

# Estimating the per Capita Rate of Population Change: How Well Do Life-History Surrogates Perform?

M. W. CHMIELEWSKI, C. KHATCHIKIAN, AND T. LIVDAHL<sup>1</sup>

Department of Biology, Clark University, 950 Main Street, Worcester, MA 01610

Ann. Entomol. Soc. Am. 103(5): 734–741 (2010); DOI: 10.1603/AN09162

**ABSTRACT** A method of estimating per capita rate of change for experimental populations in the absence of adult survival and fecundity schedules ( $r'$ ) was proposed previously (J. Anim. Ecol. 53: 573–580; 1984). The method has been used repeatedly, although there has been no attempt to verify the relationship between  $r'$  and the per capita growth rate in populations. This method was tested with laboratory populations of the mosquito *Aedes albopictus* (Skuse) (Diptera: Culicidae) growing at three larval densities. Survival and fecundity schedules enabled calculation of per capita growth rate,  $r$ , for each population, whereas measuring emergent females enabled the calculation of  $r'$ . The capacity of  $r'$  to predict  $r$  was significant, although a substantial amount of variation in  $r$  remained unaccounted for, and  $r'$  overestimated  $r$ . The degree of overestimation of  $r$  by  $r'$  was consistent across the three densities, and the regressions of  $r$  and  $r'$  versus density were similar. Overestimation of per capita rate of change by  $r'$  is attributed largely to extensive adult longevity in laboratory conditions for this species, coupled with a lengthy reproductive period, in combination with prereproductive adult mortality, both of which are assumed to be negligible with the  $r'$  method. Separate indicators of larval success were also tested for their predictions of  $r$ ; only first day emergence and average development time were significant predictors although neither performed as well as  $r'$ . The  $r'$  index accounted for the largest fraction of variation in  $r$ . Implications of overestimating  $r$  by  $r'$  to estimating other population parameters are discussed.

**KEY WORDS** competition, container mosquito, density dependence, invasive species, life table

Quantifying success of experimental populations has presented a long-standing problem for ecologists. It is particularly challenging to gather information about per capita rate of change and to synthesize it in a manner that relates to basic theoretical problems. Livdahl and Sugihara (1984) proposed a composite index of success to estimate per capita growth rate for cohorts in experimental situations,  $r'$ . This measure, and its antilog derivative  $\lambda'$ , have become favored as a tool to summarize per capita rate of change of insect populations (Livdahl and Willey 1991, Alto and Juliano 2001, Braks et al. 2004, Murrell and Juliano 2008, Juliano 2009). Despite the apparent utility of  $r'$  as a tool in population studies over a 25-yr period, the reliability of  $r'$  as a predictor of per capita growth in various competitive regimes has remained untested. Here, we assess  $r'$  as a measure of per capita growth, in populations of *Aedes albopictus* (Skuse) (Diptera: Culicidae) exposed to different levels of larval competitive stress.

Ideally, the dependent variable in quantifying population success is the per capita growth rate ( $r$ ) (Table 1). This variable forms the base currency for any model that describes population change as a function

of environmental conditions, including virtually all models for single species growth and models describing species interactions. Despite the clear value of estimating per capita growth rate and quantifying its response to environmental factors, actual values derived from experimental populations remain elusive, especially for long living species that reproduce for significant periods of their lifespan. To sidestep the practical difficulties of measuring  $r$ , experimental ecologists commonly measure presumed correlates of  $r$ . As examples, many studies have used body size at maturity or survival to maturity as correlates of success (McCown and Williams 1969, Lynch 1977, Polis and Farley 1980, Cezilly et al. 1996, Kupferberg 1997, Janzen et al. 2000, Kisdí 2004, Aldridge and Boyce 2008, Carlson et al. 2008). Implicit in the use of such variables is the assumption that population growth rates do indeed scale with such surrogate measures. For many organisms, multiple surrogate measures are accessible and may need to be considered jointly to permit overall conclusions about experimental treatments, or conjecture about how fast an experimental population could grow in response to experimental treatments. Various methods of projecting population growth have been applied to estimate rates of change within populations. Schedules for age ( $x$ ) specific sur-

<sup>1</sup> Corresponding author, e-mail: tlivdahl@clarku.edu.

**Table 1.** Equations for terms referred to in the text<sup>a</sup>

Term	Equation
(1) Innate capacity for increase	$r_m = \frac{\ln(R_0)}{\tau}$
(2) Capacity for increase (Laughlin 1965)	$r_c = \frac{\ln(R_0)}{T_c}$
(3) Net reproductive rate	$R_0 = \sum_x l_x m_x$
(4) Per capita rate of change (iterative method)	$1 = \sum_x l_x m_x e^{-rx}$
(5) Estimated per capita rate of change. $A_x$ is the number of females emerging on day $x$ ; $D$ is the estimated time between emergence and oviposition.	$r' = \frac{\ln\left[\frac{1}{N_0} \sum_x A_x f(\bar{w}_x)\right]}{D + \frac{\sum_x A_x f(\bar{w}_x)}{\sum_x A_x f(\bar{w}_x)}}$
(6) Future fecundity of females with avg. size $\bar{w}_x$ emerging on day $x$ . This study uses the relationship reported by Blackmore and Lord (2000)	$f(\bar{w}_x) = e^{2.35+0.69\bar{w}_x}$
(7) Estimated finite rate of increase	$\lambda' = e^{r'}$
(8) Cohort generation time	$T_c = \sum_x x l_x m_x / \sum_x l_x m_x \approx \tau$
(9) Generation time, corrected	$\tau = \frac{\ln(R_0)}{r}$
(10) Fecundity at age $x$	$m_x = \frac{Eggs_x/2}{Females_x + Larvae_x/2}$
(11) Survivorship to age $x$	$l_x = N_{x,t+x} / N_{0,t}$

<sup>a</sup>  $N_0$  is the initial density at time zero,  $A_x$  is the number of new adult females produced at time  $x$ ,  $D$  is the delay time between adult emergence and oviposition, and  $\bar{w}_x$  is the average wing length of females emerging on day  $x$ .

Survival ( $l_x$ ) and fecundity ( $m_x$ ) can be used to calculate the per capita growth rate  $r$  (Dublin and Lotka 1925; Lotka 1925); however, such schedules require time consuming and often difficult observations under experimental conditions. In response to this, different measures of population growth rate have been devised that generally focus on separate life-history traits as proxies for survival and fecundity data.

Andrewartha and Birch (1954) proposed an approximate measure of the capacity for increase, as a statistic to discern how quickly a population can multiply (Table 1, equation 1), and this was advocated later by Laughlin (1965) (Table 1, equation 2). Laughlin emphasized that this measure remains an estimate of the innate capacity for growth rather than actual growth, in that the observed  $r$  and its calculated value may differ. In particular, the absolute value of  $r$  may need to be  $<0.1$  for equation 2 to provide a reliable estimate (Caughley and Birch 1971). In addition, Andrewartha and Birch (1954) found that the success of equation 1 may depend on  $R_0$  (Table 1, equation 3) being close to or equaling 1. May (1976) noted that variation in distribution of age of reproduction within a cohort should be small for the most accurate estimate of  $r$  by equation 2. Although Laughlin's estimate was a convenience before the widespread use of computers, the more accurate iterative solution of the Lotka-Euler equation (Table 1, equation 4; Lotka 1925) can now be performed efficiently and requires no more information than Laughlin's  $r_c$ . Laughlin's estimate did how-

ever provide the basis for other estimates that did not rely on age specific fecundity and survival schedules.

Livdahl and Sugihara (1984) suggested an approximation of per capita growth rate ( $r'$ ), derived directly from Laughlin's  $r_c$ , which may be most applicable to experimental insect studies (Table 1, equation 5). This measure takes life-history features into account while dispensing of the need for large scale observations of fecundity and survival through the life span of all individuals for every population of interest (Livdahl and Sugihara 1984). In particular, by focusing on the relationship between adult female size and fecundity in mosquitoes [ $f(\bar{w}_x)$  is a fecundity-size relationship (Table 1, equation 6)], Livdahl and Sugihara's method sidesteps direct reproductive observations. Despite the adoption of this technique for estimating  $r$ , little is known about the applicability of  $r'$  methods across different density treatments, or the importance of multiple reproductive events to the actual per capita growth rate. A major objective of this study was to test the  $r'$  method as a predictor of  $r$  and to test its consistency at a variety of densities.

The Asian tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae), an important disease vector, provides a particularly useful model for inquiries into population growth rate methods. The species is conveniently reared in laboratory conditions. Moreover, this species has proven highly invasive, occupying much of eastern North America since its introduction in the 1980s (Hawley 1988; Cilek et al. 1989; O'Meara et al. 1992, 1995), Albania in 1979 (Adhami and Reiter 1998), other European countries since the late 1990s, and Central and South America since the 1980s (global spread is reviewed in Reiter 2010). This success has generated considerable interest in interspecies competition, dispersal, population growth, and the species' ability to withstand cold winters (Hawley et al. 1987, Moore et al. 1988, Francy et al. 1990, Novak 1992, Reiter 1998, Moore 1999).

Analyses of various aspects of the life-history of *Ae. albopictus* have been conducted in the field and laboratory. These include single species life-table studies of adults in a field population in Singapore (Chan 1971), fecundity-female size relationships (Blackmore and Lord 2000), analyses of separate aspects of larval success in competition with other species (Black et al. 1989, Ho et al. 1989), and  $r'$  methods [or derivative methods based on  $\lambda'$  (Table 1, equation 7)] to assess responses of *Ae. albopictus* to direct competition with *Aedes aegypti* (L.) (Juliano 1998) or *Aedes triseriatus* (Say) (Livdahl and Willey 1991). In addition, Armistead et al. (2008b) recently used  $r'$  to explore the effects of the introduction of *Aedes japonicus* (Theobald) on *Aedes atropalpus* (Coquillett) populations. Most of these studies have not included direct estimates of fecundity, but instead have relied upon fecundity-size relationships obtained in separate studies (Livdahl and Willey 1991, Juliano 1998, Armistead et al. 2008a) or oviposition for a predetermined period (Black et al. 1989, Blackmore and Lord 2000). None of these studies allow for a measure of the full potential fecundity of adult females throughout their life span

in conjunction with the impact of density dependent processes among larvae. As the estimate of  $r$  through  $r'$  relies on assumptions about the duration of reproductive period, it is essential to estimate  $r$  directly through life-table methods, and to concurrently calculate  $r'$  for the same experimental cohort.

With this study, we aimed to evaluate the accuracy of  $r'$  as a predictor of  $r$  for populations exposed to different levels of intraspecific larval competition, taking into account repeated reproduction by adults. We also evaluated several life-history traits for their accuracy as predictors of  $r$ .

### Materials and Methods

**Study Animals.**  $F_1$  generation *Ae. albopictus* eggs were used, with the parental generation coming from a field collection in the Bermuda Islands (United Kingdom) in 2004.

**Hatching and Larval Rearing.** Eggs were submerged in 2 liters of a 1 g/liter nutrient broth solution and allowed to hatch over 24 h. Larvae were reared at three different target densities (5, 10, and 15 larvae per 30 ml). At each density level, ten replicate sets of petri dishes (30 ml of distilled  $H_2O$  per dish) were established. Each set constituted a population, and each of these 10 populations at each larval density was begun with 48 newly hatched individuals (number was determined based on the total number of available newly hatched larvae), subdivided into dishes to obtain similar, if not identical, densities of larvae within each replicate population. As larvae were lost due to death or pupation, densities were maintained as close as possible to the target levels of 5, 10, and 15 per dish by reconstituting the dishes within each set to create densities that approximated the target densities. Exchange of larvae among dishes occurred within a replicate set of dishes but did not occur among replicate populations. Using scoops that delivered a standardized average volume of food, we fed each dish of larvae an average of 1 mg brewer's yeast and an average of 0.5 mg of ground mouse food (Charles River Laboratories, Inc., Wilmington, MA) on the first day and every 3 d thereafter.

Each day, dishes were checked for pupae, which were removed to separate containers. Pupae were checked daily for adults, which were transferred to 20-by-20-by-20-cm mesh cages (BioQuip Products, Inc., Rancho Dominguez, CA). Before being moved to cages, female wings were measured (outer wing edge less the fringe scales to the humerus and wing junction) by using a microscope and digital calipers.

**Adult Maintenance and Egg Production.** Cages of emerged adults, one for each initial larval population, were kept at 20°C and a photoperiod of 16:8 (L:D) h. The humidity was kept at >80% for the entire experiment. Adults were fed on a 20% sucrose solution placed within 50-ml Erlenmeyer flasks, which were capped with cotton dental wads. The sucrose solution was replaced every 14 d.

Each cage included an opaque plastic container ( $\approx$ 8 cm in depth, 6-cm-diameter width at opening) lined

with thoroughly moistened unbleached brown coffee filters to allow females to oviposit. Blood feeding was conducted every other day, starting on the fourth day after the first emergence. Females were provided the opportunity for a human bloodmeal (supplied by investigators) for 5 min in semidark conditions. After blood feeding, ovitrap liners were removed and replaced.

**Analysis.** Per capita growth rates for each replicate and density were generated by two methods. Fecundity and survival tables ( $m_x$  and  $l_x$  values) were generated to provide observed data on  $r$  for comparison with predictive methods. The iteratively obtained value (Table 1, equation 4) of  $r$  (Lotka 1925) was calculated with the solver tool in an Excel (Microsoft, Redmond, WA) spreadsheet. Livdahl and Sugihara's method (Table 1, equation 5, with a maturity time of  $D = 12$ ) was used to generate a preliminary set of  $r'$  values. The observed value of  $D$ , estimated by the difference between the first dates of oviposition and female emergence, was calculated ( $D = 21.25$ ) and was found to reduce bias in  $r'$  values. A regression based on these revised values was conducted to determine how well  $r'$  predicts  $r$ .

Values of  $r$  and  $r'$  were plotted against density and tested for differential density effects on these population growth statistics. The  $r$  values were regressed against individual life-history traits to determine their relative accuracy in predicting  $r$  as compared with  $r'$ . The log of survival ( $l_x$ ) was regressed against time to estimate an average death rate (slope of the regression line) for each density. In addition, the net reproductive rate ( $R_0$ ) and generation time ( $\tau$ ) values (Table 1, equations 3 and 9) were regressed against those generated in calculating  $r'$  (numerator and denominator in equation 5, Table 1, respectively) to identify the sources of differences between observed fecundity ( $r$ ) and predicted fecundity ( $r'$ ).

In the calculation of these statistics, we used the fecundity predicted by equation 11 (Table 1) divided by 2 (Blackmore and Lord 2000) to establish expected fecundity of individuals based on body size, assuming a 1:1 sex ratio of offspring. Average survival and fecundity over time were plotted against density for comparison among treatments.

As drivers of the  $r'$  equation, the net reproductive rate,  $R_0$ , and the cohort generation time,  $\tau$ , were regressed on the corresponding estimates based on a combination of wing length, larval survival, and larval developmental time to determine how these different values affect the overall aptitude of  $r'$  to predict  $r$ .

Average daily death rate was calculated for each replicate as  $-\text{slope of the log of } l_x \text{ values regressed against age}$ . Due to unequal variances, a test for differences among death rates was conducted by Welch's test for differences among group means (Zar 1999) in lieu of analysis of variance (ANOVA). Occasionally during the study, the date of death of certain females could not be assessed due to adult escape or other loss. In these cases, such data were replaced by randomizing the date of death within the appropriate time period (date of introduction to the cage to date of last

**Table 2.** Summary of life-history traits for the 10 replicates for each larval density

Parameter	Density (no. larvae per 30-ml dish)		
	5	10	15
Day of first female emergence	12	15	17
Avg. first female emergence (d) ± SE	14.2 ± 1.32	18.8 ± 2.1	20.7 ± 3.5
Average female emergence (d) ± SE	19.62 ± 0.92	29.39 ± 1.26	32.29 ± 3.38
Day of first egg	28	36	28
Avg. first egg ± SE	32 ± 2.83	43.6 ± 8.83	46.6 ± 12.44
Day of last egg	198	202	185
Avg. last egg (d) ± SE	147.6 ± 31.83	132.1 ± 33.9	130.8 ± 42.15
Adult reproductive delay (d)	17.8	24.8	25.9
Last female death (d)	216	214	195
Avg. last female death (d) ± SE	161.7 ± 35.1	147.8 ± 37.8	137.4 ± 45.31
Net rate of increase, $R_0$ ± SE	9.78 ± 2.2	11.18 ± 2.25	8.38 ± 2.19
Avg. female wing length (mm) ± SE	2.45 ± 0.03	2.37 ± 0.04	2.29 ± 0.04
Avg. female death rate ± SE	0.008 ± 0.001	0.009 ± 0.001	0.013 ± 0.003
Per capita growth rate, $r$ (ind <sup>-1</sup> · day <sup>-1</sup> ) ± SE	0.046 ± 0.13	0.023 ± 0.28	0.019 ± 0.023
Per capita growth rate estimate, $r'$ (ind <sup>-1</sup> · day <sup>-1</sup> ) ± SE	0.067 ± 0.006	0.055 ± 0.005	0.045 ± 0.004
Finite rate of increase, $\lambda$ (ind <sup>-1</sup> · day <sup>-1</sup> ) ± SE	1.047 ± 0.013	1.023 ± 0.279	1.02 ± 0.0233
Estimated finite rate of increase, $\lambda'$ (ind <sup>-1</sup> · day <sup>-1</sup> ) ± SE	1.098 ± 0.007	1.078 ± 0.005	1.065 ± 0.003
Generation time, $\tau$ (d) ± SE	72.219 ± 3.226	78.119 ± 4.203	81.994 ± 4.271

death) using random numbers generated based on atmospheric noise (Random.org 2, True Random Number Service; <http://www.random.org>).

We used model II regression (residual maximum likelihood method, for estimating variance components) to test for predictions of one variable by another in situations where there was error in the predicting variable ( $r'$ ,  $\lambda'$  cohort generation time, day of first emergence, mean day of emergence, largest female, mean female size, sum of female size, and survival to adulthood. Model II regressions failed in three cases:  $r$  regressed on survival to adulthood and  $r$  versus sum of female size, as well as  $R_0$  (based on life-table data) regressed against  $R_0$  (based on wing length and larval survival). In those instances, no convergence of parameter estimates was reached after 100 iterations, so we report the results of model I regressions, none of which approached significance.

Statistical analyses were conducted using JMP version 6.0 (SAS Institute, Cary, NC), SSPS version 15 (SPSS Inc., Chicago, IL) and Excel 2003 (Microsoft).

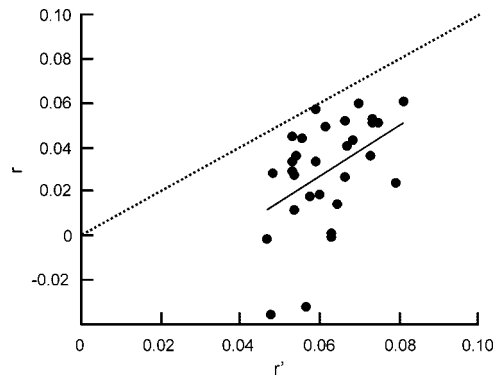
**Results**

**Egg Production and Adult Life Span.** First adult emergence spanned 12–16 d ( $n = 5$ ), 15–22 d ( $n = 10$ ), and 17–27 d ( $n = 15$ ) posthatch, depending on density (Table 2). Egg production occurred between 28–198 d ( $n = 5$ ), 32–202 d ( $n = 10$ ), and 28–185 d ( $n = 15$ ) posthatch, depending on density (Table 2). The adult populations terminated with the deaths of the last individuals in each population on days 216 ( $n = 5$ ), 214 ( $n = 10$ ), and 195 ( $n = 15$ ) posthatch (Table 2). Although the precise emergence day of the last surviving adult is not known, it is possible to surmise that the last surviving individual had been an adult for at least 189 d.

**$r$  and  $r'$**  The per capita rate of change was found to be an accurate predictor of trends in instantaneous growth rate when  $r$  was regressed on  $r'$  (Fig. 1). A very similar relationship was also found between  $\lambda$  and  $\lambda'$

(data not shown). Analysis of covariance (ANCOVA) among density groups failed to show a significant interaction between  $r'$  and density ( $F_{2,24} = 1.05$ ;  $P = 0.37$ ), indicating that the predictive capacity of  $r'$  was robust to differences in larval density conditions. Further support for the robustness of  $r'$  as a predictor is indicated by no significant departure from the overall model for any of the density groups after the interaction term had been removed (ANCOVA:  $F_{2,26} = 0.44$ ;  $P = 0.65$ ).

Regressions of  $r$  and  $r'$  on density ( $n$ ) were both significant (Fig. 2). The intercepts of these lines yield some important quantities for population predictions, the maximum per capita rate  $r_m$  (intercept at vertical axis) and the carrying capacity,  $K$  (intercept at horizontal axis). For the regression of  $r$  against  $n$ ,  $K$  is estimated at 21.04 individuals (ind) per dish and  $r_m$  at  $0.06 \pm 0.010$  (SE) ind<sup>-1</sup>d<sup>-1</sup> (Fig. 2). The linear relationship for  $r'$  versus  $n$  generated higher estimates



**Fig. 1.** Values of  $r$  (derived population growth rate) regressed on  $r'$  (projected population growth rate (model II regression:  $y = 1.14x - 0.0389$ ,  $R^2 = 0.24$ ,  $t_{23} = 2.80$ ,  $P = 0.01$ ,  $P < 0.01$ ). The dotted diagonal line through the origin represents the ideal correspondence (1:1) between  $r$  and  $r'$ . Values below the line represent overestimation and values above underestimation.



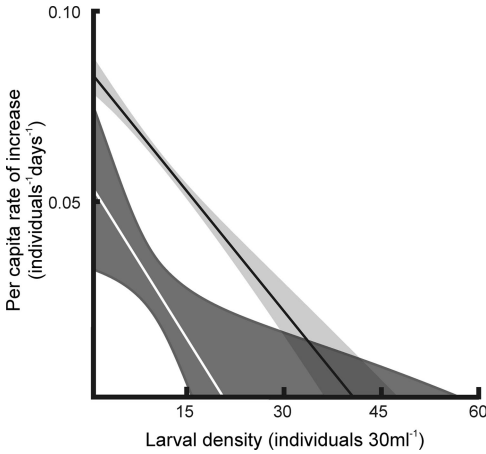


Fig. 2.  $r$  and  $r'$  regressed by larval density ( $r$ :  $y = -0.0026x + 0.0555$ ,  $R^2 = 0.2005$ ,  $F_{2,28} = 7.02$ ,  $P = 0.01$ ;  $r'$ :  $y = -0.0031x + 0.1077$ ,  $R^2 = 0.856$ ,  $F_{2,28} = 166.45$ ,  $P < 0.01$ ). The  $y$  intercept predicts  $r_{max}$  ( $r$ : 0.056;  $r'$ : 0.11), the maximum per capita rate of increase; and the  $x$  intercept predicts  $K$  ( $r$ : 21.35;  $r'$ : 34.74), the carrying capacity for the species under similar environmental conditions. The gray areas represent 95% confidence interval of the respective regressions;  $r$  depicted with a white line and dark shades for confidence intervals;  $r'$  depicted with a black line and light shades for confidence intervals.

for  $K$  (35.45 ind/30 ml dish) and  $r_m$  ( $0.08 \pm 0.002$  [SE]; Fig. 2). The slopes of these two regressions ( $-r_m/K$ ) were not different ( $F_{1,56} = 0.36$ ;  $P = 0.55$ ).

The  $R_0$  values generated using both  $r$  and  $r'$  (for the latter,  $R_0$  is calculated as the antilog of the numerator of equation 5, Table 1) methods had no significant association (Fig. 3). The direction of the deviation between the two regressions is such that  $R_0$  has been overestimated in the  $r'$  calculations relative to the

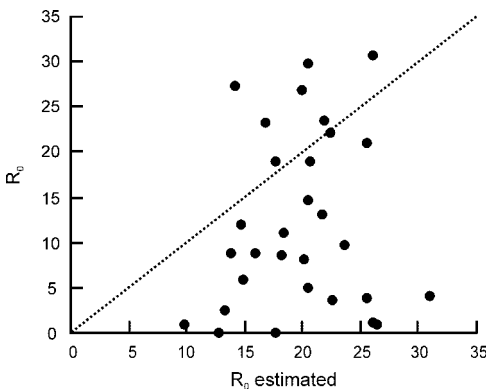


Fig. 3. Values of net reproductive rate ( $R_0$ ) derived from the life-table study regressed on the net reproductive rate ( $R_0$ ) estimated from the  $r'$  calculations (model I regression:  $y = 0.20x + 8.184$ ,  $R^2 = 0.01$ ,  $F_{1,28} = 0.29$ ,  $P = 0.59$ ). Regression line not shown. The dotted diagonal line through the origin represents the ideal correspondence (1:1) between  $R_0$  and  $R_0$  estimated with  $r'$ . Values below the diagonal line represent overestimation and values above underestimation.

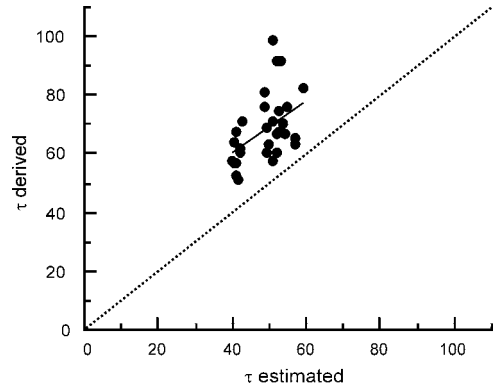


Fig. 4. Generation time ( $\tau$ ) obtained from equation 9 (see Table 1) regressed on the cohort generation time estimated from the  $r'$  calculations (denominator, equation 5, Table 1) (model II regression:  $y = 0.87x + 26.30$ ,  $R^2 = 0.24$ ,  $t_{23,6} = 2.87$ ,  $P < 0.01$ ). The dotted diagonal line through the origin represents the ideal correspondence (1:1) between  $\tau$  and  $\tau$  estimated with  $r'$ . Values below the diagonal line represent overestimation and values above underestimation.

observed  $R_0$ . When the same was done for the observed  $\tau$  and estimated  $\tau$  (the latter calculated as the denominator of equation 5, Table 1), the  $\tau$  value generated using  $r'$  methods seemed to be underestimating  $\tau$  derived via the  $r$  calculation (Fig. 4). The estimated value of  $D$  obtained from (first egg-date of first female) was weakly associated with density ( $F_{2,28} = 4.19$ ;  $P = 0.05$ ).

**Life-History Traits as Predictors of  $r$ .** Of those life-history traits considered possible predictors of  $r$ , day of first female emergence ( $t_{23,8} = 3.52$ ,  $P < 0.01$ ) and average day of female emergence ( $t_{15,7} = 2.74$ ,  $P = 0.01$ ) were the only traits that accounted for a significant portion of the variation in  $r$ . Both measures of emergence were less strongly correlated with  $r$  than  $r'$  [ $(r$  versus  $r'$ ),  $R^2 = 0.24$  ( $r$  versus first emergence day),  $R^2 = 0.16$  ( $r$  versus average female emergence time)]. Other traits commonly reported as measures of larval success showed no significant relationship, including largest female ( $t_{2,4} = 1.25$ ,  $P = 0.32$ ,  $R^2 = 0.07$ ), mean female size ( $t_{2,6} = 1.28$ ,  $P = 0.30$ ,  $R^2 = 0.07$ ), sum of female size ( $t_{28} = 0.67$ ,  $P = 0.51$ ,  $R^2 = 0.01$ ), and survival to adulthood ( $t_{28} = 0.53$ ,  $P = 0.60$ ,  $R^2 = 0.01$ ). Average death rates through the entire life span for each density were similar (Table 2; Welch ANOVA:  $F_{2,14,4} = 2.40$ ;  $P = 0.12$ ).

## Discussion

The derivation of  $r'$  (Livdahl and Sugihara 1984) relied on several assumptions. Individually, they seem unrealistic, but collectively, departures from assumptions could cancel, producing a useful estimate. The key assumptions concern the adult life table, particularly the distribution of reproduction across a variety of ages. Specifically,  $r'$  assumes that reproduction occurs only once, and if this were true, mosquitoes could not be important vectors of disease. However, it also

assumes that all females survive to reproduce. Departures from these assumptions could compensate for one another. Survival of adults through repeated reproduction would boost the net rate of increase, the numerator of indices of Andrewartha and Birch (1954) and Laughlin (1965), but this also would extend the generation time, in the denominator. The data gathered here permit the first assessment of  $r'$  estimates. We found that  $r'$  is a significant predictor of the per capita rate of change, that  $r'$  consistently overestimates the per capita rate of change, that the degree of overestimation is not influenced by these experimental density levels, and that despite its overestimating tendency,  $r'$  provides a better prediction of per capita rate of change than any other single life-history feature. We consider below the reasons for overestimation, as well as the implications of this to predictions about natural populations and species interactions.

Numerous studies (Livdahl 1982, Carpenter 1983, Hawley 1985, Edgerly and Livdahl 1992, Mahmood et al. 1997, Lord 1998) have established that container dwelling mosquito larvae have highly plastic responses to crowding and food shortages. These results for *Ae. albopictus* were consistent with previous studies of density dependent growth and emergence in container breeding species. The regressions of  $r$  and  $r'$  versus density differ in their  $R^2$  values (Fig. 2), perhaps because  $r$  is derived from lifetime egg production by females, some of which lived for several months. By contrast,  $r'$  is derived only from larval production of adults, and projections of egg production by females based on their size. Random events can therefore generate more error in  $r$  than in  $r'$ .

Despite the significant regression of  $r$  on  $r'$ ,  $r'$  overestimated the actual  $r$  values generated across populations from all three crowding densities. To determine why the  $r'$  values were not more accurate, it is important to look at the equation for  $r'$  in terms of numerator and denominator driving the overall value of  $r'$ . If  $R_0$  is overestimated, that will exaggerate  $r'$  values, whereas the opposite is true for  $\tau$ . Given that  $r'$  was overestimating  $r$ , we expected that  $R_0$  would be the overestimated value in the  $r'$  calculations, or that  $\tau$  would be underestimated.

We found that overestimates of  $R_0$  (Fig. 3) and underestimates of  $\tau$  (Fig. 4) both inflate estimates of  $r'$  relative to  $r$ . The overestimation of  $R_0$  probably has to do with the assumption that all females survive to reproduction. The underestimation of  $\tau$  may stem from the assumed value of  $D$ , the time lag between emergence and the beginning of oviposition. The assumed value of  $D$  may be inaccurate, and it seems likely that  $D$  is not constant with every population. In fact, the discovery of a weak density effect on  $D$  suggests that  $D$  is likely to vary across populations, depending on larval nutrition. There is some evidence for extended periods before egg development in anophelines (the pregravid stage) that relates inversely to female size, and probably to larval nutrition as well (Lyimo and Takken 1993), and our result may represent a similar phenomenon.

Several life-history traits (largest female, mean female size, sum of female size, survival to adulthood) taken individually were not significantly correlated with  $r$ . The only two that were, median and first emergence times, involve life stages that require rearing to adulthood. As  $r'$  more strongly predicted  $r$  than any single life-history trait, these data support the use of  $r'$  over separate indices when attempting to summarize larval success.

We obtained a substantially larger value for delay between emergence and oviposition ( $D$ ) than the value used for prior calculations of  $r'$  for *Ae. albopictus* (Livdahl and Willey 1991, Juliano 1998, Aliabadi and Juliano 2002, Armistead et al. 2008a), all of which have used the estimate of Livdahl and Willey (1991). This value could vary with experimental temperature, and differences among strains are certainly possible. The presence of sucrose solution as a carbohydrate source also could have resulted in an exaggerated preoviposition period, as found by Braks et al. (2006); however, the previous estimate of  $D$  by Livdahl and Willey (1991) also relied on adults maintained with a constant sugar water supply. Our results, along with those of Livdahl and Willey, suggest that it may be important for investigators to obtain estimates within their own experimental settings and for the particular populations being studied.

Braks et al. (2006) demonstrated plasticity of the timing of reproduction resulting from access to or deprivation from a sugar source in *Ae. albopictus*. Access to sugar water delayed and reduced fecundity, and sugar deprivation accelerated blood feeding and subsequent oviposition. Their results may indicate that the relatively high value of  $D$  obtained in our study is unrealistic relative to field populations. However, that conclusion would require knowledge that we do not have about the access that field populations have to sugar sources relative to blood sources, and the preferences they have for each. We would expect these factors to vary widely with season and location, depending on floral conditions and vertebrate host abundance and activity.

Researchers interested in accuracy of  $K$  and  $r_m$  values generated by  $r'$  must use  $r'$  with caution, however. The  $y$  intercept (as an estimate of  $r_m$ ) was overpredicted when compared with  $r$ -generated values (Fig. 2). Although  $K$  estimates were not significantly different between the two measurements, perhaps due to the large error about each prediction, the inaccuracy of the  $r'$  methods in predicting  $r$  values suggests that overestimation could be a problem in comparing the competitive abilities of different species. Based on different degrees of apparent sensitivity to inter- and intraspecific density, differences in  $K$  between competing species can be crucial in making predictions about the outcome of invasions (Livdahl and Willey 1991; Juliano 1998; Armistead et al. 2008a,b). However, a simple overestimate of  $K$ , as  $r'$  would produce for *Ae. albopictus* in this study, does not necessarily lead to a false prediction of a competitive outcome, if a comparable error is obtained for the competing species.

Additional information about interspecies effects, in the form of competition coefficients, also is needed to predict the long-term outcome of competition. A prediction based on classical theory requires the calculation of  $\alpha_{ij}$ , the per capita impact of one species on the resource base of the other, converted into the conspecific equivalent. One way to obtain  $\alpha_{ij}$  is to regress the per capita rate of change against the two species' densities, obtain the coefficients for response to heterospecific and conspecific densities, and calculate the ratio of the heterospecific coefficient to the conspecific coefficient (Livdahl and Willey 1991). Our results show that the regression coefficient of  $r$  and  $r'$  against  $N$  are very similar (Fig. 2); if this same result also applies to responses to interspecific densities, then the estimate of  $\alpha_{ij}$  would be robust, despite biases in the  $r'$  values.

Given the significant ability of  $r'$  to predict  $r$ , this study supports the use of  $r'$  as a tool for predicting general trends in population dynamics, given established size–fecundity relationships. Due to the consistency of the bias in prediction across densities, it is tempting to suggest a simple corrective calibration of  $r'$  to adjust for the overestimation. We do not advocate this because of the likely difference between survival and reproductive rates under field and laboratory conditions. Some estimates of death rates in field populations suggest that females die at rates about an order of magnitude higher than the death rates in this study. Niebylski and Craig (1994) estimated a death rate of  $0.11 \text{ ind}^{-1} \cdot \text{d}^{-1}$  for *Ae. albopictus* in Missouri and longevity of 8.2 d. Chan (1971) reported a daily female death rate of  $0.2 \text{ ind}^{-1} \cdot \text{d}^{-1}$  for a Singapore population of *Ae. albopictus*, which would yield an estimate of  $\approx 5$  d. Populations in this study yielded daily death rates of  $0.008\text{--}0.013 \text{ ind}^{-1} \cdot \text{d}^{-1}$  (Table 2), with longevity estimates ranging from 77d to 125 d. Given this difference between field and laboratory survival, as well as the likelihood that bloodmeal access in field conditions is much more difficult for females, the lengthy period of reproduction observed in this study will likely not be approached by field populations. As such, a major source of error in  $r'$  estimates could be reduced, and the predictive ability of  $r'$  could actually be improved under field conditions for the adult stage.

### Acknowledgments

We thank S. Mana Capelli, J. Baker, D. Robertson, S. Juliano, and anonymous reviewers for helpful comments of earlier versions of this manuscript. This research was supported the National Institutes of Health grant 1R15 AI062712-01 (to T.L.); the W. M. Keck Foundation; and the Department of Biology, Clark University.

### References Cited

- Adhami, J., and P. Reiter. 1998. Introduction and establishment of *Aedes (stegomyia) albopictus* Skuse (Diptera: Culicidae) in Albania. *J. Am. Mosq. Control Assoc.* 14: 340–343.
- Aldridge, C. L., and M. S. Boyce. 2008. Accounting for fitness: combining survival and selection when assessing wildlife-habitat relationships. *Isr. J. Ecol. Evol.* 54: 389–419.
- Aliabadi, B. W., and S. A. Juliano. 2002. Escape from gregarine parasites affects the competitive interactions of an invasive mosquito. *Biol. Invasions* 4: 283–297.
- Alto, B. W., and S. A. Juliano. 2001. Temperature effects on the dynamics of *Aedes albopictus* populations in the laboratory. *J. Med. Entomol.* 38: 548–556.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University Chicago Press, Chicago, IL.
- Armistead, J. S., J. R. Arias, and L. P. Lounibos. 2008a. Interspecific larval competition between *Aedes albopictus* and *Aedes japonicus* (Diptera: Culicidae) in northern Virginia. *J. Med. Entomol.* 45: 629–637.
- Armistead, J. S., N. Nishimura, R. L. Escher, and L. P. Lounibos. 2008b. Larval competition between *Aedes japonicus* and *Aedes atropalpus* (Diptera: Culicidae) in simulated rock pools. *J. Vector Ecol.* 33: 238–246.
- Black, W. C., K. S. Rai, B. J. Turco, and D. C. Arroyo. 1989. Laboratory study of competition between United States strains of *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae). *J. Med. Entomol.* 26: 260–271.
- Blackmore, M. S., and C. C. Lord. 2000. The relationship between size and fecundity in *Aedes albopictus*. *J. Med. Entomol.* 25: 212–217.
- Braks, M.A.H., N. A. Honório, L. P. Lounibos, R. Lourenço-de-Oliveira, and S. A. Juliano. 2004. Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil. *Ann. Entomol. Soc. Am.* 97: 130–139.
- Braks, M.A.H., S. A. Juliano, and L. P. Lounibos. 2006. Superior reproductive success on human blood without sugar is not limited to highly anthropophilic mosquito species. *Med. Vet. Entomol.* 20: 53–59.
- Caughley, G., and L. C. Birch. 1971. Rate of increase. *J. Wildl. Manage.* 35: 658–663.
- Carlson, S. M., E. M. Olsen, and L. A. Vøllestad. 2008. Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout. *Funct. Ecol.* 22: 663–673.
- Carpenter, S. R. 1983. Resource limitation of larval treehole mosquitoes subsisting on beech detritus. *Ecology* 64: 219–223.
- Cezilly, F., A. Viallefont, V. Boy, and A. R. Johnson. 1996. Annual variation in survival and breeding probability in greater flamingos. *Ecology* 77: 1143–1150.
- Chan, K. L. 1971. Life table studies of *Aedes albopictus* (Skuse), pp. 131–144. *In* Sterility principles for insect control or eradication. International Atomic Energy Agency, Vienna, Austria.
- Cilek, J. E., G. D. Moorer, L. A. Delph, and F. W. Knapp. 1989. The Asian Tiger Mosquito, *Aedes albopictus* in Kentucky. *J. Am. Mosq. Control Assoc.* 5: 267–268.
- Dublin, L. I., and A. J. Lotka. 1925. On the true rate of natural increase. *J. Am. Stat. Assoc.* 20: 305–339.
- Egerly, J. S., and T. Livdahl. 1992. Density-dependent interactions within a complex life cycle: the roles of cohort structure and mode of recruitment. *J. Anim. Ecol.* 61: 139–150.
- Francy, D. B., C. G. Moore, and D. A. Eliason. 1990. Past, present and future of *Aedes albopictus* in the United States. *J. Am. Mosq. Control Assoc.* 6: 127–132.
- Hawley, W. A. 1985. The effect of larval density on adult longevity of a mosquito, *Aedes sierrensis*: epidemiological consequences. *J. Anim. Ecol.* 54: 955–964.
- Hawley, W. A. 1988. The biology of *Aedes albopictus*. *J. Am. Mosq. Control Assoc.* S. 1: 1–40.

- Hawley, W. A., P. Reiter, R. S. Copeland, C. B. Pumpuni, and G. B. Craig Jr. 1987. *Aedes albopictus* in North America: probable introduction in used tires from northern Asia. *Science* 236: 1114–1116.
- Ho, B. C., A. Ewert, and L. M. Chew. 1989. Interspecific competition among *Aedes aegypti*, *Ae. albopictus*, and *Ae. triseriatus* (Diptera: Culicidae): larval development in mixed cultures. *J. Med. Entomol.* 26: 615–623.
- Janzen, F. J., J. K. Tucker, and G. L. Paukstis. 2000. Experimental analysis of an early life-history stage: selection on size of hatchling turtles. *Ecology* 81: 2290–2304.
- Juliano, S. A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79: 255–268.
- Juliano, S. A. 2009. Species interactions among larval mosquitoes: context dependence across habitat gradients. *Annu. Rev. Entomol.* 54: 37–56.
- Kisdi, E. 2004. Optimal body size, density-dependent selection gradients, and phenotypic variance under asymmetric competition. *Ecology* 85: 1460–1467.
- Kupferberg, S. J. 1997. Bullfrog (*Rana catesbeiana*) invasion of a California river: the role of larval competition. *Ecology* 78: 1736–1751.
- Laughlin, R. 1965. Capacity for increase: a useful population statistic. *J. Anim. Ecol.* 34: 77–91.
- Livdahl, T. 1982. Competition within and between hatching cohorts of a treehole mosquito. *Ecology* 63: 1751–1760.
- Livdahl, T., and G. Sugihara. 1984. Nonlinear interactions of populations and the importance of estimating per capita rates of change. *J. Anim. Ecol.* 53: 573–580.
- Livdahl, T., and M. S. Willey. 1991. Prospects for an invasion: competition between *Aedes albopictus* and native *Aedes triseriatus*. *Science* 253: 189–191.
- Lord, C. C. 1998. Density dependence in larval *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.* 35: 825–829.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams & Wilkins, Baltimore, MD.
- Lyimo, E. O., and W. Takken. 1993. Effects of adult body size on fecundity and the pre-gravid rate of *Anopheles gambiae* females in Tanzania. *Med. Vet. Entomol.* 7: 328–332.
- Lynch, M. 1977. Fitness and optimal body size in zooplankton population. *Ecology* 58: 763–774.
- May, R. M. 1976. Estimating  $r$ : a pedagogical note. *Am. Nat.* 110: 496–499.
- Mahmood, F., W. J. Crans, and N. S. Savur. 1997. Larval competition in *Aedes triseriatus* (Diptera: Culicidae): effects of density on size, growth, sex ratio, and survival. *J. Vector Ecol.* 22: 90–94.
- McCown, R. L., and W. A. Williams. 1969. Competition for nutrients and light between the annual grassland species *Bromus mollis* and *Erodium botrys*. *Ecology* 49: 981–990.
- Moore, C. G. 1999. *Aedes albopictus* in the United States: current status and prospects for further spread. *J. Am. Mosq. Control Assoc.* 15: 221–227.
- Moore, C. G., D. B. Francy, D. A. Eliason, and T. P. Monath. 1988. *Aedes albopictus* in the United States: rapid spread of a potential disease vector. *J. Am. Mosq. Control Assoc.* 4: 356–361.
- Murrell, E. G., and S. A. Juliano. 2008. Detritus type alters the outcome of interspecific competition between *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae). *J. Med. Entomol.* 45: 375–383.
- Niebylski, M. L., and G. B. Craig, Jr. 1994. Dispersal and survival of *Aedes albopictus* at a scrap tire yard in Missouri. *J. Am. Mosq. Control Assoc.* 10: 339–343.
- Novak, R. J. 1992. The Asian tiger mosquito, *Aedes albopictus*. *Wing Beats*. 3: 5.
- O'Meara, G. F., L. F. Evans Jr., A. D. Gettman, and F. D. Scheel. 1992. Invasion of cemeteries in Florida by *Aedes albopictus*. *J. Am. Mosq. Control Assoc.* 8: 1–10.
- O'Meara, G. F., L. F. Evans, Jr., A. D. Gettman, and J. P. Cuda. 1995. Spread of *Aedes albopictus* and decline of *Aedes aegypti* (Diptera: Culicidae) in Florida. *J. Med. Entomol.* 32: 554–562.
- Polis, G. A., and R. D. Farley. 1980. Population biology of a desert scorpion: survivorship, microhabitat, and the evolution of life history strategy. *Ecology* 61: 620–629.
- Reiter, P. 1998. *Aedes albopictus* and the world trade in used tires, 1988–1995: the shape of things to come? *J. Am. Mosq. Control Assoc.* 14: 83–94.
- Reiter, P. 2010. Yellow fever and dengue: a threat to Europe? *Euro Surveill.* 15: 10. (<http://www.eurosurveillance.org/ViewArticle.aspx?ArticleId=19509>).
- Zar, J. H. 1999. *Biostatistical analysis*. Prentice-Hall, Upper Saddle River, NJ.

Received 6 November 2009; accepted 3 June 2010.