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

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 Burton 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 (Hasslan 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: Taeneaera 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 Taeneaera sp. were more abundant, I established additional treatments with these species at higher densities. The Taeneaera 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