

- JIRON, L. F., AND J. SOTO-MANITUU. 1989. Field evaluation of attractants for the capture of *Anastrepha* spp. (Diptera: Tephritidae), pest of fruits in tropical America. III. Hydrolyzed protein and torula yeast. *Revista Brasileira de Entomologia*. 33: 353-356.
- LOPEZ-D, F., AND O. H. BECERRIL. 1967. Sodium borate inhibits decomposition of the protein hydrolysates attractive to the Mexican fruit fly. *J. Econ. Entomol.* 60: 137-140.
- LOPEZ-D, F., L. M. SPISHAKOFF, AND O. H. BECERRIL. 1968. Pelletized lures for trapping the Mexican fruit fly. *J. Econ. Entomol.* 61: 316-317.
- LOPEZ-D, F., L. F. STEINER, AND F. R. HOLDBROOK. 1971. A new yeast hydrolysate-borax bait for trapping the Caribbean fruit fly. *J. Econ. Entomol.* 64: 1541-1543.
- MALO, E. A. 1992. Effect of bait decomposition time on capture of *Anastrepha* fruit flies. *Florida Entomol.* 75: 272-274.
- MASON, L. J., AND R. M. BARANOWSKI. 1989. Response of Caribbean fruit fly (Diptera: Tephritidae) to modified McPhail and Jackson traps: effects of trapping duration and population density. *J. Econ. Entomol.* 82: 139-142.
- NEWELL, W. 1936. Progress report on the Key West (Florida) fruit fly eradication project. *J. Econ. Entomol.* 29: 116-120.
- SAS INSTITUTE. 1985. SAS/STAT guide for personal computers, version 6 edition. SAS Institute, Cary, North Carolina.
- SIMPSON, S. E. 1993. Caribbean fruit fly-free zone certification protocol in Florida (Diptera: Tephritidae). *Fla. Entomol.* 76: 228-233.
- SIVINSKI, J. 1990. Colored spherical traps for capture of the Caribbean fruit fly, *Anastrepha suspensa*. *Florida Entomol.* 73: 123-128.
- STEINER, L. F. 1955. Bait sprays for fruit fly control. *Agric. Chem.* 10: 32-34, 113-114.



LONGEVITY AND FECUNDITY IN THE CARIBBEAN FRUIT FLY (DIPTERA: TEPHRITIDAE): EFFECTS OF MATING, STRAIN AND BODY SIZE

JOHN M. SIVINSKI

Insect Attractants, Behavior, and Basic Biology Research Laboratory,
Agricultural Research Service, U.S. Department of Agriculture
Gainesville, FL 32604

ABSTRACT

There was no difference in the longevity of mated versus virgin female Caribbean fruit flies, *Anastrepha suspensa* (Loew), when kept without food. Females provided with food and kept with males lived a shorter period of time than single females, and females with larger males had a shorter lifespan than those kept with smaller males. Females provided with food and caged with large males did not have fecundity greater than those caged with small males. When protein was removed from the female diet, there was no difference between the fecundities of females mated to large and small males. The maximum fecundity of wild females in different size categories was correlated to thorax length. A similar analysis of longevity yielded a relationship that bor-

dered on significance. Domestic male lifespan was significantly related to size. Flies kept in colony for more than 15 years lived a shorter time than wild flies, but had greater lifetime fecundity.

Key Words: *Anastrepha suspensa*, lifespan, survival, egg production.

RESUMEN

No hubo diferencia en la longevidad de hembras pareadas comparadas a hembras vírgenes de la mosca caribeña de las frutas, *Anastrepha suspensa* (Loew) cuando estas se mantenían sin comida. Las hembras a las cuales se proporcionó de comida y que se contenían con machos vivían por un período más corto al compararse con hembras solitarias y hembras con machos más grandes tenían vidas más cortas que las que estaban con machos más pequeños. Las hembras las cuales se proporcionaba comida y las cuales se enjaulaban con machos grandes no tenían fecundidad más grande que las que fueron enjauladas con machos pequeños. Cuando se removió la proteína de la dieta de la hembra, no hubo diferencia en la fecundidad entre las hembras pareadas a machos grandes al compararse con machos pequeños. La fecundidad máxima de hembras silvestres en diferentes categorías de tamaño fue correlacionada a la largura del torax. Un análisis similar de longevidad dió una relación que acercaba significación. La longevidad de los machos fue significativamente relacionada al tamaño. Las moscas mantenidas en una colonia por más que 15 años vivían menos tiempo que moscas silvestres, sin embargo durante toda la vida su fecundidad fue mayor.

Male Caribbean fruit flies, *Anastrepha suspensa* (Loew), defend leaf territories within mating aggregations on host plants (Burk 1983). From these locations, they broadcast pheromones, acoustic signals and, probably, visual displays for approaching females (see Sivinski & Burk 1989). The behavior of females in the field, who sometimes orient toward displaying males and then leave without copulation, suggests that females discriminate among males and exercise mate choice. Laboratory studies have shown that males of choice are usually the larger of those available (Burk & Webb 1983), and that females are more likely to react to the acoustic signals typical of larger males (Sivinski et al. 1984). Why females choose larger males is unknown, though size may be correlated to beneficial genetic features. An alternative is that large males are better able to provide a material benefit or service to their mates. For example, a number of insects, including Diptera, provide nutrients in ejaculatory substances that females incorporate into their eggs or use for their own sustenance (e.g., Markow & Ankney 1984). It has been demonstrated that male-derived substance(s) move from the spermathecae to the ovaries and body of female Caribbean fruit flies (Sivinski & Smittle 1987).

There are unusual female behaviors in the Tephritidae that may have evolved because males transfer investments in their ejaculates. As male contributions toward mates or offspring increase, female competition for the best providers should increase (Trivers 1972). In extreme cases, behavioral role reversals occur where males choose mates and aggressive females fight over access to males (e.g., Gwynne 1983). In the laboratory, female Caribbean fruit flies frequently interfere with copulating pairs and appear to be attempting to interrupt copulations. Female Mediterranean fruit flies (*Ceratitis capitata* Wiedemann) approaching conspecifics perform an acoustic repertoire that is nearly identical to that of the male courtship signals (Arita & Kaneshiro 1983). It is possible that females are attempting to elicit courtship from particular males, i.e., advertising their presence to discriminating males who may pursue the courtship further.

This study presents experiments performed to determine if females used male ejaculatory substances to increase longevity. If males pass substances useful for their mates' egg production, larger males may contribute a more substantial investment. The fecundity of females who consorted with very large or unusually small males was also examined. Once these experiments were underway, it was found that other parameters of longevity and fecundity could be conveniently measured. Thus, additional observations were made to determine the effect of strain (wild and domestic) on longevity and the effect of female age on fecundity. Longevity and egg production of different sizes of females were also examined.

MATERIALS AND METHODS

Wild Caribbean fruit flies were reared from larvae collected in *Psidium guajava* (L.) picked in Dade County, Florida. Domestic flies were taken from a colony maintained at the USDA-ARS Insect Attractants, Behavior and Basic Biology Research laboratory, Gainesville, Florida, for more than 15 years. All adult flies were kept indoors at $25^{\circ}\text{C} \pm 1^{\circ}$, and on a 12:12 (L:D) photoperiod. At 1 day of age, adults were placed in cages consisting of 2 transparent plastic 500-ml cups stacked one on top of the other. The bottom cup contained water and was connected to the upper cup with a cotton wick that provided moisture for the flies. The upper cup was covered with a piece of fabric mesh. Food consisted of a mixture of 80% white granular sugar and 20% yeast hydrolysate enzymatic. This was provided to excess by filling a 1.5 cm diam plastic dish. Unless otherwise noted, fly mortality was checked daily. Moribund individuals were removed daily. When individual flies were kept for life with a member of the opposite sex, dead consorts were replaced weekly.

The following conditions were examined for their effects on Caribbean fruit fly longevity and fecundity:

Effects of Mating on the Survival of Starved Females

Male ejaculate materials have been found in the ovaries and body tissues of female Caribbean fruit flies 24 hours after insemination (Sivinski & Smittle 1987). Movement of this material may indicate a resource provided by the male to increase the number of eggs his sperm might fertilize. This could be accomplished by enhancing the nutrition of his mate. If this is the case, a possible effect of mating might be increased survival in the absence of another "food" source.

To test for differences in the longevity of starved flies that were either newly-mated or virgin, 32 caged female flies of the same age (10-15 d) were arranged in two 4×4 cage blocks. These cages contained no food. Males were introduced in one block of 16 females. When a female completed mating, the male was removed and the female in the corresponding position in the other block was set aside as a control. A total of 105 mated and 111 virgin flies were used (the difference in numbers is due to escapees). Mortality was checked daily on at least 3 occasions, at approximately 0800 hours, 1200 hours, and 1700 hours, until all flies in a replicate were dead. Statistical comparison of the mean longevity of mated and control flies was by t-test (SAS Institute 1987).

Effects of Mating and the Presence of Sexual Partners on Survival

To see if the presence of a sexual partner affected longevity when sugars and proteins were available, wild males and females were kept either isolated or with a sexual partner (from the domestic strain) until death. Thirty-eight wild males were kept without females and 41 were caged with females. Forty-six wild females each were kept with and without males.

Effect of Consort Size on Female Longevity and Fecundity

Males of different sizes were kept with females to determine if consort size affected longevity or fecundity and thus served as a basis for female choice of larger mates. In order to obtain consistently different sizes of flies, pupae were sorted with a mechanical device that separates pupae into different size and weight categories. Female pupae in the experiment had an average weight of 0.0088 g (SE = 0.0004), small males 0.0043 g (SE = .0007) and large males 0.0148 g (SE = .0007). An oviposition surface was provided in the following manner. Two 3.5-cm diam holes were cut in the lid of the previously described cages. One of these was covered with cloth mesh, and the other was filled by a piece of red-dyed beeswax-impregnated cloth. This was covered by a damp sponge and finally topped by a 5.5 cm diam petri dish. Flies oviposited freely into the wax and other locations in the cup. All eggs were counted weekly. Mortality was determined as described above. Seventy-seven females were paired with large males and 84 females were paired with small males. Comparisons of means were by t-test (SAS Institute 1987).

To maximize the effect of male nutritional contributions on fecundity, the above experiment was repeated using females that had been kept on an incomplete diet. Protein (yeast hydrolysate) was removed from holding cages when females were five days of age, and insects were given only white sugar (sucrose) tablets. When placed with males at age 10 days, they had been without protein for 5 days. Males were provided with the typical sugar and yeast diet. Flies were put into 57 large-male and 57 small-male cages and eggs were counted daily for 7 days. Females not laying eggs were discounted from further consideration. Adult male and female sizes were estimated by measuring the dorsal length of the thorax with an optical micrometer at 20 X. Analysis of data was by t-test and correlation (SAS Institute 1987).

It has been pointed out that studies of longevity based on individually caged insects often suffer from small sample size (Carey 1992). Samples of at least several hundred insects might be preferable. To compare data from single and mass-caged domestic Caribbean fruit flies, 785 flies (343 males, 442 females) were maintained at 65% RH and 12:12 (L:D) photoperiod in three 30 × 30 × 30 cm screen wire cages. Mortality was determined daily until all flies had died.

Effect of Age and Size on Fecundity and Longevity

Females of both strains were kept continuously with consorts chosen at random in cages as described above. Food, water and an oviposition surface were provided and eggs were counted weekly. Seventy-two wild and 71 domestic females were observed. Their body size was estimated by measuring the length of their thorax (from anterior margin of the prothorax to the posterior margin of the scutellum) with an optical micrometer at 20X magnification.

RESULTS

Effects of Mating on Starved-Female Survival

There was no difference between the longevitys of starved females that had mated and those that had not mated (\bar{x} not mated = 78.5 hrs (2.7), $n = 111$, \bar{x} mated = 82.5 hrs (3.2), $n = 105$; $t = 0.97$, $p = 0.33$).

Effects of Mating and the Presence of Sexual Partners on Survival

The lifespans of wild male flies accompanied by females did not significantly differ from those kept alone (\bar{x} without females = 46.8 (6.3), $n = 38$, \bar{x} with females = 54.6 (5.9), $n = 41$; $t = 0.9$, $p = 0.37$, Fig. 1). However, wild female flies kept with males

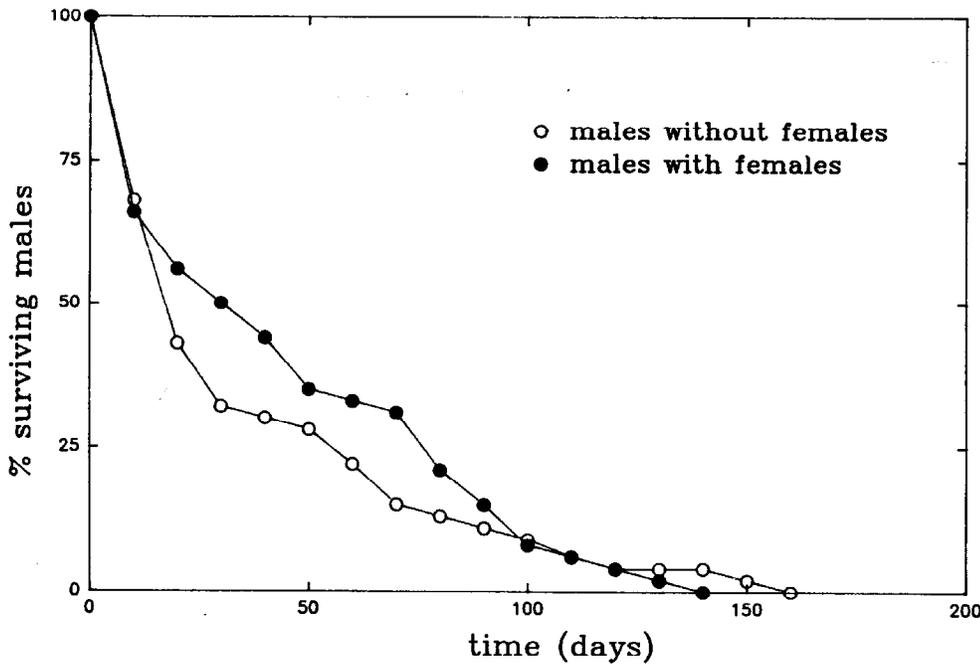


Fig. 1. The percent survival of Caribbean fruit fly males kept with females (black dot) and without females (white dot) over time.

had significantly shorter lifespans (\bar{x} without males = 115.7 (10.9), $n = 46$; \bar{x} with males 77.6 (4.6), $n = 46$, $t = 3.2$, $p = 0.002$, Fig. 2). A few solitary females lived an extended period of time. One lasted 1 day short of a year.

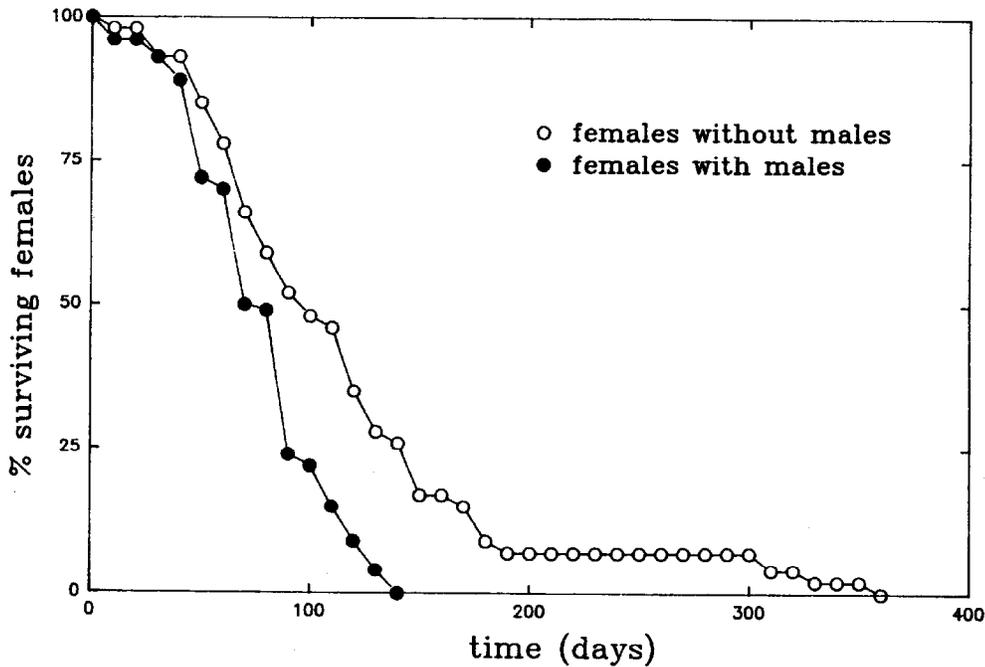


Fig. 2. The percent survival of Caribbean fruit fly females kept with males (black dot) and without males (white dot) over time.

Effect of Consort Size on Longevity and Fecundity

The size of the male consort(s) affected female longevity. Those kept with large males had a significantly shorter lifespan than those kept with small males (\bar{x} with large males = 52.6 (3.3), $n = 77$; \bar{x} with small males = 64.3 (2.9), $n = 84$; $t = 2.7$, $p = 0.009$). There was no significant effect of consort size on total egg production (\bar{x} with large males = 238.1 (25.1), $n = 77$; \bar{x} with small males = 281.7 (21.4), $n = 84$; $t = 1.3$, $p = 0.19$). Also, the number of eggs laid per day were not significantly different (\bar{x} with small male = 4.2 (0.3), $n = 84$; \bar{x} with large male = 3.7 (0.3), $n = 77$; $t = 1.3$, $p = 0.20$).

When protein-starved females were kept with large versus small males there was no difference in the numbers of eggs laid over 7 days (\bar{x} with small male = 39.2 (4.0), $n = 40$; \bar{x} with large male = 40.1 (4.6), $n = 46$; $df = 84$; $p = 0.88$). There was no significant correlation between male size (thoracic length) or a ratio of male/female size with the fecundity of their partners.

Effects of Size on Longevity and Fecundity

There was no significant correlation between thorax length and lifespan or total number of eggs laid in either wild or domestic flies. This was true even if presumably defective flies that lived less than 7 days or laid fewer than 50 eggs were deleted. However, there was evidence that the *potential* for fecundity and longevity increases with body size in wild flies. Insects with thoracic lengths ranging from 2.3 to 2.9 cm were divided into 6 size categories, i.e., 2.3 to 2.39 cm, 2.4 to 2.49 cm, etc. The maximum rate of daily egg deposition and longevity was taken in each category and correlated to size. The fecundity relationship was significant ($r = 0.86$, $p = 0.03$, Fig. 3), while that for lifespan was nearly so ($r = 0.79$; $p = 0.06$).

There was a significant correlation between size and lifespan in domestic males ($r = 0.36$, $p = 0.03$, $n = 37$) but not among wild males.

Effect of Age and Strain on Fecundity

Wild flies were significantly larger than flies obtained at random from the domestic colony (Table 1). In addition, wild flies were significantly longer lived (Table 1). However, domestic flies laid more eggs over their lifespan and had a higher daily rate of oviposition (Table 1). The difference between wild and domestic male longevity was much more pronounced than in females (Figure 4 & 5). Domestic males, on average, lived longer than wild ones (\bar{x} wild = 32.1 (6.1), $n = 48$; \bar{x} domestic = 102.9 (9.1), $n = 48$; $t = 6.5$, $p = 0.0001$).

DISCUSSION

Females are believed to choose mates on the basis of their genetic qualities, or their ability to materially invest in the female or her offspring (Thornhill & Alcock 1983). Male Caribbean fruit flies transfer substances to females that leave the sperm storage organs and migrate to the ovaries and body tissues (Sivinski & Smittle 1987). The nature and amount of these substance(s) are unknown but may increase female longevity and/or fecundity. If large males provided more of these substances than small males, then female choice of larger males might derive from the differential abilities of males to provide resources.

The predictions tested in this argument were: (1) females that have mated will have resources virgins do not, and in the absence of other nutrients, will have longer lifespans

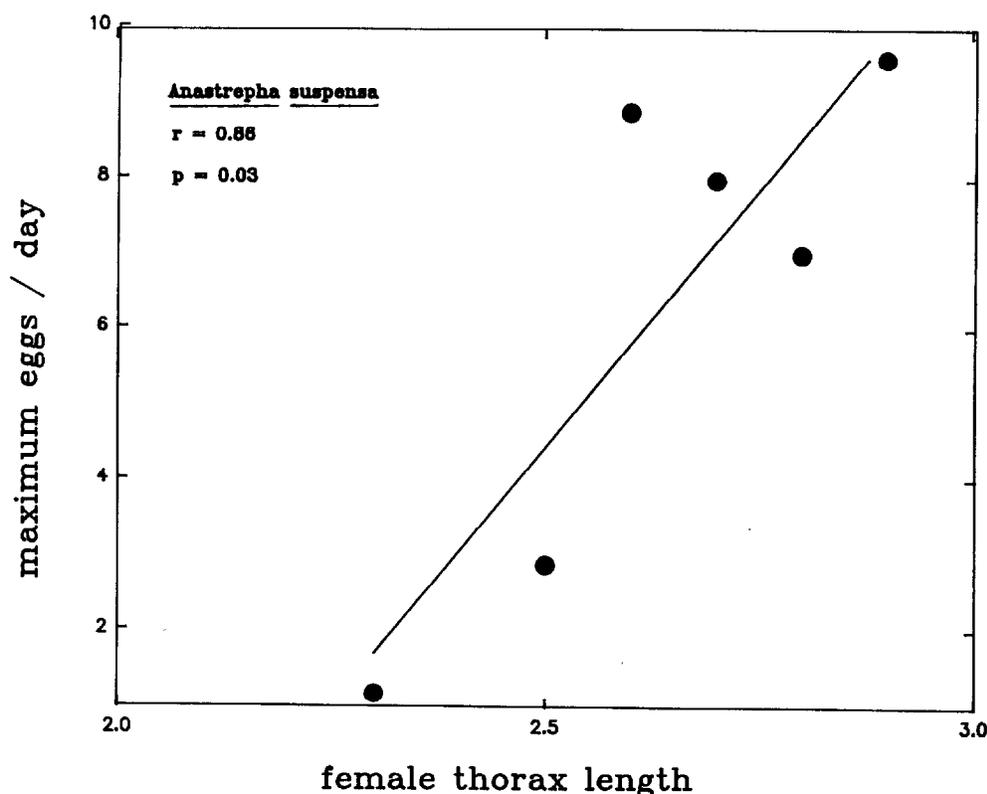


Fig. 3. The mean maximum number of eggs produced by Caribbean fruit fly females as a function of thoracic length.

than virgins, and (2) females that mate with large males will be more fecund than those that mate with small males. Neither of the above were supported in the experiments conducted.

Females kept with males lived a shorter period of time than did single females. This might be due to increased oviposition exhausting nutritional reserves (see Sivinski & Heath 1988). However, females kept with larger males lived a shorter time than those kept with small males, even though there was no difference in mean lifetime fecundity. It might be that harassment by courting males shortened lifespan and the advances of larger males were more exhausting than those of small males. In order to minimize the effect of being kept with another individual and maximize the importance of any nutritional substance donated by the male, females were separated after copulation and kept

TABLE 1. THE MEAN (SE) LIFESPAN, FECUNDITY AND SIZE OF FEMALE CARIBBEAN FRUIT FLIES OBTAINED EITHER FROM FIELD-COLLECTED FRUIT OR A COLONY MAINTAINED FOR OVER 15 YEARS.

	Wild Females	Domestic Females	t	P
Total eggs produced	161 (24.0)	237.0 (24.6)	2.2	.03
Eggs laid/day	1.9 (0.3)	3.8 (.04)	4.4	.0001
Lifespan (days)	73.6 (4.9)	55.0 (3.3)	3.1	.002
Size (thorax length)	2.71 (.02)	2.46 (.02)	8.4	.0001

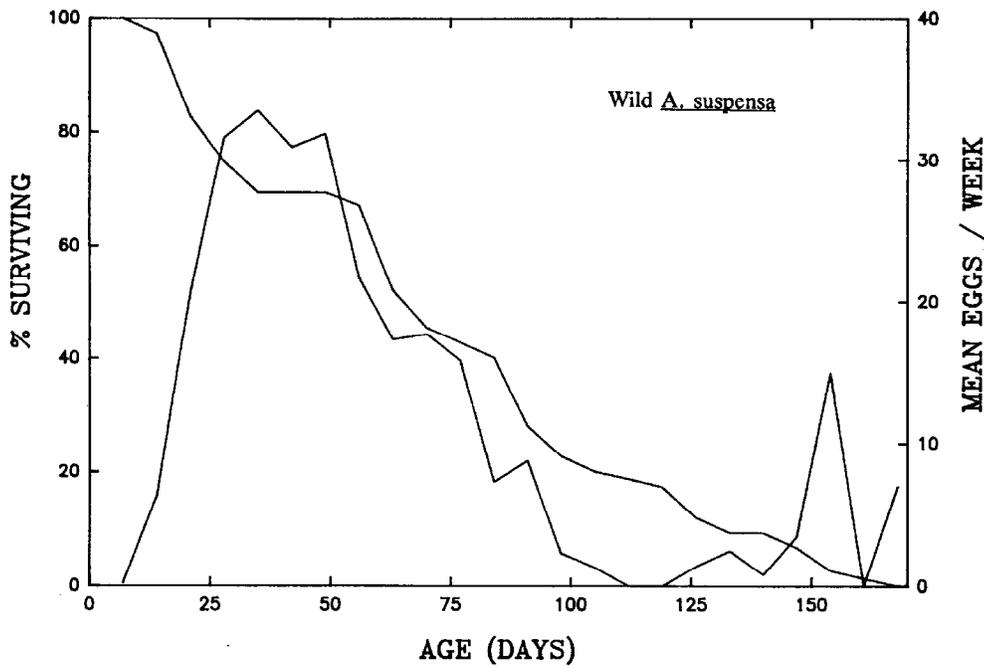


Fig. 4. The percent survival of wild Caribbean fruit flies over time and the average number of eggs laid as a function of time.

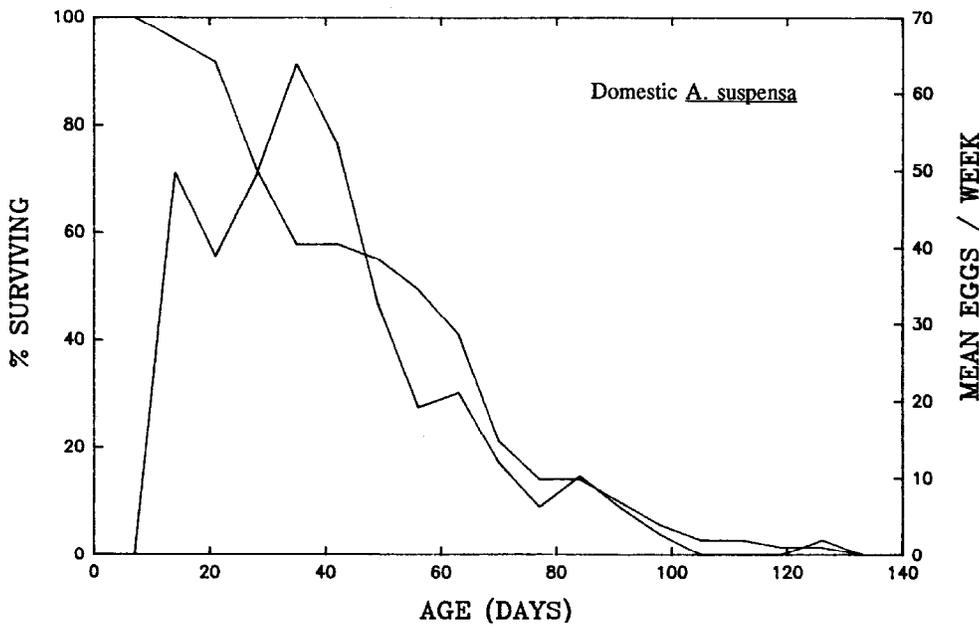


Fig. 5. The percent survival of domestic Caribbean fruit flies over time and the average number of eggs laid as a function of time.

without food. Again, there was no significant difference in the survival of mated and unmated females. There was no difference in the fecundity of females kept with large and small males and this was true whether or not protein was available.

Size is known to influence fecundity in a number of insect species (citations in Thornhill & Alcock 1988). There is considerable variance in the egg production of Caribbean fruit fly females, but the potential for daily egg production increases with size. Size is also often a factor in insect longevity (e.g., Van Dem Assam et al. 1989). Larger starved Mediterranean fruit flies *Ceratitis capitata* (Weid.) survive longer than smaller individuals (Bloem et al. 1992). Among fed wild female Caribbean fruit flies, there was a marginal relationship between lifespan and thorax length. A positive and significant relationship existed in domestic males.

Domestic female flies had greater egg production, which may result from years of adaptation to cages and wax oviposition devices and to intense selection to oviposit while young. Wild flies lived up to 1 year in age. These longevities are approached or equalled by other Tephritids (e.g., *Dacus oleae* (Gmelin) "close to a year," *Ceratitis capitata* (Wied.) "up to a year," *Anastrepha ludens* (Loew) "up to 9 months," *A. fraterculus* (Wied.) "3 to 5 months" (Fletcher 1989). A larger 785 fly sample of communally caged Caribbean fruit flies failed to uncover any extraordinary longevities that had not been discovered among the smaller number of individually caged flies. In fact, life spans were shorter in the larger sample and these data emphasize that different rearing conditions, including densities (see Nusbaum et al. 1993) may have considerable effect on longevity.

If there is no material benefit to mating with a particular male, the significance of female mate choice and apparent competition, remains undetermined. An alternative explanation is that there are genetic benefits to be obtained from certain males. Since copulations last an average of 30 minutes, the time the most attractive males with the "best genes" are available is limited and females might want to disrupt ongoing matings in order to replace the original female.

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REFERENCES CITED

- ARITA, L. H., AND K. Y. KANESHIRO. 1983. Pseudomale courtship behavior of the female Mediterranean fruit fly, *Ceratitis capitata* (Wiedman). *Proc. Hawaii Entomol. Soc.* 24: 205-210.
- BARINAGA, M. 1991. How long is the human life-span? *Science* 254: 936-938.
- BLOEM, K. A., S. BLOEM, AND D. L. CHAMBERS. 1987. Field assessment of quality: Release-recapture of mass-reared Mediterranean fruit flies (Diptera: Tephritidae) of different sizes. *Environ. Entomol.* (in Press).
- BURK, T. 1983. Behavioral ecology of mating in the Caribbean fruit fly, *Anastrepha suspensa* (Loew). *Florida Entomol.* 66: 330-344.
- BURK, T., AND J. C. WEBB. 1983. Effects of male size on calling propensity song parameters and mating success in Caribbean fruit flies (*Anastrepha suspensa* (Loew)). *Ann. Entomol. Soc. Am.* 76: 678-682.
- CAREY, J. R., P. LIEDO, D. OROZCO, AND J. W. VAUPEL. 1992. Slowing of mortality rates of older ages of large medfly cohorts. *Science* 258: 457-461.
- FLETCHER, B. 1989. Life history strategies of tephritid fruit flies, pp. 195-219 in A. Robinson and G. Hooper [eds.], *Fruit Flies: Their Biology, Natural Enemies, and Control*. Elsevier, Amsterdam.
- GWYNNE, O. T. 1983. Male nutritional investment in Tettigoniidae and other Orthoptera, pp. 337-366 in O. Gwynne and G. Morris [eds.], *Orthopteran Mating Systems*. Westview Press, Boulder, Colorado.

- MARKOW, T. A., AND P. F. ANKNEY. 1984. *Drosophila* males contribute to oogenesis in a multiple mating species. *Science* 224: 302-303.
- NUSBAUM, T. J., J. L. GRAVES, L. D. MUELLER, AND M. R. ROSE. 1993. Letter. *Science* 260: 1567.
- SAS INSTITUTE. 1987. Users guide: Statistics. SAS Institute, Cary, North Carolina.
- SIVINSKI, J., AND T. BURK. 1989. Mating behavior, pp. 343-351 in A. Robinson and G. Hooper [eds.], *Fruit Flies: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam.
- SIVINSKI, J., T. BURK, AND J. C. WEBB. 1984. Acoustic courtship signals in the Caribbean fruit fly *Anastrepha suspensa* (Loew). *Anim. Behav.* 32: 1011-1016.
- SIVINSKI, J., AND R. R. HEATH. 1988. Effect of oviposition on remating, response to pheromones, and longevity in the female Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.* 81: 1021-1024.
- SIVINSKI, J., AND B. SMITTLE. 1987. Male transfer of materials to mates in the Caribbean fruit fly, *Anastrepha suspensa* (Diptera: Tephritidae). *Florida Entomol.* 70: 233-238.
- TRIVERS, R. 1972. Parental investment and sexual selection, pp. 136-179 in B. Campbell [ed.], *Sexual Selection and the Descent of Man*. Heineman, London.
- THORNHILL, R., AND J. ALCOCK. 1983. *The Evolution of Insect Mating Systems*. Harvard University Press, Cambridge, Massachusetts.
- VAN DEN ASSEM, J., J. A. VAN DERSEL, AND R. L. LOS-DEN HARTOGH. 1989. Is being large more important for female than for male parasitic wasps? *Behavior* 108: 160-195.