to plastic containers, 20 cm diam × 16 cm deep, with fine muslin mesh at both ends. When they had recovered, the number alive and active was estimated; delayed recovery, large numbers and constant movement of the mosquitoes limited the accuracy of this estimate.

Mosquitoes were marked with powdered fluorescent pigments with a particle size range of 4–6 μm (Ciba-Geigy "Radglo"), blown into the container from a large-bulb pipette. Preliminary tests had demonstrated that this technique produced durable labels which were readily detectable and the resulting colors were distinguishable under long wavelength ultra-violet illumination.

With the exception of the first release (February 5) when approximately 50% of the adults had been caught the previous night and held for 24 h prior to labeling, marked mosquitoes were released on the night of capture, at approximately midnight. Disturbance was minimized as far as possible by allowing the majority of individuals to leave the container "voluntarily." Mosquitoes were released, on several occasions at each of 4 locations (Fig. 1), with a different color label (green, red, yellow and orange) being used for each release point.

Release point 1 was approximately 4 km E S E of the town center, and mosquitoes released at this site were labeled green. The second (red label), third (yellow label) and fourth (orange label) release points were 2.5, 5 and 9.5 km, respectively, from release point 1 (Fig. 1).

The study area contained a wide variety of environments including urban areas, irrigated rice paddies, orchards, vineyards and grazing land. Initially, recapture traps were arranged within 5 km of the first release point, at the intersection of 2 roads. Recapture stations were positioned on each road at 0.25, 0.5, 1, 2, 3, 4 and 5 km from this release point. The areas between the main axes were sampled at stations 2.5 and 5 km from the center, on each of 8 additional radial arms. One EVS trap was operated nightly, at each of these 44 recapture stations, from February 7–8 to 18–19.

From February 19–20 to 21–22, the experimental area was extended 4.5 km to the SW to include release point 4, and 13 stations were added to the recapture grid (Fig. 1). Only 23 traps were operated on the final night of trap-

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ping, February 22–23, concentrated along a SW-NE axis. The use of the 3 peripheral release points allowed the detection of movements up to 14.4 km.

Collections from recapture traps were examined for labeled individuals with an ultra-violet lamp operating at 366 nm; the presence of marking powder and its color were confirmed by microscopic examination (20–40×) of fluorescing individuals.

The effect of marking on survival was monitored in the laboratory. Ten samples each of approximately 20 labeled females were maintained in a darkened, humid environment, at ambient temperature (approximately 20–30°C) for 6 wk on a diet of 20% sucrose solution. Ten batches of control females were taken from the same night's catch before anaesthesia and labeling. Survival was recorded at intervals of 1–2 days, and the 2 populations were compared by determination of their Product Limit Survivorship Estimators (Kaplan and Meier 1958) and application of the logrank test (Peto et al. 1977).

The 4 release points and 67 trapping stations were mapped at a scale of 1:25,000. The distances between each release point and each trap were measured to the nearest 25 m, together with their angle relative to north. Although angles were measured to the nearest degree, they were grouped into quadrants, 1–90°, 91–180°, 181–270° and 271–360° for statistical analysis.

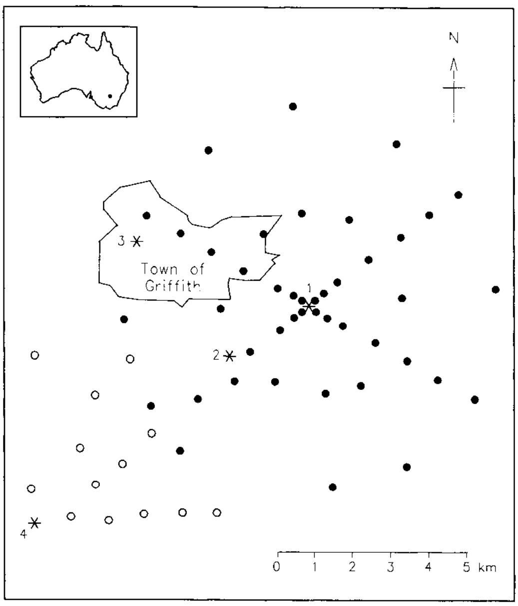

Fig. 1. The location of release points (*) and trapping stations at Griffith, N.S.W. Trapping stations marked (○) were added to the grid on 19–20 February.

Analysis of results: Taylor (1978, 1980) has suggested that the dispersal of many insects can be described by the general equation:

$$N = \exp\,(a + b\,X^c) \qquad (1)$$

where N is the density at distance X from the dispersal center (release point) and a, b and c are parameters. Apart from the parameter c, this is a generalized linear model (McCullagh and Nelder 1983) and was fitted to the recapture data by maximum likelihood methods, using the computer program Genstat V.

For each trap, for each set of releases, the recapture rate was considered as:

$$\frac{\text{Number of mosquitoes recaptured}}{\text{Number of trapping nights}}$$

which allows for variations in trapping intensity. The number of recaptured mosquitoes was assumed to be proportional to the density of labeled mosquitoes (N) and to the number of trapping nights.

The effects of release point and direction of movement on the recapture rate were examined, including extra parameters in the model for these factors and assessing their statistical significance by an analysis of deviance. The trap effect was assumed to be randomly distributed and was included as a component of the residual deviance.

The best fit of the model was determined by varying the value of the exponent c and selecting that value which minimized the deviance. The 95% confidence limits of c were derived as those values which gave a deviance that was greater than the minimum deviance by the critical chi-square value (1 d.f.) of 3.84.

Hawkes (1972) discusses the calculation of the average distance dispersed by the population under study for the specific case of $c = 0.5$. This approach may be generalized for any value of c as:

$$\text{Average distance dispersed} = \frac{\Gamma\,(3d)}{(-b)^d\,\Gamma\,(2d)} \qquad (2)$$

where Γ represents the gamma function and $d = 1/c$.

The specific forms of equation (2) appropriate to the best fit of c and its 95% confidence limits were determined and the corresponding estimates of average distance dispersed calculated. The relative numbers of mosquitoes at different distances from release points were calculated by multiplying the density, derived from equation (1), by the circumference of the circle with that distance as its radius. The maximum distance dispersed by specified proportions of the population was obtained by numerical integration of the relative numbers.

An alternative, more conservative approach was also adopted; the determination of mean distance traveled, as described by Lillie et al. (1981). Distances up to that of the observed maximum flight were divided into a series of annuli, at intervals of 100 m, up to 500 m from the release point and thereafter, at 500 m intervals. The mid-point of each annulus (z) was taken as the representative value of distance from release point and the corresponding density (N_z) was calculated by means of the fitted model. The density was multiplied by the area of the annulus (A) to give a measure of the number of (labeled) mosquitoes in each annulus. The mean distance traveled was calculated using the formula:

$$\text{Mean distance traveled} = \frac{\sum N_z \cdot A \cdot z}{\sum N_z \cdot A} \qquad (3)$$

where $\sum$ is the summation of annuli.

The terms "average distance dispersed" and "mean distance traveled" refer to the same population parameter, but are retained throughout this paper to distinguish between the 2 methods of calculation.

Date-specific labels were not used in this study, but the successive use of 4 colors made it possible to obtain estimates of the rates of movement. The minimum, maximum and median times in the field and the corresponding rates of dispersal were determined for each recaptured individual, and the mean values of these parameters calculated for the whole population. More precise estimates could be derived for 10 individuals, recaptured on either the same night as release or the following night.

RESULTS

Approximately 75,000 female *Cx. annulirostris* were released between February 5–18, 1985 as shown in Table 1 with a period of 17 days between the first release and the final trapping. Labeling did not adversely affect survival over a comparable period ($\chi^2 = 0.277$ at 1 d.f., $P > 0.5$; Fig. 2). The median longevity of the labeled population was 17 days and the maximum was 42 days.

A total of 215 labeled *Cx. annulirostris* was recovered (Table 2). Of these, 95 were labeled green, 90 red, 26 yellow and 4 orange. Nineteen were captured at distances of 5 km or more from their release point. The maximum recorded flight was 8.7 km.

The recapture rates for release points 1–4, respectively, were in the proportions 1.0, 1.8, 1.3 and 0.7. As these differences were statistically

Table 1. Labeling details and numbers of female *Culex annulirostris* released at Griffith, N.S.W., during February 1985.

Release point	Color of label	Release dates	Numbers released (approx.)
1	Green	Feb. 5–7	25,000
2	Red	Feb. 8–11*	18,000
3	Yellow	Feb. 12–15	20,000
4	Orange	Feb. 16–18	12,000
Total	—	—	75,000

* Mosquitoes were not released on February 9.

significant ($P < 0.001$), release point was taken into account in subsequent analyses.

Direction was found to exert a significant effect ($P < 0.001$), but there was also a significant interaction between release point and direction ($P = 0.01$). The effects were mainly due to lower recaptures in quadrant 2 (SE) from release points 2 and 3. As there was no indication of a consistent direction effect of the type that could, for example be due to a prevailing wind, the effect of direction was not considered further. Since the main presentation of results depends on the parameter b in equation (1) and inclusion of direction and the interaction term changed the estimate of b by less than 2%, the results are not materially affected by this decision.

The best fit of Taylor's (1978, 1980) general dispersal equation to the observed recaptures was obtained with a value of $c = 0.55$, giving a minimum deviance of 267.7 (222 d.f.). The 95% confidence limits were $c = 0.26$ and $c = 0.89$.

The specific forms of equation (2) for these values of c, the corresponding values of b and the calculated average distances dispersed by the labeled female *Cx. annulirostris* are shown in Table 3, together with the distance limits for specified proportions of the whole labeled population. The relative numbers of labeled mosquitoes by distance, derived from the fitted regressions are shown in Fig. 3. The average distance dispersed was calculated as 6.8 km, with 95% confidence limits of 4.1 km ($c = 0.89$) and 40.9 km ($c = 0.26$).

Using the method of Lillie et al. (1981) (equation 3) the mean distance traveled was 3.8 km ($c = 0.55$) with 95% confidence limits of 3.5 km ($c = 0.89$) and 4.2 km ($c = 0.26$).

The estimated rates of movement derived from all recaptured *Cx. annulirostris* ($n = 215$) were: minimum, 0.7 km/day; median, 1.1 km/day; maximum, 2.1 km/day. The rates of the 10 individuals caught within 1 day of release ranged

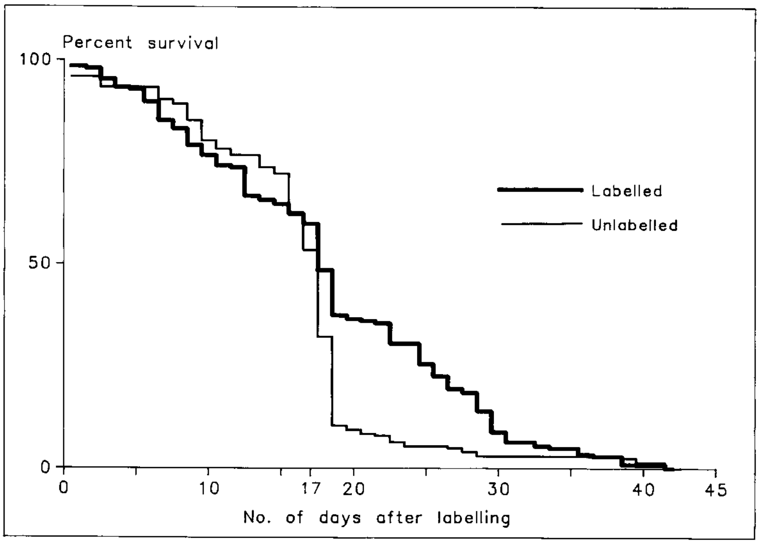

Fig. 2. The survival of labeled and unlabeled female *Culex annulirostris* in the laboratory.

Table 2. Distances from release point at which labeled *Culex annulirostris* females were recaptured and recapture rates for each distance category.

Distance from release point (km)	Total number recaptures	Total number nights	Number of recaptures per trap night (=recapture rate)
0.125–0.375	25	58	0.431
0.376–0.750	50	99	0.505
0.751–1.250	13	71	0.183
1.251–1.750	18	56	0.321
1.751–2.250	19	112	0.170
2.251–2.750	22	214	0.103
2.751–3.250	22	199	0.111
3.251–3.750	3	66	0.046
3.751–4.250	11	115	0.096
4.251–4.750	9	159	0.057
4.751–5.250	7	265	0.026
5.251–5.750	9	142	0.063
5.751–6.250	0	38	0
6.251–6.750	1	58	0.017
6.751–7.250	1	62	0.016
7.251–7.750	4	91	0.044
7.751–8.250	0	31	0
8.251–8.750	1	41	0.024
8.751–14.750	0	247	0

from 0.6 to 7.5 km/day. Two individuals exceeded 5 km in 1 day, traveling 6.5 and 7.5 km.

DISCUSSION

Movements which result in dispersal may be classified as either migratory or trivial (Johnson 1960, 1966, 1969; Kennedy 1961; Southwood 1962), the 2 types of movement being behaviorally distinct. Migratory flights are primarily locomotory with vegetative behavior, such as feeding and reproduction, suppressed. Trivial movements are the incidental result of responses to vegetative stimuli.

In mosquitoes, migratory behavior, if expressed, generally occurs shortly after emergence and before the females are reproductively active (Service 1976). Provost (1952, 1957) for example, identified a clear post-teneral migratory phase (non-appetential) in the salt-marsh species *Aedes taeniorhynchus* (Wied.), followed by a period of shorter flights (appetential) associated with feeding and reproduction. He considers this pattern to be general for mosquitoes. Southwood (1962) and Johnson (1969) equated Provost's division of mosquito flights into non-appetential and appetential with their division into migratory and trivial movements.

It is probable that the study described here was concerned primarily or solely with the measurement of dispersal by trivial movements because traps baited with dry ice, as used in the recapture grid, selectively attract those females which are seeking a blood meal. Following the hypothesis proposed by Johnson, Kennedy and Southwood, such females would have completed any migratory phase. As trivial movements are typically shorter than migrations (the main exception being Southwood's (1962) category of "vagrants") and occupy only a part of the adult's life, it is very likely that the flight ranges observed in this study underestimate the dispersal of *Cx. annulirostris.*

In the absence of transovarial transmission, infection with, and transmission of, arboviruses

Table 3. Values of average distance dispersed and distance limits for specified proportions of the labeled *Culex annulirostris* female population for the three regression equations corresponding to the best fit of *c* and its 95% confidence limits.

c	b	Form of equation (2)	Average distance dispersed (km)	Distance limits (km)		
				50%	90%	95%
0.26	−0.5725	$\frac{4783.6}{_{b}3.846}$	40.9	18.5	99.0	152.7
0.55	−0.0313	$\frac{12.558}{_{b}1.818}$	6.8	4.8	15.0	19.9
0.89	−0.00140	$\frac{2.5548}{_{b}1.124}$	4.1	3.4	8.2	10.2

Note: In the regressions and equations (2) above, distance (X) is expressed in meters. Derived distance parameters have been subsequently converted to km.

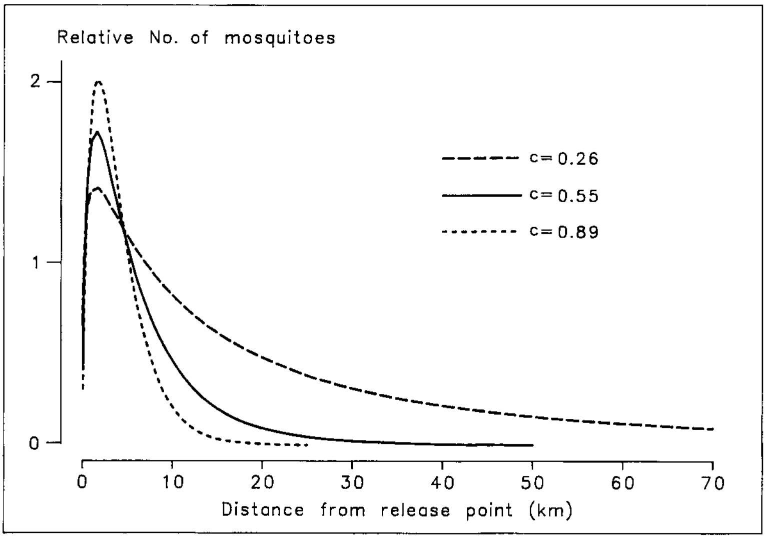

Fig. 3. The relative numbers of labeled mosquitoes by distance from release point as estimated by Taylor's (1978, 1980) model; the best fit (c = 0.55) and its 95% confidence limits (c = 0.26, c = 0.89) are shown.

will only occur in this post-migration phase and the estimates of dispersal presented here are, therefore, relevant to the consideration of *Cx. annulirostris* as a vector.

The data were evaluated by direct examination and 2 methods of modeling. From direct examination of the data, the maximum flight was 8.7 km. Of the 215 recaptured specimens, 19 had traveled 5 km or further and would have traversed the 5 km barrier zone established at Griffith during 1984. The proportion of the mosquito population reaching or passing this boundary cannot be assessed by direct examination of the data, as no account is taken of variation in sampling intensity with distance. Considering the low recapture rate (<1%), however, it is clear that flights of 5 km or more are not uncommon.

More detailed information can be obtained from the models. Taylor's (1978, 1980) general dispersal equation (1) gave a good fit to the data with c = 0.55. From the corresponding equation (2), the average distance dispersed was 6.8 km with 98% confidence limits of 4.1 km (c = 0.89) and 40.9 km (c = 0.26).

As the spatial distribution of the dispersing mosquitoes was markedly skewed (Fig. 3), the average distance dispersed has limited meaning. This qualification does not apply to the distance limits, within which specified proportions of the population dispersed, which are, therefore, more readily comprehensible and a more complete description of the dispersal process. Using c = 0.55, 50% of the population dispersed 4.8 km or more, 10%, 15 km or more and 5%, 20 km or further.

In the model-fitting approach, the expected values of density for all distances are determined and subsequent calculations, e.g., the average distance dispersed, derived from a summation of the corresponding numbers of individuals. It is, therefore, the more powerful method for an analysis of dispersal but assumes that the relationship based upon the observed recaptures retains the same form over all distances. If this assumption is valid, the calculated values of average distance dispersed and distance limits demonstrate that *Cx. annulirostris* is capable of dispersing well beyond the upper limit observed in this study and that approximately half of the population could cross a 5 km barrier zone.

The upper confidence limit, corresponding to $c = 0.26$, yielded a very high estimate of the average distance dispersed, 40.9 km and correspondingly large distance limits. In the absence of supporting observations, caution is necessary in interpreting these values, which are largely due to the low precision with which the densities of labeled mosquitoes were measured at the greater distances from the release point. The relationship between the parameters in the model is such that even relatively small variations in b, at low values of c, can have marked effects on the derived values of average distance dispersed and distance limits. As Taylor (1980) discusses, the simpler form of the model, as used here, is not a full description of the dispersal process and the development and inclusion of additional parameters is desirable.

The modeling method of Lillie et al. (1981) to determine mean distance traveled, as adapted for use in this study, is a compromise between the purely descriptive approach and the extrapolations implicit in Taylor's model. It allows the behavior of the whole population to be examined, but avoids the difficulties of extrapolation by limiting the analysis to observed dispersal distances. It is, however, conservative and underestimates dispersal because of the problems in adequately sampling the very low densities in areas distant from release points. Thus, in this study, the best fitted model gave an estimate of 3.8 km (95% c.l. 3.5–4.2 km) for the mean distance traveled compared with 6.8 km for the average distance dispersed.

The data on daily rates of dispersal are limited and, at best, approximations; but the estimates obtained are compatible with the hypothesis that *Cx. annulirostris* is capable of considerable mobility.

Only one other study of dispersal in this species is known to the authors. Russell (1986) recorded flights of up to 7 km (the limit of his trapping grid) from a larval habitat into the surrounding country, where no larval sites occurred. If his data are analyzed by the model applied in the present study, the average distance dispersed was 7.1 km, in close agreement with the results of the present study. As Russell also used EVS traps, migrants were probably also underestimated in his study.

CONCLUSIONS

Culex annulirostris is a highly mobile species; extrapolation from the results suggests that it is capable of flights up to and beyond 10 km. If this hypothesis is correct, then in areas with high mosquito population densities, such as Griffith, substantial numbers will cross a 5 km barrier zone. If the concept of a barrier zone is to be included in future control strategies, our findings suggest that it should be increased to at least 10 km. However, such an increase would entail a substantial increase in the area requiring control measures and a far greater commitment of resources. For example, if it is assumed that the Griffith town area can be encompassed within a circle of 2 km radius, a circular area of 7 km radius would have been treated in 1984. To increase the barrier zone to 10 km, a circle with a 12 km radius would have to be treated, increasing the area by a factor of 2.94. Further studies are required so that appropriate control strategies can be implemented.

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