

Population Dynamics of Mosquitoes

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The trouble with ecology is that it is fun to do, but not very interesting to read about.

— Charles Elton

One of the more interesting thing about ecology is the possibility of advance from a consideration of the dynamics of single species or pairs of species and ignoring the rest. It looks like cheating but it also seems to work.

— J.H. Lawton

Introduction

Population dynamics is a numbers game. We observe that the number of individuals in a population fluctuates from time to time or place to place and that some species are always relatively abundant whereas others are relatively rare. Population dynamics is the discipline practiced in order to gain an understanding of the causes of these fluctuations and the determination of the average levels about which the fluctuations occur. To detect and analyze the underlying mechanisms, it is usually necessary to study the intra-generation changes in numbers and relate these to long-term population trends at the generation level. The 2 common techniques that have been devised to detect such mechanisms are the analysis of determination (Mott 1966) and key-factor analysis (Varley and Gradwell 1960, 1968). Fundamentally, these 2 approaches are not different; Mott's analysis does by a regression model what Varley and Gradwell's does graphically. Essentially, changes in the population's trend index are correlated with changes in the contributing survivorship or natality functions. Both approaches evaluate age- or stage-specific variables but neither may provide deep insights into the mechanisms that cause the variations in survivorship or natality in populations.

If we think about the determination of abundance in mosquito populations it is immediately obvious that a large complex of factors could be involved in causing changes in natality or survivorship; many of them form subjects of chapters in this manual. The problem is to find out which ones are important. The factors will express themselves through the 3 fundamental components of population dynamics: survivorship/mortality, dispersal, and natality. To elucidate the effects of biotic and abiotic factors on these components of population dynamics we need estimates of the *numbers* of eggs, larvae, pupae and adults at different times. The numbers are essential, for in most definitive studies it is not sufficient to know only that the population of some life-history stage has increased or decreased; we need to know *by how much* and (or) *at what rate* and we need to know how much confidence we can place on that number — that is, we must have estimates of standard errors or confidence limits in order to know how *wrong* we might be. Existing studies of mosquitoes are deficient in two ways:

- reliable information on population sizes is scarce or altogether lacking;
- the environmental influences on survival and reproduction have not been fully explored or quantified under field conditions.

To a large extent, therefore, a population dynamics of mosquitoes can scarcely be said to exist but there have been some promising and fruitful beginnings.

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My coverage of the mosquito and population-dynamics literature has been extremely selective. I have tried to use examples that are exemplary, in a positive or a negative sense, or that provide reliable insights into demographic phenomena in mosquito populations. In some instances I have explored examples rather thoroughly because they illustrate particular points well. I have not avoided the numbers or the rigor of analysis although that has made the discourse a bit heavy in places. Population dynamics is not a field for the statistically faint of heart; the field can only benefit from the sustained efforts of workers whose primary interests are in disentangling the complex biological webs of populations but who, at the same time, have a thorough grasp of modern ecological statistics.

With few exceptions, I have ignored the large literature of theoretical population dynamics, not because it has nothing to say to the mosquito ecologist but because the present need is for carefully planned and executed experiments on real populations. Population dynamics has the distinction of being one of the few areas of modern biology in which theoretical advances regularly and rapidly outstrip the availability of reliable field data. For the most part, I have also ignored laboratory studies of mosquitoes in favor of field studies of the population dynamics, regardless of the many obvious inadequacies that emerge under the constraints of the field environment.

My review is somewhat lugubrious; I have focused on death. In order to make the dimensions of the paper manageable, I have ignored several important aspects of mosquito population dynamics but mention them here in order to at least introduce a more balanced view of the subject. Perhaps the most serious omission is the absence of a treatment of the dynamics of natality. To have included this subject would have expanded this chapter immensely. In omitting the subject, I have been guided by the few studies of mosquito dynamics that suggest that regulation is more likely to be accomplished through mortality than natality. Other subject areas that are virtually omitted but that are recognized as seminal or contributory are: life-history strategies (Crovello and Hacker 1972; Walter and Hacker 1974; Lansdowne and Hacker 1975; Schlosser and Buffington 1977); the age-structure of populations (Detinova 1968; Ungureanu 1974) (but I have dealt with the subject of survivorships derived from the age-structure of both larval and adult populations); and the genetic structure of mosquito populations (Nevo 1978; Trpiš and Häusermann 1978; Hartberg and McClelland 1973; Tabachnick and Powell 1978). I have also totally ignored the area of population modeling even though developments from the area of time-series modeling are likely to soon advance our understanding of mosquito dynamics; Weidhaas and Haile deal with this subject in Chapter 21.

Population Size: Adults

A study of the dynamics of adult-mosquito populations requires estimates of population size or abundance. Almost all studies have made use of population estimates that are relative in time or space. Useful reviews of the great variety of sampling techniques available for adult-mosquito populations are provided by Service (1976, 1977b) and Bidlingmayer (1975a). The dynamics of adult-mosquito populations are so complex that most relative estimates bear an unknown relationship to the total population size and many techniques selectively and sometimes variably sample only a portion of the population. Few investigators have examined the many sources of bias and error in relative population estimates with the result that much of the data resulting from studies of adult mosquitoes is of little value in interpreting their dynamics.

If the relationship between a relative population estimate and the total population size were known, it might be possible to make advances in studying the dynamics of populations by making use of the simple relative estimate only. However, it is rare for an investigator to make simultaneous estimates of both relative and absolute population sizes and even when this has been done, the nature of the relationship between the two types of estimates is sometimes still unclear; a variety of relationships, ranging from simple to complex, can exist between the two types of estimates (Caughley 1977). Trpiš (1971) estimated the population size of *Aedes aegypti* in a tire dump in Tanzania and, at the same time, made estimates of the man-hour biting index, a relative estimate (Table 1). Although the data set is small, there is an excellent linear correspondence between the two estimators (Table 1) so that the total population size might be estimated from a knowledge of the

biting index only. However, the few data provided by Trpiš (1971) do not permit a test of linearity; that the relationship between the relative and absolute estimates might be non-linear is suggested not only by deduction from first principles but also by the observation that another model (Table 2) provides an acceptable fit to the data. The difference in the population sizes predicted by the different models is small and probably would be of little consequence when absolute population sizes lie between, say, 500 and 2500. However, the models are based on quite different assumptions about the nature of the relationship between the relative and absolute estimates. Without additional information, estimates of absolute population size based only on the relative index would be suspect when the index is either very low or very high. Studies of mosquito populations should attempt to quantify the relationship between relative and absolute estimates.

Table 1. Correlation^a between relative and absolute estimates of population size in a population of *Aedes aegypti* in Dar es Salaam, Tanzania.

Adults/ha ^b (<i>N</i>)	Man-hour biting index ^c (<i>I</i>)
2295.28	9.6
1262.37	5.3
921.35	4.1

^a The simple least-squares regression of the man-hour biting index on population size is: $I = 0.00404 N + 0.30113 \pm 0.12948$; $r^2 = 0.9990$, $F = 996.761$, $P = 0.0202$. On theoretical grounds, a more appropriate model might be a linear model forced through the origin, in which case: $I = 0.00422 N \pm 0.1626$; $F = 5181.979$, $P = 0.0088$.

^b Petersen estimates corrected for mean-daily survivorship (0.656) and the proportion (0.059) of females taking multiple bloodmeals in a single gonotrophic cycle (Conway *et al.* 1974).

^c From Trpiš (1971)

Table 2. A comparison of the absolute population sizes predicted (inverse prediction) by 3 models of the relationship between an absolute and a relative population estimate.

Index ^a	Observed ^a	Population size predicted by model ...		
		Linear ^a	Linear – Origin ^a	Exponential ^b
1.0	—	172.97	237.23	208.85
4.1	921.35	940.24	972.66	936.73
5.3	1262.37	1237.24	1257.34	1230.85
9.6	2295.28	2301.52	2277.45	2315.38
15.0	—	3638.04	3558.51	3722.03
20.0	—	4875.57	4744.59	5054.42

^a See Table 1 for further information.

^b A linear model forced through the origin; see Table 1.

^c The model is: $I = 0.00659 N^{0.94105} \pm 0.02958$; $r^2 = 0.9977$, $F = 434.423$, $P = 0.0305$.

Analytical investigations of population dynamics and the estimation of mortality rates and their effects on populations are almost impossible without absolute estimates. Such estimates are also required for genetic and some types of biological control. For adult mosquitoes, this usually means that estimates of total population size are needed, rather than estimates of population intensity. Estimates of absolute population size in

mosquitoes are usually carried out by mark-release-recapture (MRR) techniques. Useful reviews of the assumptions and procedures of the techniques may be found in Cormack (1968, 1973), Parr *et al.* (1968), Service (1976) and Southwood (1978). A comprehensive treatment of the subject was given by Seber (1973) but the average biologist is apt to find his level of exposition a trifle bracing. Simulation studies by Manly (1970) and Bishop and Sheppard (1973) compared the performance of 3 of the better MRR models, the Fisher-Ford, Jolly and Manly-Parr models (the first two only in Bishop and Sheppard). These are helpful papers during the planning stages of a study when attempts are made to forecast the extent to which a given population will fail to satisfy the assumptions of the various MRR models. The simulations by Manly (1970) involved exceptionally high (0.1–0.75) sampling intensities so their value in planning mosquito studies, in which sampling intensity is usually lower than this, may be reduced.

The most important assumptions of the MRR techniques are that marking does not alter the behavior or survivorship of the marked individuals and that all individuals in the population have equal catchability. The deterministic MRR models (e.g. Lincoln/Petersen, Fisher-Ford, Leslie, Bailey) assume a constant survivorship over the catching period whereas the stochastic model of Jolly (1965) allows for random fluctuations in survivorship. However, the Jolly model assumes that mortality is independent of age, an assumption that should be carefully examined for a mosquito population. Violations of the equal-catchability assumption are frequent and lead to underestimates of population size. Southwood (1978) reviews the various causes of unequal catchability and discusses procedures and tests to detect it in MRR experiments. If mosquitoes are trapped at bait or hosts, the feeding habits will induce a periodicity on the availability of subgroups in the population; that periodicity will vary from simple to complex, depending on the frequency of host visits within a gonotrophic cycle and the duration of the cycle. Conway *et al.* (1974) showed how the robust method of Fisher and Ford could be modified to overcome this violation of the equal-catchability assumption.

Simulations of MRR experiments (Bishop and Sheppard 1973) suggest that if the number of sampling occasions is large and the recapture rate is high, the stochastic model usually gives a better estimate of population size and variance than do the deterministic models (in this simulation study, the deterministic model was that of Fisher and Ford). However, if there are few sampling occasions and the recapture rate is low, the deterministic models may give a more reliable estimate. In both deterministic and stochastic approaches to MRR, a relatively large proportion of the population may have to be marked in order to retrieve reliable demographic estimates.

There have been many attempts to measure the absolute size of mosquito populations. Among the relatively successful and instructive examples are assessments of *Ae. aegypti* populations in Thailand (Sheppard *et al.* 1969), India (Reuben *et al.* 1973), Tanzania (Conway *et al.* 1974) and Kenya (McDonald 1977), of *Ae. triseriatus* in Indiana (Sinsko 1976; Sinsko and Craig 1979), of *Culex pipiens fatigans* in Thailand (Lindquist *et al.* 1967; Macdonald *et al.* 1968), and of *Cx. tarsalis* in California (Nelson *et al.* 1978). The studies by Conway *et al.* (1974) and Sheppard *et al.* (1969) are particularly recommended for their careful attention to sources of violation of the MRR assumptions.

The studies of mosquito populations that have been successful and that have yielded relatively reliable demographic data have usually been carried out on populations that are small in size and (or) relatively isolated, relatively stable in time, and with restricted dispersal. The assessment of *Ae. aegypti* by Conway *et al.* (1974) was carried out in a reasonably discrete habitat of only 1 ha but even here there was evidence that the population was subdivided into a number of smaller populations (*see also* Poole 1978). The estimation of population size in adult mosquitoes is extraordinarily difficult; frequently, the estimates have been made without independent assessments of the population size so that the reliability of the estimates is questionable. Even when population size is estimated simultaneously by several models (as should be done in any MRR experiment), this does not provide an independent check on the estimates because most MRR models share a large set of assumptions. A detailed examination of a recent study of *Ae. triseriatus* (Sinsko 1976; Sinsko and Craig 1979) will serve as an exemplary and sobering case to illustrate the MRR technique, to give examples of the demographic data that can be derived from such studies and to forecast the severe problems that can be expected if MRR assessments are made for populations that are of more than trivial size.

Ae. triseriatus breeds in treeholes. Such habitats offer some noteworthy advantages in population-dynamics studies: the mosquito species that occupy them usually do not breed in other sites except artificial containers (tires, tin cans, etc.); the habitats are discrete and, at least in theory, enumerable; the small size of the habitat makes it at least theoretically possible to monitor recruitment directly, although the sampling problems with treehole habitats are not minor (Parker 1978). Sinsko (1976) and Sinsko and Craig (1979) studied a population of *Ae. triseriatus* in a small (a 10.1 ha) woodlot in Illinois; the woodlot was isolated by habitat into which the adults would rarely stray. All larval habitats were identified and pupal production (both sexes) was monitored by weekly counts. Adult populations (females) were monitored by human-bait collections; marking was carried out with fluorescent pigments. The possibility of losses due to dispersal was tested by a MRR experiment to measure movement between 2 adjacent, but isolated woodlots and by allozyme analysis of a single (esterase) locus. The latter approach yielded equivocal results but the marking experiment strongly suggested that the population in the woodlot was essentially isolated. Population estimates were made on 3 occasions, with marking and recapturing occupying 10 d on each of the 1st 2 occasions and 6 d on the 3rd. The data were analyzed by the models of Jolly (1965), Bailey (1951, 1952) and Schnabel-Thompson (Schnabel 1938).

As judged by pupal recruitment, the population was small; in 1975, total pupal production in the habitats under observation was only 4228 (1790 ♀♀, 2438 ♂♂ — distorted sex ratios were common, especially in the early part of the year). Given the method of assessing the adult population, only the production of female pupae is of interest. 7 of about 80 treeholes produced more than half the pupae. Female-pupal recruitment and estimates of the population size on the 3 occasions are given in Table 3.

Table 3. Population estimates and projections: *Aedes triseriatus* in Kramer's Woods, IL, 1975 (after Sinsko 1976).

Wk	Number of ♀ Pupae		Predicted Population Size ^a	Population Size Estimated by ...			
	Per Wk	Cumulative		Jolly ^b	Bailey triple catch	Bailey's with correction	Schnabel-Thompson
11	1	1	1.00				
12	91	92	91.38				
13	77	169	112.01				
14	138	307	180.91				
15	104	411	173.31				
16	103	514	169.40				
17	120	634	184.90				
18	169	803	239.84	780.1 ± 258.7 ^c	891.4 ± 1015.5 ^c	676.2 ± 736.0 ^c	1184.8 ± 118.9 ^c
19	144	947	235.88	(33.2%) ^f	(113.9%)	(108.8%)	(10.0%)
20	94	1041	184.37				
21	80	1121	150.63	1021.3 ± 432.7 ^d	708.9 ± 327.1 ^d	615.9 ± 436.9 ^d	1582.3 ± 306.2 ^d
22	89	1210	146.71	(42.4%)	(46.1%)	(70.9%)	(19.4%)
23	179	1389	235.21				
24	229	1618	319.11				
25	132	1750	254.25	1224.4 ± 454.6 ^e	1221.7 ± 522.4 ^e	905.3 ± 328.8 ^e	1590.1 ± 288.3 ^e
26	40	1790	137.41	(37.1%)	(42.8%)	(36.3%)	(18.1%)

^a Deterministic model assuming a constant, daily survivorship of females of 0.87192 (mean of 20 estimates of daily survivorship from the Jolly-model estimates, including 5 survivorships that were >1.0) and assuming that the probability of successful emergence = 1.0.

^b Recomputed from the raw data in Sinsko (1976).

^c Mean ± standard deviation of 8 estimates (21–29 July, inclusive)

^d Mean ± standard deviation of 8 estimates (13–21 August, inclusive)

^e Mean ± standard deviation of 4 estimates (15–29 September, inclusive)

^f Coefficient of variation.

Even though the woodlot was small, relatively large numbers of mosquitoes were marked and released (*see* Table 4), and a high recapture rate (45, 28 and 24%, respectively, for the 3 occasions) was achieved, the population estimates (Table 3) show considerable variation both within and among models. The Schnabel-Thompson model produced the highest estimates and the corrected Bailey the lowest. The Bailey model produced the most variable sets of daily estimates, the Schnabel-Thompson the least; the variation of the daily Jolly estimates was the most consistent over the 3 sampling occasions.

Sinsko (1976) and Sinsko and Craig (1979) concluded that the Jolly model yielded the most reliable results. Although this method requires that marking and recapturing be carried out over a relatively long period of time and that the recapture rate be high, if the assumptions of the model are satisfactorily met, it can yield a wealth of useful demographic data (e.g. Table 4), most of which estimates are accompanied by standard errors (Table 4).

Sinsko (1976) and Sinsko and Craig (1979) evaluated the reliability of the MRR estimates by making a totally independent forecast of the size of the female population based on pupal recruitment. Using a mean-daily survivorship of 0.87 (derived from the Jolly-model estimates) and assuming that the success rate of emergence of female pupae was 100%, they predicted the population size for the woodlot (Sinsko and Craig 1979, Fig. 2) for each week of the year, including the weeks during which the MRR estimates were made. They concluded that the Jolly method satisfactorily estimated the size of the female population; the Jolly estimates were higher than those predicted by the recruitment model but were not grossly larger and their standard errors enclosed the recruitment-model estimates.

I am unable to reproduce the recruitment-model estimates of Sinsko and Craig (1979) unless I assume that the daily survivorship of 0.87 was inserted in their model as a *weekly* survivorship. But a weekly survivorship of 0.87 implies a daily survivorship of 0.98, a value that even on first principles seems unusually high and that is higher than the estimate of mean-daily survivorship for any other mosquito (Table 5). The mean-daily survivorship of the population of *Ae. triseriatus* based on 20 Jolly estimates (5 of which were in excess of 1, some grossly), is 0.87192 (recomputed from the raw data in Sinsko 1976), implying a weekly survivorship of only 0.38311. Modeling the population size of females on that basis, using the pupal-production data of Sinsko and Craig (1979), yields estimates of female population size that are very considerably smaller than the recruitment-model estimates of Sinsko and Craig (1979) and much smaller than the population estimates from the MRR experiments (Table 3). I conclude that there is a large discrepancy between the MRR population estimates (irrespective of the model) and the independent estimates of population size based on pupal recruitment (Table 3). It is disquieting indeed to recognize that estimates of population size for such a small, isolated population of mosquitoes can inspire so little confidence!

There are many possible reasons for the discrepancy between the recruitment and MRR estimates — failure of marked insects to disperse randomly; immigration from other sites; underestimates of pupal production because habitats were missed or pupae were undetected in the recesses of treeholes. It is also conceivable that the survivorship estimates derived from the Jolly model were seriously in error; that 5 of 20 estimates exceeded 1 is cause for concern. In simulations with population sizes of 200 and 1000 using the Jolly model, Bishop and Sheppard (1973) concluded that the model consistently and considerably overestimated the survival rates. “The bias is so great that it is clear that the model must be used with great caution in studies where survival rates are important” (Bishop and Sheppard 1973, p. 241). If this source of error applies to the MRR estimates of the *Ae. triseriatus* population, it would serve to *increase* the discrepancy between the MRR and recruitment-model estimates. If we accept 0.87 as a reasonable estimate of adult survivorship on a daily basis (cf. Table 5), then the numbers of mosquitoes marked and released on a daily basis by Sinsko and Craig (1979) (sometimes >100/d) are close to the total population sizes estimated by the recruitment model (Table 3). A small number of treeholes produced most of the pupae. Failure to detect even 1 or 2 habitats could cause serious underestimates of production. The Jolly model produced estimates of daily recruitment (Table 4) that were nearly an order of magnitude higher than the pupal recruitments reported by Sinsko and Craig (1979). It appears that pupal recruitment was underestimated or that immigration was high (or both) and thus, the reliability of these MRR estimates remains a moot point. The study by Sinsko and Craig (1979) was carefully designed and apparently carefully conducted. It illustrates well the enormous problems encountered in deriving reliable estimates of the absolute sizes of mosquito populations, even when those populations are of a very minor size and relatively confined.

Table 4. Population estimates on different days together with estimates of survivorship and recruitment and their standard errors for a population of *Aedes triseriatus* in Kramer's Woods, IL, July 1975 (Jolly model^c). (In part, from Sinsko (1976) and Sinsko and Craig (1979).)

i	n_i	s_i	$\hat{\alpha}_i$	\hat{M}_i	\hat{N}_i	$\hat{\phi}_i$	\hat{e}_i	(d) ^a \hat{B}_i	$\{V(\hat{N}_i)\}^{0.5b}$	$\{V(\hat{\phi}_i)\}^{0.5}$	$\{V(\hat{B}_i)\}^{0.5}$	$\{V(\hat{N}_i N_i)\}^{0.5}$	$\{V(\hat{\phi}_i) - [\hat{\phi}_i^2(1 - \hat{\phi}_i) / \hat{M}_{i+1}]\}^{0.5}$
1	122	122	—	—	—	0.958	24.0	—	—	0.1729	—	—	0.1720
2	108	98	0.0926	116.909	1262.62	0.723	3.6	-274.53	428.582	0.1348	297.419	428.535	0.1311
3	98	98	0.2347	148.222	631.56	1.110	-9.1	176.47	142.853	0.2446	192.127	141.882	0.2446
4	84	81	0.2824	247.714	877.32	0.465	1.8	263.95	226.297	0.0975	140.513	225.714	0.0932
5	104	103	0.2115	141.816	670.40	0.966	29.4	-108.54	142.362	0.1458	129.235	141.394	0.1453
6	115	110	0.4000	215.231	538.08	1.253	-3.9	127.20	90.198	0.3130	124.531	88.641	0.3130
7	75	72	0.4400	349.800	795.00	0.892	9.3	271.87	208.709	0.2890	163.478	208.066	0.2886
8	110	110	0.3545	347.000	978.72	0.369	1.5	106.00	270.796	0.1133	78.871	270.260	0.1109
9	106	103	0.3302	154.263	467.20	—	—	—	118.038	—	—	161.900	—
10	91	0	0.4505	—	—	—	—	—	—	—	—	—	—

^a Expectation of further life = $[1/(-\log_e(\phi_i))] + 0.5$

^b N_1 (= B_0 by definition) was arbitrarily set equal to 1000 in order to compute these standard errors.

^c The symbolism and format follow Jolly (1965) (reproduced in Service (1976)). Column headings are defined below.

i Day number; day 1 = 20 July 1975.

n_i Number of ♀♀ captured on day i .

s_i Number of ♀♀ marked and released on day i ; $s_i \in n_i$ and $s_i \leq n_i$.

α_i M_i/N_i , the proportion of marked animals in the population on day i . (The caret (hat) (“^”) here and elsewhere signifies an estimate of the parameter.

M_i Total number of *marked* animals in the population at time i .

N_i Population size at the time the i_{th} sample is captured.

ϕ_i Probability that an animal alive at the moment of *release* of the i_{th} sample will survive until the time of capture of the $(i+1)_{th}$ sample (emigration is not distinguished from death) — here an estimate of *daily* survivorship.

B_i Number of new animals joining the population in the interval between the i_{th} and the $(i+1)_{th}$ samples and alive at time $(i+1)$.

$V(\hat{N}_i)$ Variance of the estimates of population size (includes a component due to real variation and a component due to errors of estimation of the parameter itself); the square root of the variance (here and elsewhere) yields the standard error.

$V(\hat{\phi}_i)$ Variance of the estimates of survivorship (includes a component due to real variation and a component due to errors of estimation of the parameter itself).

$V(\hat{B}_i)$ Variance of the estimates of recruitment.

$V(\hat{N}_i|N_i)$ The component of $V(\hat{N}_i)$ due to estimation of the parameter itself.

$V(\hat{\phi}_i) - [\hat{\phi}_i^2(1 - \hat{\phi}_i) / \hat{M}_{i+1}]$ The component of variance of $\hat{\phi}_i$ due to estimation of the parameter itself. If survivorship > 1 , this component is set equal $V(\hat{\phi}_i)$.

Survivorship: Adults

A knowledge of the survivorship of the adults in a mosquito population provides important insight into the dynamics of the population. Reliable estimates of survivorship are also required in order to correct for mortality in long-running MRR experiments and, of course, estimates of survivorship are of indispensable significance in the construction of epidemiological models. In a study of the sensitivity of insect-population models to changes in the parameters, Miller *et al.* (1973) found that daily survivorship of the adults is the most significant parameter; a 5% increase in daily survivorship in some models roughly doubled the number of eggs expected of an adult. Field studies of the survivorship of adult mosquitoes offer nothing near that degree of precision.

Survivorship in adult mosquitoes can be measured in a number of ways; Service (1976) provides a useful review and carefully discusses the assumptions of the various methods. Theoretically, survivorship could be measured directly by estimating adult recruitment and then making successive population estimates, provided that recruitment took place over a narrow time span. However, the difficulties associated with absolute population estimates make this approach impracticable so that survivorship must be assessed in other ways. Frequently, survivorship of adult mosquitoes (especially females) is assessed by determining the infection rate with a pathogen or (only for females) the parous rate. There are critical assumptions involved in the use of these indirect methods and Service (1976) should be consulted before they are used.

A completely different approach to the estimation of adult survivorship is the use of data from MRR experiments. The Jolly model (*see* Table 4) produces estimates of daily survivorship. Alternatively, estimates of survivorship can be derived from the decline with time of the recaptures of marked animals; this approach usually combines losses due to mortality and losses due to dispersal so that survivorship is underestimated.

A summary of estimates of survivorship of adult mosquitoes is given in Table 5. When possible, I have also given the 95% confidence limits and range, which, in many instances, had to be computed from the raw data. Such errors should always be estimated; frequently they are surprisingly large. In spite of the fact that these data (Table 5) have been drawn from populations over a wide geographical range and involve many species with different reproductive and life-history strategies, the variance of the mean-daily survivorship is remarkably small; most estimates fall within the range 0.75–0.90 (Table 5). 2 important observations to be drawn from these data are that males suffer higher daily mortality rates than do females and different techniques often give quite different estimates of daily survivorship. A good example of the latter problem is provided by a study of *Cx. tarsalis* by Nelson *et al.* (1978) (Table 6). Survivorship of females was estimated by rates of recapture of marked females and also by the parous rate; not only was the survivorship estimated by the parous-rate method higher, the monthly fluctuations in survivorship were ranked differently by the 2 methods (Table 6). If similar confidence could be had in both methods, it might be possible to view the difference between the estimates of daily survivorship from the parous rates and those from the recapture data as a measure of dispersive loss.

Survivorship of adult mosquitoes sometimes shows surprisingly little variation from time to time; rather, it often remains relatively constant within a species, even over time spans in which the conditions to which the population is exposed could be expected to change markedly. Sheppard *et al.* (1969) found no difference in the mean-daily survivorship of *Ae. aegypti* populations over a 12-mo period (Table 5) and the survivorship of *Cx. tarsalis* did not change over the period from June to September (Nelson *et al.* 1978; Table 7). In such cases, mean-daily survivorship is probably best represented by a pooled set of data, not by a simple average (Table 7).

Table 5. Some estimates ^a of mean-daily survivorship (p) of adult mosquitoes under field conditions. Unless otherwise specified, the quoted survivorship is for females only and no distinction was made between true mortality and losses due to dispersal.

Species	p	95% limits	Range	Method	Reference
<i>Ae. aegypti</i> ($\sigma\sigma$) ^b	0.697	0.635–0.759	0.529–0.849	Fisher-Ford	Sheppard <i>et al.</i> 1969
<i>Ae. aegypti</i> ($\text{♀}\text{♀}$) ^b	0.814	0.767–0.861	0.671–0.917	Fisher-Ford	Sheppard <i>et al.</i> 1969
<i>Ae. aegypti</i> ($\sigma\sigma$) ^c	0.720	0.659–0.781	0.554–0.873	Fisher-Ford	Sheppard <i>et al.</i> 1969
<i>Ae. aegypti</i> ($\text{♀}\text{♀}$) ^c	0.845	0.800–0.890	0.695–0.943	Fisher-Ford	Sheppard <i>et al.</i> 1969
<i>Ae. aegypti</i> ($\sigma\sigma\&\text{♀}$) ^d	0.883	0.849–0.917	0.783–0.959	Fisher-Ford	Sheppard <i>et al.</i> 1969
<i>Ae. aegypti</i> ($\sigma\sigma$)	0.770	—	—	MRR ^e	McDonald 1977
<i>Ae. aegypti</i> ($\text{♀}\text{♀}$)	0.890	—	—	MRR	McDonald 1977
<i>Ae. aegypti</i> ($\sigma\sigma$) ^f	0.755	0.692–0.825	—	MRR	McDonald 1977
<i>Ae. aegypti</i> ($\text{♀}\text{♀}$) ^f	0.855	0.831–0.880	—	MRR	McDonald 1977
<i>Ae. aegypti</i>	0.625	—	—	MRR	Reuben <i>et al.</i> 1973
<i>Ae. aegypti</i>	0.575	0.416–0.734	0.440–0.680	Jolly estimates	Reuben <i>et al.</i> 1973
<i>Ae. aegypti</i> ^g	0.849	—	—	MRR	Conway <i>et al.</i> 1974
<i>Ae. aegypti</i> ^g	0.656	—	—	Fisher-Ford	Conway <i>et al.</i> 1974
<i>Ae. africanus</i>	0.926	—	—	Parous rate (June)	Germain <i>et al.</i> 1977
<i>Ae. africanus</i>	0.950	—	—	Parous rate (October)	Germain <i>et al.</i> 1977
<i>Ae. triseriatus</i> ^h	0.872	0.712–1.032	0.369–1.558	Jolly estimates	Sinsko 1976
<i>Ae. albopictus</i> ⁱ	0.824	0.803–0.844	0.677–0.940	Parous rate	Chan 1971
<i>Ae. albopictus</i> ^j	0.788	0.727–0.842	—	Parous rate	Chan 1971
<i>Cx. tarsalis</i> ^k	0.704	0.655–0.758	0.641–0.770	MRR	Nelson <i>et al.</i> 1978
<i>Cx. tarsalis</i> ^k	0.839	0.819–0.859	0.811–0.865	Parous rate	Nelson <i>et al.</i> 1978
<i>Cx. vishnui</i> ^l	0.870	0.866–0.873	0.630–0.940	Parous rate	Reuben 1963
<i>Cx. fatigans</i>	—	—	0.790–0.800	<i>Wuchereria</i>	Laurence 1963
<i>Cx. fatigans</i>	—	—	0.760–0.840	Parous rate	Laurence 1963
<i>Cx. fatigans</i>	0.833	0.788–0.881	—	MRR	Lindquist <i>et al.</i> 1967
<i>Cx. tritaeniorhynchus</i> <i>summosus</i>	0.489	—	—	MRR	Wada <i>et al.</i> 1969
<i>An. funestus</i>	0.834	—	—	Sporozoite rate	Garrett-Jones 1970
<i>An. funestus</i>	0.850	—	—	<i>Wuchereria</i>	Garrett-Jones 1970
<i>An. peditaeniatus</i>	—	—	0.760–0.850	<i>Wuchereria</i>	Laurence 1963
<i>An. peditaeniatus</i>	—	—	0.770–0.800	Parous rate	Laurence 1963

^a This table is intended to be representative, not exhaustive.

^b Mean of 12 monthly determinations (Table 4 in Sheppard *et al.* 1969). A 2-way ANOVA without replication (using the interaction mean square as residual) showed no difference in survivorship from month to month ($F = 2.043$, $P = 0.126$) but a highly significant difference in mean-daily survivorship between the 2 sexes ($F = 16.616$, $P = 1.832 \times 10^{-3}$).

^c Mean of 12 monthly determinations (Table 13 in Sheppard *et al.* 1969), corrected for dispersal of adults out of the study area. A 2-way ANOVA without replication (using the interaction mean square as residual) showed no difference in survivorship from month to month ($F = 2.136$, $P = 0.112$) but a highly significant difference between the 2 sexes ($F = 20.446$, $P = 8.695 \times 10^{-3}$).

^d Mean of 14 estimates corrected for population size and emergence (see Table 17 in Sheppard *et al.* 1969). Considered by Sheppard *et al.* to be a best estimate.

^e Mark-release-recapture experiment. Survivorship usually determined by regressing the logarithm of the number of marked recaptures on the age of the marked individuals recaptured.

^f Computed by regression analysis of the capture data given in Table 3 of McDonald (1977).

^g A number of assumptions concerning the feeding behavior of the females are involved in the computation of these estimates.

^h Mean of 20 Jolly-model estimates, including 5 estimates that exceeded 1.0. Recomputed from the raw data in Sinsko (1976).

ⁱ Outdoor human-bait collection, assuming a 3-d gonotrophic cycle.

^j Indoor human-bait collection, assuming a 3-d gonotrophic cycle.

^k Common estimate for 4 monthly determinations. Recomputed from the data in Nelson *et al.* (1978). Parous-rate estimates assume that the length of the gonotrophic cycle is 4.5 d; Nelson *et al.* (1978) computed survivorship based on both 4- and 5-d gonotrophic cycles.

^l Recomputed from the raw data in Table II of Reuben (1963) assuming an average gonotrophic-cycle duration of 3 d. Weighted mean based on 19 monthly observations; weighted-mean parous rate = 0.658. The range is for survivorships computed for gonotrophic cycles of 2–5-d duration.

Table 6. A comparison ^a of the mean-daily survivorship in an isolated population of *Culex tarsalis* in Kern County, California, determined simultaneously by 2 methods (after Nelson *et al.* 1978).

Month	Estimated survivorship with lower and upper 95% confidence limits based on ...					
	Mark-release-recapture ^b			Parous rate ^c		
	Lower CL	Survivorship	Upper CL	Lower CL	Survivorship	Upper CL
June	0.631	0.735	0.856	0.776	0.825	0.865
July	0.557	0.641	0.738	0.825	0.865	0.899
August	0.552	0.668	0.810	0.760	0.811	0.853
September	0.657	0.770	0.903	0.811	0.853	0.889
Common ^d	0.655	0.704	0.758	0.819	0.839	0.859

^a A 2-way ANOVA using the interaction mean square as residual showed no difference among months ($F = 0.956, P = 0.514$) but a difference between methods ($F = 17.202, P = 0.025$). The product-moment correlation is -0.0329 ; the Spearman rank-correlation coefficient is -0.200 .

^b See Table 7 for the common regression based on the mark-release-recapture estimates. Because the confidence limits are derived from a logarithmic curve, they are not symmetrical.

^c Assuming the duration of the gonotrophic cycle is constant and equal to 4.5 d (Nelson *et al.* (1978) provided estimates of survivorship based on a gonotrophic-cycle duration of both 4 and 5 d — see their table 4). The parous rates were 0.42, 0.52, 0.39 and 0.49 for June–September inclusive, based on samples of 100 ♀♀ (not blood-fed, not gravid). The confidence limits for June–September were obtained from Table 1.4.1. in Snedecor and Cochran (1967); confidence limits for the pooled data were computed from the normal approximation to the binomial.

^d See Table 7 for common regression. For parous rates, there was no difference among months ($\chi^2 = 4.396, P = 0.222$). The common parous rate was 0.455.

Table 7. Mean-daily survivorship of adults in an isolated population of *Culex tarsalis* in Kern County, California, as determined by mark-release-recapture studies (after Nelson *et al.* 1978).

	Jun	Jul	Aug	Sep	Common ^a
Number of recapture days	9	9	10	9	10
Number marked ♀♀ recaptured	301	134	256	133	824
Slope of regression line ^b	-0.30849	-0.44439	0.08305	-0.26139	-0.3507
Standard error of slope	0.06454	0.05939	0.08305	0.06730	0.0359
r^2	0.76546	0.88887	0.74626	0.68306	0.7487
r	-0.87490	-0.94280	-0.86387	-0.82647	-0.8652
F^c	22.85	55.99	23.53	15.09	91.32
Probability of a larger F	2.013×10^{-3}	1.393×10^{-4}	1.271×10^{-3}	6.021×10^{-3}	4.064×10^{-11}
Mean-daily survivorship ^b	0.735	0.641	0.668	0.770	0.704
Lower 95% confidence limit	0.631	0.557	0.552	0.657	0.655
Upper 95% confidence limit	0.856	0.738	0.810	0.903	0.758

^a An analysis of covariance showed no difference ($F = 1.351, P = 0.277$) between the slopes of the regression lines for the 4 mo. The “common” column represents the data for the common regression line.

^b Assume the daily survivorship, p , is constant. Then the number of marked females (A) recaptured on the n_{th} day after release is given by $A = Nap^n$ (or: $\log_e A = n \log_e Na$) where N = total number of marked females released and a = the recapture rate. Thus, the slope of the least-squares regression of $\log_e A$ on n estimates $\log_e p$ and therefore $\hat{p} = \exp(\log_e p)$.

^c A test of the null hypothesis that the slope of the least-squares regression line is zero. For all 4 months this hypothesis is soundly rejected.

Flight Behavior: Migration and Dispersal

The movement of adult mosquitoes is a fundamental element of their population biology. Not only is movement extensively involved in the life histories of some species (e.g. migrants) but also, patterns of movement comprise sources of serious error and confounding in the estimation of many critical demographic parameters. The quantitative analysis of movement in mosquitoes is expensive, time-consuming and often frustrating (e.g. Eddy *et al.* 1962) and, as a result, many workers have chosen to ignore it, assuming (no doubt incorrectly) that there was no net movement into or out of their study area. Useful reviews of mosquito movement are provided by Service (1976) and Provost (1974).

In general, mosquitoes exhibit 2 classes of movement: *migration* and *dispersal*. Migration is a “persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it” (Kennedy 1961). When migration occurs in mosquitoes it is typically synchronous and involves mass movements of young adults in a sustained flight that takes place shortly after emergence and before the 1st gonotrophic cycle (Provost 1974). Johnson (1969) would class such migratory flights as “type-I”; the other classes of mosquito “migration” that he considers are more properly considered as dispersal. True migration in mosquitoes is relatively uncommon; it has been studied most thoroughly, in both the field and laboratory, in the saltmarsh mosquito, *Ae. taeniorhynchus* (Haeger 1960; Nielsen 1958; Nielsen and Haeger 1960; Provost 1952, 1953, 1957, 1960, 1974; Nayar and Sauerman 1969, 1971). Less-well-documented instances of migration are known in a few other species (Service 1976). Such migrations can result in the rapid displacement of large portions of a population over relatively great distances; species that have such migratory flights can be expected to present challenging abatement problems.

*Dispersal*² is the net displacement of a population (or part of it) that occurs as a result of the summation of the movements of the constituent individuals. In mosquitoes, such movements may be aimless and non-specific (Corbet 1961) or, more commonly, may take place in conjunction with activities such as mating, nectar- and blood-feeding, oviposition, etc. Although dispersal has inherent elements of stochasticity, the process is not necessarily entirely random because the spatial distribution of breeding sites, host plants and animals, local topography and wind conditions, etc. may generate distinctive patterns of displacement (Klassen and Hocking 1964; Petruchuk 1972b).

A study of the movement patterns of mosquitoes is important for the following reasons:

- Movement patterns will determine, in part, the degree of “isolation” of a population and hence the very definition of the population itself. The boundaries and degree of isolation of a population are clearly of fundamental interest in demography and population genetics but as well, the extent of movement will contribute to decisions about the dimensions of abatement areas and their buffer zones.
- Movement patterns will contribute to estimates of demographic parameters such as age structure, survivorship, population size, recruitment, etc. Failure to correct for immigration or emigration may result in serious errors of estimation. The carefully analyzed study of the population dynamics of *Ae. aegypti* by Sheppard *et al.* (1969) provides an instructive and exemplary case.
- Some biological-control programs (e.g. genetic control) require knowledge of the rate and extent of movement of mosquitoes into or out of an abatement area.

Rather more is known of the biology and demography of migration than of dispersal but much of what is known is restricted to *Ae. taeniorhynchus*. In *Ae. taeniorhynchus* migration is preceded by a “milling” behavior that is typical of many migratory insects (Haeger 1960; Hocking 1953a); migration is initiated by the mosquitoes flying upward and then with the wind. The initial vertical flight, ranging from 3–12 m, is an

² Mosquito biologists (e.g. Lindquist *et al.* 1967) have not always been careful to distinguish between “dispersal” and “dispersion”; dispersal is the process whereby displacements occur whereas dispersion, in ecology (not statistics), is the spatial pattern of a population (Armstrong 1977).

essential part of the migration for, in rising to this height, the mosquitoes place themselves at a level at which the wind speed makes it impossible for them to control their orientation (Taylor 1960, 1974). Once above the boundary level in which oriented flight is possible, the mosquitoes are carried by the wind.

The distance traveled by mosquitoes during migratory flights depends on wind speed and the duration of the flight. The latter in turn depends on meteorological conditions and the extent of the energy reserves at the time of migration (Haeger 1960; Hocking 1953; Nayar and Sauerman 1972, 1973; Provost 1974). Mosquitoes have been recorded remaining airborne for 30 h or more (Klassen and Hocking 1964). If mosquitoes do not feed (on nectar) prior to migration (and they usually do not (Provost 1974)), the duration and distance of migration are reduced (Haeger 1960). Records of distanced traveled range from 3–5 to >50 km (Haeger 1960; Johnson 1969; Klassen 1968; Provost 1952, 1957) but the distance is highly variable (Provost 1974). The distance flown and the speed of flight may differ between the sexes; males fly for a shorter time than do females and consequently, they sometimes do not fly as far (Haeger 1960; Provost 1957).

Dispersal associated with the normal day-to-day activities of mosquitoes is relatively poorly understood and what is known is largely restricted to a small group of species that share some or all of the following features: great economic importance, usually as vectors; peridomestic habits; immatures in container habitats; populations small in size and with near-stable age structures (or at least populations in which recruitment occurs over relatively long periods of time and at low rates so that population fluctuations are damped by comparison with, for example, temperate-zone snow-melt *Aedes*). Thus, several intensive investigations of dispersal have been carried out with urban and (or) container-breeding mosquitoes in tropical regions (*inter alia*: Sheppard *et al.* 1969; Reuben *et al.* 1972; Rajagopalan *et al.* 1973; Wada *et al.* 1969; Yasuno *et al.* 1972a, 1972b, 1973; Lindquist *et al.* 1967).

In many studies the emphasis has been on the determination of maximal flight ranges (see Table 16 in Service (1976)) although from a population-dynamics or epidemiological point of view, maximal flight ranges are of little interest. More-recent studies have emphasized the dynamic aspects of dispersal and have attempted to quantify the statistics of the process: mean flight ranges (with standard errors); rates of dispersal; rates of decline of density with distance from a known source; and the influence of age, mortality rates and sex on dispersal.

Most studies of dispersal in mosquitoes involve MRR techniques even though it is often feared and sometimes strongly suspected (Dow 1971; Sheppard *et al.* 1969) that the actual marking process may accentuate post-marking dispersal. Other studies have introduced an easily reared taxon into an area from which it is normally absent (e.g. Morlan and Hayes 1958) or have used genetically marked strains (e.g. Reuben *et al.* 1972). In most studies (except those conducted on very small, relatively confined populations), the recapture rates of marked insects of been disappointingly small, making it necessary to draw important conclusions about dispersal behavior based on few individuals. In many instances, the failure to achieve an adequate recapture rate is at least partly due to a failure to increase the sampling intensity with increasing distance from the release site. The exponential increase in area with increasing distance from the release site, when combined with mortality of the marked individuals, bring about an often-overlooked, exceedingly rapid decrease in the density of marked individuals at only moderate distances from the release site and within a short time of the release (Table 8). For species that have mean dispersal rates of more than 50–100 m per day (as is probably the case for many temperate-zone mosquitoes (Provost 1974; Petruchuk 1972a)), this rapid decline in density with time and distance makes the reliable analysis of dispersal very difficult. In a study of the dispersal of *Ae. aegypti* in India, Reuben *et al.* (1972) did not increase the sampling intensity with distance (even though this species has a very modest dispersal ability) nor did they make any independent assessment of mortality. As a result, the picture of the distribution of marked individuals (Table 9) is a confounded mixture of losses due to mortality, losses due to dispersal, and errors due to the sampling program itself.

Table 8. A hypothetical example to illustrate the effect of mortality and dispersal on the density of marked mosquitoes released from a central point. Consider an initial release (on day 0) of 10 000 marked females. Suppose the net daily dispersal rate is 200 m (this is fairly modest), unidirectional (this is simplistic), and that marking does not induce increased dispersal. Further, suppose that the daily survival rate is 0.80 (this is fairly typical) and constant (unlikely). The trapping intensity desired is 10 traps km⁻².

Day	# mosquitoes	Dispersal area (km ²)	Density (# km ⁻²)	Traps needed
0	10 000	—	—	—
1	8 000	0.126	63 661.977	1
2	6 400	0.503	12 732.395	5
3	5 120	1.131	4 527.074	11
4	4 096	2.011	2 037.183	20
5	3 276	3.142	1 042.783	31
6	2 620	4.524	579.147	45
7	2 096	6.158	340.397	61
8	1 676	8.042	208.394	80
9	1 340	10.179	131.647	101
10	1 072	12.566	85.307	125

Table 9. Dispersal rates and survivorship of marked *Aedes aegypti*^a in Delhi, India (after Reuben *et al.* 1972).

Days after Release	Males ^b		Females ^c	
	<i>n</i>	Mean distance (m) ± SE	<i>n</i>	Mean distance (m) ± SE
1	62	1.855 ± 0.589	160	1.531 ± 0.313
2	9	8.889 ± 4.148	72	4.931 ± 0.836
3	2	5.000 ± 0.000	41	6.098 ± 0.964
4	1	5.000 ± 0.000	29	7.931 ± 1.151
5	0	—	15	6.333 ± 1.579
6	0	—	8	8.750 ± 2.631
7	0	—	9	5.556 ± 1.303
8	0	—	1 ^e	5.000 ± 0.000

^a On day 0, 4101 marked mosquitoes (1157 ♂♂, 2944 ♀♀) were released.

^b Daily survivorship estimated from the frequency of recaptures is 0.249 with 95% confidence limits of 0.107–0.583.

^c Daily survivorship estimated from the frequency of recaptures is 0.542 with 95% confidence limits of 0.453–0.647.

^d Female dispersal fits the model: mean distance = 8.3642 - 6.7183 d⁻¹ ± 1.2433 (*F* = 16.1, *P* = 0.0102, *r*² = 0.763).

^e This point was omitted in fitting the dispersal model.

The results of a study of the dispersal of *Cx. pipiens fatigans* by Lindquist *et al.* (1967) are representative (Table 10). Dispersal is modest in extent; about 80% of the marked adults were recaptured within about 550 m of the release site. The recapture rate was typically small (0.1808%). Males dispersed less than females (Table 10); this difference has been noted in several species and may reflect both inherent sex-specific

dispersal behavior and sex differences in survivorship (female mosquitoes have higher survivorship than males — Table 5). In a study of *Ae. aegypti*, Sheppard *et al.* (1967) found that although females dispersed more slowly than males, their net displacement was greater because they lived longer. Lindquist *et al.* (1967) did not attempt to estimate the loss of marked individuals from the study area. The study of dispersal in *Ae. aegypti* by Sheppard *et al.* (1969) showed that this loss rate (estimated to be 40% in that study) can be astonishingly high, even in populations that have poor dispersal capabilities and (or) low dispersal rates. Undetected dispersive losses of marked adults beyond the boundaries of the study area will depress estimates of survivorship and of the extent and rate of dispersal.

Table 10. Dispersal of marked adults of *Culex pipiens fatigans* in the Kemmendine area of Rangoon, Burma (after Lindquist *et al.* 1967).

Distance (x) from release site (yd)	Number of Collecting Stations	Number of adults (N)			
		Males ^b		Females ^c	
		Sample size	Marked	Sample size	Marked
200	4	3 985	18		22
400	4	6 078	8		28
600	6	4 998	5		14
800	8	4 139	3		13
1000	8	8 322	0		6
Sums	30	27 522	34		83

^a The mean distance dispersed (\pm SE) for males was 358.82 ± 34.589 and for females 486.75 ± 27.254 . Females dispersed significantly farther than males ($t = 2.664$, $P = 8.83 \times 10^{-3}$).

^b Male dispersal fits the model: $N = -1.82051 + 3963.07692x^{-1}$; $r^2 = 0.99946$, $F = 3703.0$, $P = 2.699 \times 10^{-4}$.

^c Female dispersal fits the model: $N = 40.18722 \exp(-0.00168x) \pm 0.29736$; $r^2 = 0.81027$, $F = 12.81$, $P = 0.0373$.

The relationship between density and distance of dispersing mosquitoes is complex. Most studies have revealed a rapid, nonlinear decline of density with distance. However, a plot of distance dispersed against frequency of dispersers usually yields a regression that is species-, sex-, terrain- and sometimes season-specific. This is not surprising, for the pattern of dispersal will come to reflect the dispersion of the biological requirements of mosquitoes in a particular terrain as stimuli (hosts, nectar sources, resting sites, oviposition sites, etc.) arrest or alter flight patterns. The many models that have been fitted to density-distance data (Service 1976; Wolfenbarger 1946, 1958) lack generality and sometimes biological interpretability; they serve only as convenient descriptions of particular data sets (e.g. Table 10). General models of the relationship between density and distance of dispersing insects have yet to be found for any group of insects (Taylor 1978) and will certainly have to embody more parameters than the distance from a dispersal site.

It is clear that the pattern of local dispersal flights of mosquitoes will depend on the peculiarities of the species and on environmental conditions. Some species, such as *Coquillettidia perturbans*, regularly fly several miles between the breeding/resting sites and host areas (Snow and Pickard 1957). Many species of temperate-zone *Aedes* rest in wooded areas or shrubbery but feed in open areas (Bidlingmayer 1967, 1971; Haufe and Burgess 1960). The times at which dispersal flights occur will depend on environmental conditions as well as innate periodicities.

A large array of environmental factors can be expected to influence the dispersal behavior of mosquitoes. Among the more-important factors are light (Davies 1975; Wright and Knight 1966; Bidlingmayer 1964; Klassen 1968; Wellington 1974), temperature and humidity (Platt et al. 1957, 1958; Haufe 1963; Bidlingmayer 1974), wind (Bidlingmayer 1971; Schreck *et al.* 1972; Snow 1976, 1977; Klassen and Hocking 1964; Gillies 1974; Petrushuk 1972b), vegetation (Bidlingmayer 1967, 1971, 1974, 1975b; Giglioli 1965; Hocking and Hudson 1974; Klassen and Hocking 1964), and physical barriers and topography (Lindquist *et al.* 1967; Gillies and Wilkes 1978). An important feature of the dispersal behavior of mosquitoes and one that is overlooked in many studies is their vertical stratification during dispersal. Many species have characteristic elevations at which they disperse (Gillies and Wilkes 1976; Gillies 1974; Burgess and Haufe 1960). It is reasonable to expect that the dispersion of resources will also affect the dispersal behavior of mosquitoes. All these features should be borne in mind in the design and interpretation of dispersal experiments on mosquitoes.

Population Dynamics: Larvae

An understanding of the demography of the immature stages is a key element in the explanation of the abundance and population fluctuations of mosquitoes. Knowledge of the population dynamics of the larval stages is also important because many biological-control agents are directed against this stage. Some authors (e.g. Chan 1971; Weidhaas *et al.* 1971; Southwood *et al.* 1972) have shown or suspected that important density-dependent mortality occurs in the larval stages of several species of mosquitoes; such density-dependent mortality could be a "key factor" (Varley and Gradwell 1960). In a carefully designed study of the population dynamics of the North American pitcher-plant mosquito, *Wyeomyia smithii*, Istock *et al.* (1975) found that larval abundance was more tightly regulated than the abundance of other stages in the life cycle; egg and pupal numbers fluctuated extensively whereas larval numbers fluctuated in a damped fashion, suggesting strong regulation at this stage. Survival of larvae was found to be relatively inelastic until the later stages of larval growth and pupation when food-dependent mortality differences appeared suddenly.

In spite of the importance of the larvae in mosquito population dynamics, there have been relatively few attempts to estimate such important demographic parameters of larval populations as mortality rates and survivorship. From the few studies that have been done, a diversity of mortality patterns has emerged (Table 11). In many cases, the larvae show an age- or stage-dependent mortality that increases or decreases with time so that the resulting survivorship curve is similar to the type I or type IV of Slobodkin (1963) (Table 11). However, in a few cases (Table 11), mortality is age-independent. It is clearly premature to generalize on the patterns of larval mortality that occur in mosquitoes.

A study of the larval population dynamics requires relative or absolute estimates of population size as well as estimates of the age structure of the larval population. The paucity of information on larval population dynamics is at least partly attributable to the complexity of larval habitats and the dispersion of larvae in the habitat, both of which factors seriously complicate the problem of sampling larvae (Service 1976). The dispersion of the larvae is one of the most important (and often ignored) components involved in the development of a sampling program. Commonly, the larvae are aggregated, sometimes exceedingly so (Hocking 1953b; Nielsen and Nielsen 1953; Nayar and Sauerman 1968), so that the variance exceeds the mean density irrespective of the sampling method (Table 12). The larval dispersion is not a static phenomenon; it may change with the age of the larvae (Service 1976), conditions in or around the pool, and possibly also with the type of pool. Failure to account for the sampling bias attributable to contagious distributions of larvae will seriously affect population estimates and the statistics derived from such estimates and may invalidate statistical comparisons among populations.

Table 11. Representative patterns of larval-pupal survivorship of mosquitoes under field conditions.

Species	Locale	Survivorship ^a	Reference
<i>An. gambiae</i>	Kenya	I – II	Service 1971, 1973, 1977a
<i>Ae. aegypti</i>	Thailand	III – IV ^b	Southwood <i>et al.</i> 1972
<i>Ae. albopictus</i>	Singapore	I ^c	Chan 1971
<i>Ae. cantans</i>	England	IV	Lakhani and Service 1974
<i>Ae. euedes</i>	Canada	II – III ^d	Enfield and Pritchard 1977b
<i>Ae. mercurator</i>	Canada	II – III ^d	Enfield and Pritchard 1977b
<i>Cx. pipiens fatigans</i>	India	I ^e	Rajagopalan <i>et al.</i> 1975a

^a The symbolism follows Slobodkin (1963). In a type-I survivorship pattern, mortality is age-specific and acts most heavily on older individuals. The survivorship curve is convex. In type-II survivorship, a constant number die per unit time yielding a constantly changing, age-specific mortality pattern and a survivorship curve that is linear when the ordinate (L_x) is arithmetic. In type-III survivorship, mortality is age-independent, a constant proportion of the larvae or pupae dying per unit time. The survivorship curve is linear when the ordinate is logarithmic. In type-IV survivorship, mortality is age-dependent and acts most heavily on younger individuals. The survivorship curve is concave.

^b Southwood *et al.* (1972) obtained several life tables for *Ae. aegypti* in Wat Samphaya. The survivorship curves were generally close to a type IV but were variable both among habitat types and months of the year. During the cool season (October–February) there was relatively little mortality between instars 2–4; thus the survivorship curves were close to type IV. However, during the warm season (March–August), high late-instar mortalities were found, yielding survivorship curves that were more nearly of the type-III variety.

^c Larval habitats were experimental and were covered as soon as eggs were found in them, thus excluding predators and preventing further oviposition. Thus, the results are possibly not typical of the normal survivorship pattern of this species.

^d Survivorship was inferred from rates of decline of total population size. The data did not permit a selection between a linear and a logarithmic model so that survivorship may be either type-II or type-III.

^e In this survivorship curve (and many others for mosquitoes), the curve is sigmoid. Thus, in *Cx. fatigans*, mortality was low for the very young larvae and late stages of development but was high for intermediate stages.

If the dispersion of the larvae in a pool can be satisfactorily modeled, the design of a statistically reliable sampling strategy is made considerably easier (Rojas 1964; Mackey and Hoy 1978). Of several contagious probability distributions, the negative-binomial is perhaps the most useful for mosquito larvae (Service 1971; Table 12) but even this model often fails to adequately describe the patterns observed (e.g. Table 12). Studies of the population dynamics of larval mosquitoes should be preceded by investigations designed to assess the larval dispersion so that reliable sampling schemes can be developed.

A wide variety of methods is available for making both relative and absolute estimates of larval-population sizes; Service (1976) provides a thorough and critical review of most of the common procedures. Theoretically, all the conventional techniques for making estimates of the absolute population size of adults by MRR are available for assessing larval populations but the difficulties of individual marking have resulted in the Petersen or Bailey procedures being most commonly used (Service 1976; Croset *et al.* 1976; Papierok *et al.* 1973; Rioux *et al.* 1968; Nayar *et al.* 1979). For certain types of habitats such as rock pools or treeholes from which the investigator can, within a short period of time, remove a detectable portion of the population, absolute estimates of population size can be made by regressing the accumulated catch on the catch per unit effort (e.g. Wada 1962). Occasionally, absolute estimates of population size are made by extrapolation from density indices derived from replicated-dipping or other area-sampling methods (e.g. Enfield and Pritchard 1977a). Some investigators (e.g. Service 1971) have made simultaneous estimates of larval populations by both MRR techniques and by extrapolations from density indices and have found almost perfect disagreement between the 2 methods. Service (1971) recommended that extrapolations of relative estimates to give total population sizes should be restricted to comparisons of similar-sized pools. On the other hand, Croset *et al.* (1976) found that the dipping method yielded estimates of population size that were in good agreement with independent estimates made by conventional MRR methods. The reliability of estimates made by extrapolation from indices may be site- and species-dependent.

Table 12. Representative frequency distributions of number of larvae (x) per dip in populations of *Anopheles gambiae* in Kenya (after Service 1971). Although the distributions are commonly of the aggregated variety (typical of many species of larval mosquitoes), the negative-binomial distribution does not always provide a reasonable model.

Number of dips having x larvae					
Kisumu, Experiment #1			Kisumu, Experiment #3		
x	Observed	Expected ^a	x	Observed	Expected ^a
0	122	109.433	0	44	42.164
1	28	63.120	1	17	22.950
2	46	37.628	2	19	13.529
3	32	22.674	3	5	8.179
4	26	13.736	4	5	5.006
5	6	8.348	5	4	3.087
6	4	5.084	6	3	1.913
7+	4	7.978	7+	3	3.172
	\bar{x}	1.500		\bar{x}	1.490
	s^2	3.007		s^2	3.545
	$k_3 \pm SE^b$	0.937 \pm 0.173		$k_3 \pm SE^b$	0.858 \pm 0.239
	$U \pm SE^c$	-0.893 \pm 0.412		$U \pm SE^c$	-0.533 \pm 0.678
	$T \pm SE^c$	-3.858 \pm 3.391		$T \pm SE^c$	-4.314 \pm 6.171

^a On the basis of a negative-binomial distribution, the parameters of which were estimated by maximum likelihood (Bliss and Fisher 1953).

^b k_3 is the maximum-likelihood estimate of k , using the symbolism of Bliss and Fisher (1953).

^c For an explanation of the computation and interpretation of these moment goodness-of-fit statistics, see Evans (1953). If the statistic \pm its standard error brackets zero, it can be concluded that the distribution fits a negative-binomial model. Thus, the frequency distribution of number of larvae/dip in Kisumu, Experiment #3 fits a negative-binomial; that of experiment #1 does not.

Rarely, estimates of larval or pupal population sizes are required for their intrinsic worth. More commonly, such estimates are intended to permit the construction of life tables or budgets and the estimation of stage- or age-specific mortality/survivorship rates. Life tables are convenient formats for summarizing age- or stage-specific demographic data. They permit estimates of survivorship through the various developmental stages of mosquitoes and they may provide insights into possible regulatory mechanisms in populations by drawing attention to the stages at which and the intensity with which natural mortality acts. Life tables have sometimes been proposed as adjuncts or aids in the design of abatement strategies (Southwood 1978) but their value in pointing the way to novel pest-management techniques for mosquito populations has yet to be robustly demonstrated.

Various methods for deriving the data for and constructing life tables or budgets are given in Southwood (1978), Service (1976) and Krebs (1978). Specialized life-table techniques are found in Lakhani and Service (1974) and Southwood *et al.* (1972). It is important to recognize that there are 2 fundamentally different types of life tables; both have been used in the study of mosquito populations. For insects with discrete generations (this includes many mosquitoes), the age-specific (cohort) life table is preferred or required. In this case, the mortality in a real cohort of animals is observed; this requires observations over the duration of the life-history for which the life table is required. For populations that have overlapping generations so that individual generation-cohorts are not distinguishable or in which several life-history stages are present simultaneously, it is possible to construct a time-specific (static) life table by assessing the mortality rates at a specific point

in time and assuming that these rates will persevere for the duration of the life history. If the age-specific mortality rates are constant in time and if the population is at equilibrium, the cohort and static life tables will yield the same estimates of age-specific mortality; otherwise (and this will be the common situation), the 2 tables will yield different (but hopefully similar) estimates.

2 basic approaches for obtaining the data for life tables have been used in the study of mosquito populations. One can make direct observations of the survivorship of a known cohort (e.g. Enfield and Pritchard 1977b) or, more commonly, one can infer the demographic data from observations of the age structure either at one point in time (for time-specific life tables) or at a series of times (for age-specific life tables) (Service 1971, 1977; Lakhani and Service 1974). Southwood *et al.* (1972) took advantage of the small population size and discrete habitats of *Ae. aegypti* to construct both time- and age-specific life tables for that species. That paper should be consulted for the special techniques devised for the study. We can illustrate the construction of life tables from observations of the age structure by reference to a study of *Ae. cantans* by Lakhani and Service (1974). Although the techniques developed there were used to construct a cohort life table, the same fundamental approach has been used to construct time-specific life tables for tropical anophelines (Service 1971, 1973, 1977a).

By sampling known proportions of the oviposition and emergence areas of a pool, Lakhani and Service (1974) were able to make estimates of the absolute abundance of *Ae. cantans* in a pool in Monks Wood (Table 13); these data were obtained each year for 3 yr, permitting comparisons of mortality from year to year. Estimates of egg and adult recruitment permit estimates of the total mortality during the larval and pupal stages (Table 13). In *Ae. cantans*, about 90% (90–93%) of the population die as larvae or pupae. No direct estimate of the recruitment of 1st-instar larvae was made, but in the laboratory, the hatching success of eggs was very high. Although a large proportion of the population dies during the larval-pupal period, the daily survivorship is high (≈ 0.97) (Table 13), in part because the development period is prolonged (87 d).

Table 13. Population sizes of eggs and adults in a population of *Aedes cantans* in Monks Wood, England (after Lakhani and Service 1974).

Year	Number of Viable Eggs	Number of Emerging Adults	Survivorship	
			Overall ^c	Mean daily ^d
1969	197 062	13 045	0.066	0.96927
1970	204 258	15 812	0.077	0.97102
1971	454 202	47 427	0.104	0.97436
Total	855 522	76 283	0.089	0.97260

^a Estimated from 100 samples representing 0.03125 of the available oviposition area and corrected for the efficiency of the egg-extraction technique (0.83) and the proportion (0.0125) of eggs that fail to hatch.

^b Estimated from emergence-trap collections. Emergence cages covered either 0.04155 of the pool area (1969 and 1970 (latter date incorrectly reported in Lakhani and Service as 1971) or 0.1061 (incorrectly given in Lakhani and Service as 0.10288) of the pool area (1971). No corrections for trap efficiency were made.

^c The probability that a viable egg will give rise to an adult; hence, a measure of generation survivorship, assuming all eggs in a given year are derived only from the population in the preceding year.

^d An estimate of the constant, daily survivorship based on an estimated duration of the larval-pupal stages of 87 d.

Such data (Table 13) permit an estimate of the overall intensity of immature-stage mortality but it is not possible to determine whether mortality affects some stages more than others. In order to estimate the age- or stage-specific mortality, Lakhani and Service (1974) made regular collections (100 dips at 7-d intervals) during the developmental period; the frequencies of the stages are enumerated and summed for the entire

season (Table 14). The frequency with which a given stage is represented in the collections is a function of its survivorship and its duration (Bates 1941). Thus, if the duration of the instars is known, it is possible to reconstruct a survivorship profile for the population. Lakhani and Service (1974) made independent, laboratory estimates of stage durations (Table 15) using temperature regimes that were similar to those actually experienced by larvae and pupae in the field. This step in the construction of life tables is critical because errors in the estimation of stage durations will have profound effects on the estimates of mortality rates. It is well known that laboratory estimates of stage duration (which are commonly done under conditions that are more favorable for development than those actually existing in the field) may seriously underestimate the true stage durations (e.g. Southwood *et al.* 1972).

Table 14. Stage frequencies of the aquatic stages of *Aedes cantans* in Monks Wood, England (Lakhani and Service 1974).

Year	Number of individuals collected in instar / stage ...				
	1	2	3	4	Pupae
1969	3 945	1 017	393	420	130
1970	4 661	1 350	539	371	173
1971	6 358	1 688	935	811	209
Total	14 964	4 055	1 867	1 602	512

If the stage frequencies are divided by their respective durations, a histogram results; this histogram resembles the survivorship function of the population. The histogram bars are centered on the instar mid-points, which are easily computed from the cumulative developmental durations (Table 15). However, in order to construct the life table, we must know the number of individuals that *enter* each stage (i.e. the number alive at the beginning of each stage), not the mean number alive during the stage. The problem then is to reconstruct the survivorship curve from the survivorship histogram; this is a deceptively difficult exercise.

Table 15. Temporal data for a population of *Aedes cantans* in Monks Wood, England (after Lakhani and Service 1974).

Stage	Duration (d)	Cumulative (d)	Midpoint (d) ^a
1	24	24.0	12.00
2	20.5	44.5	34.25
3	16.5	61.0	52.75
4	19	80.0	70.50
Pupa	7	87.0	83.50

^a If the midpoint of stage *i* is M_i and the cumulative time for that stage is C_i , then $M_i = (C_i + C_{i-1})/2$.

In their method "A", Lakhani and Service (1974) drew smooth, free-hand curves through the histogram, yielding a survivorship function from which one can interpolate the number of individuals that enter the various stages (i.e. the numbers alive at times 0, 24, 44.5 ... d; *see* Table 15). The values reported by Lakhani

and Service (1974) for each of the 3 yr and for the combined 3-yr data set are reproduced in Table 16 (italized values). This is a highly subjective approach to curve fitting; although the curve can confidently be fitted by eye for the middle periods, the possibility for error at the 2 tails of the curve is very large indeed. A plausible and much more rapid approach to the problem of fitting survivorship curves is polynomial-regression analysis. A 4th-order (higher-order polynomials are not permitted because there are only 5 data points) provides an excellent fit to the survivorship histogram (Table 16) and the number of individuals alive at the beginning of each instar can be determined by the regression equation. For the most part, there is excellent agreement between the estimates of the numbers entering a stage derived from the free-hand curve and those derived from the regression analysis (Table 16). The advantages of regression analysis are speed and the possibility of undertaking the entire exercise by computer.

Table 16. Number of individuals of *Aedes cantans* entering each stage in a population in Monks Wood, England: a comparison of the values obtained by Lakhani and Service (1974) (“graph”) by free-hand survivorship curves and values obtained by polynomial-regression analysis (“regression”).

Stage	Age (d) at beginning of stage	Numbers entering stage							
		1969		1970		1971		All 3 years	
		Graph	Regression ^a	Graph	Regression ^b	Graph	Regression ^c	Graph	Regression ^d
1	0	296	288	327	357	478	533	1125	1178
2	24	87	87	105	106	128	132	310	325
3	44.5	31	30	44	44	66	63	138	137
4	61	22	22	25	25	46	51	94	98
Pupa	80	19	20	20	21	34	33	76	74
Adult	87	18	16	19	31 [†]	29	28	70	74 [†]
Generation survival ^e		0.061	0.056	0.058	0.053	0.061	0.053	0.062	0.059

^a Let instar-frequency/instar duration at time t be N_t . The regression equation is then:

$$N_t = 287.85503854 - 12.57360606 \times t + 0.20519097 \times t^2 - 0.00126176 \times t^3 + 0.00000174 \times t^4; r^2 = 1.00000000$$

^b $N_t = 357.39202503 - 17.76728977 \times t + 0.39666393 \times t^2 - 0.00433006 \times t^3 + 0.00001864 \times t^4; r^2 = 1.00000000.$

^c $N_t = 533.11252825 - 29.85889385 \times t + 0.71245548 \times t^2 - 0.00757784 \times t^3 + 0.00002950 \times t^4; r^2 = 1.00000000.$

^d $N_t = 1178.35959176 - 60.19978967 \times t + 1.31431038 \times t^2 - 0.01316966 \times t^3 + 0.00004988 \times t^4; r^2 = 1.00000000.$

^e Number entering the adult stage divided by the number entering the 1st instar.

[†] These 2 values were the only serious discrepancies produced by the regression curves. In calculations that follow, these clearly erroneous values were replaced by those of Lakhani and Service (1974).

Once a survivorship curve has been fitted and the number of individuals entering the various stages predicted, we can construct a life table for the population (Table 17). In *Ae. cantans*, the largest absolute and instantaneous losses occur during the 1st-instar-larval stage; mortality suffered by 3rd- and 4th-instar larvae and especially by pupae is relatively low by comparison. Thus, the survivorship curve is of the type-IV variety.

Recognizing the problems associated with the free-hand fitting of survivorship curves, Lakhani and Service (1974) tested the reliability of their method by fitting the survivorship curve in quite another manner. They devised a model of survivorship on the assumption that the instantaneous mortality within an instar was constant but that mortality rates could vary among instars. Thus, the cohort could be expected to decline in an exponential fashion within each instar but possibly at different rates among instars. Using the 5 exponential declines in cohort size, Lakhani and Service (1974) derived a series of 5 nonlinear equations in 6 unknowns (i.e. the 5 instantaneous mortality rates and the size of the recruited 1st-instar-larva population). To force a unique solution, a 6th equation was derived from either the relationship between the number of eggs and the

number of adults (Table 13; their method “B”) or an inferred linear relationship between the instantaneous mortality rates in instars 2 and 3 as determined from the survivorship curve previously fitted by eye (method “C”). The 6 equations must be solved by computer; Lakhani and Service (1974) provided a linear approximation that can be solved by simple matrix-algebra techniques but the approximation is rather poor. Method “C” yielded estimates of the instantaneous mortality rates that were satisfyingly close (Table 18) to those obtained by the freehand fitting of a survivorship curve.

Table 17. A life table ^a for a population of *Aedes cantans* based on the computation of the numbers entering each stage by polynomial-regression analysis. (Data from Lakhani and Service 1974)

Stage (<i>i</i>)	N_i	l_i	d_i	q_i	λ_i	e_i
1	1178	1000.000	724.109	0.724	-0.0537	20.75
2	325	275.890	159.593	0.578	-0.0421	26.29
3	137	116.299	33.107	0.285	-0.0203	29.64
4	98	83.192	20.374	0.245	-0.0148	22.06
Pupa	74	62.818	3.396	0.054	-0.0079	7.28
Adult	70	59.423	59.423	1.000	— ^b	—

^a The terminology of the table is as follows:

N_i Number entering the stage.

l_i The number entering the stage (i.e. alive at the beginning of the stage) scaled to $N_0 = 1000$.

d_i The number dying during the stage.

q_i The stage-specific mortality rate — the proportion of individuals dying during a stage.

λ_i Instantaneous mortality rate during instar i computed from the relationship: $\lambda_i = \{\ln(l_{i+1}/l_i)\}/t_i$ where t_i is the duration of stage i in days. Thus, these rates are per day. Lakhani and Service (1974) refer to the λ_i as “relative mortality rates” and give them as positive values.

e_i Expectation of further life, days.

^b No rate is computed because the longevity of adults is unknown.

Table 18. Instantaneous mortality rates for larvae and pupae of *Aedes cantans* in Monks Wood, England (after Lakhani and Service 1974).

Instar	Instantaneous Mortality Rate	
	Method A ^a	Method C ^b
1	-0.0537	-0.0599
2	-0.0395	-0.0358
3	-0.0233	-0.0211
4	-0.0112	-0.0123
Pupa	-0.0117	-0.0065

^a Mortality rates were computed from the decline in the numbers entering a stage as determined from a survivorship curve fitted by eye to the field data of stage frequencies and developmental periods.

^b Mortalities determined by solving a set of nonlinear equations in 6 unknowns; the 6th equation is derived from the relationship between the instantaneous mortality rates of 2nd- and 3rd-instar larvae as determined by method A.

The important contribution of Lakhani and Service (1974) was to show that the first method (“A”) of deriving life-table statistics for a mosquito population produces reasonable estimates of age-specific mortality rates. By comparison to the exact method, the free-hand-curve method underestimated mortality in 1st-instar larvae and pupae (by 12 and 44%, respectively) and overestimated mortality in the 2nd-, 3rd-, and 4th-instar larvae (by 9, 9, and 10%, respectively). Not surprisingly, the largest discrepancies between the 2 methods are at the tails of the curve — on the one hand because the estimation of the number of 1st-instar larvae entering the population is exceedingly difficult and on the other because the number of pupae is relatively small and the sampling errors are correspondingly large. The derivation of life-table statistics from survivorship curves has been undertaken by several workers but none has assessed the reliability of the estimates in the manner used by Lakhani and Service (1974). It would be interesting to have such checks run on the life tables for other species of mosquitoes. Further attention is needed to the important problem of reconstructing the survivorship function from stage-frequency data. Several methods for the extraction of demographic statistics from stage-frequency data (e.g. Manly 1974a, 1974b, 1976) assume a constant mortality rate over all instars, making them inappropriate for populations of larval mosquitoes.

If absolute estimates of larval/pupal population sizes are available for a cohort on successive occasions, it may be possible to infer the pattern of mortality from the regression of numbers on time. Enfield and Pritchard (1977a, 1977b) investigated the dynamics of the immature stages of several species of mosquitoes in a pool in Alberta. To estimate larval mortality, these workers estimated the population density in the pool on successive occasions and produced total-population estimates by extrapolation to the total area of the pool (Table 19). For some species the data could not be analyzed because the population estimates showed no obvious trend, possibly because of staggered recruitment or the inadequacy of the sampling method for some species or stages. For *Ae. euedes* and *Ae. mercurator*, however, a highly significant regression of numbers on time was found (Table 19). Nevertheless, the pattern of mortality experienced by these populations is not clear from the population estimates because the regression of numbers on time fits both logarithmic and linear models quite well (Table 19). These models imply radically different patterns of larval mortality: the logarithmic model implies an age-independent mortality rate whereas the linear model implies a continuously increasing, age-dependent mortality rate. The 2 models also predict quite different estimates of total recruitment (Table 19). The mean daily survivorship of larvae, on the assumption of the logarithmic model, was 0.914 for *Ae. euedes* and 0.931 for *Ae. mercurator*; these values are not significantly different (Table 19) and are close to the mean-daily survivorship of *Ae. cantans* (Table 13). If the larval mortality rates are truly constant from instar to instar, the pattern of mortality in these species is substantially different from that found in most other species of mosquitoes in which these rates have been measured.

Patterns of larval/pupal mortality are known for only a few species of mosquitoes; mortality rates differ markedly among the instars and species, leading to varied and complex patterns of larval mortality and a variety of survivorship curves. For the most part, the causes of larval mortality are not well understood in a population-dynamics sense nor is it known for most species whether any of the age-specific mortality rates are regulatory, that is whether certain of the mortality rates account for most of the fluctuations in population size in the adult stage or in subsequent generations. In part this is due to a failure on the part of most studies to quantify the causes of larval mortality and in part because we lack complete (i.e. egg → adult → egg) life tables for all species. Service (1971) believed that of the many possible larval mortality factors (competition, limited food supply, parasites, pathogens, predators), predators were the most important. Later studies (Service 1973, 1977a) showed that parasites and epibionts were important mortality factors but differences in the shapes of survivorship curves among habitats were correlated with the predator fauna. Much is known of the diversity of predators, pathogens and parasites of mosquitoes (other papers in this volume) but for the most part, the intensity with which these agents act on populations or whether they are in any way regulatory are not known.

Table 19. Mortality in larval populations of *Aedes euedes* and *Aedes mercurator* in Alberta (after Enfield and Pritchard 1977a, 1977b).

Day ^a	Estimated population size (all instars) ± SE	
	<i>Aedes euedes</i> ^b	<i>Aedes mercurator</i> ^c
4	106 630 ± 8 530	70 270 ± 8 990
8	80 420 ± 7 540	33 630 ± 6 540
12	77 120 ± 9 670	41 540 ± 9 910
19	38 730 ± 6 830	34 510 ± 6 970
22	34 400 ± 5 330	16 590 ± 3 570
25	45 750 ± 6 300	29 740 ± 7 240
28	17 690 ± 3 930	14 450 ± 2 560
31	4 846 ± 1 783	4 846 ± 2161

	Estimates of mean-daily survivorship ^d	
	<i>Aedes euedes</i>	<i>Aedes mercurator</i>
Survivorship	0.914	0.931
Lower 95% CL	0.87	0.89
Upper 95% CL	0.961	0.974

Model	Estimated Population size on day 0 (95% CL)	
	<i>Aedes euedes</i>	<i>Aedes mercurator</i>
Linear	114 572.5 (96 117.1 – 133 027.9)	64 538.5 (44 089.0 – 84 988.1)
Logarithmic	196 243.6 (69 855.6 – 551 302.0)	90 988.0 (35 881.9 – 230 724.1)

^a Day 0 = 19 April 1975 = day of hatching.

^b The regression of larval numbers on time fits the following 2 models where N = numbers on day t :

(1): $N = 114\,572.52 - 3429.49t \pm 9372.64$ ($r^2 = 0.9368$, $F = 88.88$, $P = 8.097 \times 10^{-5}$).

This linear model implies a constant loss rate of 3429 larvae/d and hence a continuously changing age-dependent mortality rate.

(2) $\log(N) = 5.2928 - 0.0390t \pm 0.2278$ ($r^2 = 0.7638$, $F = 19.41$, $P = 4.542 \times 10^{-3}$).

This logarithmic model implies a constant, age-independent mortality rate.

^c The regression of larval numbers on time fits the following 2 models:

(1) $N = 64538.52 - 1816.99t \pm 10385.37$ ($r^2 = 0.7720$, $F = 20.32$, $P = 4.070 \times 10^{-3}$).

(2) $\log(N) = 4.9590 - 0.0309t \pm 0.2052$ ($r^2 = 0.7149$, $F = 15.05$, $P = 8.181 \times 10^{-3}$).

^d ANCOVA of the logarithmic regressions shows no difference in the larval-mortality rates between species ($F = 0.46$, $P = 0.51$).

In a few instances, sufficient life-table data have been collected to permit the ranking of the age-specific mortality rates and to suggest the means by which they operate. In an extensive and detailed study of larval/pupal mortality in *Ae. aegypti*, Southwood *et al.* (1972) identified key factors by a modification of the method of Varley and Gradwell (1960), giving no consideration to natality. In the cool season, most of the variation in generation (i.e. egg → pupa) mortality was due to variation in the death of 4th-instar larvae (Table 20, k_4) but an interesting shift occurred in the warm season when death of young larvae (Table 20, k_1) caused most of the variation in generation mortality. k_1 was shown to be density dependent (as determined by the regres-

sion of k_1 on the log-transformed population sizes on which the factor acts) but k_4 was density independent. Southwood *et al.* (1972) thought that the regression of k_1 on log population size indicated overcompensating mortality among young larvae but there is perhaps insufficient evidence to confidently declare that the slope of the regression line is greater than 1 ($t = 1.021$, $P = 0.171$ (1-tailed hypothesis)). In Wat Samphaya, predators were few and Southwood *et al.* (1972) thought that the mortality in both young and old larvae resulted from competition, presumably for food, but there was no direct evidence that this was so.

Table 20. Correlation matrices and tests for density dependence for k factors ^a from life tables for *Aedes aegypti* breeding in water jars in Wat Samphaya, Bangkok, for the cool season, the warm season, and for the entire year (after Southwood *et al.* 1972).

Cool season: October 1967 – February 1968 ($n = 4$)

	k_2	k_3	k_4	K
k_1	-0.459	0.723	-0.631	-0.368
k_2		-0.944	-0.223	-0.472
k_3			-0.080	0.207
k_4				0.953 *

* $P = 0.047$

Warm season: March – August 1968 ($n = 5$)

	k_2	k_3	k_4	K
k_1	-0.750	0.262	0.606	0.975 *
k_2		-0.426	-0.705	-0.782
k_3			-0.233	0.331
k_4				0.667

* $P = 0.0047$

Entire year: October 1967 – August 1968 ($n = 9$)

	k_2	k_3	k_4	K
k_1	-0.713	0.034	0.328	0.672 *
k_2		0.095	-0.429	-0.332
k_3			-0.203	0.384
k_4				0.663 †

* $P = 0.047$; † $P = 0.051$

Tests for density dependence:

$$k_1 = 1.4727 \log(\# \text{ eggs}) - 4.2682 \pm 0.2019; F = 10.1135, P = 0.016.$$

$$k_4 = 0.1322 \log(\# \text{ 4}^{\text{th}}\text{-instar larvae}) + 0.0998 \pm 0.2925; F = 0.1285, P = 0.731.$$

^a The mortality factors are as follows:

k_1 = death from eggs to 1st-instar larvae;

k_2 = death from 2nd-instar larvae to 3rd-instar larvae;

k_3 = death from 3rd-instar larvae to 4th-instar larvae;

k_4 = death from 4th-instar larvae to pupae;

K = death from eggs to pupae.

In the limited life-table data for *Ae. cantans* (Lakhani and Service 1974), there is some evidence (Table 21) that much of the fluctuation in the mortality from egg to adult stage is due to fluctuations in the mortality of 3rd-instar larvae (k_3). As well, high mortality in instar 2 may be compensated for by low mortality in the 4th-instar larvae and pupae (Table 21). There is no evidence for density dependence in the action of k_3 but the data are very slim. In a study of the density dependence of larval mortality in *Cx. pipiens fatigans*, Rajagopalan *et al.* (1975b) found that larval mortality was undercompensating in the late-summer and monsoon seasons, compensating in the post-monsoon and early-summer seasons and overcompensating in winter. The causes of the mortality and the reasons for the shifts in the intensity of density dependence with season are not known.

Table 21. Matrix of simple correlation coefficients for k -factors for 3 life tables of *Aedes cantans*^a

	k_2	k_3	k_4	k_5	K
k_1	-0.5715	-0.8185	0.5214	0.8840	-0.8348
k_2		-0.0037	-0.9982 ^b	-0.8888	0.0252
k_3			0.0634	-0.4550	0.9996 ^c
k_4				0.8598	0.0346
k_5					-0.4805

^a The raw data for the construction of the life tables may be found in Table 16. The k -values are determined as the difference in the logarithms (base-10) of successive estimates of the number of individuals entering each stage. The subscripts refer to the instars with pupae designated by "5". In the absence of information on fertility, K was computed as the difference in the logarithms of the number of individuals entering instar 1 and the number of emerging adults.

^b $P = 0.038$

^c $P = 0.018$

Epilog

Our understanding of the population dynamics of mosquitoes is at a very rudimentary stage. Other chapters in this manual have illustrated that there is much information about the mortality factors that might be important for mosquito populations but, for the most part, the quantification of mosquito mortality is just beginning. The need is clearly for sustained, long-term observations on a few species; promising results have been achieved with a small cadre of tropical, peridomestic species and a few others. Even with small, confined populations, the problems of obtaining statistically reliable estimates of demographic parameters of mosquito populations may be virtually insurmountable. Until more reliable sampling methods are devised, it is doubtful whether much progress can be made in understanding the population dynamics of large, unstable populations of mosquitoes, especially the dynamics of the adults.

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Survivorship Estimates

Lalharid Service (1974)

Aedes cantans - mortality decreasing with age - (But see my Appendix)

In. An. gambiae, most. was heavier among 4th-instar larvae (Service 1974b, 1973b - ref in L+S) Southwood et al (1972) found that A. aegypti in 1st instar, highest mort. in 1st instar, in warm season

Using data pooled over 3 years.

Method C

Instar	Dist. Mort Rate	Finite Mort Rate	Finite Survival Rate
1	- 0.0599	0.05814	0.94186
2	- 0.0358	0.03517	0.96483
3	- 0.0211	0.2088	0.97912
4	- 0.0123	0.9222	0.98778
P	- 0.0065	0.00648	0.99352

$\bar{x} = 0.97342$

Method B	Dist. Mort Rate	Finite Mort Rate	Finite Survival Rate
1	- 0.0517		0.94961
2	- 0.0504		0.95085
3	+ 0.0014		—
4	- 0.0359		0.96474
P	+ 0.0738		—

$\bar{x} = 0.95507$

Method A	Dist. Mort Rate	Finite Mort Rate	Finite Survival Rate
1	- 0.0537		0.94772
2	- 0.0395		0.96127
3	- 0.0233		0.97697
4	- 0.0112		0.98886
5	- 0.0117		0.98837

$\bar{x} = 0.97264$

Using their data from Table V (p. 274) for larvae only

Entering L1 = 1175, Entering L5 = 75

∴ instantaneous daily mortality rate = -0.03439 Duration is 80 days.

Survival₈₀ = 0.96619 (higher than my study, but development period is longer)

Reusians et al 1993.

Compute larval survivorship

Pond 1 1989

Entering L1 12000

Entering L5 800 (pupae)

Duration of larval stages = 58 days

$$\text{Instantaneous mortality rate} = (\log_e(800) - \log_e(12000)) / 58 = -0.04669$$

$$\text{Daily survival rate} = 0.95438$$

Pond 2, 1989

Entering L1 285

Entering P 10

Duration of larval stage = 59 d

$$\text{Inst. mortality rate} = -0.05678$$

$$\text{Daily survival} = 0.94480$$

Pond 2, 1990

Entering L1 265

Entering P 25

Duration 51 days

$$\text{Instantaneous mortality rate} = -0.04629$$

$$\text{Daily survival rate} = 0.95431$$

Average over the 3 sites = 0.95131.

Leushaw - continued

Estimate total # collected from Fig 5.

Pond 1 1989	Order	Height of Micropip	Duration	# Collected
?	1	9100 or 910?	15	136500
axi wrong.	2	3300	15	49500
	3	1800	13	23400
	4	1600	15	24000
	P	100	12	1200

Pond 2, 1989	Order	Height	Duration	# Collected	SE
	1	260	15	3900	0.00214
	2	190	15	2850	0.00495
	2	150	14	2100	0.01360
	4	10	15	150	0.03388
	P	15	13	195	0.09824

Pond 2, 1989	Order	Height	Duration	# Collected	SE
?	1	22			
axi wrong,	2	14			
	3	12			
	4	3			
	P	2			