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A Mortality Cost of Virginity at Older Ages in Female Mediterranean Fruit Flies

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Abstract

Mortality rates were measured over the lifetime of 65,000 female Mediterranean fruit flies, *Ceratitis capitata*, maintained in either all-female (virgin) cages or cages with equal initial numbers of males, to determine the effect of sexual activity and mating on the mortality trajectory of females at older ages. Although a greater fraction of females maintained in all-female (virgin) cages survived to older ages, the life expectancy of the surviving virgins was less than the life expectancy of surviving non-virgins at older ages. This was due to a mortality crossover where virgin flies experience lower mortality than mated flies from eclosion to Day 20 but higher mortality thereafter. These results suggest that there are two consequences of mating—a short-term mortality increase (cost) and a longer term mortality decrease (benefit).

Keywords: Mediterranean fruit fly, *Ceratitis capitata*, cost of reproduction, cost of mating, life tables, age-specific mortality

1. Introduction

The concept of mortality cost of mating and reproduction in insects is fundamental to ecology, evolution, population biology, and gerontology because it provides a framework for life history tradeoffs between reproduction and longevity (Bell and Koufopanou, 1986; Partridge and Harvey, 1988; Reznick, 1985). Altering longevity by manipulating reproductive activity has been used to study the evolution of aging and thus provides material for the study of its genetic mechanisms. Comparisons of male and female differences in mortality also shed light on the effects of sex-specific reproductive processes on life span (Carey and Liedo, 1995a,b).

Virgin insects are widely used in experiments concerned with the mortality effects of mating and reproduction since virginity is generally considered "cost free"; survival to older ages is usually greater for unmated than for mated individuals (Bell and Koufopanou, 1986; Bilewicz, 1953; Smith, 1958). An implicit assumption of virtually all studies concerned with cost of mating and reproduction is that because survival to older ages is higher in virgins than in non-virgins, mortality at older ages is greater in non-virgins. Because of the central importance of the reproductive and mating cost concept to theories of aging (Kirkwood and Rose, 1991; Rose and Charlesworth, 1980) and for understanding male-female mortality differentials (Hazzard, 1986, 1990), we conducted experiments to determine whether the effects of mating in females were beneficial at older ages relative to virginity, as reflected in mortality rates of virgin and non-virgin cohorts. The current paper builds on the general findings from previous research on the mortality dynamics of the Mediterranean fruit fly, *Ceratitidis capitata* (Carey, 1999; Carey and Liedo, 1999a,b; Carey et al., 1998, 1999; Müller et al., 1997a,b, 2001; Vaupel et al., 1998) including a recent modeling paper in which the data presented in this paper were used to test the hypothesis that oxidative damage accounted for differences in the mortality trajectory of virgin versus mated medflies (Novoseltsev et al., 2000).

2. Methods

We studied Mediterranean fruit flies at Moscamed, a large rearing facility in Metapa, Mexico, where we were provided with essentially unlimited numbers of pupae of the same age. The Mediterranean fruit fly strain currently reared at the facility was started from several hundred field-collected individuals in 1983 in Antigua, Guatemala, is maintained at 2–3 million breeding adults, and has a weekly pupal production rate averaging 500 million. Technical details on the production process, larval and adult diets, seeding densities, and environmental conditions are given in Carey (1999), Schwartz et al. (1981), and Vargas (1989). Adult flies in the trials were maintained under the following environmental conditions: 12:12 light/dark cycle, 24.0°C ($\pm 2^\circ$), and 65% relative humidity ($\pm 9\%$). Mediterranean fruit flies were maintained in each of two mesh-covered, 15 × 60 × 90 cm³ aluminum cages. Adults were given a diet of sugar and water, ad libitum, and each day dead flies were removed, counted and their sex determined.

For the experiments, around 1500 individuals of each sex were placed in one cage for monitoring death rates of females with access to males and 3000 females were placed in

another cage for monitoring death rates of females denied access to mates. We replicated this design 19 times to obtain mortality data on approximately 35,000 females maintained in all-female (virgin) cages and 30,000 females maintained in mixed-sex (non-virgin) cages. Cohorts that totaled over 30,000 flies were used to ensure that mortality rates at both young and old ages would be based on large numbers. Minor contamination of several all-female cages was discovered by the technicians while counting dead flies. A total of eight male Mediterranean fruit flies were found in cohorts intended to be all females. We made no adjustment in our analyses inasmuch as the number of male "contaminants" was extremely small relative to the total number of females (8 out of 35,162 or approximately 1 male in 4400 females).

For the estimation of trajectories of mortality, we used the statistical techniques as described in Müller et al. (1997b) and Wang et al. (1998), which allow to estimate a hazard rate from a cohort lifetable. For statistical testing each cohort was treated as an independent unit, as the flies within one cohort do not necessarily constitute an independent sample.

3. Results

The greater survival rate of virgin females relative to non-virgins was consistent with findings on other insect species (Bell and Koufopanou, 1986) as presented in table 1. For example, the survival rates to Day 20 for females maintained in mixed-sex and all-female cages were around 23% and 33%, respectively. The expectations of life at eclosion for females maintained in mixed-sex and all-female cages were 14.7 and 16.1 days, respectively. Thus the life expectancy difference between virgins and non-virgins was 1.3 days for females. The leveling off of mortality at older ages is consistent with the findings of a previous study on 1.2 million Mediterranean fruit flies (Carey et al., 1992).

Table 1. Number of female Mediterranean fruit flies alive at age x (N_x) and fraction of initial number surviving to age x (l_x) for cohorts maintained in either all-female or mixed-sex cages

Age	Mixed-sex		All-female	
	N_x	l_x	N_x	l_x
0	30,003	1.0000	35,162	1.0000
10	18,110	0.6036	22,394	0.6369
20	6837	0.2279	11,505	0.3272
30	2425	0.0808	3494	0.0994
40	757	0.0252	856	0.0243
50	236	0.0079	212	0.0060
60	55	0.0018	52	0.0015
70	4	0.0001	11	0.0003
80	0	0.0000	0	0.0000

The trajectories of age-specific mortality maintained under the two different mating regimes are shown for all 19 cohorts in figure 1 and as a composite in figure 2. Mortality rates for virgin females were slightly higher than for non-virgins at young ages. However, these

mortality differences had little impact on life expectancy differences because the absolute levels of mortality were low at the young ages. Mortality in virgin females increased to about 0.08 after 7 days, declined to about 0.06, and then increased again to about 0.13, where it remained relatively steady. Mortality in non-virgin females increased to 0.10 after about 8 days and then began leveling off. This early leveling off of non-virgins and the continual increase of mortality in virgins caused the two schedules to crossover at about 3 weeks so that the mortality of virgin females was 1–4% higher than mortality in non-virgins at older ages. Note that both virgins and mated flies show a peak of mortality around Day 10, indicating that both have a vulnerable period around this age (Müller et al., 1997 a,b), but at a much higher level of mortality for mated flies (probably reflecting “cost of mating”).

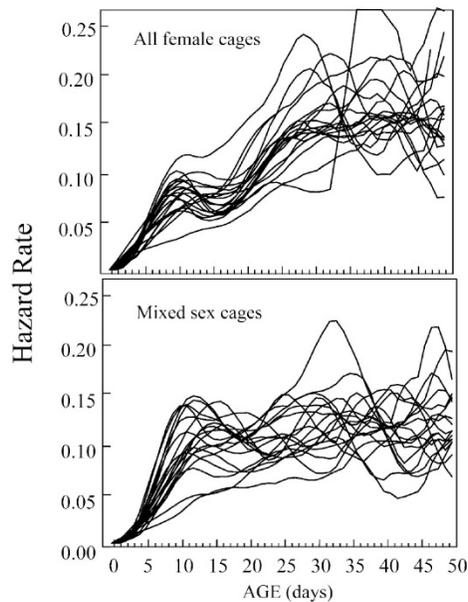


Figure 1. Smoothed hazard rates for 33 female Mediterranean fruit fly cohorts maintained in either mixed sex (a) or female-only (b) cages. Each curve is based on deaths in approximately 1000 flies.

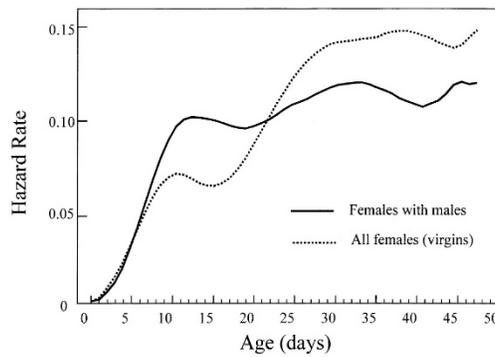


Figure 2. Mean hazard rates for the 33 female Mediterranean fruit fly cohorts shown in figure 1. Each curve is based on deaths in a total of over 33,000 individuals.

The mortality crossovers between cohorts of virgins and non-virgins at older ages for each sex reversed the life expectancy advantage. Female life expectancy advantage favored virgins only until Day 16, at which time it switched to non-virgins. At 50 days, the expectation of life for both virgin and non-virgin females was nearly identical. The death rates from 0 to 20 days of mated females were substantially higher than for unmated females, but from 21 to 45 days the death rates were considerably lower in mated females than in virgin females. χ^2 tests for differences in 5-day death rates between females maintained in mixed-sex cages and females in all-female cages were highly significant ($P < 0.001$) for all ages except 45–50 days. The effects on relative survival of 30-day-old females of the mortality crossover are shown in table 2. For example, over 30 and 9% of females maintained in mixed-sex cages (non-virgins) survived to 40 and 50 days, respectively, whereas around 25 and 6% of females maintained in all-female cages (virgins) survived to these respective ages. This is a reversal of relative survival of these two groups of females compared to young ages. Statistical comparisons of mean differences for virgin and mated females at selected ages are given in table 3. All comparisons are highly significant, with the first two (0 and 10 days) showing longer remaining lifetimes for the virgins and the latter two (20 and 30 days) showing longer remaining lifetimes for the mated flies.

Table 2. Number of female Mediterranean fruit flies alive at age x (N_x) and fraction of initial number surviving to age x (l_x , normalized using the number alive at 30 days (N_{30})) for cohorts maintained in either all-female or mixed-sex cages

Age	Mixed-sex		All-female	
	N_x	l_x	N_x	l_x
30	2425	1.0000	3494	1.0000
40	757	0.3122	856	0.2450
50	236	0.0973	212	0.0607
60	55	0.0227	52	0.0149
70	4	0.0016	11	0.0031
80	0	0.0000	0	0.0000

Table 3. Table of two-sample comparisons for log transformed average remaining lifetimes calculated for each cage, comparing cages with virgin and mated medflies (the means, variances, and standard deviations of the log average remaining lifetimes for the two groups, and the values of the *t*-test statistics and associated *P*-values are given below. The groups are defined as *V* = virgins and *M* = mated. The subscript *x* after *V* and *M* denotes that remaining lifetime after age *x* is considered; e.g., *V*₂₀ indicates the values for remaining lifetime life expectancy at Day 20 for virgins. The *t*-test is based on the transformed (natural log) average remaining lifetimes for each cage. If we ignore possible dependencies of lifetimes for flies raised within the same cage, all *P*-values are smaller than 0.0001).

Group Statistic	<i>T</i> > 0		<i>T</i> > 10		<i>T</i> > 20		<i>T</i> > 30	
	<i>V</i> ₀	<i>M</i> ₀	<i>V</i> ₁₀	<i>M</i> ₁₀	<i>V</i> ₂₀	<i>M</i> ₂₀	<i>V</i> ₃₀	<i>M</i> ₃₀
Mean	2.8013	2.7182	2.4762	2.3106	2.1323	2.2501	1.9926	2.1605
Variance	0.0110	0.0231	0.0196	0.0296	0.0216	0.0220	0.0125	0.0295
Standard deviation	0.1717	0.1050	0.1519	0.1399	0.1721	0.147	0.1483	0.112
<i>t</i> -test		1.96		3.25		-2.46		-3.57
df		36		36		36		36
<i>P</i>		0.0577		0.0025		0.0188		0.0010

4. Discussion

Higher survival rates of virgins relative to non-virgins have been reported in other insect studies including those on *Drosophila* (Fowler and Partridge, 1989; Smith, 1958); the housefly *Musca domestica* (Ragland and Sohal, 1973); the bruchiid beetle *Callosobruchus maculatus* (Tatar et al., 1994); the tribolium beetle *Tribolium castaneum* (Sonleitner, 1961, Mertz, 1975); grasshoppers, *Melanoplus* spp. (Dean, 1981); the bug *Dysdercus fasciatus* (Clarke and Sardesai, 1959); the leaf miner *Agromyza frontella* (Quiring and McNeil, 1984); the apple maggot fly *Rhagoletis pomonella* (Roitberg, 1989); and the moth *Ephestia kuhniella* (Norris, 1933). However, a study of *D. virilis* (Aigaki and Ohba, 1984) revealed that mating status has a reverse effect on survival of female and male flies—unmated females lived around 14% longer than mated females whereas unmated males lived about 12% shorter than mated males. A study on the backswimmer, *Corixa punctata* (Calow, 1977), and another study on *D. subobscura* (Lamb, 1977) reported no survival differences between virgin and mated individuals. We could find no studies on insects in which mortality rates of virgins and non-virgins were examined at older ages. However, our findings are similar to those on *Drosophila melanogaster* in which the cost of mating to the individual is an immediate but short-term increase in mortality at the time of mating (Partridge, 1986; Partridge and Andrews, 1985). The cumulative effect is to reduce the fraction of individuals that attain older ages.

There are several explanations for why the mortality rate of female Mediterranean fruit flies maintained in all-female cages crossed over the mortality rate of females Mediterranean fruit flies maintained in cages with males. One explanation is that the changing mortality pattern in each cohort was due to heterogeneity at the cohort level (Vaupel and Carey, 1993). That is, in cages where females were maintained with males, the most frail

females may have died at young ages due to mating costs and thus, the most robust subgroup of females (i.e., those with the lowest death rates) survived to the older ages (Vaupel et al., 1979).

A second explanation is that the differences in mortality patterns were an artifact of the particular environmental conditions. For example, it is possible that the longevity advantage would favor virgins over mated females throughout their lives if both mated and unmated females were given a protein source for food. For example, we found that the male-female mortality crossover occurred later and was less pronounced in cohorts provided with protein than in cohorts that were protein deprived (Müller et al., 1997a,b).

A third explanation for the relative changes in the mortality schedules of both treatments is that age changes in the reproductive biology and behavior of individuals alter their age-specific vulnerability and, in turn, the age-specific mortality trajectory. For example, it is possible that the short-term survival advantage of virgins may eventually disappear due to costs associated with the constant arousal and subsequent thwarting of the sex drive (Morris, 1955), due to the possible absence of protective hormones elicited by mating or reproduction (Engelmann, 1970), or due to the elicitation of costly behaviors associated with the opposite sex (Arita and Kaneshiro, 1983; Daly, 1978; Whittier and Shelly, 1993). For example, when Mediterranean fruit fly females are maintained as virgins several days beyond the optimum sexual maturation period, females begin to mimic the courtship actions of the male such as "pseudomale" behavior in Mediterranean fruit fly females (Arita and Kaneshiro, 1983; Morris, 1955).

A fourth explanation is that the findings are consistent with a protective effect of reproduction which comes to bear at later ages, as opposed to a fairly immediate cost of mating. For example, increased throughput of eggs with many eggs present in early oogenic stages may have a protective effect, so that in particular the flies which remain active in egg laying and reproduction are protected in older ages. This is consistent with earlier findings by Müller et al. (2001) that individual mortality is associated with the time-dynamics of the egg-laying trajectory in medflies.

The results of this study demonstrate that the implicit assumption from previous studies on the life expectancy of virgin fruit flies that mortality is lower in virgins at all ages is likely to be either incorrect or considerably more complicated than the idea that mortality differences over all age classes between virgin and non-virgin cohorts are constant. Additional studies are needed where the mortality rates of virgin and non-virgin cohorts are monitored over all ages before it is known whether the current results are general or restricted to medfly females.

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References

- Aigaki, T., Ohba, S., 1984. Effect of mating status on *Drosophila virilis* lifespan. *Exp. Gerontol.* 19, 267–278.
- Arita, L. H., Kaneshiro, K. Y., 1983. Pseudomale courtship behavior of the female Mediterranean fruit fly *Ceratitis capitata* (Wiedemann). *Proc. Hawaiian Entomol. Soc.* 24, 205–210.
- Bell, G., Koufopanou, V., 1986. The cost of reproduction. In: Dawkins, R., Ridley, M. (Eds.). *Oxford Surveys in Evolutionary Biology*. Oxford University Press, Oxford, pp. 83–131.
- Bilewicz, S., 1953. Experiments on the reproductive length of life of *Drosophila melanogaster*. *Folio. Biol.* 1, 177–194.
- Calow, P., 1977. Ecology, evolution and energetics: a study in metabolic adaptation. *Adv. Ecol. Res.* 10, 1–61.
- Carey, J. R., 1999. Population study of mortality and longevity with gompertzian analysis. In: Yu, B. P. (Ed.). *Methods in Aging Research*. CRC Press, Boca Raton, FL, pp. 3–24.
- Carey, J. R., Liedo, P., 1995a. Sex mortality differentials and selective survival in medfly cohorts: implications for human sex mortality differentials. *Gerontologist* 35, 588–596.
- Carey, J. R., Liedo, P., 1995b. Sex-specific life table aging rates in large medfly cohorts. *Exp. Gerontol.* 30, 315–325.
- Carey, J. R., Liedo, P., 1999a. Measuring mortality and reproduction in large cohorts of the Mediterranean fruit fly. In: Sternberg, H., Rimiras, P. S. (Eds.). *Studies of Aging*. Springer, Berlin, pp. 111–124.
- Carey, J. R., Liedo, P., 1999b. Mortality dynamics of insects: general principles derived from aging research on the Mediterranean fruit fly (Diptera: Tephritidae). *Am. Entomol.* 45, 49–55.
- Carey, J. R., Liedo, P., Orozco, D., Vaupel, J. W. 1992. Slowing of mortality rates at older ages in large medfly cohorts. *Science* 258, 457–461.
- Carey, J. R., Liedo, P., Müller, H.-G., Wang, J.-L., Vaupel, J. W., 1998. Dual modes of aging in Mediterranean fruit fly females. *Science* 281, 996–998.
- Carey, J. R., Liedo, P., Müller, H.-G., Wang, J.-L., Chiou, J.-M., 1999. Mortality oscillations induced by periodic starvation alter sex-mortality differentials in Mediterranean fruit flies. *J. Gerontol.: Biol. Sci.* 54A, B424–B431.
- Clarke, K. U., Sardesai, J. B., 1959. An analysis of the effects of temperature upon growth and reproduction of *Dysdercus fasciatus* Sign (Hemiptera, Pyrrhocoridae). *Bull. Entomol. Res.* 50, 387–405.
- Daly, M., 1978. The cost of mating. *Am. Nat.* 112, 771–774.
- Dean, J. M., 1981. The relationship between lifespan and reproduction in the grasshopper *Melanoplus*. *Oecologia* 48, 385–388.
- Engelmann, F., 1970. *The Physiology of Insect Reproduction*. Pergamon Press, Oxford.
- Fowler, K., Partridge, L., 1989. A cost of mating in female fruitflies. *Nature* 338, 760–761.
- Hazzard, W. R., 1986. Biological basis of the sex differential in longevity. *J. Am. Geriatr.* 34, 455–471.
- Hazzard, W. R., 1990. The sex differential in longevity. In: Hazzard, W. R., Andres, R., Bierman, W. L., Blass, J. P. (Eds.). *Principles of Geriatric Medicine and Gerontology*. McGraw-Hill, New York, pp. 37–47.
- Kirkwood, T. B. L., Rose, M. R., 1991. Evolution of senescence: late survival sacrificed for reproduction. *Phil. Trans. R. Soc. Lond.* 332, 15–24.
- Lamb, M. J., 1977. *Biology of Ageing*. Wiley, New York.

- Mertz, D. B., 1975. Senescent decline in flour beetle strains selected for early adult fitness. *Physiol. Zool.* 48, 1–23.
- Morris, D., 1955. The causation of pseudomale and pseudofemale behavior—a further comment. *Behavior* 8, 46–56.
- Müller, H.-G., Wang, J.-L., Capra, W. B., Liedo, P., Carey, J. R., 1997a. Early mortality surge in protein-deprived females causes reversal of sex differential of life expectancy in Mediterranean fruit flies. *Proc. Natl Acad. Sci.* 94, 2762–2765.
- Müller, H.-G., Wang, J.-L., Capra, W. B., 1997b. From lifetables to hazard rates: the transformation approach. *Biometrika* 84, 881–892.
- Müller, H.-G., Carey, J. R., Wu, D., Vaupel, J. W., 2001. Reproductive potential determines longevity of female Mediterranean fruit flies. *Proc. R. Soc. Lond. B* 268, 445–450.
- Norris, M. J., 1933. Contributions toward the study of insect fertility. II. Experiments on the factors influencing fertility in *Ephesia kuhniella*. *Proc. Zool. Soc. Lond.* 903, 342–354.
- Novoseltsev, V. N., Carey, J. R., Liedo, P., Novoseltseva, P., Yashin, A. I., 2000. Anticipation of oxidative damage decelerates aging in virgin female medflies: hypothesis tested by statistical modeling. *Exp. Gerontol.* 35, 971–987.
- Partridge, L., 1986. Sexual activity and life span. In: Collatz, K.-G., Sohal, R. S. (Eds.). *Insect Aging*. Springer, Berlin, pp. 45–54.
- Partridge, L., Andrews, R., 1985. The effect of reproductive activity on the longevity of male *Drosophila melanogaster* is not caused by an acceleration of ageing. *J. Insect Physiol.* 31, 393–395.
- Partridge, L., Harvey, P. H., 1988. The ecological context of life history evolution. *Science* 241, 1449–1455.
- Quiring, D. T., McNeil, J. N., 1984. Influence of intraspecific larval competition and mating on the longevity and reproductive performance of females of the leaf miner *Agromyza frontella* (Rondani) (Diptera: Agromyzidae). *Can. J. Zool.* 62, 2197–2203.
- Ragland, S. S., Sohal, R. S., 1973. Mating behavior, physical activity and aging in the housefly, *Musca domestica*. *Exp. Gerontol.* 8, 135–145.
- Reznick, D., 1985. Costs of reproduction: an evaluation of the empirical evidence. *Oikos* 44, 257–267.
- Roitberg, B. D., 1989. The cost of reproduction in rosehip flies *Rhagoletis basiola*: eggs are time. *Evol. Ecol.* 3, 183–188.
- Rose, M., Charlesworth, B., 1980. A test of evolutionary theories of senescence. *Nature* 287, 141–142.
- Schwarz, A. J., Zambada, A., Orozco, D. H. S., Zavala, J. L., Calkins, C. O., 1981. Mass production of the Mediterranean fruit fly at Metapa, Mexico, Florida *Entomol.* 68, 467–477.
- Smith, J. M., 1958. The effects of temperature and of egg-laying on the longevity of *Drosophila subobscura*. *J. Exp. Biol.* 35, 832–842.
- Tatar, M., Carey, J. R., Vaupel, J. W., 1994. Long term cost of reproduction with and without accelerated senescence in *Callosobruchus maculatus*: analysis of age-specific mortality. *Evolution* 47, 1302–1312.
- Vargas, R., 1989. Mass production of tephritid fruit flies. In: Robinson, A. S. & Hooper, G. (Eds.), *World Crop Pests. Fruit Flies: Their Biology, Natural Enemies and Control*. pp. 141–152. Amsterdam: Elsevier.
- Vaupel, J. W., Carey, J. R., 1993. Compositional interpretations of medfly mortality. *Science* 260, 1666–1667.
- Vaupel, J. W., Manton, K. G., Stallard, E., 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16, 439–454.

- Vaupel, J. W., Carey, J. R., Christensen, K., Johnson, T. E., Yashin, A. I., Holm, N. V., Iachine, I. A., Kannisto, V., Khazaeli, A. A., Liedo, P., Longo, V. D., Zeng, Y., Manton, K. G., Curtsinger, J. W., 1998. Biodemographic trajectories of longevity. *Science* 280, 855–860.
- Wang, J.-L., Müller, H.-G., Capra, W. B., 1998. Analysis of oldest-old mortality: life tables revisited. *Ann. Stat.* 26, 126–163.
- Whittier, T. S., Shelly, T. E., 1993. Productivity of singly vs. multiply mated female Mediterranean fruit flies, *Ceratitis capitata* (Diptera: Tephritidae). *J. Kansas Entomol. Soc.* 66, 200–209.