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Interactions of mating, egg production and death rates in females of the Mediterranean fruit fly, *Ceratitis capitata*

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Costs of reproduction include costs of producing eggs and of mating itself. In the present study, we made an experimental investigation of costs of reproduction in the Mediterranean fruit fly (medfly, *Ceratitis capitata*). We demonstrated that virgins live longer than non-virgin females. However, in strong contrast to most findings within the Diptera, non-virginity had no detectable effect on egg production. Therefore the increased longevity of the virgin females cannot be attributed to an increase in egg production in non-virgin females, and instead indicates a cost of mating. A comparison of the life spans of normal females and those sterilized by low doses of X-irradiation, revealed an additional cost of egg production. There were no significant differences in remating levels between females that did and did not lay eggs, showing that the cost of producing eggs is independent of mating frequency. Medfly females therefore suffer a decrease in survival as a result of egg production and of mating, and these costs are independent of one another. To put our results into context, we reviewed the existing literature on the effects of mating on longevity, egg production and sexual receptivity for 64 species of Diptera, and examined the pattern of mating effects that emerged.

Keywords: *Ceratitis capitata*; mating; egg production; death rates

1. INTRODUCTION

In many insects, there is a marked cost associated with reproduction, typically manifested as an increased death rate of non-virgin relative to virgin females (e.g. Partridge *et al*. 1986; Partridge & Fowler 1990), or of frequent as compared to less frequent maters (e.g. Fowler & Partridge 1989). Reproductive activities can be costly because they make high energetic demands on available resources. For example, high rates of egg production can lead to a decrease in survival (e.g. Partridge *et al*. 1987), and abolishing egg production (using irradiated or ovary-less females) can lead to an extension in life span (e.g. Maynard Smith 1956, 1958*a*). In addition to energetic costs of reproduction, mating itself can also carry a cost. Female *Drosophila melanogaster* that mate at high frequencies have shortened life spans (Fowler & Partridge 1989), an effect that is solely due to the transfer of seminal fluid molecules from males (Chapman *et al*. 1995).

In addition, in many insects, non-virgin females lay more eggs and are less sexually receptive than virgin females (e.g. Leopold 1976; Chen 1984; Gillot 1988; Ridley 1988; Miller *et al*. 1994; Eberhard 1996; Chapman 1998). The switch from virgin to non-virgin behaviour is often effected through substances passed from males to females at mating. The nature of these signals varies, and effects of sperm (e.g. Manning 1962; Cunningham *et al*. 1971; Nakagawa *et al*. 1971) and of molecules secreted by the male reproductive tract, e.g. by the accessory glands (e.g. Chen *et al*. 1988; Herndon & Wolfner 1995) and the ejaculatory duct (e.g. Riemann *et al*. 1967; Morrison *et al*. 1982), have been reported. In addition, the physical stimulus provided by the act of mating itself can also alter female behaviour (e.g. Daviescole *et al*. 1993; Clutton-Brock & Langley 1997). A switch in behaviour and physiology between the virgin and non-virgin state makes sense from an evolutionary point of view. High rates of egg production will be initiated only once mating has occurred and sperm has been received, thus avoiding sterile egg production, which may be energetically costly.

Previous studies have rarely quantified or tested for separate longevity costs of egg production and of mating itself, to determine which might be the major contributor to the total cost of reproduction. It is important to do so, because of the fact that mating itself can affect egg production directly (e.g. Bilewicz 1953; Hihara 1981; Chapman & Partridge 1996*a*) and *vice versa* (Trevitt *et al*. 1988; Chapman *et al*. 1994; Chapman & Partridge 1996). The species that has previously been explored in most detail in this regard is *Drosophila melanogaster*. In *D. melanogaster* females, manipulations of egg-production rate, by varying either the amount of protein in the diet or the availability of oviposition sites, has shown that high rates of egg production can lead to a decrease in survival (Partridge *et al*. 1987; Chapman *et al*. 1994). In addition, the rate of egg production itself can affect remating frequency, high rates leading to increased receptivity (Trevitt *et al*. 1988; Fuyama 1995; Chapman *et al*. 1994; Chapman & Partridge 1996; C. M. Sgrò, unpublished data). Mating costs in this species are caused by

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seminal fluid molecules made in the male accessory gland 'main cells', which are transferred along with sperm at mating (Chapman *et al*. 1995). These molecules increase the fitness of the mating male, by elevating the number of eggs that the female lays, decreasing her receptivity (Chen *et al*. 1988; Kalb *et al*. 1993), displacing previously stored sperm and promoting the storage of his sperm (Harshman & Prout 1994; Wolfner 1997). At least two components of accessory fluid are known to affect egg production; the 36-amino-acid 'sex peptide' (Chen *et al*. 1988) and the accessory fluid protein 26Aa (ACP 26Aa) (Herndon & Wolfner 1995). The sex peptide also causes a decrease in female receptivity, and the effects of the sex peptide on egg production and receptivity are coupled (Chen *et al*. 1988).

Functional sex peptides are found in all members of the *melanogaster* species subgroup of *Drosophila* (Chen & Balmer 1989; T. Schmidt & E. Kubli, unpublished data). The sex peptides of each of the eight species in this group all cause an increase in egg production coupled with a decrease in female receptivity. They also show high sequence homology and are functionally cross-reactive, eliciting responses in the other group members. The sex peptides of *D. melanogaster*, *D. simulans*, *D. mauritiana* and *D. sechellia* differ by 1–3 amino acids, and those of *D. erecta*, *D. orena*, *D. yacuba* and *D. teissieri* differ by 4–6 amino acids (T. Schmidt & E. Kubli, unpublished data). The sex-peptide sequence of more distant relatives is more divergent; that of *D. suzuki* is a 41-amino-acid peptide (Schmidt *et al*. 1993*b*) and the sex peptide gene of *D. subobscura* is duplicated (Cirera & Aguadé 1998). Other molecules that stimulate ovulation in more distantly related drosophilids have also been reported (e.g. Fuyama 1983; Ohashi *et al*. 1991; Sato *et al*. 1997).

In contrast to the congruency of the effects of mating within the Drosophilidae, the published data on the effects of virginity and of mating on longevity, receptivity and fecundity in seven species of Tephritid fruit flies (including the medfly), are equivocal. The Tephritid family includes many species that are major fruit fly pests of economic importance, which attack a wide range of soft fruits. Studying this group will not only help to shed light on the generality and evolution of mating effects, but may also provide novel routes for pest control. Excluding the results of this study, five studies report that non-virginity (Sivinski 1993; Carey & Liedo 1995) or that mating itself (Carey *et al*. 1986; Opp & Prokopy 1986; Mangan 1997) decreases life span in the Tephritids, and two report that non-virginity (Whittier & Kaneshiro 1991) or mating (Whittier & Shelly 1993) does not decrease longevity. However, in none of these studies was the distinction made between the effects of mating itself and the effects of egg production. Nine studies report higher egg production or egg fertility in non-virgins in comparison with virgins (Cavalloro & Delrio 1970*a*; Cavalloro & Delrio 1970*b*; Prokopy & Bush 1973; Delrio & Cavalloro 1979), or in multiply mated females compared with singly mated females (Neilson & McAllan 1965; Opp & Prokopy 1986; Saul & McCombs 1993; Whittier & Shelly 1993; Telang *et al*. 1996; Mangan 1997), and one study reports lower egg production in twice-mated compared with once-mated females (Myers *et al*. 1976). Finally, although nine studies report decreased receptivity after mating (Cavalloro & Delrio 1970*a*,*b*; Katiyar & Ramirez 1970; Nakagawa *et al*. 1971; Delrio & Cavalloro 1979; Opp & Prokopy 1986; Bloem *et al*. 1993; Kuba & Itô 1993; T. Miyatake, T. Chapman & L. Partridge, unpublished data), the mechanism by which the receptivity effect is mediated seems uncertain.

We aim here to test the effect of mating itself on death rate and on egg production in the medfly and to probe the underlying mechanisms involved, dissecting any association between egg production and remating frequency. We tested the effect of mating on female death rate and on egg production by comparing the death rates and egg production of virgin and non-virgin females held singly and in groups. Finally, using females that could not lay eggs (owing to X-irradiation treatment) we tested whether egg production itself is costly for females, by comparing the death rates of non-virgin females that could and could not lay eggs. We could therefore dissect the effect of remating frequency on egg production by comparing the number of eggs laid by virgin and non-virgin females. Using irradiated females we could further test whether egg production affects mating frequency, by comparing the number of matings by non-irradiated and irradiated females. Finally, to put our results into a wider context, we compared our results to a review of the existing data on the effects of mating in the Diptera as a whole. We examined the patterns of the effects of mating on death rate, egg production and receptivity that emerged.

2. MATERIALS AND METHODS

(a) *Stocks and culture methods*

The medflies used were a subculture of the Moscamed mass rearing factory strain from Guatemala, Central America, which was established there in 1984 (Rendon 1996). Medflies were cultured at 25 °C, 65–75% relative humidity and 12:12 h light/dark. Adults were kept in plastic cages (28 cm × 22 cm × 13 cm). Eggs laid through gauze in the side of population cages fell into water troughs below, were collected and then added to 500 ml larval culture medium (Robinson *et al*. 1986) in 17 cm × 13 cm × 5 cm containers. The larvae developed under conditions of 'relaxed' larval density. At the third-instar larval stage, the cultures were placed into pupation boxes in which the floors were covered in sand to a depth of 1 cm, to allow 'jumping' larvae to exit the culture boxes and pupate. Development time from egg to adult under these conditions is *ca*. 21 days.

Three days before emergence, pupae were sieved from the sand and placed into small cages (22 cm × 15 cm × 8 cm; 400 pupae per cage) containing water and adult food (4:1 sugar: yeast-extract paste). Virgins were collected by sorting emerging flies within 24 h after eclosion using light CO_2 anaesthesia followed by sorting on ice. Experimental adults were then stored in groups in small cages with water and adult food.

(b) *Effect of virginity on survival and egg production*

To investigate the effects of virginity on survival and on egg production we compared the death rates and egg production of virgin and non-virgin females held singly and in groups.

(i) *Singletons and pairs*

One hundred and ninety-two 3–4-day-old virgin females were randomly assigned to two groups: 'virgin' and 'non-virgin'.

Ninety-six virgins were placed individually in 100-ml plastic pots and 96 non-virgin females were placed individually in pots, each with two 3–4-day-old males. Each pot was supplied with water through a filter paper wick and adult food in an Eppendorf cap, replaced every week. Females laid eggs through gauze in the side of the pot, which then dropped into a small weighing boat containing water. Eggs were collected every two days by passing this water through a fine silk cloth on which a grid was imprinted. The eggs in each square of the grid were then counted under a dissecting microscope. Female deaths were scored daily and any dead males replaced in the non-virgin group with males of the same age.

(ii) *Groups*

Five groups, each of 400 males and virgin females, were collected and stored in small cages. Virgin females (1–2 days old) were then randomly assigned to two groups and placed in 250-ml plastic pots as follows: the 'virgin' group consisted of 25 replicate pots of 40 virgins per pot, giving a total sample size of 1000 virgin females; the 'non-virgin' group comprised 25 replicate pots of 20 females and 20 1–2-day-old males, giving a total sample size of 500 non-virgin females. Each pot received water through a filter paper wick and food by an Eppendorf cap filled with adult medium. Females laid eggs through gauze in the lid of each pot. Egg-samples (24 h) were collected twice a week by brushing the eggs through a funnel into Eppendorf tubes, and then counting them on the fine silk cloth, as described above. Food was replaced twice weekly, and deaths scored daily. To ensure that the females in the non-virgin groups received equal exposure to males throughout the experiment, the sex ratio in each pot was maintained at 1:1 by replacing any dead males with ones of the same age, or removing males when females died.

(c) *Cost of egg production*

To test whether egg production is costly in female medflies, we compared the death rates of egg producing (non-irradiated) and non-egg producing (X-irradiated) non-virgin females. In the main experiment, two doses of X-irradiation were used, 2.5 and 5 krad (1 krad = 10 Gy). In a separate experiment, we compared the life spans of non-virgin untreated females and females treated with a higher radiation dose (7.2 krad). To test whether shutting-off egg production alters female receptivity, we compared the remating frequency of X-irradiated (at 2.5, 5 and 7.2 krad) and untreated females.

(i) *Death rates of non-virgin females treated with 2.5, 5 and 7.2 krad*

In the main experiment, two batches of pupae were X-irradiated 1–2 days before emergence at 451 rad min^{-1} for 5.5 min and 11 min to give doses of 2.5 and 5 krad, respectively. Virgin males and females emerging from all pupae were collected and stored in single-sex groups of 400, and 1–3-day-old virgin females and males were placed in pots as follows: ten replicate 250-ml pots of 20 non-irradiated females and 20 males ($n=200$ non-virgin females); seven replicate pots of 20 females treated with 2.5 krad and 20 males ($n=140$ non-virgin females); and nine replicate pots of 20 females treated with 5 krad and 20 males ($n=180$ non-virgin females). All males were non-irradiated. Water was supplied through a filter paper wick from below as before, and food was replaced every two days. Deaths were scored every day and the sex ratio in the non-virgin groups maintained as previously.

In a separate experiment, we used a higher irradiation dose. Pupae were X-irradiated 1–3 days before emergence at 451 rad min^{-1} for 16 min to give a total dose of 7.2 krad. Virgin females and males (1–3 days old) were then placed in pots as follows: ten replicate pots of 20 non-irradiated females and 20 males each ($n=200$ non-virgin females); and 12 replicate pots of 20 females treated with 7.2 krad and 20 males each ($n=240$ non-virgin females). All males were non-irradiated. Water and food were supplied, deaths scored daily and the sex ratio maintained at 1:1, as described above.

(ii) *Receptivity of non-virgin females treated with 2.5, 5 and 7.2 krad*

Receptivity was scored by recording the number of matings by untreated females, and by females treated with 2.5 and 5 krad, every 2 h in the 6 h after lights on, on days 2, 4, 6, 9, 11 and 13 of the main experiment. In the higher-dose experiment, we compared the receptivity of untreated females and those treated with 7.2 krad every 2 h for the 6 h after lights on, on days 3, 8, 13 and 15.

All statistical analysis was done using JMP statistical software for the Macintosh computer (version 3.1, SAS 1994).

3. RESULTS

(a) *Effect of virginity on survival and egg production*

(i) *Singletons and pairs*

Virgin females (mean survival = 16.5 days) had significantly longer life spans than non-virgin females (mean survival = 14.4 days) (log rank test (Miller 1981), $\chi^2=11.13$, $p=0.0008$; figure 1*a*). The difference became apparent midway through the experiment, (no significant differences in survival, $p>0.05$, until after day 15 of the experiment) owing to a slowing down in the mortality rate of virgin females. Virginity had no significant effect on egg production (figure 1*b*). There was a significant difference in egg production between the groups on one day only, non-virgin females laid significantly more eggs than virgins on day 6 (Mann–Whitney tests, $p<0.05$, corrected for multiple comparisons using the sequential Bonferroni method (Rice 1989)). The pattern of egg production by virgin and non-virgin females was very similar and did not provide any evidence of a switch to high egg production caused by mating.

(ii) *Groups*

Survival curves for the 50 individual replicate pots (figure 2*a*) shows that in general, non-virgin groups had higher death rates than virgin groups. A *t*-test of the mean survival times of the pots in each group reveals this effect as highly significant ($t=5.2$, $p<0.0001$). There were no significant differences between the replicates within the virgin group (log rank $\chi^2=32.5$, $p>0.05$) and slightly significant differences between replicate pots in the non-virgin groups ($\chi^2=38.2$, $p=0.03$). Collapsing the data into two groups (figure 2*b*) reveals a long tail in female survival probability, although unlike in the previous experiment, the survival differences between virgin and non-virgin groups were apparent and remained consistent from the first week of the experiment.

Mean egg production per female per pot was calculated for each of the five 1-day egg samples taken in this experiment. The means of the replicate pots for each group were then *t*-tested against each other for each egg sample. There were no significant differences in egg production between virgin and non-virgin females in any

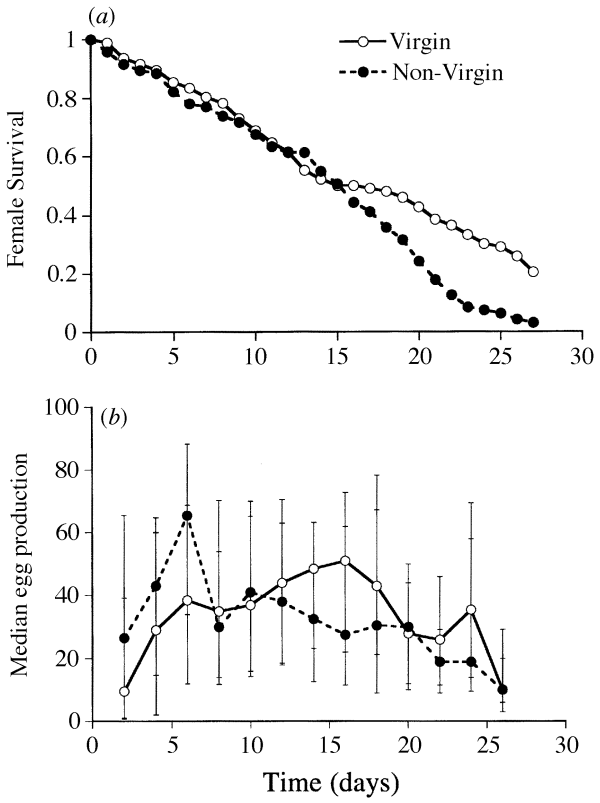

Figure 1. (*a*) Cumulative female-survival probability against time in days, for singleton virgin females (open circles, solid line), or non-virgin females kept individually with two males each (closed circles, dotted line). (*b*) Median (and inter-quartile range) number of eggs produced per two days against time in days, by the virgin (open circles, solid line) and non-virgin females (closed circles, dotted line) shown in (*a*).

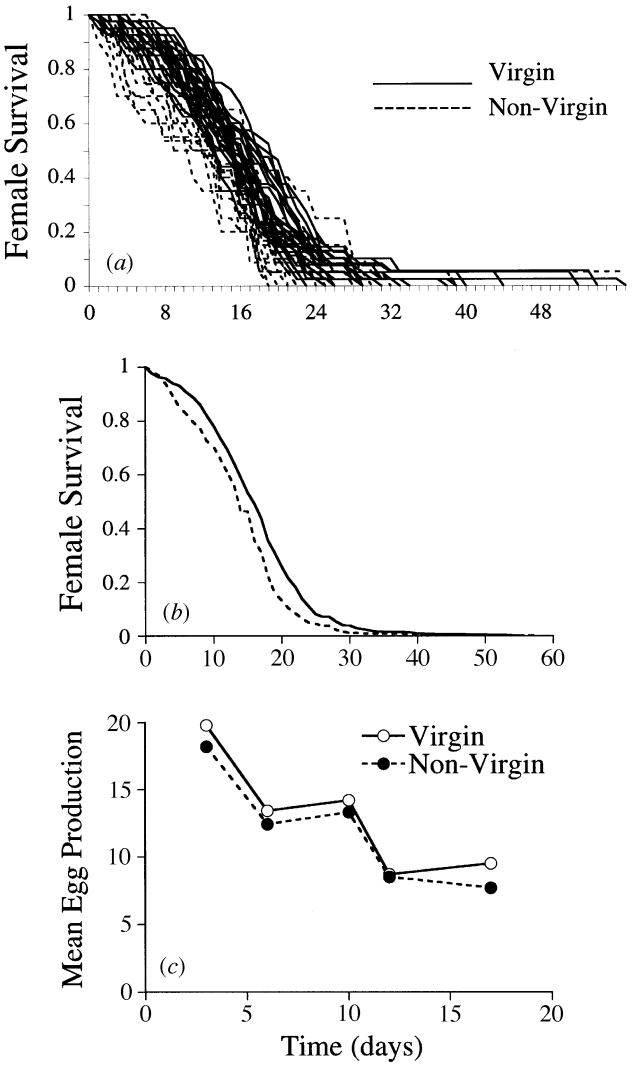

Figure 2. (*a*) Cumulative female-survival probability against time in days, for 25 replicates each of virgin (solid lines) and non-virgin females (dotted lines). Virgins were kept in groups of 40, and non-virgins in groups of 20 pairs. (*b*) Cumulative female-survival probability against time in days, for the females shown in (*a*), after grouping replicate pots. Virgins (solid line) and non-virgin females (dotted line). (*c*) Mean number of eggs laid per female per replicate per 1-day sample against time in days, for the virgin (open circles, solid line) and non-virgin females (closed circles, dotted line) shown in (*a*, *b*); replicates were grouped together.

of the samples ($p > 0.05$). The data are shown collapsed into the virgin and non-virgin groups (figure 2*c*). The results were therefore consistent with the previous experiment.

To further confirm the finding that non-virginity does not increase egg production, we also used a recently collected wild-type stock, which had been held in the laboratory for only one year. We compared the life spans and egg production of three replicate pots of 40 virgin females ($n=120$) and three replicate pots of 20 females and 20 males ($n=60$). There were no significant differences in survival between non-virgin and virgin females (log rank $\chi^2=3.14$, $p>0.05$, data not shown), which is perhaps not surprising given the large sample sizes needed to demonstrate the mating cost in our earlier experiments. The number of eggs laid by five of the six non-virgin and virgin replicate groups of females did not differ significantly ($p>0.05$). The sixth group of virgins laid atypically low numbers of eggs; although the reason for this was not clear, the data support the finding that mating has no effect on egg production.

(b) *Cost of egg production*

(i) *Death rates of non-virgin females treated with 2.5, 5 and 7.2 krad*

Samples of females treated with 2.5, 5 and 7.2 krad were dissected in phosphate-buffered saline to assess the degree of sterility. Only 1–2% of females in the groups treated with 2.5 and 5 krad laid eggs, and dissection treatment revealed that the ovaries of females treated with 5 krad were generally completely structureless and significantly more atrophied than those of the females treated with 2.5 krad. Females treated with 2.5 krad often had identifiable nurse cells at the termini of their ovarioles. The ovaries of females treated with 7.2 krad were completely atrophied and none of these females laid eggs.

Replicate pots within each group in the experiments with 2.5 and 5 krad did not differ in survival (except for a slight difference among the non-irradiated females; log rank $\chi^2=18.35$, $p=0.03$). Survival curves for replicates collapsed together within a group are shown in figure 3*a*. Analysis of variance on the mean survival times of each replicate pot within each group show that there are highly significant differences in survival between the

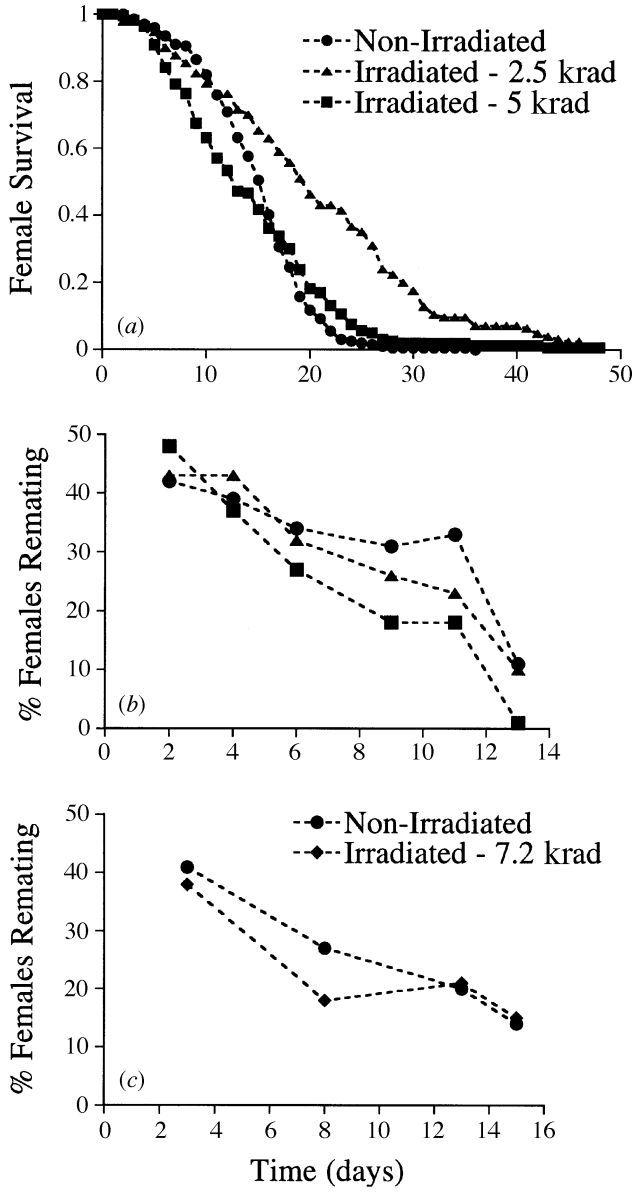

Figure 3. (*a*) Cumulative female-survival probability against time in days, for non-virgin females that were non-irradiated (circles), or irradiated with 2.5 krad (triangles) or 5 krad (squares); replicates were grouped together. (*b*) Percentage of females remating in 6-h observation periods against time in days, for the females in (*a*). (*c*) Percentage of females remating in 6-h observation periods against time in days, for non-virgin females that were non-irradiated (circles) and irradiated with 7.2 krad (diamonds); replicates were grouped together.

groups ($F=22.95$, $p<0.0001$). This difference is clearly attributable to the significantly lower death rate of females treated with 2.5 krad (mean survival = 20.6 days; Tukey–Kramer multiple comparisons, $p<0.01$) relative to those treated with 5 krad and to untreated females, which did not differ significantly from one another (mean survival = 14.2 and 15.0 days, respectively; $p>0.05$).

A *t*-test of mean pot survival in the higher-dose experiment showed that non-virgin females treated with 7.2 krad (mean survival = 13.4 days) did not differ in survival compared with untreated non-virgin females (mean survival = 14.6 days; $t=1.46$, $p>0.05$, data not shown).

(ii) *Receptivity of non-virgin females treated with 2.5, 5 and 7.2 krad*

For untreated females and females treated with 2.5 and 5 krad, the percentage that remated each day was initially high and decreased as females aged (figure 3*b*). The data were analysed using a χ^2 test, to compare the number of females that did and did not remate on each of the six test days. There were no significant differences in female remating frequency on any of the days ($p>0.05$, corrected for multiple comparisons (Rice 1989)). In the separate experiment using higher doses of irradiation, the percentage of 7.2-krad-irradiated and non-irradiated females that remated was again high and then decreased (figure 3*c*). As before, there were no significant differences between the remating frequency of irradiated and non-irradiated females on any of the four days tested ($p>0.05$, corrected for multiple comparisons). The data from both experiments show that female receptivity is independent of the rate of egg production.

4. DISCUSSION

The data from the first two experiments both indicate a small, but nevertheless highly significant, cost of reproduction in female medflies, with virgins living significantly longer than non-virgin females. In addition, a striking but very clear result from both of these experiments is that mating does not alter the rate or pattern of egg production. This finding was also supported by the results of the experiment using the more recently introduced stock. In all experiments, non-virgin females were continuously exposed to males and remated at high frequency (e.g. figure 3*b*,*c*); virgin females never mated.

The results of the experiments that compared the number of eggs laid by non-virgin and virgin females provide no evidence that molecules in males can enhance egg production. This conclusion is also supported by direct evidence from the injection of extracts from medfly male accessory glands. Females injected with either male accessory gland extract or saline did not differ in egg production (T. Chapman, unpublished data). This finding is intriguing because it is clear that the transfer of seminal fluid at mating does have an effect on receptivity (T. Miyatake, T. Chapman & L. Partridge, unpublished data). Because egg production did not differ between non-virgin and virgin females, the difference in longevity between these females must have been due to the costly effects of mating itself. We have therefore identified a cost of mating in the medfly that is independent of the rate of egg production. The magnitude of this effect, however, is much smaller than that seen in *D. melanogaster* (Fowler & Partridge 1989; Chapman *et al*. 1995).

The experiments with irradiated females provide evidence that egg production itself also carries a separate cost. In the absence of differences in remating frequency (figure 3*b*), non-virgin females treated with 2.5 krad had significantly longer life spans than untreated females, or females treated with 5 krad. Females treated with 5 and 7.2 krad did not differ in lifespan from their respective groups of untreated females, presumably because any benefit they gained through the abolition of costly egg production was negatively balanced by the deleterious side effects of the higher irradiation doses used. In the

females treated with a lower dose of 2.5 krad, the full benefit of abolishing costly egg production was expressed, leading to a significant increase in life span, indicating that egg production can incur a survival cost. This interpretation is also supported by Carey & Liedo (1995) who reported that irradiation (15 000 roentgens), produced a 2.3-day increase in life expectancy in non-virgin medfly females. Treatment with 2.5 krad is a low dose, but still results in most females laying no eggs. At 1 krad, female egg production is indistinguishable from that of untreated females (T. Chapman, unpublished data).

Another striking result of our study is that the rate of oviposition or ovulation is not correlated with receptivity (figure 3*b*,*c*). The irradiated females that were unable to lay eggs did not differ in remating frequency from untreated females. The effect occurred at all of the irradiation doses tested (2.5, 5 and 7.2 krad). This indicates that remating frequency and egg production vary independently. Therefore, the cost of egg production is independent of female mating status (virgin or non-virgin) and represents a separate cost to that of mating itself. These results are in direct contrast to the situation in *Drosophila melanogaster*, where mating frequency affects egg production and *vice versa* (e.g. Fuyama 1985; Partridge *et al*. 1987; Trevitt *et al*. 1988; Chapman *et al*. 1994; Chapman & Partridge 1996; C. M. Sgrò, unpublished data).

The comparable remating frequency of irradiated and non-irradiated females suggests that there is no feedback between the ovary or spermathecae to sites that regulate receptivity, which are probably receptors in the brain (Tompkins & Hall 1983). This is again contrary to what is reported in *D. melanogaster*, where the receptivity of eggless or irradiated females is low (Fuyama 1995; C. M. Sgrò, unpublished data). This result has implications for the females that are released in sterile-insect-technique programmes (Klassen *et al*. 1994) that do not use genetic sexing strains for 'male-only' releases. Sterilized females are not more likely than any other female to refuse matings on the basis of their current rate of egg production or number of sperm they have in store. Such females could therefore act as a 'sink' for the sperm of wild-type males.

Further evidence on the contribution of reproduction to mortality is provided by the shape of the survival curves. In both of the first two experiments, the survival curves flattened off slightly with age, showing a decrease in the mortality rate of old females (Carey *et al*. 1992). The flattening off in mortality rate of virgin relative to non-virgin females was significant after day 15 in the first experiment. In the second experiment, the difference in mortality rates was apparent from the first week of the experiment and remained constant; the mortality rates of both non-virgin and virgin females decreased at the very end of the experiment. The discrepancy could be due to differences in density or in the numbers of interactions between individuals between the two experiments. In addition, the first experiment was unreplicated and the second consisted of two groups of 25 replicates each, some of which showed mortality patterns similar to the first experiment. The females still alive at the ends of the experiments were post-reproductive, laying very few eggs. They may represent a subset of females in which life expectancy was increased through a reduction in costly reproductive activities, including mating and egg production, which both decrease as flies age (Carey *et al*. 1992; Carey & Liedo 1995).

The finding that virgin females maintain high rates of egg production in the absence of mating presents a paradox, especially given that egg production is costly. The absence in medflies of a switch-type mechanism to turn on egg production only after mating, might suggest that medfly females have a vanishingly small probability of remaining unmated in the field. However, it is difficult to conceive a reason for this that is specific to medflies and not to other species with similar ecology. It is possible that the high rate of egg production in non-virgin females is a side-effect of adaptation to the laboratory environment. However, this seems unlikely because high egg production in virgin females was also seen in the more recently introduced stock. In addition, why laboratory adaptation should have led to the abolition of a switch to turn on egg production in medflies and not in other species, which have also undergone considerable adaptation to laboratory conditions, is unclear.

The differences between our results and previous studies that differ in their conclusions (Whittier & Kaneshiro 1991; Whittier & Shelly 1993) is almost certainly due to differences in the experimental method. We used continuous exposure to males to give the maximum difference in remating frequency between non-virgin and virgin females (which did not mate at all) and measured egg production and longevity until all females were dead. This was important as differences sometimes became apparent only after half of the females had already died (see figure 1*a*). In addition, we used very large sample sizes to increase statistical power, which is essential given the small magnitude of the mating cost.

Our study has revealed some unexpected findings, and to put the results of our experiments in context, we have also assessed the data on the effects of mating on female survival, egg production and sexual receptivity for the Diptera as a whole (for a phylogeny of the Diptera, see http://phylogeny.arizona.edu/tree/phylogeny.html). Our aim was to establish whether there is a typical pattern of mating effects on female behaviour and physiology, to test whether our findings differ consistently from the results for other Diptera.

Table 1 shows the published data for the effect of mating on female survival, egg production and receptivity for 64 species of Diptera. Where known, the substances such as sperm, accessory fluid, etc. that mediate these effects are included, together with an indication of whether implant or injection experiments were done. However, in isolation, a response elicited by an extract or peptide injection does not necessarily confirm that the response actually occurs. Studies that produced similar results within species are grouped together. Multiple entries for one species occur where the studies investigated different phenomena, or where the data are equivocal. Uncertain results are indicated by the presence of question marks. To summarize the data (table 2), mating is reported to decrease female survival in ten species (and not to do so in nine), increase egg production in 38 species (and not to do so in three) and decrease female receptivity in 47 species (and not to do so in

Table 1. *Effect of mating on female survival, egg production and sexual receptivity in the Diptera*

(Abbreviations: S, sperm; AF, accessory fluid; EJ, ejaculate (sperm+accessory fluid), PHYS=physical stimulus. Studies that produced similar results within species are grouped together. Multiple entries for one species occur where the studies investigated different phenomena, or where the data are equivocal. Uncertainty is indicated by the presence of question marks.)

					does mating decrease survival?		does mating increase egg production?		does mating decrease receptivity?		confirmed by implant (IMP) or		
sub-order	division	group	family species		Y/N	mediated by	Y/N	mediated by	Y/N	mediated by	injection (INJ)?	refs[a]	notes
Nematocera													
			Ceratopogonidae										
				Culicoides mellus					Y			(1)	
			Culicidae										
				Aedes aegypti	Y		Y					(2, 3)	Mating decreases survival only in starved females. Fecundity effect is on pre-ovipostition and egg development. *A. albopictus* SF increases egg development in *A. aegypti*.
				Aedes aegypti			Y (+ fertility)					(4)	
				Aedes aegypti					Y	AF		(5)	
				Aedes aegypti			Y	AF	Y	AF ('Matrone')	INJ	(6–9)	Matrone is a large protein with two subunits (30+60 kDa); α and β subunits together decrease receptivity, α alone increases oviposition.
				Aedes aegypti			Y (+ fertility)	AF	Y	AF	IMP	(4, 10–14)	
				Aedes aegypti	Y/N							(15)	Longevity effect is dependent on the length of male and female association: it increased if short, but decreased if new males were introduced every two weeks.
				Aedes aegypti					Y	AF	IMP	(16)	
				Aedes albopictus			Y	AF			IMP	(10)	
				Aedes albopictus					Y	AF	IMP	(10, 16)	*A. albopictus* accessory fluid also increases oviposition in *A. aegypti*.
				Aedes taeniorrhynchus			Y	AF				(17, 18)	The fecundity effect is on egg development.
				Aedes atropalpus					Y	AF	IMP	(14, 16)	
				Aedes mascarensis					Y	AF	IMP	(16)	
				Aedes polynesiensis					Y	AF	IMP	(16)	
				Aedes scutellaris					Y	AF	IMP	(16)	
				Aedes sierrensis					Y	AF	IMP	(16)	
				Aedes togoi					Y	AF	IMP	(16)	
				Aedes triseratus			Y		Y	AF	IMP	(14, 16)	*A. triseratus* accessory fluid also causes an increase in oviposition in *A. aegypti* and a decrease in receptivity in *A. atropalpus*.

(*Continued*)

Table 1. (*Continued*)

sub-order	division	group	family	species	does mating decrease survival? Y/N	does mating decrease survival? mediated by	does mating increase egg production? Y/N	does mating increase egg production? mediated by	does mating decrease receptivity? Y/N	does mating decrease receptivity? mediated by	confirmed by implant (IMP) or injection (INJ)?	refs[a]	notes
				Aedes vitattus					Y	AF	IMP	(16)	
				Anopheles freeborni					Y	EJ		(19)	Remating induced by incomplete sperm transfer.
				Anopheles quadrimaculatus					Y	AF	IMP	(16)	
				Culex pipiens			Y	AF	Y		IMP	(16, 20)	Accessory fluid of *A. aegypti* and *D. melanogaster* also causes an increase in fecundity and decrease in receptivity in *C. pipiens*.
				Culex tarsalis			Y (fertility)	AF	Y	AF	INJ	(21, 22)	The *C. tarsalis* accessory fluid protein is small (2 kDa) in comparison to matrone of *A aegypti*. Mating increases fertility, not egg number.
			Chironomidae										
				Chironomous riparus					Y	male extract	INJ	(23)	
			Cecidomyiidae										
				Mayetiola destructor			Y	EJ	Y	PHYS + EJ	INJ	(24)	
			Bibionidae										
				Plecia nearctica	N							(25)	Remating before the initiation of egg production increased longevity, because females usually lay eggs and die after their first mating.
Brachycera													
	Cyclorrhapha												
		Schizophora											
			Diopsidae										
				Cyrtodiopsis whitei	N		N		N			(26)	Longevity was measured over the first 2 weeks of life.
				Cyrtodiopsis dalmanni	N		Y/?		N			(27)	Females mated four times produced more (but not significantly more) progeny than singly-mated females.
			Tephritidae										
				Rhagoletis pomonella	Y		Y (+ fertility)		Y	S		(28–30)	Females mated twice had lower sperm loads than those refusing to mate. Egg production was also increased by the presence of males in the absence of mating.
				Rhagoletis pomonella			N					(31)	No statistics and small samples, but females mated twice produced fewer eggs than once-mated females.
				Rhagoletis completa			Y (+ fertility)					(32)	Multiply mated females laid more eggs and had higher fertility than females mated once, but differences were statistically non-significant.

Anastrepha suspensa	Y						(33)	Mating cost only evident when females were provided with food.
Anastrepha ludens	Y		Y(?)				(34)	Fecundity effect varied among strains.
Ceratitis capitata					Y	S	(35–37)	Correlation shown between the number of sperm in the spermatheca and remating frequency.
Ceratitis capitata			Y(?)		Y(?)	S(?)+AF(?)	IMP (38, 39)	No statistics and difficult to interpret results with certainty.
Ceratitis capitata	Y		N		Y	S, PHYS(?)+AF(?)	(40, 41)	Egg production also costly (this paper).
Ceratitis capitata	N		Y				(42, 43)	
Ceratitis capitata			Y (fertility)				(44)	
Ceratitis capitata	Y						(45, 46)	
Bactrocera cucurbitae					Y	AF (?)	(47)	
Bactrocera (*Dacus*) *oleae*			Y(?)	EJ(?)	Y(?)	S(?)	(48)	Results uncertain as no statistics are quoted, but 'higher' % females remated after mating to aspermic or exhausted males than to normal males.
Coelopidae								
Coelopa frigida	N		N		N		(49)	Comparisons of set numbers of copulations (1, 2, 3, 4 and 5 versus none) and 0 versus 48-h exposure across different conditions, food and temperature.
Coelopa ursina	N						(50)	Virgin versus singly-mated female longevity compared.
Coelopa nebularum	N						(50)	Virgin versus singly-mated female longevity compared.
Coelopa pilipes	N						(50)	Virgin versus singly-mated female longevity compared.
Rhis whitlei	N						(50)	Virgin versus singly-mated female longevity compared.
Drosophilidae								
Drosophila melanogaster	Y		Y				(51)	
Drosophila melanogaster	Y						(52, 53)	
Drosophila melanogaster	Y	AF					(54, 55)	Egg production also costly (Partridge *et al*. 1987; Trevitt *et al*. 1988).
Drosophila melanogaster					Y	S + AF	(56, 57)	
Drosophila melanogaster					Y	S	(58–62)	
Drosophila melanogaster			Y	AF	Y	AF	IMP/INJ (63–67)	
Drosophila melanogaster			Y	AF			IMP (68)	
Drosophila melanogaster			Y	AF	Y	AF	(69)	
Drosophila melanogaster			Y	AF	Y	AF (SP)	INJ (70–74)	*D. melanogaster* sex peptide (SP) is a peptide of 36 amino acids.
Drosophila melanogaster			Y	AF (ACP 26Aa)	Y	AF	(75, 76)	Accessory fluid protein 26Aa (ACP 26Aa)

(*Continued*)

Table 1. (*Continued*)

sub-order	division	group	family species	does mating decrease survival? Y/N	mediated by	does mating increase egg production? Y/N	mediated by	does mating decrease receptivity? Y/N	mediated by	confirmed by implant (IMP) or injection (INJ)?	refs[a]	notes
			Drosophilidae (*continued*)									
			Drosophila simulans			Y	AF (SP)	Y	AF (SP)	INJ	(77, 78)	All *melanogaster* species subgroup SPs are peptides of 35–36 amino acids with high homology to the *D. melanogaster* SP.
			Drosophila mauritiana			Y	AF (SP)	Y	AF (SP)	INJ	(77, 78)	(SP) = *D. mauritiana* sex peptide.
			Drosophila sechellia			Y	AF (SP)	Y	AF (SP)	INJ	(77, 78)	(SP) = *D. sechellia* sex peptide.
			Drosophila yacuba			Y	AF (SP)	Y	AF (SP)	INJ	(78)	(SP) = *D. yacuba* sex peptide.
			Drosophila erecta			Y	AF (SP)	Y	AF (SP)	INJ	(78)	(SP) = *D. erecta* sex peptide.
			Drosophila orena			Y	AF (SP)	Y	AF (SP)	INJ	(78)	(SP) = *D. orena* sex peptide.
			Drosophila teissieri			Y	AF (SP)	Y	AF (SP)	INJ	(78)	(SP) = *D. teissieri* sex peptide.
			Drosophila ananassae			Y	AF (SP)	Y	AF (SP)	INJ	(78)	
			Drosophila pulchrella			Y	AF (SP?)	Y	AF (SP?)	INJ	(79)	
			Drosophila suzukii			Y	AF (SP & OSS)	Y	AF (SP)	INJ	(79–81)	*D. suz* sex peptide (SP), a 41 amino-acid peptide that is homologous to *D. mel* SP. Ovulation stimulating substance (OSS) is a peptide of at least 35 amino acids.
			Drosophila biarmipes			Y	AF (SP & OSS)	Y	AF (SP)	INJ	(82)	(SP)=*D. biarmipes* sex peptide.
			Drosophila funebris			Y	AF (PS-2)	Y	AF (PS-1)	INJ	(83, 84)	*D. funeb* paragonial substance 1 (PS-1) (27 amino acids) and PS-2 (glycine carbohydrate derivative) are non-homologous to the *D. mel* SP.
			Drosophila mojavensis			Y	seminal feeding				(85)	
			Drosophila subobscura	Y				Y	S(?) or testis substance		(86–89)	
			Drosophila subobscura			Y	courtship feeding				(90)	
			Drosophila subobscura			Y	AF (SP)	Y	AF (SP)	INJ	(91)	*D. subobscura* AF extract tested by injection into *D. melanogaster*. *D. sub* SP is homologous to *D. mel* SP and the *D. sub* SP gene is duplicated.
			Drosophila pseudoobscura			Y					(92–94)	This species may exhibit seminal feeding (Bownes & Partridge 1987).
			Drosophila hydei			Y/N					(95)	The fecundity effect depends on remating interval. If matings are close together, there is no increase in fecundity, but if they are spaced apart by 24-h intervals, there is.
			Drosophila mercatorum	Y							(96)	
			Agromyzidae									
			Agromyza frontella	Y		Y					(97)	

Calliphoridae									
Lucilia cuprina			Y	testis + AF	Y	AF	INJ	(98–100)	
Lucilia sericata					Y	AF	IMP	(101)	
Phormia regina					Y	male extract	INJ	(102)	Tested by injection of extract into *Musca domestica*.
Cochliomyia hominivorax					Y	male extract	INJ	(102)	Tested by injection of extract into *Musca domestica*.
Anthomyiidae									
Delia antiqua			Y	AF	Y	AF	INJ	(103, 104)	Some cross reactivity between *D. antiqua*, *D. platura* and *D. radicum* accessory gland extracts.
Delia platura			Y	AF	Y	AF	INJ	(104)	Some cross reactivity between *D. antiqua*, *D. platura* and *D. radicum* accessory gland extracts.
Delia radicum			Y	AF	Y	AF	INJ	(104)	Some cross reactivity between *D. antiqua*, *D. platura* and *D. radicum* accessory gland extracts.
Hylema brassicae			Y	AF	Y	AF	INJ + IMP	(105)	
Muscidae									
Musca domestica	N		Y	AF	Y	ejaculatory duct fluid	INJ + IMP	(106–108)	There are no defined accessory glands in this species. Virgin = mated life span in flies kept together for six days.
Musca domestica					Y	reproductive tract fluid	INJ	(102, 109)	
Stomoxys calcitrans			Y	AF	Y	median ejaculatory duct	IMP	(110, 111)	*S. calcitrans* extract had no effect on receptivity in *Musca domestica*, *Sarcophaga bullata* and *Phormia regina*.
Glossinidae									
Glossina morsitans	Y	PHYS						(112)	
Glossina morsitans			Y	PHYS	Y	PHYS + AF	INJ	(113)	Physical and accessory fluid stimuli required for full response.
Glossina morsitans					Y	PHYS(?) + AF		(114)	Aspermic and normal males decrease receptivity equally.
Glossina pallidipes					Y	EJ(?)		(115)	

[a] References: (1) Linley & Adams (1975); (2) Yeh & Klowden (1990); (3) Klowden & Chambers (1991); (4) Young & Downe (1982); (5) Dickinson & Klowden (1997); (6) Fuchs *et al.* (1968); (7) Fuchs *et al.* (1969); (8) Fuchs & Hiss (1970); (9) Hiss & Fuchs (1972); (10) Leahy & Craig (1965); (11) Judson (1967); (12) Speilman *et al.* (1967); (13) Adlakha & Pillai (1975); (14) Ramalingam & Craig (1976); (15) Liles (1965); (16) Craig (1967); (17) Borovsky (1985); (18) O'Meara & Evans (1977); (19) Yuval & Fritz (1994); (20) Leahy (1967); (21) Young & Downe (1983); (22) Young & Downe (1987); (23) Downe (1973); (24) Bergh *et al.* (1992); (25) Thornhill (1976); (26) Wilkinson & Presgraves (unpublished data); (27) Cowdery, Fowler & Pomiankowski (unpublished data); (28) Neilson & McAllan (1965); (29) Opp & Prokopy (1986); (30) Prokopy & Bush (1973); (31) Myers *et al.* (1976); (32) Telang *et al.* (1996); (33) Sivinski (1993); (34) Mangan (1997); (35) Nakagawa *et al.* (1971); (36) Bloem *et al.* (1993); (37) Katiyar & Ramirez (1970); (38) Cavalloro & Delrio (1970*a*); (39) Delrio & Cavalloro (1979); (40) this paper; (41) Miyatake, Chapman & Partridge (unpublished data); (42) Whittier & Kaneshiro (1991); (43) Whittier & Shelly (1993); (44) Saul & McCombs (1993); (45) Carey *et al.* (1986); (46) Carey & Liedo (1995); (47) Kuba & Itô (1993); (48) Cavalloro & Delrio (1970*b*); (49) D. M. Shuker (unpublished data); (50) A. S. Gilburn (unpublished data); (51) Bilewicz (1953); (52) Malick & Kidwell (1966); (53) Partridge *et al.* (1986); (54) Fowler & Partridge (1989); (55) Chapman *et al.* (1995); (56) Manning (1962); (57) Manning (1967); (58) Pyle & Gromko (1978); (59) Pyle & Gromko (1978); (60) Gilbert *et al.* (1981); (61) Gromko *et al.* (1984); (62) Letsinger & Gromko (1985); (63) Kummer (1960); (64) Garcia-Bellido (1964); (65) Leahy & Lowe (1967); (66) Merle (1968); (67) Burnet *et al.* (1973); (68) Leahy (1966); (69) Hihara (1981); (70) Chen & Diem (1961); (71) Chen & Bühler (1970); (72) Chen *et al.* (1988); (73) Schmidt *et al.* (1993*a*); (74) Kubli (1996); (75) Herndon & Wolfner (1995); (76) Kalb *et al.* (1993); (77) Chen & Balmer (1989); (78) T. Schmidt & E. Kubli (unpublished data); (79) Fuyama (1983); (80) Ohashi *et al.* (1991); (81) Schmidt *et al.* (1993*b*); (82) Sato *et al.* (1997); (83) Baumann (1974*a*); (84) Baumann (1974*b*); (85) Markow *et al.* (1990); (86) Maynard Smith (1956); (87) Maynard Smith (1958*a*); (88) Maynard Smith (1958*b*); (89) Maynard Smith (1963); (90) Steele (1986); (91) Cirera & Aguadé (1998); (92) Beckenbach (1978); (93) Pruzan-Hotchkiss *et al.* (1981); (94) Turner & Anderson (1983); (95) Markow (1985); (96) Ikeda (1974); (97) Quiring & Mcneil (1984); (98) Smith *et al.* (1989); (99) Smith *et al.* (1990); (100) Cook (1992); (101) Pollock (1971); (102) Nelson *et al.* (1969); (103) Spencer *et al.* (1992); (104) Spencer *et al.* (1997); (105) Swailes (1971); (106) Leopold (1970); (107) Riemann *et al.* (1967); (108) Riemann & Thorson (1969); (109) Adams & Nelson (1968); (110) Morrison *et al.* (1982); (111) Venkatesh & Morrison (1980); (112) Clutton-Brock & Langley (1997); (113) Gillot & Langley (1981); (114) Daviescole *et al.* (1993); (115) Leegwater-van der Linden & Tiggelman (1984).

Table 2. *Effect of mating on female survival, egg production and sexual receptivity in the Diptera*

	yes		no	
(*a*) Does mating decrease survival?				
number of species:	10		9	
genera: (number of species)	*Aedes* (1) *Anastrepha* (2) *Rhagoletis* (1) *Ceratitis* (1)	*Drosophila* (3) *Agromyza* (1) *Glossina* (1)	*Plecia* (1) *Cyrtodiopsis* (2) *Coelopa* (4) *Rhis* (1)	*Musca* (1)
families: (number of species)	Culicidae (1) Tephritidae (4) Drosophilidae (3) Agromyzidae (1) Glossinidae (1)		Bibionidae (1) Diopsidae (2) Coelopidae (5) Muscidae (1)	
(*b*) Does mating increase egg production?				
number of species:	38		3	
genera: (number of species)	*Aedes* (4) *Culex* (2) *Cyrtodiopsis* (1) *Mayetiola* (1) *Rhagoletis* (2) *Anastrepha* (1) *Bactrocera* (1) *Drosophila* (17)	*Agromyza* (1) *Lucilia* (1) *Delia* (3) *Hylema* (1) *Musca* (1) *Stomoyxs* (1) *Glossina* (1)	*Cyrtodiopsis* (1) *Ceratitis* (1) *Coelopa* (1)	
families: (number of species)	Culicidae (6) Diopsidae (1) Cecidomyiidae (1) Tephritidae (4) Drosophilidae (17)	Agromyzidae (1) Calliphoridae (1) Anthomyidae (4) Muscidae (2) Glossinidae (1)	Diopsidae (1) Tephritidae (1) Coelopidae (1)	
(*c*) Does mating decrease receptivity?				
number of species:	47		3	
genera: (number of species)	*Culicoides* (1) *Aedes* (10) *Anopheles* (2) *Culex* (2) *Chironomous* (1) *Mayetiola* (1) *Rhagoletis* (1) *Ceratitis* (1) *Bactrocera* (2)	*Drosophila* (14) *Lucilia* (2) *Phormia* (1) *Cochliomyia* (1) *Delia* (3) *Hylema* (1) *Musca* (1) *Stomoxys* (1) *Glossina* (2)	*Cyrtodiopsis* (2) *Coelopa* (1)	
families: (number of species)	Ceratopogonidae (1) Culicidae (14) Chironomidae (1) Cecidomyiidae (1) Tephritidae (4)	Drosophilidae (14) Calliphoridae (4) Anthomyidae (4) Muscidae (2) Glossinidae (2)	Diopsidae (2) Coelopidae (1)	
(*d*) Are increased egg production and decreased receptivity both caused by the transfer of seminal fluid?				
number of species:	29		4	
genera: (number of species)	*Aedes* (3) *Culex* (2) *Mayetiola* (1) *Bactrocera* (1) *Drosophila* (14) *Lucilia* (1)	*Delia* (3) *Hylema* (1) *Musca* (1) *Stomoxys* (1) *Glossina* (1)	*Cyrtodiopsis* (2) *Ceratitis* (1) *Coelopa* (1)	
families: (number of species)	Culicidae (5) Cecidomyiidae (1) Tephritidae (1) Drosophilidae (14)	Calliphoridae (1) Anthomyidae (4) Muscidae (2) Glossinidae (1)	Diopsidae (2) Tephritidae (1) Coelopidae (1)	

three). In most cases (58 out of these 64 species), females exhibit either an increase in egg production, or a decrease in sexual receptivity, or both, after mating. In 29 species (but not in four), the increase in egg production and decrease in sexual receptivity has been shown to be linked, and caused by the transfer of components of the male ejaculate during mating.

Comparisons of the number of species in table 1 that share features are, however, subject to a number of important caveats, the most important of which is shared phylogeny resulting in non-independence (Harvey & Pagel 1991). Counting species numbers would therefore result in pseudo-replication. However, examining not only the number of species, but also genera and families show that, for example, mating-induced decreases in receptivity are distributed among 16 genera in nine families and mating-induced increases in egg production are distributed among 15 genera in ten families. The widespread nature of mating effects across genera and families within the Diptera and in insects as a whole (e.g. Leopold 1976; Chen 1984; Gillot 1988; Ridley 1988; Miller *et al*. 1994; Eberhard 1996) lend weight to the generality of these patterns. Another caveat is negative results, there are many blanks in the table because traits have not been tested, or results not reported.

The existing data on the effect of virginity and mating on the female life span are equivocal and no clear pattern of increase or decrease emerges from table 1. However, variation in experimental method is likely to be critical to the interpretation of results here. For example, the measurement of the effect of mating on survival in *D. melanogaster* depends upon remating frequency itself, length of exposure to males, and nutrition. Females kept on poor-quality food (where remating frequency and egg production is low) show no mating costs whatsoever; however, costs become apparent and successively larger in magnitude with increasing quality of nutrition, remating frequency and egg production (Chapman & Partridge 1996*a*). There is also usually no attempt to distinguish between or control the different and possibly confounding component costs, such as exposure to males, egg production and mating itself. In addition, large sample sizes are often required to detect survival differences (Carey *et al*. 1992). The results of several carefully controlled, large-scale or replicated experiments, show that mating can reduce survival (Maynard Smith 1958*b*; Fowler & Partridge 1989; Chapman *et al*. 1995; Clutton-Brock & Langley 1997; Mangan 1997). Our results are consistent with these findings and identify separate costs of egg production and of mating itself, as found for *D. melanogaster* (Partridge *et al*. 1987; Fowler & Partridge 1989).

A much clearer pattern emerges in terms of the pattern of egg production and receptivity after mating. The males of many dipteran species contain seminal fluid molecules that enhance the rate of egg production after their transfer at mating. In addition, a characteristic pattern of decreased receptivity and increased egg production after mating is evident. In this study, we found no evidence that mating, or substances transferred during it, increase egg production in the medfly. However, mating and the transfer of seminal fluid do reduce female receptivity (T. Miyatake, T. Chapman & L. Partridge, unpublished data). This uncoupling of seminal-fluid-mediated effects on egg production and receptivity is unusual in the Diptera, may represent a novel pattern and certainly merits further investigation.

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