



## Effect of physiological state of young *Ceratitis capitata* females, on resource foraging behavior

Hadass Cohen & Hillary Voet

Hebrew University, P.O. Box 12, Rehovot 76100, Israel (E-mail: hadassc@bezeqint.net)

Accepted: September 5, 2002

**Key words:** food resources, foraging behavior, *Ceratitis capitata*, Diptera, Tephritidae, physiological state

### Abstract

We investigated the influence of the physiological state of young female *Ceratitis capitata* (Diptera: Tephritidae) on resource foraging behavior and mating propensity in field cage studies. Three kinds of diets were supplied prior to release on host plants: (1) 2% sucrose, (2) 20% sucrose, and (3) protein hydrolysate. Laboratory-cultured *C. capitata* females of different ages, ranging between 3–9 days old, were released in field cages containing two potted citrus tree seedlings, each consisting of either proteinaceous or carbohydrate sources. Flies 3–7 days old, exposed to 2% sucrose, showed no preference for either source, while other groups, at the same age, displayed a significant influence of diet. Conversely, the behavior of flies within the age 8–9 days old was governed only by their reproductive needs, all three groups being significantly attracted to protein. In additional field-cage studies, mating propensity of similar groups was observed. Copulation was significantly higher among immature flies fed on proteinaceous diet than those exposed to carbohydrate sources prior to their release.

### Introduction

Adult tephritids fruit flies acquire necessary nutrients for survival and reproduction from a large variety of food sources in the environment, mostly carbohydrates and proteins (Christenson & Foot, 1960; Bateman, 1972; Hendrichs & Hendrichs, 1990; Hendrichs et al., 1991; Warburg & Yuval, 1997). When foraging, they encounter resources that differ in distribution, abundance, and quality. Adjustments in behavior of individuals to such variability may affect their foraging efficiency and reproductive success. Factors that might influence those activities which have been studied for tephritid fruit flies include: genetics (Prokopy et al., 1984; Papaj et al., 1987), the physiological state of adults (Malavassi & Prokopy, 1992; Averill & Prokopy, 1993), and the previous experience of individuals (Papaj & Prokopy, 1989; Prokopy et al., 1989b; Averill et al., 1996). This last aspect has been studied in particular for the Mediterranean fruit fly, *Ceratitis capitata*, through consideration of effects of quality and availability of food on foraging behavior (Prokopy et al., 1987; Prokopy & Roitberg, 1989;

Hendrichs & Hendrichs, 1990). Studies of several species focusing on factors determining responses to specific attractants and phagostimulants, showed that both feeding history and age had an effect. In *Anastrepha ludens*, protein hunger dramatically increased attraction to bacterial volatiles. Sugar hunger, whether age-dependent or deprivation-induced, caused more attraction of flies to a fruit-derived bait than to proteinaceous lures (Robacker, 1991; Robacker & Garcia, 1993; Robacker & Moreno, 1995). In the Mediterranean fruit fly, protein-deprived females responded more readily to protein than did protein-fed flies (Prokopy et al., 1992; Cangussu & Zucoloto, 1995). A similar response was seen in *Rhagoletis pomonella* (Malavassi & Prokopy, 1992; Prokopy et al., 1993) and *Dacus cucurbitae* (Lui et al., 1995).

With these findings as background, this report further evaluates the effect of the physiological state of the Medfly immature female, prior to egg maturation (Hanna, 1938; Williamson, 1989), on two elements of their behavior: feeding and copulation. Generally, females' willingness to copulate or their receptivity is known to be affected by their physiological state

(Ringo, 1996). Available knowledge on sexual behavioral patterns of Mediterranean fruit flies, as reflected from their resource feeding behavior, has been acquired mainly for males, with hardly any work having been done on females (Yuval & Hendrichs, 2000).

The emphasis in our study on immature females hinges on the assumption that these flies may be of special importance for future development of management strategies aimed towards controlling the buildup of populations at the beginning of the season. Heath and co-workers (1995, 1997), found a high percentage of unmated Mediterranean females (by checking egg maturation), captured in traps baited with food-based synthetic attractants. In the current study, we assess the preferences of laboratory-cultured flies to sugar or protein resources and their propensity to mate, in field cage experiments. Studies on laboratory cultures are the first step prior to tests with wild flies. There is a strong carryover effect of high larval protein into adulthood, and this needs to be borne in mind when interpreting data from laboratory-bred flies. Nevertheless, the quantitative effects we report are robust. Furthermore, it has been shown that medflies from laboratory cultures responded to host-fruit associated stimuli similarly to wild flies (Prokopy et al., 1989a; Papaj et al., 1987). Using laboratory strains allow us to control the status, genotype, and numbers of flies being used in tests. The objectives of this work were to address the following factors: (1) the hierarchies of feeding decisions associated with the behavioral patterns of *C. capitata* immature females, (2) the factors governing mating propensity of that age range, both as affected by type of diet and age.

#### Materials and methods

Flies used in field cage tests originated from a laboratory colony, reared at the fruit fly facility of the Israeli Citrus Board. The strain used, designated 'Sade', has been routinely refreshed with natural males by introducing them into mating cages. Larvae were fed a standard diet of bran, sugar, and yeast. One hundred pupae selected according to date of pupation were used for each test. Pupae were maintained at 25 °C and L14: D10 photoperiod, in 30 × 30 × 30 plastic screened cages. Emerging flies were segregated by sex and provided with different experimental diets.

All series of screen field cage experiments involved two parameters, diet and age. Three different types of diet were supplied to females: (1) a low concentrated

carbohydrate diet, containing 2% sucrose in distilled water (Nitzan, 1981), (2) near-optimal carbohydrate diet, containing 20% sucrose in distilled water (Warburg & Galun, 1992), and (3) a protein diet, consisting of yeast hydrolysate and sucrose (1:2). The yeast hydrolysate (INC Biomedicals Inc) contained 60% protein enriched with vitamins and minerals. Flies had free access to all diets, which were provided on soaked cotton wool up to the time of testing. Four age groups were identified: (1) 1–3 days (post emergence), (2) 4–5 days, (3) 6–7 days, and (4) 8–9 days in accordance with the different stages of egg maturity as described by Hanna (1938) and, with more detail, by Williamson (1989). The first two groups represent females containing immature eggs, whereas the two other groups represent stages of egg maturation within the female ovary.

All field-cage trials were carried out from 08:00–15:00 h, in 2 m tall × 2 m<sup>2</sup> surface clear nylon screen field cages. Two potted orange seedling trees (30 cm canopy in diameter and 90 cm high) were located (an opposite side) of the cage. Each seedling accommodated a 5 cm diameter cotton wool patch, containing either one of the two offered sources: 20% sucrose in distilled water or 5 g. protein hydrolysate in water. Food dye coloring (in concentrations of 20%–25%) was added to each food source, either red (E-122 preserving material) or green (consisting of blue No. 1 plus yellow sunset) (Elite Industries Ltd, Ramat-Gan, Israel) as food source markers.

Three experimental series were conducted in field cages, with different groups of flies selected according to the two variables described above: (a) control trials, (b) two-choice foraging tests, and (c) mating propensity observations. In each trial, 50 males and 50 females were aspirated from plastic cages and released into the field screen cages. After 6–7 h, all flies were collected and chilled at 3 °C for 5–7 min. Subsequently, the presence of dye in their abdomen was determined, indicating their choice of food. On average, only 5% of flies showed mixed colors (indicating double feeding). These were excluded from the data.

**Control trials.** These included two tests: color preference and attraction to patches containing water versus one of the two food sources. The first test offered released females a choice of two colors of food dye, red or green, provided on water soaked cotton wool, excluding food resources. The flies participating in this experiment were collected from the two well-fed groups supplied with either 20% sucrose or protein,

prior to their release. The second test offered two differently colored patches: one consisting of water and the other of either sugar or protein. Flies participating in these experiments were collected from one diet group only 20% sucrose. The group of 4–5 days old females was the only 'age group' involved in all control tests. Number of replicates varied from 3–4 per test.

**Foraging behavior.** Three series of tests involving two age groups were each conducted for a specific prerelease diet group: 2% sucrose, 20% sucrose, or protein. The number of replicates varied from 4–6 per test.

**Mating propensity.** The observations included three series of tests similar to the foraging tests, involving all three diet groups but only two age groups: 4–5 and 8–9 days old. In each test, 50 males and 50 females were released into field cages. Mated pairs were collected once an hour throughout the trial.

**Statistics.** Data were analyzed by Student *t* test comparisons and by multifactorial analysis of variance, followed by pairwise comparisons with the LSD test. The number of females marked by one of the two colors was expressed as the mean number of live flies ( $\pm$ SEM) collected at the end of each experiment. Data were transformed to square root ( $x+1$ ) to stabilize their variance. A significance level of 0.05 was used for all statistical tests. The SAS software (6.12) was used for all statistical analyses.

## Results

**Control trials.** Results from the trial checking the first factor, response of young females to colors, indicated no preference for either of the tested colors, regardless of the food source associated with the color (Table 1). The second factor, attraction to food, showed significantly lower numbers of flies responding to pure water patches, only 11–12%, in comparison to 50% and 70% females responding to patches containing water solutions of sugar and protein, respectively (Table 2). Neither factor, color or food, showed a significant influence on young females' feeding behavior.

**Foraging behavior.** In the second series of experiments we studied the effect of two main factors, age

and diet, on foraging behavior of young females. Each main factor was tested at three levels. The two-way analysis of variance revealed a significant interaction between age and diet on the foraging behavior of young females ( $F_{4,23}=5.33$ ;  $P=0.0003$ ). Females within the age ranges of 2–3 and 4–5 days old, fed with enriched prerelease diets containing 20% sucrose or protein, showed a consistent trend of feeding on sugar rather than on protein (Table 3). In the same age ranges, deprived females fed on 2% sucrose did not show any preference for sugar or protein sources. In the succeeding age group, 6–7 days old, both 2% and 20% sucrose-fed females responded similarly to the two food sources, in contrast to the third group, protein-fed females, which showed a definite preference for sugar. As they aged (8–9 days old), all females, regardless of their prerelease diets, showed a significant preference for the proteinaceous source (Table 3).

**Mating propensity.** The number of mated couples among flies fed on carbohydrate diets (2% and 20% sucrose), within the younger age range (4–5 days), differed significantly from their siblings fed on protein diet. Copulation among protein-fed females averaged 31% in comparison to only 16% among protein deprived females (Table 4). Two-way analysis of variance revealed no interaction between age and diet but did show a significant influence of diet ( $F_{2,21}=4.53$ ;  $P=0.023$ ) on mating behavior. Older females within the age range of 8–9 days old did not differ significantly among diet groups, in their propensity to copulate.

## Discussion

Our results indicate a significant influence of the nutritional state of the individual young female on both its foraging and mating behavior (Tables 3 and 4). We will first discuss results referring to foraging behavior studies. Young females reared on various diets responded differently to the two food sources offered. Medfly females fed either 20% sucrose or protein prerelease diets of 3–5 days old showed a significant preference for sugar rather than for protein (Table 3). The high tendency at females that age range to feed on sugar is consistent with previous studies suggesting carbohydrate is an essential element in the diet of young medfly females (Galun et al., 1985; Nestel et al., 1985). Furthermore, carbohydrate feeding

Table 1. Preference of *C. capitata* sugar or protein fed females (4–5 days old) for one of two colors used as food source markers in field cage trials

Prerelease diet	No. replicates	Attractant	% feeding individuals (Mean±SEM)	P
20% sucrose	3	Green	24.2 ± 2.5	0.1994
20% sucrose		Red	30.7 ± 6.0	
Protein		Green	29.0 ± 10.1	0.7033
Protein		Red	16.2 ± 5.2	

Table 2. Attractiveness of *C. capitata* carbohydrate fed females (4–5 days old) to 'wet patches' soaked with only water or water with additional food resource (either 20% sucrose or yeast hydrolysate)

Attractant	No. replicates	% feeding individuals (Mean±SEM)	P
20% sucrose	4	50.5 ± 13.2	0.017
Water		11.2 ± 2.6	
Protein	3	70.0 ± 16.4	0.006
Water		12.1 ± 7.9	

Table 3. Attraction to sugar (versus protein) by *C. capitata* females of different ages following different prerelease diets (Mean±SEM of % attracted to sugar) (in brackets, Mean±SEM number of females responding to treatments is indicated). In the bottom line mean, the significance of difference from 50% is given

Age (days)	2% sucrose	20% sucrose	Protein
2–3	43.3 ± 2.98b	75.24 ± 5.80a	77.97 ± 5.54a
	(61.7 ± 6.7)	(71.0 ± 5.5)	(52.8 ± 4.2)
	P = 0.3902	P = 0.0002	P = 0.0004
4–5	39.01 ± 5.92b	70.51 ± 4.93a	70.60 ± 7.86a
	(59.8 ± 4.0)	(63.2 ± 6.4)	(73.6 ± 13.3)
	P = 0.0986	P = 0.0023	P = 0.0038
6–7	47.10 ± 2.63b	34.95 ± 2.19b	81.65 ± 5.27a
	(49.4 ± 3.2)	(68.8 ± 8.6)	(51.9 ± 3.5)
	P = 0.7128	P = 0.0825	P = 0.0001
8–9	22.06 ± 8.56a	13.28 ± 4.47a	34.49 ± 6.19a
	(62.0 ± 5.3)	(51.4 ± 3.1)	(64.4 ± 2.5)
	P = 0.0002	P = 0.0001	P = 0.0248

\*Means followed by the same letter did not differ significantly ( $P < 0.05$ , LSD) within the same row.



Table 4. Differences in rate of courtship among *C. capitata* females of two age groups fed on 3 types of diets prior to their release in field cages

Age (no. days)	No. replicates	Prerelease diet	Mean $\pm$ SEM % mated individuals	P
4-5	5	2% sucrose	16.4 $\pm$ 3.2b	0.0207
	5	20% sucrose	16.3 $\pm$ 2.5b	
	5	Protein	31.4 $\pm$ 5.4a	
8-9	4	2% sucrose	20.3 $\pm$ 4.3a	0.3200
	4	20% sucrose	20.4 $\pm$ 3.2a	
	4	Protein	27.5 $\pm$ 3.3a	

Columns marked with the same letter are not significantly different (t-test,  $P=0.05$ ).

has been shown to be associated with longevity of Medfly females, prior to egg production (Cangussu & Zucoloto, 1992) has also been indicated for *Anastrepha serpentina* (Jacome et al., 1999). Nevertheless, age-related patterns of feeding vary among different tephritid species. In *Anastrepha suspensa*, both sugar and protein feeding increase during the first five days of adult life (Landolt & Davis-Hernandez, 1993), whereas in *A. ludens* flies up to four days old prefer sugar to protein and feed about equally on both resources, throughout sexual maturation, between 5-9 days old (Robacker, 1991). In our study, the shift from sugar preference to protein throughout the first week of Medfly female's life differs among groups, depending on their nutritional state. Older 6-7 days old, carbohydrate-fed (20% sucrose) females, showed no significant preference for either of the two offered resources, while their protein-fed conspecifics showed a significantly higher tendency to feed on sugar rather than protein (Table 3). The effect of diet type on foraging behavior of Medfly females older than six days has been shown previously in different bioassays (Prokopy et al., 1992; Cangussu & Zucoloto, 1995). Those studies indicated a higher consumption of protein among exclusively carbohydrate-fed females as they aged. The similarity in preference for protein by 8-9 day-old females of various prerelease diet groups, on the one hand, and the significant differences in their response to the two resources offered in earlier ages, on the other, suggests that the influence of diet is limited to the first week in a Medfly female's life. Once females reach the stage of egg maturation (Tsitsipis, 1989), their feeding history apparently becomes less significant. Feeding at that stage (8-9 days), can simply be explained by the necessity of tephritid females to guarantee egg maturation by feeding on protein (Bateman, 1972; Fletcher, 1989).

In contrast to flies fed protein or 20% sucrose, foraging behavior among poorly nourished females fed on 2% sucrose did not vary within the different age groups ranging between 3-7 days. No flies showed preferences for either one or other resource type (Table 3). Evidence of a similar feeding behavior has been shown in starved Medfly females, though for only 24 h following deprivation (Warburg & Yuval, 1996). Such a behavioral pattern might be explained as a compensating reaction to deprivation of both protein and sucrose. Data from both Nitzan (1981) and Nestel et al. (1985) suggest this possibility, documenting an irreversible loss to the lipogenic potential of *C. capitata* flies under prolonged starvation. Furthermore, results by Warburg & Galun (1992) and Warburg & Yuval (1996) show a strong correlation between nutritional stress and lipid reserve depletion. In our study, concerning poorly nourished females rather than totally starved ones, that trend has been evident throughout the first week of female adult life. Beyond that age, as mentioned above, feeding shifted towards a definite preference for protein, similar to the two other diet groups.

Additional observations on young females mating propensity, in relation to their nutritional state, revealed a significant effect of diet at the early age of 4-5 days (Table 4). The effect of quality and quantity of diet on mating behavior of tephritid females has been proved to be associated with their maturation state (Webster & Stoffolano, 1978; Landolt & Sivinsky, 1992). Studies considering the mating behavior of young *Drosophila melanogaster* females indicated an increase in receptivity (willingness to mate) only among protein-fed females when tested against sugar-fed individuals (Cook & Connolly, 1976; Chapman et al., 1994). Similarly, the 3-5 days old, protein-deprived Medfly females in our study showed signif-

icantly lower copulation rates (16% for both 2% and 20% sucrose-fed females) than protein-fed females (31.4%), as they may have not yet reached the point of reproductive maturity. As females aged they no longer differed in their willingness to copulate, regardless of the pre-release diet they were given. Maturation is generally accompanied by a change in behavioral priorities of the individual female, from feeding to reproducing (Ringo, 1996). Sawabe & Kanda (1990) demonstrate this by showing mating preference of deprived mature mosquitoes when offered free access to sugar.

We conclude that both age and diet govern foraging behavior and mating propensity of *C. capitata* young females in the stage prior to egg laying (1–7 days old). As females age, both foraging behavior and mating propensity are governed by reproductive necessities. The findings suggest a distinct shift to protein feeding, regardless of the individual's nutritional state, plus a much higher propensity to mate, once flies complete their first week of adulthood. Virgin Mediterranean fruit flies had already been proven to be more attracted to male pheromones than their mated conspecifics (Jang et al., 1998). Therefore, we can assume that a deployment of traps consisting of both food-based protein attractants and male pheromone may contribute to Medfly management. Such traps, which have been proven in their high attractiveness to medfly females upon other traps in use (Gazit et al., 1998), will reduce the proportion of damage-producing females when replaced in the beginning of the season.

#### Acknowledgements

Our thanks to Boaz Yuval on his professional supervision, to Y. Rossler and R. Akiva of the Citrus Marketing Board for providing the flies used in these experiments, and to Alona Achsanov for technical assistance. This work was supported by a grant from the Israel Citrus Marketing Board.

#### References

- Averill, A. L. & R. J. Prokopy, 1993. Foraging of *Rhagoletis pomonella* flies in relation to interactive food and fruit resources. *Entomologia Experimentalis et Applicata* 66: 179–185.
- Averill, A. L., R. J. Prokopy, M. M. Sylvia, P. P. Conner & T. T. Y. Wong, 1996. Effect of recent experience on foraging in Tephritid fruit flies. *Journal of Ins. Behav.* 4: 571–583.
- Bateman, M. A., 1972. The ecology of fruit flies. *Ann. Rev. Ent.* 17: 493–518.
- Cangussu, J. A. & F. S. Zucoloto, 1992. Nutritional value and selection of different diets by adult *Ceratitis capitata* flies (Diptera: Tephritidae). *J. Ins. Physiol.* 38: 485–491.
- Cangussu, J. A. & S. Zucoloto, 1995. Self-selection and perception threshold in adult females of *Ceratitis capitata* flies (Diptera: Tephritidae). *J. Ins. Physiol.* 41: 223–227.
- Chapman, T., S. Trevitt & L. Partridge, 1994. Remating and male-derived nutrients in *Drosophila melanogaster*. *J. Evol. Biol.* 7: 1–69.
- Cook, R. M. & K. Connolly, 1976. Sexual behavior of a female-sterile mutant of *Drosophila melanogaster*. *J. Ins. Physiol.* 22: 1727–1735.
- Christenson, L. D. & R. H. Foot, 1960. Biology of fruit flies. *Ann. Rev. Ent.* 5: 171–192.
- Fletcher, B. S., 1989. Life history strategy of tephritid fruit flies. In: A. S. Robinson & G. Hooper (eds), *Fruit Flies: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 195–208.
- Galun, R., S., Gothilf, S., Blonheim, J., Sharp, M., Mazor & A. Lachman, 1985. comparison of aggregation and feeding responses by normal and irradiated fruit flies *Ceratitis capitata* and *Anastrepha suspensa* (Diptera: Tephritidae). *Environ. Ent.* 14: 726–732.
- Gazit, Y., Rossler, Y., N. D. Epsy & R. R. Heath, 1998. Trapping females of the Mediterranean fruit fly (Diptera: Tephritidae) in Israel: Comparison of lures and trap type. *J. Econ. Ent.* 91: 1355–1359.
- Hanna, A. D., 1938. Studies on the Mediterranean fruit fly *Ceratitis capitata* Weid. the structure and operation of the reproductive organs. *Bulletin de la Soci  t  * 22: 39–52.
- Heath, R. R., N. D. Epsy, A. Guzman, B. D. Dueben, A. Manukian & W. L. Meyer, 1995. Development of a dry plastic insect trap with food-based synthetic attractant for the Mediterranean and Mexican fruit flies. *J. Econ. Ent.* 88: 1307–1315.
- Heath, R. R., N. D. Epsy, B. D. Dueben, J. Rizzo & F. Jeronimo, 1997. Adding methyl-substituted ammonia derivatives to a food-based synthetic attractant on capture of the Mediterranean and Mexican fruit flies (Diptera: Tephritidae). *J. Econ. Ent.* 90: 1584–1589.
- Hendrichs, J. & M. A. Hendrichs, 1990. Mediterranean fruit fly (Diptera: Tephritidae) in nature: location and diel pattern of feeding and other activities on fruiting and nonfruiting hosts and nonhosts. *Ann. Ent. Soc. Am.* 83: 632–641.
- Hendrichs, J., B. I. Kastoyannos, D. R. Papaj & R. J. Prokopy, 1991. Sex differences in movement between natural feeding and mating sites and tradeoffs between food consumption, mating success and predator evasion in Mediterranean fruit flies (Diptera: Tephritidae). *Oecologia* 86: 223–231.
- Jacome, I., M. Aluja & P. Liedo, 1999. Impact of adult diet on demographic and population parameters of the tropical fruit fly *Anastrepha serpentina* (Diptera: Tephritidae). *Bull. Ent. Res.* 89: 165–175.
- Jang, E. B., D. O. McInnis, D. R. Lance & L. A. Carvalho, 1998. Mating-induced changes in olfactory-mediated behavior of laboratory-reared normal, sterile and wild female Mediterranean fruit flies (Diptera: Tephritidae) mated to conspecific males. *Ann. Ent. Soc. Am.* 91: 139–144.
- Landolt, P. J. & Sivinski, 1992. Effects of time of day, adult food, and host fruit on incidence of calling by male Caribbean fruit flies (Diptera: Tephritidae). *Environ. Ent.* 21: 382–387.
- Landolt, P. J. & K. M. Davis-Hernandez, 1993. Temporal patterns of feeding by Caribbean fruit flies (Diptera: Tephritidae) on sucrose and hydrolyzed yeast. *Ann. Ent. Soc. Am.* 86: 749–755.

- Lui, Y. C. Chang, Y. C. Lui & C. Chang, 1995. Attraction of food attractants to melon fly *Dacus cucurbitae* Coquillett. *Chin. J. Ent.* 15: 69-80.
- Malavassi, A. & R. J. Prokopy, 1992. Effect of food deprivation on the foraging behavior of *Rhagoletis pomonella* females for food and host fruit. *J. Ent. Sci.* 27: 185-193.
- Nestel, D. R. Galun & S. Friedman, 1985. Long term regulation of sucrose intake by the adult Mediterranean fruit fly *Ceratitis capitata*. *J. Ins. Physiol.* 31: 533-536.
- Nitzan, Y., 1981. Feeding nutrition and gustatory sensilla of the Mediterranean fruit fly *Ceratitis capitata*. Ph.D. Thesis, Tel Aviv, Israel.
- Papaj, D. R. & R. J. Prokopy, 1989. Ecological and evolutionary aspects of learning in phytophagous insects. *Ann. Rev. Ent.* 34: 315-350.
- Papaj, D. R., R. J. Prokopy, P. McDonald & T. T. Y. Wong, 1987. Differences in learning between wild and laboratory *Ceratitis capitata* flies. *Ent. Exp. Appl.* 45: 65-72.
- Prokopy, R. J. & B. D. Roitberg, 1989. Fruit fly foraging behavior. In: A. S. Robinson & G. Hooper (eds), *Fruit Flies: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 293-306.
- Prokopy, R. J., P. T. McDonald & T. T. Y. Wong, 1984. Interpopulation variation among *Ceratitis capitata* flies in host acceptance pattern. *Ent. Exp. Appl.* 35: 65-69.
- Prokopy, R. J., D. R. Papaj, S. B. Opp & T. T. Y. Wong, 1987. Intra-tree foraging behavior of *Ceratitis capitata* flies in relation to host fruit density and quality. *Ent. Exp. Appl.* 45: 251-258.
- Prokopy, R. J., M. Aluja & T. T. Y. Wong, 1989a. Foraging behavior of laboratory cultured Mediterranean fruit flies on field-caged host trees. *Proc. Hawaii. Ent. Soc.* 29: 103-110.
- Prokopy, R. J., T. A. Green & T. T. Y. Wong, 1989b. Learning to find fruit in *Ceratitis capitata* flies. *Ent. Exp. Appl.* 53: 65-72.
- Prokopy, R. J., D. R. Papaj, J. Hendrichs & T. T. Y. Wong, 1992. Behavioral responses of *Ceratitis capitata* flies to bait spray droplets and natural food. *Ent. Exp. Appl.* 64: 247-257.
- Prokopy, R. J., S. S. Cooley, L. Galarza & C. Bergweiler, 1993. Bird droppings compete with bait sprays for *Rhagoletis pomonella* (Walsh) flies (Diptera: Tephritidae). *Can. Ent.* 125: 413-422.
- Ringo, J., 1996. Sexual receptivity in insects. *Ann. Rev. Ent.* 41: 473-494.
- Robacker, D. C., 1991. Specific hunger in *Anastrepha ludens* (Diptera: Tephritidae): effects on attractiveness of proteinaceous and fruit-derived lures. *Environ. Ent.* 20: 1680-1686.
- Robacker, D. C. & J. A. Garcia, 1993. Effects of age, time of day feeding history, and gamma irradiation on attraction of Mexican fruit flies (Diptera: Tephritidae), to bacterial odor in laboratory experiments. *Environ. Ent.* 22: 1367-1374.
- Robacker, D. C. & D. S. Moreno, 1995. Protein feeding attenuates attraction of Mexican fruit flies (Diptera: Tephritidae) to volatile bacterial metabolites. *Fla. Ent.* 78: 62-69.
- Sawabe, I. & K. Kanda, 1990. Studies on the effective attractants of anopheline mosquitoes. I. Blood feeding of female *Anopheles balabacensis* (Diptera: Culicidae). *Appl. Ent. Zool.* 25: 231-238.
- Tsitsipis, J. A., 1989. Nutrition requirements. In: A. S. Robinson & G. Hooper (eds), *Fruit Flies: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 103-119.
- Warburg, I. & R. Galun, 1992. Effects of diet and activity on lipid levels of adult Mediterranean fruit flies. *Physiol. Ent.* 21: 151-158.
- Warburg, M. S. & B. Yuval, 1996. Effects of diet and activity on lipid levels of adult Mediterranean fruit flies. *Physiol. Ent.* 21: 151-158.
- Warburg, M. S. & B. Yuval, 1997. Circadian patterns of feeding and reproduction of Mediterranean fruit fly (Diptera: Tephritidae) on various hosts in Israel. *Ann. Ent. Soc. Am.* 90: 487-495.
- Webster, R. P. & J. G. Stoffolano, Jr, 1978. The influence of diet on the maturation of the apple maggot *Rhagoletis pomonella*. *Ann. Ent. Soc. Am.* 71: 844-849.
- Williamson, D. L., 1989. Oogenesis and spermatogenesis. In: A. S. Robinson & G. Hooper (eds), *Fruit Flies: Their Biology, Natural Enemies and Control*. Elsevier, Amsterdam, pp. 141-151.
- Yuval, B. & J. Hendrichs, 2000. Behavior of flies in the genus *Ceratitis* (Dacinae: Ceratitidini). In: M. A. Aluja & A. L. Norrbom (eds), *Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior*. CRC Press, pp. 429-457.