

Effect of larval host on life history traits of the mediterranean fruit fly, *Ceratitis capitata*

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Summary. Demographic parameters for the Mediterranean fruit fly reared on each of twenty four different hosts from sixteen different plant families are reported. These include cohort parameters of development, survival, pupal size, and fecundity as well as population parameters such as intrinsic rate of population increase (r) and mean generation time. Major findings include the following: i) no consistent quantitative relationships existed between r and its chief demographic determinants such as preadult developmental time and adult fecundity; and ii) few correlations existed among the cohort life history parameters themselves. The principle conclusion is that the medfly is a successful generalist frugivore because of its developmental ability to offset the effect of the value for a host-specific trait that tends to lower r with one that tends to increase r , the net result of which is to maintain a relatively high r .

Key words: Mediterranean fruit fly – *Ceratitis capitata* – Insect demography – Insect polyphagy – Insect-host relations

Community diversity among plant hosts has been related to the evolution of phytophagous insect life histories such as formation of host races (Bush 1975; Wood and Guttman 1981), evolution of specialized herbivores (Ehrlich and Raven 1964; Scriber 1982, 1983; Smiley 1978) and maintenance of polyphagy (Cates 1980, 1981; Wiklund 1975). Approaches for studying host-specific life histories of generalist insects have historically fallen into two general categories according to the type of development for the insect studied. Hemimetabolous arthropods such as aphids and tetranychid mites are typically observed throughout all stages of their life cycle on a preselected host species. Since the feeding habits of all stages are the same, the observed effect of the host on the entire life cycle is relatively straightforward. However, studies of holometabolous insects such as lepidopterans and herbivorous dipterans are often limited to observing only the host-feeding (typically larval) stage. A frequent assumption for this case in the context of life history theory is that adaptation at the host-feeding stage (i.e. survival, development and ultimate size) is the primary determinant for overall adaptation of the species. The major problem with this assumption is that the demographic traits

of the non-host feeding adults are seldom independent of their host origin (e.g. Barbosa et al. 1983).

The specific objective of this study was to determine how immature development and survivorship and adult fecundity and survivorship of a generalist herbivore, the Mediterranean fruit fly (medfly) *Ceratitis capitata* (Wiedemann), are affected by larval host. The medfly is a highly polyphagous species with a host range of over 250 fruits (Christenson and Foote 1960; Mourikis 1965). Although Carey (1984) studied several aspects of the host-specific demography of this species, his assumption for computing population parameters was that the larval host had no effect on the subsequent adult parameters. That is, a single fecundity schedule was applied to cohorts reared from each of a variety of hosts.

Our broad goal for this research was to examine in a demographic context why the medfly is a successful generalist. We do this by addressing three questions: i) are the major medfly demographic traits correlated within a cohort?; ii) how consistent are medfly demographic parameters among cohorts which are reared on different hosts?; and iii) what life history tradeoffs exist in the medfly for maximizing its population growth rate?

Materials and methods

Source material and environmental conditions

Flies were obtained from a colony reared at the USDA Tropical Fruit and Vegetable Laboratory in Honolulu, Hawaii. This colony was considered ideal for our study because i) it has been reared upon the same diet for several generations, thus reducing intra-population genetic variability; and ii) life history parameters are remarkably similar to that of wild strains found in Kenya (Abasa 1972), Israel (Rivnay 1950), Greece (Carey 1984) and Hawaii (Harris and Carey unpublished work). Rearing conditions were 30° C ($\pm 5^\circ$), 65% RH ($\pm 10\%$), 12:12 L:D. Adults were fed a 3:1 volumetric mixture of commercial sugar and enzymatic yeast hydrolysate and water.

Hosts screened

Thirty hosts were used for medfly life history screening (Table 1). Only hosts visually determined to be at peak of ripeness were used. All of these have been reported as medfly hosts except for blackberry, raspberry, and blue-

Table 1. Family, scientific name and common name of hosts used in medfly life history studies

| Family | Species | Common name |
|------------------------|---------------------------------|----------------------------|
| Rosaceae | <i>Fragaria virginiana</i> | Strawberry |
| | <i>Malus silvestris</i> | Apple ^a |
| | <i>Prunus americana</i> | Plum |
| | <i>Prunus armeniaca</i> | Apricot |
| | <i>Prunus avium</i> | Cherry |
| | <i>Prunus domestica</i> | Prune |
| | <i>Prunus persica</i> | Peach |
| | <i>Prunus persica nectarina</i> | Nectarine |
| | <i>Pirus communis</i> | Pear |
| | <i>Pirus sp.</i> | Asian Pear |
| | <i>Rubus idaeus</i> | Raspberry |
| | <i>Rubus rubrisetus</i> | Blackberry |
| | Rutaceae | <i>Citrus aurantifolia</i> |
| <i>Citrus limon</i> | | Lemon |
| <i>Citrus paradisi</i> | | Grapefruit |
| <i>Citrus sinensis</i> | | Orange |
| Actinidiaceae | <i>Actinidia chinensis</i> | Kiwi ^a |
| Anacardiaceae | <i>Mangifera indica</i> | Mango |
| Bromeliaceae | <i>Ananas ananassoides</i> | Pineapple ^a |
| Caricaceae | <i>Carica papaya</i> | Papaya |
| Cucurbitaceae | <i>Cucumis sativus</i> | Cucumber ^a |
| Ericaceae | <i>Vaccinium corymbosum</i> | Blueberry |
| Guttiferae | <i>Mammea americana</i> | Mammee Apple |
| Lauraceae | <i>Persea americana</i> | Avocado |
| Moraceae | <i>Ficus carica</i> | Fig |
| Musaceae | <i>Musa acuminata</i> | Banana |
| Palmae | <i>Cocos nucifera</i> | Coconut ^a |
| Sapindaceae | <i>Litchis sinensis</i> | Lychee |
| Solanaceae | <i>Lycopersicon esculentum</i> | Tomato |
| Vitaceae | <i>Vitis vinifera</i> | Grape |

^a No larvae survived

berry. Twelve hosts were in family Rosaceae and four in family Rutaceae. The remaining sixteen were from different families.

Preadult traits

Egg hatch of 97% and a 2-day development period were assumed constant and independent of host (Carey 1984). Larval survivorship was determined by randomly placing one hundred newly-emerged first instar larvae on one gram of each host on moist filter paper in a petri dish. New food was added several times daily to avoid spoilage. Larval survivorship was recorded as the number of pupae recovered from each host.

Preadult development and survival and size of pupae were determined for each host by randomly placing several hundred eggs on host pulp just prior to hatch. Fresh host material was added to each treatment as necessary. All hosts were set in perforated trays in shallow pans to allow pupation, and each day all pupae were collected, sized, and held for emergence.

Adult traits

From 15 to 60 pairs of newly eclosed adult flies reared from each host were placed in separate 30 cm³ screened cages for daily observations of mortality and fecundity. Two types of eggging recepticals were employed. The first was a half-slice of apple with the severed portion sealed

in paraffin. This host receptical was used until each cohort was fifteen days old. The second type was a perforated condiment cup containing a sponge soaked in fruit juice. These cups were used for the remainder of the experiments. The change in eggging recepticals was necessary to allow eggs to be frozen and shipped to Davis, California, USA, for counting.

Demographic and statistical methods

Demographic and life table methods used are described by Carey (1982, 1984) and Chiang (1984). Statistical correlations were performed using a Spearman rank statistical test (Zar 1974).

Results and discussion

Preadult parameters

Development and survivorship. Of the cohorts that produced pupae, larval survival ranged from 1% for those reared on apricot and papaya to 68% for those reared on blackberry (Table 2). These values are generally below those reported by Carey (1984). Larval survivorship was less than 20% for larvae reared on eight hosts, while larval survivorship on six hosts was 50% or greater. Three hosts with high survivorship (blackberry, raspberry, blueberry) are cultivated outside the present range of the medfly (Jennings 1979) and were not previously classified as in-situ medfly hosts (Christenson and Foote 1960).

Larval development times ranged from 6.9 days for larvae reared on tomato to 11.7 days for those reared on grape. The mean development time of larvae from three-quarters of all hosts was less than 10 days. Rivnay (1950) and Carey (1984) obtained similar results for medflies reared on many of these same hosts.

Pupal survivorship was 59 to 96% but was greater than 75% for those reared on about three quarters of all hosts. Pupal duration was between 8.5 and 11 days. Pupal survival and development reported here are in general agreement with those reported by Carey (1984).

Pupal size. Mean diameters of medfly pupae ranged from 1.71 (e.g. tomato) to 1.97 mm (e.g. lychee) (Table 2). Pupae with the largest mean diameters were recovered from cohorts reared from rutaceous hosts. The largest individual pupa recovered exceeded the diameter of the smallest by nearly 2-fold (Fig. 1). There was no significant correlation between mean pupal size and larval development time ($r_s = -0.003$, $P > 0.05$). Thus, larger pupae do not necessarily have longer larval developmental times.

Adult parameters

Survivorship. Life expectancy at eclosion was 22 days or greater for cohorts reared from 70% of the hosts (Table 3). Over 90% of the female cohorts reared on rosaceous hosts but less than 70% of cohorts reared on other hosts lived an average of 20 days or more. The average female fly from plum, which is the host that produced the longest lived flies, lived nearly twice as long as the average female from mammee apple, which produced the shortest lived flies (Fig. 2). The cohort reared from plum experienced neg-

Table 2. Larval and pupal survival (Surv.) and development (Dev.) in days and mean pupal diameter (Diam.) in mm for medflies reared on various fruit hosts

| Host | Larval | | Pupal | | | Preadult | |
|-----------------------|--------|--------------|-------|--------------|-----------------|----------|-------|
| | Surv. | Dev. (SD) | Surv. | Dev. (SD) | Diam. (mm) (SD) | Surv. | Dev. |
| Rosaceae | | | | | | | |
| Strawberry | 0.42 | 11.49 (1.65) | 0.67 | 9.00 (0.00) | 1.81 (0.13) | 0.28 | 20.49 |
| Plum | 0.58 | 7.78 (1.16) | 0.96 | 10.00 (0.27) | 1.89 (0.12) | 0.56 | 17.78 |
| Apricot | 0.01 | 9.80 (0.68) | 0.93 | 9.00 (0.00) | 1.87 (0.11) | 0.00 | 18.80 |
| Cherry | 0.63 | 9.70 (1.30) | 0.75 | 9.06 (0.23) | 1.87 (0.08) | 0.47 | 18.76 |
| Prune | 0.28 | 11.35 (1.87) | 0.97 | 10.43 (0.52) | 1.74 (0.15) | 0.27 | 21.78 |
| Peach | 0.09 | 7.51 (0.99) | 0.96 | 10.75 (0.48) | 1.73 (0.12) | 0.09 | 18.26 |
| Nectarine | 0.25 | 7.96 (0.87) | 0.92 | 9.50 (0.13) | 1.88 (0.12) | 0.23 | 17.46 |
| Pear | 0.47 | 8.72 (1.75) | 0.97 | 10.24 (0.29) | 1.81 (1.81) | 0.46 | 18.96 |
| Asian Pear | 0.07 | 11.82 (1.75) | 0.98 | 10.23 (0.48) | 1.83 (0.11) | 0.07 | 22.05 |
| Raspberry | 0.50 | 8.85 (1.49) | 0.63 | 10.35 (0.41) | 1.74 (0.13) | 0.32 | 19.20 |
| Blackberry | 0.68 | 8.40 (1.13) | 0.97 | 11.00 (0.39) | 1.71 (0.15) | 0.66 | 19.40 |
| Rutaceae | | | | | | | |
| Lemon | 0.21 | 11.42 (1.14) | 0.59 | 9.97 (0.49) | 1.85 (0.13) | 0.12 | 21.39 |
| Grapefruit | 0.15 | 8.35 (0.91) | 0.76 | 10.26 (0.38) | 1.88 (0.12) | 0.11 | 18.61 |
| Orange | 0.33 | 8.08 (1.05) | 0.97 | 10.05 (0.33) | 1.89 (0.10) | 0.32 | 18.13 |
| Other families | | | | | | | |
| Mango | 0.57 | 9.39 (1.82) | 0.97 | 8.99 (0.22) | 1.76 (0.11) | 0.55 | 18.38 |
| Papaya | 0.01 | 7.68 (0.92) | 0.92 | 9.50 (0.52) | 1.79 (0.12) | 0.00 | 17.18 |
| Blueberry | 0.56 | 8.30 (0.18) | 0.68 | 10.05 (0.51) | 1.71 (0.04) | 0.38 | 18.35 |
| Mammee Apple | 0.11 | 10.80 (1.54) | 0.75 | 10.24 (0.35) | 1.80 (0.12) | 0.08 | 21.04 |
| Avocado | 0.39 | 8.16 (0.88) | 0.99 | 8.78 (0.42) | 1.78 (0.11) | 0.39 | 16.94 |
| Fig | 0.19 | 8.22 (1.43) | 0.94 | 10.42 (0.49) | 1.79 (0.13) | 0.18 | 18.64 |
| Banana | 0.36 | 9.95 (1.27) | 0.65 | 10.44 (0.46) | 1.73 (0.12) | 0.23 | 20.39 |
| Lychee | 0.28 | 7.33 (0.68) | 0.75 | 9.00 (0.00) | 1.97 (0.08) | 0.21 | 16.33 |
| Tomato | 0.33 | 6.94 (0.90) | 0.73 | 10.00 (0.25) | 1.71 (0.13) | 0.24 | 16.94 |
| Grape | 0.13 | 11.74 (1.83) | 0.74 | 9.00 (0.00) | 1.84 (0.10) | 0.10 | 20.74 |

Table 3. Cohort size for females (F) and males (M) and life expectancy at eclosion (e_c) and at day 30 (e_{30}) (days) for adult medflies reared on different hosts

| Host | F | M | F Survivorship | | M Survivorship | |
|-----------------------|----|----|----------------|---------------|----------------|---------------|
| | | | e_c (SD) | e_{30} (SD) | e_c (SD) | e_{30} (SD) |
| Rosaceae | | | | | | |
| Strawberry | 15 | 11 | 24.21 (9.32) | 8.00 (5.35) | 22.95 (14.83) | 9.75 (2.86) |
| Plum | 38 | 32 | 32.21 (12.29) | 7.84 (11.10) | 26.85 (12.32) | 7.90 (8.58) |
| Apricot | 32 | 22 | 19.28 (9.62) | 5.15 (3.92) | 20.88 (10.11) | 3.74 (1.86) |
| Cherry | 51 | 43 | 23.72 (7.35) | 2.17 (2.82) | 20.93 (8.35) | 4.68 (4.70) |
| Prune | 58 | 45 | 24.47 (6.64) | 2.32 (2.92) | 26.96 (11.67) | 8.20 (8.22) |
| Peach | 50 | 50 | 28.73 (4.63) | 2.43 (2.64) | 24.86 (10.80) | 3.96 (3.86) |
| Nectarine | 51 | 52 | 28.88 (8.11) | 4.53 (4.83) | 30.18 (8.67) | 6.88 (5.00) |
| Pear | 51 | 48 | 25.14 (9.38) | 5.60 (7.53) | 25.98 (8.14) | 4.86 (3.02) |
| Asian Pear | 50 | 55 | 29.30 (10.65) | 10.18 (8.15) | 22.28 (9.53) | 3.87 (4.44) |
| Raspberry | 43 | 38 | 21.82 (15.31) | 12.23 (14.27) | 18.11 (10.53) | 3.10 (3.16) |
| Blackberry | 56 | 52 | 27.15 (9.47) | 5.67 (6.01) | 23.82 (7.94) | 6.88 (5.95) |
| Rutaceae | | | | | | |
| Lemon | 51 | 39 | 17.52 (9.31) | 3.17 (4.06) | 20.71 (16.44) | 14.48 (13.86) |
| Grapefruit | 15 | 16 | 21.40 (10.00) | 3.65 (0.48) | 15.99 (11.67) | 4.00 (0.00) |
| Orange | 47 | 50 | 21.16 (9.74) | 3.23 (3.05) | 21.54 (7.28) | 1.25 (2.17) |
| Other families | | | | | | |
| Mango | 51 | 63 | 23.58 (10.91) | 5.59 (7.02) | 17.11 (9.56) | 7.87 (5.90) |
| Papaya | 42 | 51 | 20.83 (10.61) | 5.48 (3.76) | 22.34 (10.39) | 5.92 (3.38) |
| Blueberry | 46 | 49 | 23.20 (6.89) | 3.59 (3.38) | 23.48 (8.85) | 5.92 (5.92) |
| Mammee Apple | 59 | 43 | 17.33 (10.20) | 6.86 (5.36) | 20.22 (12.83) | 10.10 (9.23) |
| Avocado | 57 | 63 | 28.96 (8.83) | 4.44 (3.73) | 21.61 (6.35) | 2.90 (2.55) |
| Fig | 41 | 42 | 25.95 (4.81) | 2.12 (1.87) | 31.27 (9.11) | 7.89 (5.26) |
| Banana | 51 | 34 | 19.03 (8.77) | 5.00 (3.27) | 14.83 (10.18) | 10.67 (1.25) |
| Lychee | 37 | 26 | 21.13 (9.66) | 2.15 (1.88) | 22.54 (6.85) | 3.67 (1.25) |
| Tomato | 63 | 40 | 25.39 (10.70) | 5.21 (3.18) | 23.54 (13.85) | 7.72 (7.31) |
| Grape | 22 | 21 | 26.20 (11.46) | 6.44 (7.64) | 23.96 (13.99) | 7.68 (10.24) |

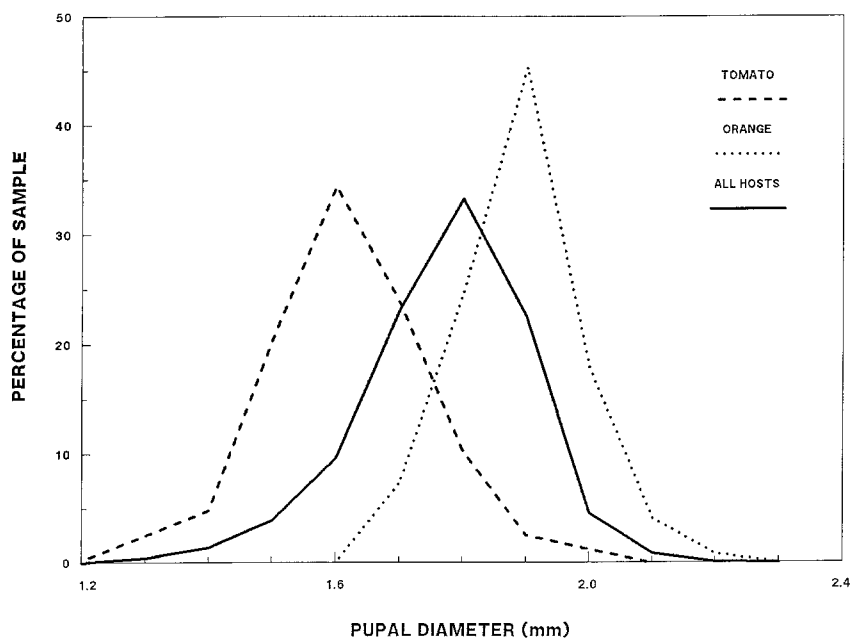


Fig. 1. Frequency distributions of pupal diameters for medflies reared on tomato (host that produced the smallest pupae), orange (host that produced among the largest pupae), and all hosts

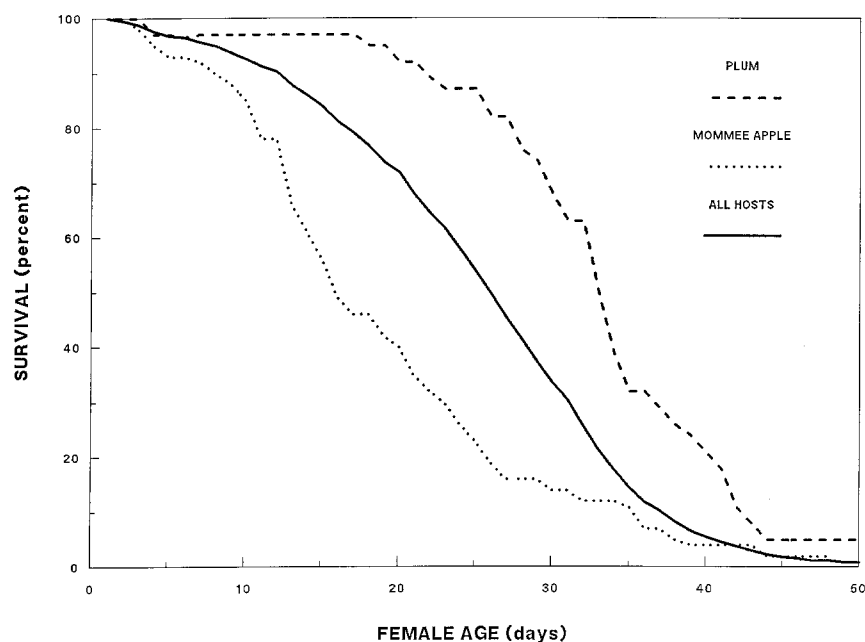


Fig. 2. Survivorship schedules for adult female medflies reared on plum (host producing the longest lived flies), mammee apple (host producing the shortest lived flies) and all hosts

ligible mortality the first 20 days while over 50% of the cohort reared from mammee apple died during this time period.

The expectation of life for females was correlated with that for males from the same host ($r_s = 0.51$, $P < 0.005$) but there were exceptions. For example, life expectancy of flies reared from asian pear favored females by about one week but life expectancy of flies reared from fig favored males by this same amount. Life expectancies for medflies in this study are in agreement with the findings of Bozzini and de Murtas (1975), Rossler (1975), and Shoukry and Hafez (1979).

Reproduction. Gross fecundity of females reared from three fourths of the hosts was between 490 and 690 eggs/female, and net fecundity of females reared from half of the hosts

was between 350 and 450 eggs/female (Table 4). The highest gross and net fecundity rates (from plum-reared flies) were twice the lowest rates (from banana-reared flies). Gross fecundity rates are similar to those reported by Shoukry and Hafez (1979) at equivalent temperatures, but are less than those reported by Carey (1984) at 25° C. This difference may have been due to temperature differences between studies (Rivnay 1950).

Age of first reproduction was 3 to 4 days for all cohorts (Fig. 3), which is similar to findings by Rivnay (1950), Abasa (1972), and Carey (1984). Mean age of gross fecundity was between 14 and 20 days for most cohorts with a peak on or before day 20 for flies reared from every host.

Daily egg production ranged from 8.5 eggs/female for flies reared from raspberry to 19.7 eggs/female for flies

Table 4. Reproduction parameters for medflies reared on different hosts

| Host | Fecundity | | Mean eggs ^a | | Mean age fec. ^b | |
|-----------------------|-----------|--------|------------------------|----------------|----------------------------|-------|
| | Gross | Net | Per Day | Per insect day | Gross | Net |
| Rosaceae | | | | | | |
| Strawberry | 494.47 | 361.40 | 10.75 | 14.93 | 16.73 | 12.16 |
| Plum | 1019.24 | 618.64 | 12.13 | 19.21 | 29.01 | 15.74 |
| Apricot | 576.09 | 362.68 | 13.72 | 18.81 | 14.98 | 11.13 |
| Cherry | 580.74 | 404.45 | 13.83 | 17.05 | 17.41 | 11.59 |
| Prune | 477.55 | 409.70 | 11.94 | 16.74 | 13.99 | 12.30 |
| Peach | 642.13 | 567.34 | 16.46 | 19.75 | 17.00 | 15.21 |
| Nectarine | 681.67 | 597.88 | 14.20 | 20.70 | 14.79 | 13.01 |
| Pear | 525.27 | 448.63 | 8.34 | 17.85 | 13.31 | 11.69 |
| Asian Pear | 469.47 | 417.80 | 6.61 | 14.26 | 13.39 | 11.65 |
| Raspberry | 517.74 | 297.03 | 7.19 | 13.61 | 19.28 | 12.11 |
| Blackberry | 681.08 | 372.35 | 11.54 | 13.72 | 26.71 | 15.18 |
| Rutaceae | | | | | | |
| Lemon | 550.62 | 304.21 | 12.81 | 17.36 | 16.57 | 11.03 |
| Grapefruit | 681.18 | 489.53 | 19.46 | 22.88 | 14.43 | 12.33 |
| Orange | 833.30 | 540.07 | 20.37 | 25.52 | 16.54 | 12.88 |
| Other families | | | | | | |
| Mango | 606.04 | 384.41 | 10.45 | 16.30 | 18.73 | 13.09 |
| Papaya | 830.58 | 519.12 | 18.06 | 24.93 | 16.88 | 12.76 |
| Blueberry | 492.51 | 388.96 | 11.73 | 16.77 | 14.94 | 11.92 |
| Mammee | 753.41 | 376.26 | 15.70 | 21.71 | 17.61 | 12.04 |
| Apple | | | | | | |
| Avocado | 718.99 | 585.68 | 16.34 | 20.22 | 16.08 | 13.04 |
| Fig | 596.49 | 533.78 | 16.12 | 20.57 | 14.04 | 12.46 |
| Banana | 407.85 | 241.82 | 10.20 | 12.71 | 16.55 | 12.36 |
| Lychee | 655.68 | 483.88 | 17.72 | 22.90 | 13.43 | 11.15 |
| Tomato | 646.29 | 466.74 | 14.36 | 18.38 | 17.41 | 14.28 |
| Grape | 561.04 | 420.59 | 10.79 | 16.05 | 16.63 | 14.08 |

^a Mean eggs per day is daily egg production by a medfly female living to the maximum possible age; per insect day is daily egg production weighted by females living at age x

^b Mean age gross fecundity is the mean age of egg production of a female living to the maximum possible age; mean age net fecundity is average age of egg production of females weighted by their survivorship

reared from orange. Daily egg production was strongly correlated with gross fecundity ($r_s = 0.72$, $P < 0.001$) but no significant correlation existed between gross fecundity and expectation of life ($r_s = 0.3$, $P > 0.05$). This suggests that flies with high fecundity produced more eggs because their daily production was higher and not necessarily because they lived longer. For example, the expectation of life for females reared from mammee apple was the lowest among all cohorts but their gross fecundity was the fourth highest. Conversely, the expectation of life for females reared from asian pear was second highest but their gross fecundity was second lowest.

No significant correlation existed between gross fecundity and pupal size ($r_s = 0.28$, $P > 0.05$). For example, mean pupal size for flies reared on peach and banana were the same, but gross fecundity of flies from peach was 40% higher. Although Krainacker (1986) found that large flies have higher fecundity than do small flies reared from the same host, the current findings suggest that size may not

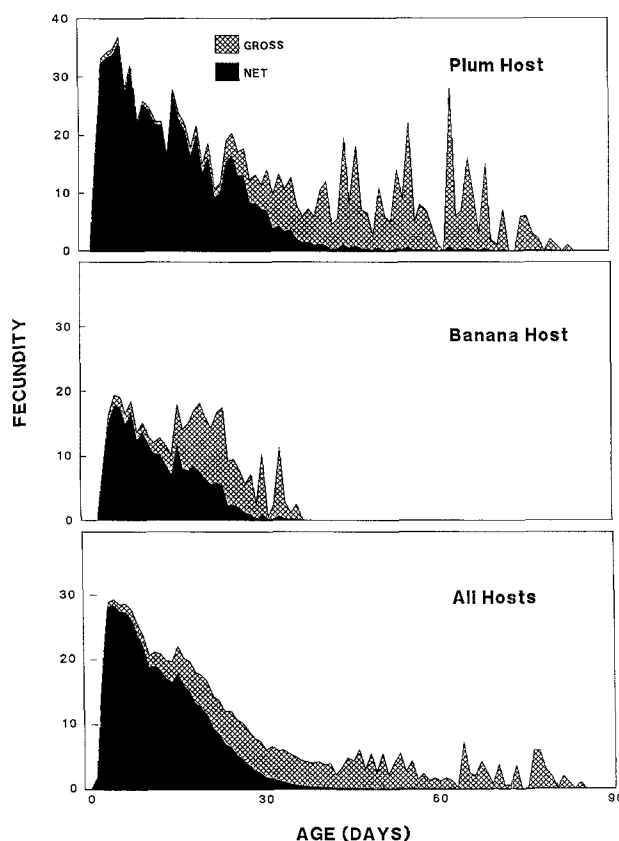


Fig. 3. Gross and net fecundity schedules for medflies reared on plum (cohort with highest gross fecundity), banana (cohort with lowest gross fecundity), and composite of all hosts

be the predominant factor in determining fecundity differences between flies reared from different hosts.

Population parameters

Net reproductive rate (R_0) for over half of all cohorts was less than 60 eggs (Table 5). However, R_0 -values varied widely, with the highest (plum-reared) exceeding the lowest (mammee apple-reared) by over 10 fold. Similarly, intrinsic rates of increase differed by 2-fold between plum-reared ($r = 0.17$) and mammee apple-reared ($r = 0.08$) cohorts.

Intrinsic birth rates were generally uniform (approximately 0.19), but tended to be lower in the rosaceous-reared cohorts. In contrast, intrinsic death rates ranged from 0.02 (blackberry) to 0.14 (apricot). Mean generation times ranged from 26.6 days for flies reared on lychee to 34.8 days for flies reared on grape. Mean generation times of cohorts reared on rosaceous hosts were consistently longer than 30 days. Doubling times ranged from 4.2 days on plum to 9.0 days on asian pear. The doubling time for nearly 70% of all cohorts was less than 6 days.

A rank ordering of medfly cohorts by host according to r -value (highest to lowest) is given in Table 6 along with the relative rank (1 to 24) for each of four major life history components typically associated with fitness (r) — preadult development time and survival and female expectation of life and fecundity. Several aspects of this table merit comment. *First*, the only consistent trend between r and any of the four demographic parameters was between preadult survival and r . Cohorts in the first quartile of r -values had

Table 5. Population parameters of medflies reared on different hosts

| Host | Growth rate ^a | | | | | Growth time ^b | |
|-----------------------|--------------------------|------|------|------|------|--------------------------|------|
| | R ₀ | r | λ | b | d | T | DT |
| Rosaceae | | | | | | | |
| Strawberry | 49.23 | 0.12 | 1.13 | 0.17 | 0.05 | 31.63 | 5.63 |
| Plum | 167.07 | 0.17 | 1.18 | 0.20 | 0.03 | 30.68 | 4.15 |
| Apricot | 16.37 | 0.09 | 1.10 | 0.23 | 0.14 | 30.28 | 7.51 |
| Cherry | 92.86 | 0.15 | 1.16 | 0.18 | 0.03 | 30.17 | 4.62 |
| Prune | 53.96 | 0.12 | 1.13 | 0.19 | 0.07 | 33.21 | 5.77 |
| Peach | 23.77 | 0.09 | 1.10 | 0.22 | 0.13 | 33.97 | 7.43 |
| Nectarine | 66.69 | 0.14 | 1.15 | 0.22 | 0.08 | 30.07 | 4.96 |
| Pear | 99.20 | 0.15 | 1.16 | 0.19 | 0.04 | 30.33 | 4.57 |
| Asian Pear | 13.80 | 0.08 | 1.08 | 0.20 | 0.12 | 34.07 | 8.97 |
| Raspberry | 45.38 | 0.13 | 1.13 | 0.18 | 0.05 | 30.48 | 5.54 |
| Blackberry | 119.19 | 0.15 | 1.16 | 0.17 | 0.02 | 32.02 | 4.64 |
| Rutaceae | | | | | | | |
| Lemon | 18.26 | 0.09 | 1.10 | 0.16 | 0.08 | 32.43 | 7.74 |
| Grapefruit | 26.36 | 0.11 | 1.12 | 0.22 | 0.12 | 30.13 | 6.38 |
| Orange | 83.85 | 0.15 | 1.16 | 0.21 | 0.07 | 29.81 | 4.67 |
| Other families | | | | | | | |
| Mango | 103.08 | 0.16 | 1.17 | 0.19 | 0.03 | 29.56 | 4.62 |
| Papaya | 57.80 | 0.13 | 1.14 | 0.21 | 0.08 | 30.14 | 5.15 |
| Blueberry | 71.83 | 0.14 | 1.16 | 0.19 | 0.04 | 29.67 | 4.81 |
| Mammee | 15.06 | 0.08 | 1.09 | 0.20 | 0.12 | 33.38 | 8.53 |
| Apple | | | | | | | |
| Avocado | 112.72 | 0.17 | 1.18 | 0.21 | 0.04 | 28.35 | 4.16 |
| Fig | 46.23 | 0.13 | 1.14 | 0.22 | 0.09 | 30.11 | 5.44 |
| Banana | 27.45 | 0.10 | 1.11 | 0.18 | 0.07 | 32.41 | 6.78 |
| Lychee | 49.28 | 0.15 | 1.16 | 0.23 | 0.09 | 26.67 | 4.74 |
| Tomato | 54.52 | 0.13 | 1.14 | 0.21 | 0.08 | 29.97 | 5.19 |
| Grape | 19.62 | 0.09 | 1.09 | 0.20 | 0.11 | 34.84 | 8.11 |

^a R₀ = net reproductive rate; r = intrinsic rate of increase (daily); λ = finite rate of increase (daily); b = intrinsic birth rate; d = intrinsic death rate

^b T = mean generation time (days); DT = population doubling time (days)

highest preadult survival and cohorts in the fourth quartile among the lowest survival. *Second*, host effects on other demographic determinants of r were inconsistent. For example, developmental time for blackberry-reared cohorts was one of the longest, yet were in the first quartile of r-values. Conversely, tomato-reared cohorts experienced the third shortest development time, yet were in the third r-value quartile. The adult parameters of survival and fecundity show similar inconsistencies when compared to r. *Third*, there are no relationships between those life history parameters that are commonly thought to be correlated. That is, long-lived flies did not necessarily produce more eggs, nor did flies with short larval development times have reduced larval survivorship. *Fourth*, r-values (as well as other demographic parameters) showed no trend within a taxonomic grouping. For example, r-values of medflies reared from many closely related species, specifically pear and asian pear, were within the first and fourth quartiles, respectively. Similarly, plum-reared cohorts had the second highest larval survivorship while apricot-reared larvae had the lowest even though both apricot and plum are in the genus *Prunus*.

Table 6. Rank ordering of medfly hosts by r-value for medflies reared from each and associated rank^a of four major host-specific life history traits: i) preadult development time; ii) preadult survival; iii) adult female survival; and iv) female fecundity

| Rank by r-value | Host | Preadult rank | | Adult rank | |
|--|--------------|---------------|----------|------------|-----------|
| | | Develop-ment | Survival | Survival | Fecundity |
| First quartile (r ≥ 0.150) | | | | | |
| 1 | Plum | 6 | 2 | 1 | 1 |
| 2 | Avocado | 2 | 6 | 3 | 5 |
| 3 | Mango | 10 | 3 | 14 | 12 |
| 4 | Cherry | 13 | 4 | 13 | 14 |
| 5 | Pear | 15 | 5 | 10 | 18 |
| 6 | Blackberry | 20 | 1 | 6 | 6 |
| Second quartile (0.130 ≤ r ≤ 0.149) | | | | | |
| 7 | Orange | 7 | 8 | 19 | 2 |
| 8 | Lychee | 1 | 15 | 18 | 9 |
| 9 | Nectarine | 5 | 13 | 4 | 6 |
| 10 | Blueberry | 9 | 7 | 15 | 21 |
| 11 | Raspberry | 17 | 8 | 16 | 19 |
| 12 | Papaya | 4 | 23 | 20 | 3 |
| Third quartile (0.100 ≤ r ≤ 0.129) | | | | | |
| 13 | Fig | 12 | 16 | 8 | 13 |
| 14 | Tomato | 3 | 12 | 9 | 10 |
| 15 | Strawberry | 16 | 10 | 12 | 20 |
| 16 | Prune | 23 | 11 | 11 | 22 |
| 17 | Grapefruit | 11 | 18 | 17 | 6 |
| 18 | Banana | 18 | 14 | 22 | 24 |
| Fourth quartile (r ≤ 0.099) | | | | | |
| 19 | Apricot | 14 | 24 | 21 | 15 |
| 20 | Peach | 8 | 20 | 5 | 11 |
| 21 | Lemon | 22 | 17 | 23 | 17 |
| 22 | Grape | 21 | 19 | 7 | 16 |
| 23 | Asian Pear | 24 | 22 | 2 | 23 |
| 24 | Mammee Apple | 19 | 21 | 24 | 4 |

^a Preadult development time ranked from shortest (i.e. no 1) to longest (i.e. no 24); all other traits ranked from highest to lowest values

Discussion

Population growth rate (r) is a parameter commonly associated with fitness (e.g. Lewontin 1965). In this study the intrinsic rate of increase was high (≥ 0.08) for medflies reared from all hosts studied. This is in spite of the broad range of values for the major parameters that determine r. For example, preadult survivorship ranged from 1 to 66%, female expectation of life ranged from 17 to 32 days, and gross fecundity ranged from 409 to 1019 eggs per female.

A major point here is that the value of a medfly life history trait that would tend to lower r was frequently offset by the value of another that would tend to increase it. Although the medfly may not possess the genetic capacity to evolve the maximal response for every life history constituent over a wide range of hosts, its collective response to a given host as expressed by r is uniformly high. For example, the low adult survivorship of flies reared from mammee apple was offset by high fecundity and the long development time of blackberry-reared flies was offset by high larval survival. We suggest that the compensation of life histo-

ry constituents is one reason that the medfly is such a successful generalist. This notion also has implications involving broader aspects of medfly life histories including maintenance of polyphagy and expansion of host range.

Maintenance of polyphagy

If population growth rate can be considered a measure of fitness, it may be instructive to ask why the medfly has not become specialized upon hosts that yield exceptionally high growth rates (i.e. plum). Specialization and host race formation has been suggested to occur in other tephritids (Bush 1969; Huettel and Bush 1972). Current plant-herbivore theory predicts host specialization to occur if: 1) differential fitness is observed on different host species; and 2) resource availability is predictable (Wiklund 1982). Condition 1 is clearly fulfilled in the medfly. However, Condition 2 may not apply. Although the fruiting seasons of many tropical and subtropical fruits are fairly predictable (Sampson 1980), a multivoltine, non-diapausing species such as the medfly is faced with several host environments throughout the year (Bateman 1972). For example, Wong et al. (1983) indicated that in Maui, Hawaii, the host environment changes from one dominated by loquat (*Eriobotrya japonica*) in winter to peach in spring and summer to fig in the fall. Minor hosts show similar fluctuations. Since successive generations (or even the same individuals) do not always have the same hosts available to them, long term selection for a particular host preference cannot occur.

Dethier (1980) suggested that mechanisms that allow for specialization on a given host decrease the ability to generalize. Based on Dethier's hypothesis, behavioral mechanisms that allow the medfly to discriminate among the mosaic of potential hosts in one environment may reduce fitness when that host environment changes. Rather, the medfly may be cueing on general fruit characteristics such as round shape or size (Nakagawa et al. 1978; Sanders 1968). Prokopy et al. (1984) found that medfly females from a population having access to a wide range of potential hosts (unpredictable through time) showed only slight differences in their ovipositional preferences. The differences were determined to be caused by a general cue (size) as opposed to a specific cue, such as host volatiles. These studies suggest that the medfly has not evolved mechanisms to discriminate finely among hosts. The lack of such mechanisms may contribute to the polyphagous nature of this species.

Expansion of host range

There were several hosts in this study in which the medfly was observed to oviposit, or has been reported to oviposit (Back and Pemberton 1918) but in which no larvae survived. Carey (1984) reported similar results with a wild strain of medflies from Greece. The tendency to oviposit in plants which cannot support larval growth is common among phytophagous insects (e.g. Chew 1975; Dowell and Steinberg 1979; Rauscher 1979). Wiklund (1975) attributed the tendency of *Papilio machaon* L. females to oviposit on plants outside the larval host range to the existence of two separate gene complexes controlling female ovipositional behavior and larval survival. A similar condition may exist for the medfly. However, the potential larval host range of the papilionids was apparently determined by larval food preference. In contrast, larvae in our study fed on all hosts

presented, suggesting that larval food preference may not be responsible for the host range in the medfly.

Futuyma (1983) suggested that once behavioral barriers to establishment on a new host are broken, evolution of physiological mechanisms to accommodate that host may occur rapidly. Two behavioral barriers – ovipositional preference and larval feeding tendency – have been broken in nearly all hosts presented to the medfly, including those on which the larvae cannot survive. The key component needed to expand the host range is physiological adaptation. The nearly indiscriminate ovipositional behavior of medfly females may be a mechanism by which host range is expanded. A small investment of reproductive effort in a novel host could expand host range if the larvae possess the physiological and genetic capacity to adapt to that host.

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