Fitness and Its Correlates Assessed by Intra- And Interspecific Interactions among Tree-Hole Mosquitoes

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FITNESS AND ITS CORRELATES ASSESSED BY INTRA- AND INTERSPECIFIC INTERACTIONS AMONG TREE-HOLE MOSQUITOES

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SUMMARY

(1) Larvae of *Aedes geniculatus* from southern England (U.K.) and *A. sierrensis* from western Oregon (U.S.A.) were reared alone or together at varying densities and on varying amounts of natural tree-hole substrate from each locality.

(2) The major determinants of fitness (replacement rate) in both species were the linear effects of substrate level, larval density and source of substrate; each of the linear effects was greater than that of higher order interactions combined.

(3) Neither species achieved higher fitness than the other at low density but *Aedes geniculatus* was competitively dominant to *A. sierrensis* at high density.

(4) The interaction between the two species did not depend upon the source locality (U.S.A., U.K.) or upon holes within localities; consequently, tree holes provide replicate habitats for these two species over intercontinental distances.

(5) Factors affecting fitness in single-species populations of either species persisted in interspecific encounter but some factors that have no effect on single-species populations affected fitness during interspecific encounter.

(6) Individual correlates of fitness accurately reflected the major, proximal factors affecting fitness in both species but no one of them was consistently, linearly correlated with fitness. Composite, rather than component, indices of fitness therefore still provide the best comparative assessment of the effect of environmental variables on fitness both within and between species.

INTRODUCTION

Fitness of populations exposed to varying resources is usually assessed by considering one or a few correlates rather than the per capita rate of change itself (Livdahl & Sugihara 1984). Livdahl & Sugihara (1984) aptly point out that such studies presume a linear relationship between individual fitness traits and per capita rate of change over the same range of environmental conditions. Livdahl (1982) examined per capita rate of increase of the tree-hole mosquito, *Aedes triseriatus*, when reared at varying densities, cohort structures, and levels of food on natural tree-hole substrate in outdoor jars. Livdahl (1982) found that non-linearities in components of fitness did not persist in the per capita rate of change calculated from the same data. Hard, Bradshaw & Malarkey (1989)

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compared separately determined per capita rates of increase of *Aedes triseriatus* and *A. geniculatus* when reared at varying densities and varying levels of artificial food in the laboratory. In the latter case, non-linearities of fitness correlates persisted in the per capita rate of change of *A. triseriatus* but not *A. geniculatus*. The difference in *A. triseriatus* between the two studies may have been due to a higher density used by Hard, Bradshaw & Malarkey (1989) than by Livdahl (1982) and/or to the differences in food (= substrate) in the two studies. Neither study considered actual interspecific interaction. The present paper compares the effect of food level, density and substrate type on the finite rate of increase and several of its correlates within and between two species of tree-hole mosquitoes.

Two species are considered, *Aedes geniculatus* (Olivier) from southern England (U.K.) and *A. sierrensis* (Ludlow) from western Oregon (U.S.A.), that live in convergent habitats and similar climatic zones (Bickmore & Shaw 1963; NOAA 1968; Steinhauser 1970) on western continental slopes. At their respective sites, both species are univoltine (Yates 1979; Jordan 1980). Neither species encounters larval predators (Rohnert 1950; Kitching 1971; Hawley 1985c), although at least *A. sierrensis* may suffer larval parasitism (Corliss & Coats 1976; Hawley 1985c; Washburn & Anderson 1986). Both species encounter limiting resources and/or densities in their native tree holes (Hawley 1985a; Bradshaw & Holzapfel 1986). To avoid the problem of the introduction of vectors, we mimic reciprocal transplantation by rearing tree-hole mosquitoes either alone or together on both native and foreign tree-hole substrates in the laboratory.

Limiting resources may be manifest as limiting food or limiting density or both. In higher Diptera (Sullivan & Sokal 1963; Bhalla & Sokal 1964; Prout & McChesney 1985; Black & Krafsur 1986) and mosquitoes (Terzian & Stahler 1949; Colless & Chellapah 1960; Kierans & Fay 1968; Moore & Fisher 1969; Barbosa, Peters & Greenough 1972; Gilpin & McClelland 1979; Moeur & Istock 1980; Fish & Carpenter 1982; Steinwascher 1982; Chambers 1985; Hawley 1985a, b, c), food or individual density has a consistent effect on per capita fitness. At lower food levels or higher densities, individuals tend to delay development, grow more slowly, weigh less at maturity, exhibit lower adult fecundity and suffer greater size-dependent mortality than at higher food levels or lower densities. These same effects persist under conditions of both varying food and density (Wada 1965; Nayar 1969; Istock, Wasserman & Zimmer 1975; Livdahl 1982; Carpenter 1983; Hard, Bradshaw & Malarkey 1989). None of these studies examined the extent to which food–density interaction is substrate-specific within or between species or persists among inter- as well as intraspecific interactions. The present study addresses the following specific questions:

(a) Do species that live in convergent habitats have similar comparative responses to food, density and their interaction on both native and foreign substrates?

(b) Do species realize a competitive advantage on their own as opposed to a foreign substrate? Specifically, does the interaction between two species depend upon the origin of the substrate with respect to continental locality or individual tree hole?

(c) Do the same correlates of fitness track a composite index (replacement rate) equally well for both inter- and intraspecific encounters? Specifically, in the absence of a species-specific transformation, is any particular correlate of fitness linearly correlated with replacement rate?

(d) Do interaction effects occur consistently in replacement rate and its correlates for both intra- and interspecific encounters?

MATERIALS AND METHODS

Experimental design

To mimic tree-holes in Oregon and England, mosquitoes were reared on natural tree-hole substrate brought into the laboratory from duplicate tree-holes at each locality. Tree-hole leaf litter and sediment were collected from four trees, two large-leaf maple (*Acer macrophyllum* Pursh) from Eugene, Oregon, U.S.A. (44°03′N, 123°04′W) and two beech (*Fagus sylvatica* L.) from Silwood Park, Ascot, U.K. (51°30′N, 0°30′W). Tree hole 1 (Table 1) is a large, permanent, rot hole. It is the only one of forty holes in the vicinity of Eugene, Oregon, that has never dried up and that regularly contains *Orthopodomyia signifera*, mosquitoes that are attracted only to more permanent holes (Zavortink 1968; Bradshaw & Holzapfel 1983, 1988). Tree hole 4 is a smaller rot hole that dries up every year and contains only *A. sierrensis*. Tree hole 16 is a large, highly exposed buttress hole that is readily colonized by *Culex torrentium* as well as by *A. geniculatus*. Tree hole 35 is a smaller, cryptic buttress hole of the type avoided by *C. torrentium* and occupied by *Anopheles plumbeus* as well as by *Aedes geniculatus* (Bradshaw & Holzapfel 1986).

For each hole the sediment was separated into leaf litter (all material of 1 cm or more maximum dimension), a coarse fraction (remaining material greater than 1 mm maximum dimension) and a fine fraction (all remaining solid and soluble material). These components were dried in shallow pans at 22 ± 1.5 °C. Once their weights remained constant over a period of 5 days, the ratio of leaf:coarse:fine fractions was determined (Table 1); these ratios were used for each tree-hole when setting up experiments. All experiments were run in clear plastic dessert dishes 9 cm in diameter and 4 cm deep, covered by a clear plastic lid with a 2-mm diameter air-hole in the centre. The experimental containers were set up at two food levels by preparing, for each hole, fourteen dishes with 3 g total of the three sediment fraction, and fourteen dishes with 6 g total of the three fractions. To each dish, 150 ml of distilled water was added; all dishes were left standing at 22 ± 1.5 °C for 1 week to permit rehydration of the sediment.

TABLE 1. Ratios of leaf:coarse:fine sediment in tree-holes used in the experiment, with adjusted mean replacement rate ($R_0 \pm 95\%$ C.L.) attained by both *A. geniculatus* and *A. sierrensis*

Hole	Type of tree; type of hole	Leaf:Coarse:Fine	R_0	
			A.g.	*A.s.*
1 (U.S.)	Large-leaf maple; rot*	1:6·0:1·0	25·90 ±1·67	24·06 ±1·93
4 (U.S.)	Large-leaf maple; rot	1:11·5:2·5	15·68 ±1·65	14·37 ±0·95
16 (U.K.)	Beech; pan,* exposed buttress	1:3·2:0·8	5·77 ±2·07	5·98 ±1·71
35 (U.K.)	Beech; pan, cryptic buttress	1:4·0:10·0	9·01 ±2·23	3·13 ±0·35

A.g. = *A. geniculatus*.
A.s. = *A. sierrensis*.
* Type of hole defined as by Kitching (1971).

Stemflow has been shown to make a contribution to larval nutrition in laboratory microcosms (Carpenter 1982) but stemflow was omitted in this study for several reasons. (i) Carpenter found no significant effect of stemflow on survivorship or pupation success over the duration of his study, although stemflow probably affected the rate of female development. (ii) Beech and maple stemflow, as shown by Carpenter, are poorer in nutrients compared with oak stemflow. (iii) The effect of leaf litter on female development was three times greater than that of stemflow. (iv) Carpenter used leaf litter collected from baskets and groundcloths only, not whole tree-hole detritus as in the present study.

Eggs of *Aedes geniculatus* and *A. sierrensis* were taken from laboratory populations collected from the same area as their respective tree-holes. Both populations had been maintained for four generations in the laboratory on a larval diet of ground guinea-pig chow and freeze-dried brine shrimp (2:1 by volume) to remove environmental (maternal) effects that might have carried over from wild-caught individuals. Larvae used in the experiments all hatched on the same day. For each tree-hole at each food level two replicates were set up of each of the following treatments with the freshly hatched first instars: ten or twenty *A. geniculatus* alone; ten or twenty *A. sierrensis* alone; ten *A. geniculatus* with ten *A. sierrensis*; and four replicates of five *A. geniculatus* larvae with five *A. sierrensis* larvae. The number of replicates was doubled in the last case to assure adequate numbers of both sexes. To provide equal numbers of replicates for subsequent statistical analyses and to avoid a posteriori bias in pooling these replicates, they were labelled A, B, C and D before the start of the experiment. It was determined a priori that, for the analyses, replicates A and B were to be pooled with each other, as were C and D. The overall experiment was then full-factorial for food level (two), larval density (two), hole at each location (two), location (two), species composition (three) and replicate (two). All dishes were placed in a constant temperature room at 15 ± 0.5 °C, with a light:dark regime of 16:8 hours, giving both species unambiguous long days to promote direct development. Light was provided by a 20 W cool-white fluorescent bulb 1 m above the experimental containers. The dishes were checked daily for pupae. Each pupa was gently blotted on tissue paper, weighed to the nearest 0·01 mg, sexed and identified as either *A. geniculatus* or *A. sierrensis*. After 6 months, over 98% of the initial larvae had pupated or died and fewer than one individual was pupating per week. Consequently, the experiment was terminated on day 179 and each of the remaining twenty-eight fourth instars was weighed to the nearest 0·01 mg as above.

The raw data were then converted into fitness correlates for each of the species for each replicate in each treatment, using equations determined from wild populations. These correlates were mean male and female pupal weight (mg), mean male and female development time (days), degree of protandry (mean male development time subtracted from mean female development time) (days), pupation success (proportion of larvae pupating), sex ratio (proportion of pupae that were female), and total biomass (cumulative sum of pupal weight plus total weight of fourth instars remaining at the end of the experiment) (mg). The replacement rate (R_0) was calculated for each species in each dish from:

$$R_0 = \frac{\Sigma(\text{eggs per batch X expected number of batches})}{\text{initial cohort size}}.$$

For *Aedes sierrensis* (Hawley 1985a, c): eggs per batch = $-12 \cdot 32 + 38 \cdot 85$ pw; pw = individual female pupal wet weight (mg); expected number of batches = $P/(1-P)$; P = parous rate of females = $-0 \cdot 100 + 0 \cdot 296$ pw $-0 \cdot 0369$ pw^2.

For *Aedes geniculatus* (W. E. Bradshaw & C. M. Holzapfel, unpublished): eggs per batch = $-35\cdot5+90\cdot94$ ln pw; expected number of batches = $P/(1-P) = 0\cdot337$; P = parous rate of females = $0\cdot508$.

Analysis

To ensure non-heterogeneity of variance and to approximate normality for the analyses, mean pupal weight ($\times$ 10), total biomass ($+1$), mean development time, degree of protandry ($+1$) and replacement rate ($+1$) values were transformed by the base -10 logarithm. Pupation success and pupal sex ratio data were subjected to the arcsine square-root transformation.

The General Linear Model procedure (SAS Institute 1985) was used to determine which regression elements reduced the amount of variance observed (Fig. 1). The model used was:

$$Y = B_0 + B_1F + B_2D + B_{12}FD + B_3L + B_4H(L) + B_5S +$$
$$B_{51}SF + B_{52}SD + B_{512}SFD + B_{53}SL + B_{54}SH(L) + e$$

where Y is the expected value of the model variable (R_0 or a correlate of fitness), e is the residual error, and the B values are constants. A type I test was performed. This method entered the variables sequentially so that the linear effect of food (F), density (D) and their interaction (FD) as well as locality (L) and holes within locality (H(L)) had been accounted for before testing, in sequence, for significant effects of accompanying species (S), food $\times$ accompanying species interaction (FS), density $\times$ accompanying species interaction (DS), food $\times$ density $\times$ accompanying species interaction (FDS), accompanying species $\times$ locally interaction (SL) and accompanying species $\times$ holes within locality interaction (SH(L)). The type I test permits testing the significance of the interaction terms, especially the last two variables, more critically, after having taken into account all of the additive factors.

As the presence of *A. sierrensis* had a significant effect on the R_0 of *A. geniculatus* (Fig. 1a), the adjusted means of the factors affecting fitness (Table 2) were calculated using the MGLH procedure of SYSTAT (Wilkinson 1987).

RESULTS

Fitness

Altogether, the eleven variables considered accounted for 73% and 82% of the total variation in replacement rate for *A. geniculatus* and *A. sierrensis*, respectively (Fig. 1). Four variables were prominent factors contributing to fitness in both species: food level, larval density, locality of substrate origin and holes within localities. Of these variables, food was a more important contributor to fitness in *A. geniculatus* than in *A. sierrensis*, while substrate locality and hole within locality were more important in *A. sierrensis* than in *A. geniculatus*. Both species achieved higher fitness on U.S. than U.K. substrates (Table 1), but there was no significant interaction between accompanying species in a dish (alone vs. together) and either locality of origin or tree-hole within locality (Fig. 1) for either *A. sierrensis* or *A. geniculatus*.

The food $\times$ density interaction was a significant contributor to fitness in *A. sierrensis*. Two additional factors were significant contributors to fitness in *A. geniculatus*: accompanying species and density $\times$ accompanying species interaction. Thus, in *A. geniculatus* but not *A. sierrensis*, intraspecific effects differed from interspecific effects
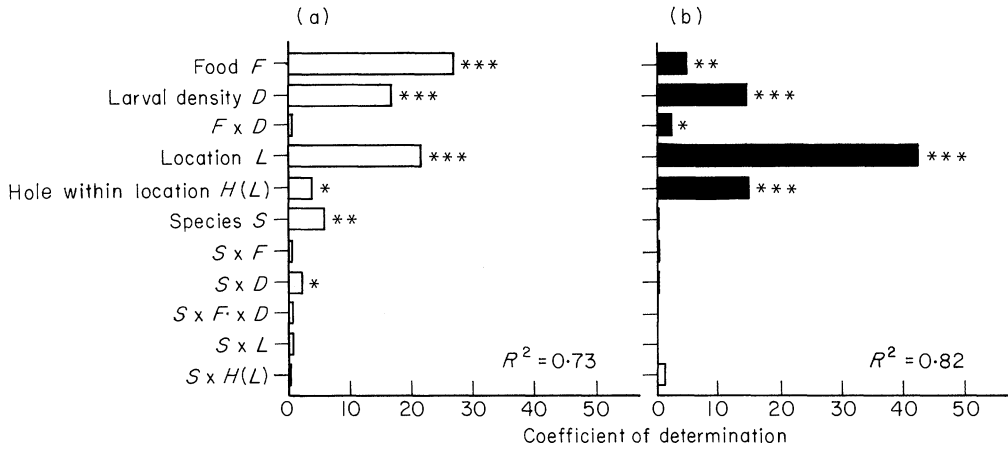
FIG. 1. Effect of environmental variables on replacement rate (R_0) in (a) *Aedes geniculatus* and (b) *Aedes sierrensis*. Variables were entered into regression from top to bottom so that the linear effects were taken into account before the interaction terms. The bars plot the increment in coefficient of determination (R^2) attributable to each variable. $*P<0.05$; $**P<0.01$; $***P<0.001$; otherwise, $P>0.05$.

both directly and in response to density. For *A. geniculatus*, a higher fitness, measured from adjusted mean replacement rate values (Table 2a), was achieved when it was accompanied by *A. sierrensis* than when it was the only species in the treatment. At high larval density (Table 2b), the presence of the second species increased the fitness of the *A. geniculatus* individuals above that achieved when at low density, either alone or with *A. sierrensis*. However, when alone the *A. geniculatus* larvae achieved lowest fitness at higher density.

The four remaining variables did not have any significant effect on fitness in either species: accompanying species × food level interaction, accompanying species × food level × density interaction, accompanying species × substrate locality interaction and accompanying species × hole within locality interaction.

TABLE 2. Factors affecting fitness in *A. geniculatus*; the table shows adjusted mean replacement rate ± 95% C.L.

(a) Accompanying species		(b) Density and accompanying species		
			Accompanying species	
Accompanying species		Density	Alone	+*A.s.*
Alone	11·95 ± 4·77	10	13·88 ± 4·42	14·02 ± 3·74
+*A.s.*	16·02 ± 4·16	20	9·77 ± 4·53	18·14 ± 3·87

A.s. = *A. sierrensis*.

Table 3. Coefficients of determination (r^2 values) relating separate fitness correlates to the composite index of fitness, replacement rate ranked by geometric mean r^2

	Mean r^2	*Aedes geniculatus*		*Aedes sierrensis*	
		Alone	+*A.s.*	Alone	+*A.g.*
Pupation success (PS)	0·63	0·78***	0·71***	0·48***	0·60***
Male PW (MPW)	0·61	0·48**	0·69***	0·76***	0·54***
Female PW (FPW)	0·61	0·56***	0·67***	0·80***	0·47***
Female DT (FDT)	0·50	0·50***	0·60***	0·56***	0·37**
Protandry (PR)	0·47	0·48**	0·57***	0·57***	0·30**
Male DT (MDT)	0·30	0·28*	0·35**	0·20*	0·39***
Sex ratio (SR)	0·16	0·11	0·11	0·17	0·33**

Rank of fitness correlates by decreasing r^2 with R_0.

$r^2 > 0·5$

A.g. alone PS > FPW > FDT
A.g. +A.s. PS > MPW > FPW > FDT > PR
A.S. alone FPW > MPW > PR = FDT
A.s. +A.g. PS > MPW

M, males; F, females; PW, pupal weight; DT, development time.
*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

Table 4. Coefficients of determination (%) relating fitness and its correlates to environmental variables of food (F), density (D), substrate (S) and their interaction in *Aedes triseriatus* and *A. geniculatus**

	F	D	FD	L	H(L)	S	SF	SD	SFD	SL	SH(L)
A. geniculatus											
R_0	**22**	**16**	.	**21**	**4**	**6**	1	**2**	.	1	.
S	**10**	**19**	.	**33**	2	**6**	.	.	.	2	3
MPW	**18**	**29**	.	**13**	**19**	.	1	.	.	.	2
FPW	.	**37**	.	**15**	**14**	**4**	.	**2**	.	.	4
MDT	**7**	**23**	.	**14**	**13**	3	.	.	2	.	2
FDT	1	**36**	1	**12**	**24**	**5**	.	.	.	.	3
PR	1	**24**	**7**	**31**	.	.	.	.	.	.	9
SR	**17**	.	**2**	.	.	.	5	3	.	.	5
A. sierrensis											
R_0	**5**	**15**	**2**	**43**	**15**	.	.	.	.	.	1
PS	**2**	**8**	**2**	**41**	**27**	.	.	.	.	.	1
MPW	**18**	**41**	.	**11**	**7**	3	.	.	.	.	.
FPW	**6**	**27**	.	**11**	**27**	1	**2**	.	.	**1**	.
MDT	**15**	**24**	**10**	4	3	.	.	.	.	.	.
FDT	**12**	**25**	**2**	**24**	**9**	**4**	.	.	.	**1**	.
PR	**12**	**24**	**12**	**16**	**7**	**4**	**2**	**2**	.	.	**2**
SR	**6**	**13**	**12**	**11**	2	2	3	.	.	.	1

*Environmental variables: F–SH(H) abbreviated as in Fig. 1; fitness correlates abbreviated as in Table 3. Bold numbers represent a significant effects ($P < 0·05$); all others are non-significant ($P > 0·05$); a period (.) in place of a number denotes a coefficient of determination less than 1%.

Fitness correlates

All of the fitness correlates, except sex ratio, were significantly correlated with replacement rate in both species, regardless of whether each species was reared alone or together with the other species (Table 3).

When reared alone, the best correlate of fitness for *A. geniculatus* was pupation success followed by female pupal weight and development time, while other correlates accounted for less than 50% of fitness variation. The best correlates of fitness for *A. sierrensis* when reared alone were female and male pupal weight, degree of protandry and female development time, while the other correlates each accounted for less than 50% of variation in fitness.

When reared together, the best correlates of fitness for both *A. geniculatus* and *A. sierrensis* were pupation success and male pupal weight. In addition, female pupal weight and development time and degree of protandry of *A. geniculatus* were also highly correlated to fitness. The remaining correlates each accounted for less than 50% of the variation in fitness.

Species-specific interactions affected R_0 only in *A. geniculatus* (S and SD) and not at all in *A. sierrensis* (Table 4). In *A. geniculatus*, four of seven fitness correlates did not differ between intra- and interspecific encounters, and none reflected the significant effect of species × density interaction. By contrast, some fitness correlates indicated significant species interactive effects not reflected in R_0. In *A. geniculatus*, male pupal weight was significantly affected by species × food interaction (SF) and prodandry by species × hole interaction within localities (SH(L)). In *A. sierrensis*, female development time differed between intra- and interspecific encounter (S).

DISCUSSION

Fitness (R_0) in both *A. geniculatus* and *A. sierrensis* was affected by density, food level and source of tree-hole detritus, both between localities (U.S.A. vs. U.K.) and between holes within localities (Fig. 1). These four factors accounted for 63% and 77% of the total variation in R_0 in *A. geniculatus* and *A. sierrensis*, respectively. The addition of all the other variables accounted for an additional 10 and 5%, respectively. The linear effects of food, substrate and density therefore had the major impact on fitness in both species and all higher order interactions only a lesser effect.

Both of the U.S. holes are superior in quality than the two from the U.K., regardless of the mosquito species (Table 1). The difference in quality may relate to the tree species and to the type of hole. The U.S. tree holes are both rot holes in large-leaf maple, while the U.K. tree-holes are buttress holes in beech (Table 1). According to Fish & Carpenter (1982), maple leaf-litter decomposes more rapidly than that of beech, so that nutrients may become available faster from the U.S. than the U.K. substrates. Rot holes, unlike buttress (pan) holes, are not lined with bark, and the cavity penetrates into the hardwood (Kitching 1971). The additional component of decomposing wood may also contribute to the greater resource quality in rot (U.S.) than in buttress (U.K.) holes.

Fitness achieved by *A. sierrensis* relative to *A. geniculatus* is very similar across localities and tree-holes (Table 1). For both species, there are significant effects of locality and hole within locality (Fig. 1) but for neither species is there a significant effect of species × locality or species × hole within locality. Consequently, neither species achieves relatively higher fitness on its own than on foreign substrate, regardless of whether it develops by itself or together with the other species. In terms of overall fitness, both species are

responding similarly to substrates of highly different quality and from highly different sorts of holes. Tree holes are therefore replicate habitats for *A. geniculatus* and *A. sierrensis* across intercontinental distances, even though these holes may differ both within and between localities. Thus, convergent habitats, even across intercontinental distances, may provide similar opportunities and exigencies that are exploited and solved by resident organisms in similar ways.

Food × density interaction affected fitness in *A. geniculatus* ($r^2 = 2.4\%$) but not in *A. sierrensis* ($R^2 = 0.3\%$) (Fig. 1). This interaction was not affected by the presence of *A. geniculatus* (SFD: $r^2 = 0.1\%$) so that factors affecting fitness assessed in single-species populations of either *A. geniculatus* or *A. sierrensis* persisted in interspecific encounters as well.

Fitness in *A. geniculatus* but not *A. sierrensis* differs between intra- and interspecific encounter (S: $r^2 = 5.6\%$ and 0.4%, respectively). In parallel, the effect of density on fitness in *A. geniculatus* but not *A. sierrensis* differs between intra- and interspecific encounters (SD: $r^2 = 2.2\%$ and 0.3%, respectively). Thus, interspecific interactions may depend upon factors that have no significant effect on fitness in single species populations.

A. sierrensis achieves the same level of fitness regardless of the presence or absence of *A. geniculatus* (Fig. 1b). *Aedes geniculatus* at high density, by contrast, achieves higher fitness in the presence than in the absence of *A. sierrensis* (Table 2a). Combined replacement rate of both species together does not differ from the average of both species reared separately at the same density and food level and tree-hole source (*t*-test for paired comparisons: mean difference ± 95% C.L. = -0.17 ± 2.22, $t_{15} = 0.16$, $P > 0.05$). This result indicates that the two species do not enjoy exclusive resources and *A. geniculatus* probably achieves greater fitness than *A. sierrensis* at higher density through competitive dominance. Consequently, if reciprocal introductions were made between these two populations, *A. geniculatus* should persist in England but exclude *A. sierrensis* in Oregon unless adult survivorships vary dramatically between the two localities. This prediction must be tempered by the results of Rosen *et al.* (1976) who found that competitive dominance observed in the laboratory (Rozeboom 1971; Lowrie 1973a, b) did not predict the outcome of an actual introduction attempt in nature. Unlike the present study, however, Rozeboom and Lowrie reared inbred laboratory strains on artifical diet and substrate.

Determination of a composite index of fitness such as replacement rate requires meaningful estimates of size-specific fecundity and survivorship in nature (Dye 1984; Hawley 1985a, b). In the present study, replacement rate was estimated from transformations of the number and weight of female pupae based on weight-specific fecundity and survivorship in nature. These transformations, however, are difficult to obtain. It would be far easier to monitor some component or correlate of fitness that accurately reflects the response of the composite index to environmental variables (habitat, food, density) including inter- as well as intraspecific interactions. Coefficients of determination relating separate fitness correlates to replacement rate (Table 3) vary at least 23% between species and between conditions of inter- and intraspecific encounter. The ranks of coefficients of determination are not similar for the two species or for inter- and intraspecific encounter within a species.

Likewise, correlates provide an uneven impression of replacement rate in terms of response to proximal environmental variables (Table 4). The relative importance of food, location, hole within location and species interaction, both within and between species, depends upon whether one considers a given fitness correlate or replacement rate itself (Table 4). We therefore conclude that using correlates to identify major environmental

factors affecting fitness is probably acceptable. However, as concluded earlier, using correlates in lieu of replacement rate or another composite index to identify higher order interactions (Livdahl & Sugihara 1984), or to compare the effects of proximal environmental variables on fitness within and between species (Hard, Bradshaw & Malarkey 1989) leads to equivocal and/or contradictory conclusions. Comparative studies, at least in mosquitoes and probably in other organisms as well, should examine the response of an appropriate composite index of fitness rather than one or even several of its correlates.

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