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# Estimating competition coefficients: strong competition among three species of frugivorous flies

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**Abstract** Despite the abundance of studies on competitive interactions, relatively few experiments have been used to fit explicit competition models and estimate competition coefficients. Such estimates are valuable for making contact between theoretical and empirical studies, which tend to measure competition in different units. To quantify the strength of competitive interactions among the larvae of three species of frugivorous flies, I manipulated the densities of each species to investigate all three pairwise interactions. The densities of each species were changed independently (i.e., using a response surface experimental design), which allowed maximum likelihood estimation of the competition coefficients for each species, based on the Hassell and Comins competition model. The effects of competitor density on larval survival, time to emergence, and the weight of emerging adults were also analyzed to investigate the responses of individual species to density. The estimates of the competition coefficients suggest that the larvae of these flies experience strong asymmetric competition for resources, and raise questions as to how these species coexist. For each pair, one of the species was largely unaffected by interspecific competition, but decreased the performance of the other.

**Key words** Interspecific competition · Response surface experimental design · Frugivorous insects · *Apeiba membranacea*

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## Introduction

Hundreds of experimental and observational studies have demonstrated the importance of intraspecific and interspecific competition in natural communities (see reviews in Schoener 1983; Goldberg and Barton 1992; Gurevitch et al. 1992). Theoretical studies also predict an important role for competitive interactions in determining coexistence (Atkinson and Shorrocks 1981; Shmida and Ellner 1984), and for influencing population dynamics (Hairston et al. 1960; Hassell and Comins 1976), and coevolution (Iwao and Rausher 1997). Unfortunately, empirical and theoretical studies of competitive interactions often discuss the strength of competition in different terms. Models of competition commonly describe the effects of competitive interactions with competition coefficients, which describe the per capita effect of one competitor on the performance (typically recruitment) of another. Empirical studies of competition have rarely employed an experimental design that allows the fitting of dynamic competition models to the data, and thus cannot provide meaningful estimates of these competition coefficients (Connolly 1986; Goldberg and Scheiner 1993; Inouye 1998b). Instead, empirical studies of competition often aim to detect a statistically significant effect of intraspecific or interspecific competitors at a certain density on single components of a competitor's performance, such as growth, survival, or fecundity.

For studies whose aim is to connect theoretical and empirical methods, the results of experiments must be expressed in units that are appropriate to the models in question. Here I report the results of an experiment that was used to estimate the strength of pairwise competitive interactions among the frugivorous larvae of three fly species. Because this experiment was part of a larger study on the coexistence of competitors (B.D. Inouye, unpublished data), it was necessary to measure competition using per capita competition coefficients. These coefficients enable one to evaluate whether competition is strong enough for competitive exclusion, and a proposed mechanism of coexistence. While most competition experiments hold either the total density of competitors or the density of one species constant, in this experiment, the densities of all competitors were varied. Since these densities were varied separately (response surface methodology: Box et al. 1978; or response surface experimental design sensu Goldberg and Scheiner 1993), I was able to estimate competition coefficients for a single competition model (Hassell and Comins 1976). This commonly used discrete-time model describes the per capita effects of competitors on a focal species. The effects of intraspecific and interspecific density were also analyzed separately for different components of fly performance: the probability of larvae surviving until emergence, the weight of emerging adults, and the time required until emergence.

The results presented here demonstrate the feasibility of using response surface experimental designs to generate the parameter estimates needed for evaluating the assumptions and predictions of ecological and evolutionary models. Response surface experimental designs vary the densities of two competitors separately over a range of densities, often by using factorial combinations of two species' densities. The use of this experimental design in ecological studies of competition is still rare, and there are very few published examples (but see Ayala et al. 1973; Law and Watkinson 1987). Response surface experimental designs have been criticized for being unnecessarily complex and labor intensive (Cousens 1991), but for most studies with an ecological or evolutionary focus they have several advantages that outweigh these potential drawbacks. Experimental designs that only vary the density of one species (additive designs, sensu Goldberg and Scheiner 1993) or that hold the total density of competitors constant ("DeWitt" or replacement designs) are inherently unsuitable for estimating competition coefficients and fitting explicit models (Connolly 1986; Inouye 1998b). Furthermore, the regression and maximum likelihood methods used for fitting models to response surfaces have the advantage that all model parameters are estimated simultaneously. Methods that estimate parameters sequentially compound any error or uncertainty in the first estimates with estimates for each additional parameter (Pascual and Kareiva 1996).

## Materials and methods

### Experimental system

*Apeiba membranacea* Spruce ex Benth. (Tiliaceae) (Piene de mico) is a canopy tree in lowland central American rainforests. Its disc-shaped fruits are 40–70 mm in diameter and 15–30 mm thick, with a woody, spiny shell, and many hard seeds distributed in a pulp. A wide range of pulp-eating insects rapidly colonizes fruits after they fall, become wet, and begin to rot. I have collected nearly 50 species of insects from inside these fruits, with about a dozen found consistently in the fruits under most *A. membranacea* trees. The common species include pulp-feeding flies, pulp-feeding, seed-feeding and predatory beetles, pulp-feeding moths, and predatory earwigs. In the experiments reported here, I used larvae of the three most abundant fly species found in *A. membranacea* fruits: *Taeneaptera* sp. (Micropezidae), *Richardia* sp. (Richardiidae), and *Chlorops* sp. (Chloropidae). All three flies colonize *A. membranacea* fruits rapidly, and are frequently found together in the same fruits. A more detailed description of this community can be found in Inouye (1998a).

### Experimental design

For each pair of species, the number of larvae per fruit was varied independently so that both the total number of larvae per fruit and the relative frequency of each competitor varied. I used all factorial two-species treatments of 0, 4, and 8 larvae of each species per fruit. Because larvae of *Chlorops* sp. and *Taeneaptera* sp. were more abundant, I established additional treatments with these species at higher densities. The *Taeneaptera* sp. larvae were used at the additional density of 12 larvae per fruit, and the *Chlorops* sp. larvae at the additional densities of 2, 12, 16, and 24 larvae per fruit, although the higher-density treatments were not fully factorial (most possible two-species combinations were not used). These densities cover a large proportion of the densities encountered in the field (B.D. Inouye, unpublished data). A total of 978 larvae in 117 fruits were used. For each combination of species and densities there was a mean of 2.3 replicates (median = 2), with a range of 1–9 replicates of each treatment.

I collected fruits and larvae for the experiment from underneath more than 30 different *A. membranacea* trees at the La Selva Biological Research Station, Heredia, Costa Rica. Each fruit was opened and inspected for all insects and larvae longer than 1 mm. Fly larvae for use in the competition experiments were put into 250-ml containers along with a small amount of fruit pulp, and kept at ambient conditions until there were enough larvae to start several replicates (1–3 days). Each container held only one species of larvae. Fresh pulp without any larvae was put into 250-ml plastic containers, with the pulp from several trees mixed in a single container. Containers of pulp were frozen at −4°C for up to a week before use, to kill any remaining larvae. The emptied woody shells were also stored in a freezer until use.

Before use, the pulp and shells were defrosted and moistened. Each replicate was started with 3.6 ml of pulp in a shell. This is slightly more than the average volume of pulp in a fruit (about 3 ml), but well within the observed range (approximately 1–6 ml). Larvae were then placed into the pulp, after recording the length of each larva to the nearest 0.1 mm. I used larvae that were as small as practical in order to maximize the period of competition inside the fruits, but I excluded the very smallest as well as the largest larvae. The shells were wrapped with cotton thread to hold them closed. Fruits were put into individual mesh-topped plastic cups with a small amount of leaf litter for pupation. The cups were misted with water daily, kept at ambient temperatures, and checked at least once per day for emerging adults. Live weights of recently emerged flies were recorded to the nearest milligram using an electronic Mettler balance. The experimental fruits were started in five temporal blocks over a period of 3 weeks during June and July 1997.

### Model fitting

Three responses were recorded for each species: the number of days until adult emergence, adult live weight, and the probability of survival from larva to adult. I analyzed each of these response variables both separately and as a composite measure of the adult biomass produced per initial larva. To obtain the composite measure of biomass, I added the weights of all flies emerging from a replicate, and discounted the weights of all flies that emerged later than the earliest emerging individual of that species (over all replicates) by 3% per day. This penalty for later emergence was included to account for predation, which in the field reduces the survival of late-instar larvae and pupae that remain in the fruits (unpublished data). In addition, I recorded the sex of adult flies of *Taeneaptera* sp. and *Richardia* sp. and the emergence of any parasitoids. A total of seven *Eucoilini* sp. parasitoids emerged from 262 *Taeneaptera* sp. larvae. No other parasitoids were reared, and parasitism rates of field-collected pupae and late-instar larvae was similarly low (unpublished data). Parasitized individuals were removed from the analyses of life history components, but for the biomass data were assigned the average weight for their species, as were five other flies that escaped or were mangled before they could be weighed.

The aggregate biomass data were analyzed by fitting the competition model:

$$A_{\mathrm{Xt}} = X_{\mathrm{t}} r[1 + c(X + \beta_{\mathrm{XY}} Y_{\mathrm{t}} + \beta_{\mathrm{XZ}} Z_{\mathrm{t}})]^{-b}$$

where $A_{\mathrm{Xt}}$ is the biomass of adults of species X, $X_{\mathrm{t}}$, $Y_{\mathrm{t}}$, and $Z_{\mathrm{t}}$ represent the larval densities of the focal species and two competitors, respectively, at time *t*, *r* is the population growth rate, $\beta_{\mathrm{XY}}$ is the effect of species Y on species X (the competition coefficient), and *b* affects the form of the response to competition (i.e., scramble vs contest). This is a modification of the Hassell and Comins (1976) model, which uses $X_{\mathrm{t+1}}$, the larval density of X in generation $t+1$, in place of $A_{\mathrm{Xt}}$ (see below). To avoid reusing data from the single-species replicates in separate analyses, I fit the data for all three species simultaneously. Thus the equations fitted to the data had five parameters to be estimated. The competition model was fit using maximum likelihood methods, assuming normally distributed error. To use the assumption of normally distributed error, those replicates in which no larvae survived to emergence were excluded from this analysis (see discussion of survival data below). Inspection of the residuals for the remaining replicates showed that the normality assumption was approximately met. The confidence intervals and significance of the parameters were evaluated with log-likelihood ratio tests (Edwards 1992; Hilborn and Mangel 1997). All of the likelihood calculations were programmed and evaluated using S-plus 4.0 (Mathsoft, Seattle, Wash.).

The Hassell and Comins model is based on a comparison of densities in two generations (comparing $X_{\mathrm{t}}$ to $X_{\mathrm{t+1}}$); however, I fit the model to data on the biomass of adults ($A_{\mathrm{Xt}}$) resulting from a given number of larvae ($X_{\mathrm{t}}$, $Y_{\mathrm{t}}$, $Z_{\mathrm{t}}$), and not the actual number of adults in the previous generation. Although the competition experiments did not last an entire generation, the estimated competition coefficients still provide an accurate description of the competitive interactions in this system if two reasonable assumptions are met. The first of these assumptions is that all competition between these species happens during the larval stage, i.e., the adult insects do not compete. I also assumed that each unit of adult biomass results in a certain number of larvae in the following generation, according to an unknown linear function $X_{\mathrm{t+1}} = \varphi A_{\mathrm{Xt}}$. This assumption may not hold in extreme cases, but the relationship between biomass and recruitment may be linear over the range of values used in the experiments (cf. Ives 1991; Leonard and Juliano 1995). Therefore, by fitting the model as $\varphi A_{\mathrm{Xt}} = X_{\mathrm{t}} f(X_{\mathrm{t}}, Y_{\mathrm{t}}, Z_{\mathrm{t}})$, the parameters *r*, *c*, and *b* from the competition equation must all be corrected by the unknown scalar $\varphi$ in order to predict the population dynamics of the competitors. Because the value of $\varphi$ is unknown, I do not report the maximum likelihood estimates for *r*, *c*, and *b*. The competition coefficients ($\beta$s) are independent of $\varphi$.

To pinpoint the particular life history components that were responsible for the aggregate responses to competition, I also fit models to each separate response (survival, weight at emergence, time until emergence), again using maximum likelihood methods. The weights of emerging flies and the number of days until emergence were modeled separately as simple linear regressions of a vector $\theta_1$ with normally distributed error. I let $\theta_1 = [\beta_1 + \beta_2(X + \beta_3 Y + \beta_4 Z) + \beta_5 C]$, where *X* represents the initial density of the focal species, *Y* and *Z* represent the initial number of larvae of competing species, and *C* represents covariates such as temporal block, the diameter of the fruit shell, or average initial larval size. Note that either *Y* or *Z* is 0 in each replicate. The magnitude of $\beta_2$ determines whether intraspecific competition is significant, while $\beta_3$ and $\beta_4$ determine the strengths and direction of interspecific interactions. I tested the significance of intraspecific and interspecific competition terms with likelihood ratio tests. The weights and number of days to emergence were Box-Cox transformed before analysis so that they more closely met the error assumptions of the model.

The test for significant effects of competition on survival was similar to that described above, but used one additional parameter. Predacious mites infected some fruits, killing all of the larvae in the fruit, but I could not confidently determine the presence or absence of mites in most fruits. Thus when no survivors emerged, I was unsure whether it was due to the negative effects of competition on survival or to mites or other extrinsic factors. To account for this uncertainty, I represented the probability of *k* survivors emerging from *j* larvae as

$$p = \begin{cases} 0 & \text{with probability } \dfrac{e^{\theta 0}}{1 + e^{\theta 0}} \\[2ex] \dbinom{j}{k} \theta_1^k (1 - \theta_1)^{j-k} & \text{with probability } \dfrac{1}{1 + e^{\theta 0}} \end{cases}$$

This mixed model allows for ‘extra’ observations of no survivors above what is expected from a binomial model. Using the exponential form for $\theta_0$ means that the maximum likelihood algorithm can be greatly simplified to a negative log likelihood of:

$$-\ln(L) = -n \ln\left(1 + e^{\theta 0}\right) + \sum_n I \ln\left(e^{\theta 0} + \left(1 + e^{\theta 1}\right)^j\right) + \sum_n (1 - I) \ln\left(e^{\theta 1 * k}\left(1 + e^{\theta 1}\right)^{-k}\right)$$

which finds $\theta_0$ and $\theta_1$ simultaneously, assuming binomial error. In this expression, *n* is the number of replicates, $I = 0$ for replicates with no survivors and 1 otherwise, *j* is the initial number of larvae in a replicate, and *k* is the number of surviving adults in a replicate.

## Results

Initial analyses of the three separate life histories found no significant effects of starting date, and so all blocks were lumped for further analysis (results not shown). For both *Taeneaptera* sp. and *Richardia* sp., the emergence weights and larval periods for male and female flies were normally distributed (grouped over all density treatments) and were not significantly different (*t*-tests, $P > 0.5$), so the sex of emerging flies was also not used in the subsequent analyses. Additionally, the shell diameter of experimental fruits and the mean initial size of larvae in a fruit were not significant covariates in 16 of 18 life history responses ($\alpha = 0.05$ per regression), and thus were ignored in the analysis of compound biomass.

### Competition coefficient estimates

The Hassell and Comins equation (1976) provided a relatively good fit to the biomass data for each species (approximate *F*-tests for lack of fit using the ratio of the mean-squared model deviations to the pure error mean square were not significant, all $P > 0.2$; Rawlings et al. 1998, p. 240). The maximum likelihood estimates (MLEs) of the competition coefficients are summarized in Table 1. The 95% confidence intervals for each of the parameter estimates were calculated using the chi-square

**Table 1** Maximum likelihood estimates of the competition coefficients (β) and their 95% confidence intervals (from likelihood ratio tests). The intraspecific competition coefficients equal 1 by definition

| Effect on | Effect of | | |
|---|---|---|---|
| | *Taeneaptera* sp. | *Richardia* sp. | *Chlorops* sp. |
| *Taeneaptera* sp. | 1 | −0.05 (−0.42, 0.19) | −0.11 (−0.14, 0.07) |
| *Richardia* sp. | 0.68 (0.24, 1.64) | 1 | −0.06 (−0.13, 0.09) |
| *Chlorops* sp. | 9.55 (1.74, 14.03) | 4.19 (−10.76, 12.88) | 1 |

approximation for the likelihood ratio test (Edwards 1992), with all other parameters fixed at their maximum likelihood values. The confidence intervals for the competition coefficients were very weakly dependent on the values of the other parameters. The MLEs and confidence intervals for the parameters $r$ and $c$ covary more strongly (results not shown, see Materials and methods). Likelihood ratio tests were also used to estimate the $P$-values when testing whether parameters were significantly different from zero. Parameter estimates with 95% confidence intervals that include zero are not significantly different from zero ($\alpha = 0.05$). Recall that in the Hassell and Comins model, the interspecific competitive effects are expressed relative to the strength of intraspecific competition, which is defined as a strength of one. The MLEs for the parameter $b$ are all less than one (*Taeneaptera* sp. $b = 0.35$, *Richardia* sp. $b = 0.65$, *Chlorops* sp. $b = 0.10$). This suggests that competition in these species is more like the ‘contest’ form; however, the confidence intervals for this parameter are very large, and none of the estimates differ significantly from one.

Based on the MLEs of the competition coefficients, larvae of *Taeneaptera* sp. were the best competitors of these three species (Table 1). *Taeneaptera* sp. experienced significant intraspecific competition ($P < 0.001$), but no significant effects of interspecific interactions. In fact, although the MLEs of the effects of interspecific competition on *Taeneaptera* sp. were not significantly different from zero (no interaction), the MLEs are slightly less than zero, which means that on average *Taeneaptera* sp. larvae performed slightly better in the presence of the other species. The larvae of *Richardia* sp. were intermediate in competitive ranking. *Richardia* sp. also experienced significant intraspecific competition ($P < 0.001$), and interspecific competition from *Taeneaptera* sp. larvae ($P = 0.02$) but not from *Chlorops* sp. larvae. The larvae of *Chlorops* sp. were the least competitive species in this experiment. They experienced significant effects of interspecific competition from both of the other species; however, they did not suffer from significant intraspecific competition, even though the range of densities tested was higher for *Chlorops* sp. than for the other species. The MLEs of the interspecific competition coefficients for *Chlorops* sp. were both high (Table 1), but only the effect of *Taeneaptera* sp. larvae was significant ($P = 0.05$).

Although *Chlorops* sp. experienced statistically significant competition only from *Taeneaptera* sp. larvae, I suspect that the interspecific competition from *Richardia* sp. larvae is biologically significant. The MLE for the per capita effect of *Richardia* sp. larvae on *Chlorops* sp. biomass production is 4.19 (Table 1), indicating a relatively strong per capita competitive effect. However, because there were relatively few replicates for this interaction ($n = 16$ for emerging adults due to scarcity and high mortality of *Richardia* sp. larvae), the 95% confidence intervals for this parameter are large and encompass zero.

The three separate life history components (time until emergence, weight at emergence, survival) responded differently to competition (Table 2). While increasing the density of larvae in a fruit tended to decrease the weight of emerging adults, the effects of intraspecific and interspecific competition on the weights of emerging flies were not significant for any of the three species (all $P > 0.10$). Increasing the density of competitors also increased the number of days until adult flies emerged, but only three of the responses were statistically significant. There was a significant effect of intraspecific

**Table 2** Direction and $P$-values for pairwise effects on the three life history components that contribute to the composite adult biomass measure: survival to emergence, weight at emergence, and the number of days until emergence. The species are represented by their generic initials (*T Taeneaptera*, *R Richardia*, *C Chlorops*), with the focal species listed first. $P$-values greater than 0.15 are shown as *n.s.* All effects are in the direction of decreased survival and weight, and increased time until emergence, except for the effect of *Richardia* sp. on *Taeneaptera* sp. survival

| Response | Competitors | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | T, T | T, R | T, C | R, T | R, R | R, C | C, T | C, R | C, C |
| Survival | 0.05<br>− | 0.01<br>+ | n.s.<br>− | n.s.<br>− | 0.02<br>− | n.s.<br>− | < 0.01<br>− | n.s.<br>− | n.s.<br>− |
| Weight | 0.12<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− | n.s.<br>− |
| Time | n.s.<br>− | < 0.01<br>− | 0.06<br>− | 0.11<br>− | 0.03<br>− | n.s.<br>− | 0.06<br>− | n.s.<br>− | 0.04<br>− |

competition on the number of days until emergence for *Richardia* sp. ($P = 0.03$), and *Chlorops* sp. ($P = 0.04$), and *Richardia* sp. affected the time until emergence for *Taeneaptera* sp.

The MLEs for the survival model suggest that approximately 10% of the fruits were infested with mites, or experienced some factor other than competition that resulted in no survivors. This mortality was similar for all three species. There was a significant effect of intraspecific competition on survival of two of the three species (Table 2, *Taeneaptera* sp., $P = 0.05$, $n = 51$ fruits with survivors, and *Richardia* sp., $P = 0.02$, $n = 40$). There were also two significant interspecific competitive effects on survival. Survival of *Taeneaptera* sp. larvae was weakly positively affected by *Richardia* sp. larvae ($P = 0.01$, $n = 17$) and the survival of *Chlorops* sp. larvae was lower in the presence of *Taeneaptera* sp. larvae ($P = 0.004$, $n = 21$). The remaining competitive interactions were not significant (all $P > 0.10$), but in each case, the trend was for decreasing survival with increasing density of intraspecific and interspecific competitors.

## Discussion

Despite the abundance of both empirical and theoretical studies of competition, there has been relatively little direct contact between the two approaches. Experimental field studies of competition most often report the effects of intraspecific and interspecific density on short-term survival or growth rates, whereas models usually express the strength of competition in terms of competition coefficients. In this study, the effects of intraspecific and interspecific density were analyzed in two ways. I looked for significant effects of competition on separate life history characteristics, such as survival, which allows a qualitative comparison with the results of other studies of competition for patchy and ephemeral resources. In the second analysis, I estimated interspecific competition coefficients by fitting the Hassell and Comins model to the aggregate biomass response. In conjunction with models of competition and coexistence, the estimates of the competition coefficients from this study could be used to make predictions about the persistence of these species (B.D. Inouye, unpublished data).

### Competition on patchy and ephemeral resources

The results of the competition experiments described above indicate that interspecific competition for a patchy and ephemeral resource can be much stronger than intraspecific competition. Other experiments on competition for resources such as rotting fruits, dung, and fungi have also documented strong competition for the limited resources in each patch, although most studies do not fit explicit competition models (there are linear models implicit in some statistical tests). For example, competition among dung beetles can have both strong intraspecific (Giller and Doube 1994) and interspecific (e.g., Ridsdill-Smith 1993) components, but none of the competition experiments using dung beetles have estimated competition coefficients (Hanski and Cambefort 1991; Ridsdill-Smith 1991). There is also much experimental evidence that carrion-breeding flies compete within carcasses (e.g., Denno and Cothran 1976; Beaver 1977; Ives 1991) and that *Drosophila* species compete within rotting mushrooms (e.g., Grimaldi and Jaenike 1984) and fruits (Sevenster 1992), but few of these studies separate the effects of intraspecific and interspecific competition. Other systems that have demonstrated competition for a patchy and ephemeral resource include mosses that use moose and wolf dung (Marino 1991a, 1991b), and mosquitoes in small ephemeral pools (Sota et al. 1994; Juliano 1998).

This study also describes the effects of competition on the flies' separate life history characteristics (Table 2). Previous experiments with carrion-breeding calliphorid and sarcophagid flies (Denno and Cothran 1976; Beaver 1977 and references therein; Ives 1991) and fungal-breeding *Drosophila* (Grimaldi and Jaenike 1984) all found strong effects of intraspecific or interspecific competition on the size (weight or wing size) of emerging adult flies. These studies found that although adult size was sensitive to larval competition, survival decreased only at extremely high larval densities, if at all. In contrast, I found no significant effects of intraspecific or interspecific competition on the weight of emerging flies, but competition at natural densities did significantly affect both survival and the time to emergence, at least for some species. Since all of these studies investigated the effects of competition on flies that exploit patchy and ephemeral resources, the differences in the responses cannot be explained by gross taxonomic or habitat differences.

A caveat to the results of this experiment is that higher-order interactions are ignored. To test for the presence of higher-order interactions or to estimate the magnitude of these interactions, it would be necessary to replicate some of the experimental fruits with larvae of all three species present. Although higher-order interactions are of interest for many ecologists, the logistics of working with this particular community precluded such a large experiment.

### Implications for coexistence

The results described above provide evidence that for each species pair there is one for which the effects of interspecific competition are much stronger than those of intraspecific competition (Table 1). For two of the three species pairs, the MLEs of the interspecific competition coefficients are greater than one for one species, the superior competitor, and less than one (approximately zero) for the other species, the inferior competitor. The estimates in Table 1 may even underestimate the true effects of competition, as the replicates with no survivors of the focal species were excluded from the analysis (see Materials and methods). Some cases when no larvae of a given species survived were likely due to competitive interactions, instead of predation by mites or other external factors.

In theory, the coexistence of two competitors depends not only on the competition coefficients, but also their carrying capacities. I was unable to estimate directly the carrying capacity of these flies from the competition experiment (see Materials and methods). However, repeated field observations on the densities of these species over 5 years and larval rearings suggest that such differences are not sufficient to negate the relatively large differences in their competitive abilities (personal observation).

Because of its strong effects on the other two species, *Taeneaptera* sp. would be likely to exclude the other flies from any collection of fruits after a few generations, unless the negative effects of interspecific competition are ameliorated by some coexistence mechanism(s). Resource partitioning among different species of fruits is an unlikely candidate, since these flies seem to specialize on *A. membranacea* fruits, at least at this site. Resource partitioning at the scale of *A. membranacea* fruits has not been observed either (B.D. Inouye, unpublished data). The mechanism most probably promoting the coexistence of these competitors is spatial heterogeneity, in the form of high intraspecific aggregation among fruits combined with variation in the distributions among trees (Inouye 1999). The independently aggregated distributions that are observed for the larvae of these flies have the consequence of lowering the frequency of interspecific relative to intraspecific competition (Inouye 1999).

It is not too surprising that the larvae within fallen *A. membranacea* fruits compete, as the fruits offer high-quality resource patches with a fixed initial amount of resource. All pulp in a fruit is generally eaten or otherwise removed within a single generation (unpublished data). The overall competitive rankings, with *Chlorops* sp. being the worst competitor, match the rankings of these three species based on size. *Taeneaptera* sp. adults (mean = 71 mg) weigh over four times as much as *Chlorops* sp. adults (15 mg) and about one-third more than *Richardia* sp. adults (55 mg). These differences in adult size also reflect the differences in maximum larval size. However, the rankings of these three species based on average time until emergence do not coincide with their rankings based on competitive ability, as *Taeneaptera* sp. (mean 27 days, one-third as pupae) tends to emerge slightly earlier than *Richardia* sp. (32 days, one-third as pupae), but *Chlorops* sp. adults consistently emerge before the other two species (13 days, 3 days as pupae).

The results of this study provide valuable estimates of competition coefficients for multiple insects under relatively natural conditions, but more studies that use sophisticated experimental designs and fit explicit models are needed. Of the previous studies that have fit explicit competition models to experimental data, most have manipulated plant densities in a greenhouse (e.g., Law and Watkinson 1987; Antonovics and Kareiva 1988). Some early studies with pairs of insects or microorganisms in the laboratory, such as *Paramecium* spp. (Gause 1934), protozoa (Vandemeer 1969), *Drosophila* spp. (summarized in Shorrocks et al. 1984), and *Tribolium* spp. (Park 1948), estimated competition coefficients, but the sequential parameter estimates used by some studies are suspect, since each estimate compounds any errors in the previous steps. Field studies that estimate competition coefficients generally use observational data rather than direct experimental density manipulations (e.g., Seifert and Seifert 1976; Pfister 1995), which presents a different set of statistical limitations (but see Juliano 1998). For investigating the effect of competition on a specific coexistence mechanism, I have only fit a single competition model, which is the same as that used in related studies (B.D. Inouye, unpublished data). However, for more detailed studies of population dynamics, the functional forms of responses to competition by different species can be compared by fitting multiple models to the data (Inouye 1998b).

## Conclusions

The experiment described above is one of few studies to use a response surface experimental design to investigate competitive interactions and explicitly fit a competition model. The estimates of the competition coefficients in this system paint a picture of strong asymmetric competition within fruits. Analysis of separate life history characteristics for these flies further demonstrates that larvae of the three species respond to intraspecific and interspecific competition. Competition among the fly larvae in this system seems to be strong enough that simple models would not predict the coexistence of these three species, although in the field there appears to be sufficient spatial heterogeneity to allow coexistence (B.D. Inouye, unpublished data).

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