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Female access and diet affect insemination success, senescence and the cost of reproduction in the male Mexican fruit fly *Anastrepha ludens*

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Abstract. Hypotheses exploring the influence of dietary conditions on the life-history trade-off between survival and reproductive success are extensively tested in female insects but only rarely explored in males. The present study examines the impact of dietary quality and female access on age-specific reproduction and survival of the male Mexican fruit fly *Anastrepha ludens* Loew (Diptera: Tephritidae). There is a clear cost of female access for males with access to dietary protein, measurable as a decrease in life expectancy, which is further influenced by the age when females are introduced. A protein deficient diet reduces the lifespan benefit of virginity and masks the detrimental effect of female access on male life expectancy. Dietary protein is not necessary for reproductive success, although access to protein at eclosion improves the lifetime reproductive success of males compared to when it is delayed. Overall, reproductive success diminishes as the male flies age, regardless of the dietary conditions, providing evidence for reproductive senescence in males. Delaying the males' access to a protein source fails to influence the negative effect of age on reproductive ability. Because age-specific reproductive rates decline with age, regardless of diet, male fitness does not benefit from lifespan extension. Therefore, males can be expected to allocate available resources towards reproductive effort in favour of an extended lifespan, regardless of mate and protein availability.

Key words. Cost of mating, life-history trade-offs, male ageing, male reproduction, resource allocation, senescence, Tephritidae.

Introduction

When nutritional scarcity is encountered in an environment, reduced rates of senescence are often observed in animals, resulting in an extension in lifespan, whereas reproductive effort is reduced or arrested (Weithoff, 2007; Carey *et al.*, 2008). By avoiding the cost of reproduction and allocating available nutrients to somatic upkeep during unfavourable dietary conditions, organisms may improve their fitness by surviving until successful reproduction can begin or resume (Wiley, 1974; Tuljapurkar, 1990; Barrett *et al.*, 2009). Although there is extensive literature on the physiological response to dearth periods, most research conducted on the factors affecting reproductive trade-offs in insects focuses primarily on females in response to dietary restriction and the timing of egg production (Awmack & Leather, 2002; Boggs & Freeman, 2005; Carey *et al.*, 2008; Harwood *et al.*, 2013). By contrast, studies investigating reproductive trade-offs in male insects are uncommon, with research primarily focused on the cost of reproduction in the absence of interactions with nutritional

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conditions (Partridge & Farquhar, 1981; Kotiaho & Simmons, 2003; Paukku & Kotiaho, 2005; Papadopoulos *et al.*, 2010). Those studies that do test the effects of dietary conditions on male reproductive trade-offs in insects find that poor nutritional conditions result in a decline in reproductive effort, although the effects of the suboptimal diets on survival are inconsistent (Hunt *et al.*, 2004; Judge *et al.*, 2008; Attisano *et al.*, 2012).

In male insects, reproductive costs are linked to many of the sexual behaviours and physiological processes related to courtship, signalling, mating and insemination (Martin & Hosken, 2004; Kuijper *et al.*, 2006; Papadopoulos *et al.*, 2010). Accordingly, male reproductive effort is expected to be postponed when the likelihood of successful reproduction is low, thereby preventing the cost of reproduction until the probability of reproductive success improves (Perrin & Sibly, 1993). Such a deferment in the cost of reproduction is well documented in the females of several species in the family Tephritidae (Carey, 2003). Specifically, female tephritids will enter a waiting period characterized by little or no reproductive effort and a lowered risk of mortality during unfavourable reproductive conditions. When conditions improve, the waiting period ends and the females experience an increase in age-specific reproductive ability and a reduced risk of mortality (Carey *et al.*, 1998).

In male tephritids, the lack of female access alone will not elicit a comparable waiting period because males will still form leks and produce and release sexual attractant pheromones in the absence of females, each of which potentially contributes to the cost of reproduction (Liedo *et al.*, 2002; Johansson *et al.*, 2005; Zhang *et al.*, 2006). A source of dietary protein appears to be essential for maximizing male tephritid reproductive ability, with copulation frequency, sexual signalling rate, pheromone production and participation in leks all being dependent on diet (Aluja *et al.*, 2001; Yuval *et al.*, 2002; Liedo *et al.*, 2013). Therefore, the absence of certain dietary resources appears to prevent or reduce the reproductive effort of males. This reduced reproductive effort as a result of poor dietary conditions is expected to allow males to avoid the cost of reproduction and allow nutritional resources to be used for somatic upkeep, thereby improving life expectancy (Hunt *et al.*, 2004; Attisano *et al.*, 2012), especially when females are not available. Because an extended lifespan is assumed only to be adaptive if it results in greater reproductive success later in life (Bonduriansky *et al.*, 2008), such an improvement in lifespan is expected to result in greater reproductive potential at advanced ages. Results in contrast to this hypothesis are reported for some dipteran species in which male reproductive rates and attractiveness are observed to decrease with age (Bonduriansky & Brassil, 2005; Papanastasiou *et al.*, 2011), such that lifespan extension cannot be expected to improve male fitness.

Accordingly, the effects of dietary conditions and female availability on the longevity and age-specific insemination success of the male Mexican fruit fly *Anastrepha ludens* Loew are tested to determine whether male reproductive effort can be delayed, thus extending male lifespan and slowing reproductive senescence, if observed. The Mexican fruit fly, a significant economic pest (Dominguez *et al.*, 2010), represents a useful model organism for understanding demographic trade-offs (Carey *et al.*, 2008; Carey & Molleman, 2010). Much of what is known about the reproductive behaviour and life history of the male Mexican fruit fly is derived from studies focused on its effectiveness in the sterile insect technique (Shaw *et al.*, 1967; Robacker & Garcia, 1993). These studies rarely focus on the trade-offs between reproduction and survival in males, and male reproductive ability is not known to be observed through the entire lifespan (Aluja *et al.*, 2000, 2008). Therefore, the data reported in the present study regarding male Mexican fruit fly life-history characteristics will be helpful for interventions aiming to control their populations, as well as for informing hypotheses regarding life-history trade-offs in male insects.

Materials and methods

Husbandry

Flies were obtained from the Moscafrut mass-production facility at Metapa de Domínguez, Chiapas, Mexico, and reared using the techniques described by Dominguez *et al.* (2010). When these experiments were conducted, the colony was approximately 170 generations old. Wild flies have been introduced into this colony periodically to maintain genetic diversity. All experiments were conducted under laboratory conditions (LD 12 : 12 h at 23 ± 3 °C and 60–75% relative humidity). Adults were separated by sex at eclosion and 450 males were each housed individually in Plexiglas cages ($4 \times 4 \times 10$ cm) from eclosion until death. Treatments consisted of combinations of dietary conditions and female availability, with 50 males assigned to each treatment. All flies were provided daily access to water and to one of two solid diets *ad libitum* depending on the treatment type: (i) full diet, which included a carbohydrate and a yeast derived protein source (3 : 1 ratio mixture of sugar to yeast hydrolysate enzymatic; MP Biomedicals, LLC, Santa Ana, California) or (ii) a diet consisting only of a carbohydrate (sugar-only diet). The experimental control consisted of 50 males provided solid full diet *ad libitum* from eclosion, adult age 0 days, until death and never paired with females.

The difference in life expectancy of males with female access, as described below, compared with those in the control group served as a proxy for the cost of reproduction. Cohorts of reproductive virgin females (aged 10–15 days) were housed in large cages with several hundred females of the same age and provided with constant access to water and full diet. Cohorts of virgin females were maintained for the duration of the study and resupplied with new females weekly to maintain the availability of 10–15-day-old flies. In the appropriate treatments, a single female was introduced into each of the male cages. After 24 h of access, the female was removed and a new virgin female was presented to each male.

Diet and female access

Three treatments were used to establish the cost of reproduction and the influence of diet type, as outlined above, on male longevity. Treatment 1a comprised a full diet from eclosion until death with constant female access, in which males received access to a new virgin female daily for their entire lifespan. Treatment 2a comprised a sugar diet from eclosion until death with constant access to virgin females for the entire lifespan. Treatment 3a comprised a sugar-only diet with no female access. The cost of female access and the effect of diet quality on male lifespan were estimated by comparing the life expectancy of the males in each treatment with that of males in the experimental control group (full diet from eclosion with no female access).

Truncated reproduction

To describe the influence of prior female access on male lifespan after females were no longer available, 50 males were assigned to two truncated access treatments. Treatment 1b comprised constant access to full diet for the entire lifespan, with virgin females only provided from eclosion until age 20 days. Treatment 2b comprised a sugar diet for the entire lifespan, with virgin females only provided until age 20 days. These two treatments were compared with the control group (full diet with no female access) and those testing the effect of diet and female access as described above.

Delayed reproduction

In an attempt to delay reproduction in males, access to virgin females or to full diet, as well as to both females and full diet, were delayed for 20 days after eclosion. Fifty males were tested under each of the specific delayed reproduction treatments. Treatment 1c comprised constant access to full diet from eclosion until death, whereas access to virgin females was delayed for 20 days, after which females were provided daily until death. Treatment 2c comprised a sugar diet provided until age 20 days, after which full diet was provided until death, whereas virgin females were provided daily from eclosion until death. Treatment 3c comprised both a full diet and virgin females delayed until age 21 days, prior to which males were given sugar diet and not provided females. The treatment in which full diet and female access was constant for the entire lifespan (treatment 1a with respect to diet and female access) was included for a factorial design to determine whether delayed diet or female access improved the males life expectancy compared with when reproduction was expected to be continuous.

Diet and age-specific reproduction

To quantify the effect of age and dietary conditions on male lifetime reproductive ability, the insemination success of 20 males from the treatments when (treatment 1a) full diet and female access were constant, (treatment 2a) sugar-only diet and female access were constant, and (treatment 2c) full diet was delayed for 20 days, whereas female access was constant, were monitored every fifth day beginning at eclosion. The 60 females (20 from each of the three treatments) associated with these males on the observation days were removed after being paired and then held for 15 days in individual cages with an egg-laying substrate (silicon coated mesh) and access to water and full diet. Eggs were collected, placed inside a plastic petri dish on a moist sponge wrapped in black satin, and observed for larval hatch over an additional 15-day period. The presence of larvae indicated successful insemination for the male at the age when it was paired with the female, whereas a lack of larval hatch was interpreted as failed insemination. Daily insemination success was recorded as the proportion of males associated with larval production at each observation period.

Statistical analysis

The effect of diet and female access on male life expectancy was tested with two linear regressions. The first assumed the control (full diet from eclosion until death, with no female access) as the baseline for estimating the effects of constant diet, constant female access and truncated female access on the male lifespan. The second assessed the effects of delaying female access, delaying full diet and delaying both on lifespan compared with when both female access and a full diet were constant (treatment 1a). This treatment (1a) was selected as the baseline to determine whether delaying access to females and/or full diet would lead to lifespan extension compared with when reproduction was assumed to be constant. Additional pairwise comparisons were made among treatments with two-tailed *t*-tests. A final linear regression model analyzed the effects and interaction of diet type and age, on male insemination success, with treatment 1a (full diet and female access are constant) selected as the intercept, and age being analyzed as a continuous independent variable.

Results

Diet and female access

The life expectancy of males fed a full diet and never paired with females was 70.32 days. Female access reduced the life expectancy of males fed a full diet by 20.74 days ($t = -5.11$, $P < 0.001$), although female access was not observed to reduce the probability of survival until after age 20 days (Figs 1 and 2). The life expectancy of males on a sugar diet without female access was reduced by 26.94 days compared with when a full diet was provided ($t = -6.64$, $P < 0.001$) (Fig. 2). When a sugar diet was combined with constant female access, the male life expectancy was 25.04 days less than that of control flies ($t = -3.95$, $P < 0.001$), although it was not significantly different from the life expectancy of males supplied a full diet and constant female access ($t = -1.31$, $P = 0.20$) (Fig. 2). There was no significant difference in the life expectancies of sugar-fed males with and without female access ($t = -0.61$, $P = 0.54$) (Fig. 2) and age-specific survival was similar in both of these treatments (Fig. 1).

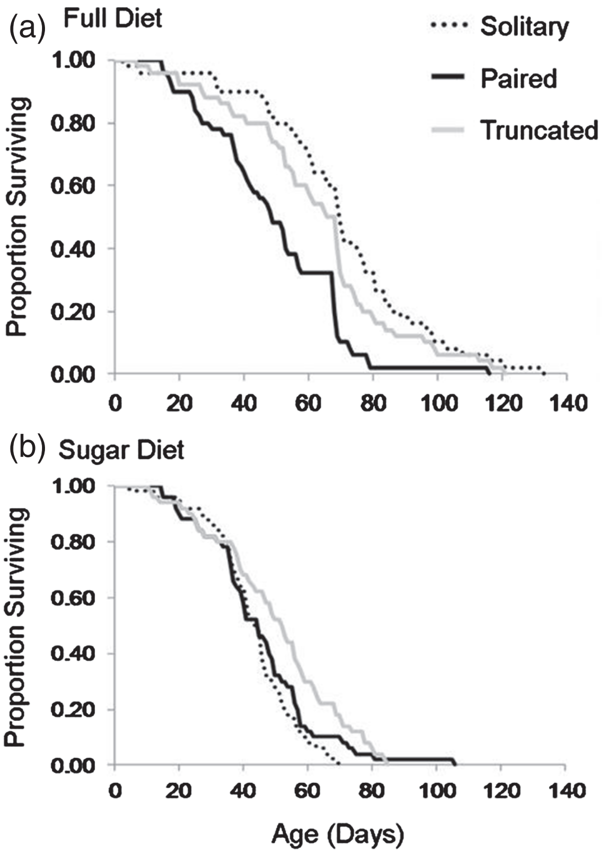

Fig. 1. Age-specific survival of the adult male Mexican fruit fly *Anastrepha ludens* when fed either (a) a full diet (3 : 1 sugar to yeast protein) or a sugar-only diet (b), when female access was prevented (solitary), constant from eclosion until death (paired) or only provided until age 20 days (truncated).

Truncated female access

Truncated female access combined with a full diet did not reduce the life expectancy of males relative to the control ($t = -1.84$, $P = 0.07$) and extended the lifespan relative to those that had constant female access by 13.10 days ($t = 3.27$, $P = 0.001$) (Fig. 2). In combination with a sugar diet, the truncated female access resulted in a significant loss of life expectancy compared with the control ($t = 1.75$, $P = 0.01$) but lessened the loss of life expectancy associated with the sugar diet by 7.30 days ($t = -2.15$, $P = 0.03$) and also appeared to improve age-specific survival after age 40 days compared with the other sugar diet treatments (Fig. 1). The life expectancy of males with truncated access to females was not significantly different from those sugar-fed males with constant female access ($t = -1.40$, $P = 0.16$) (Fig. 2).

Delayed reproduction

Relative to the life expectancy of males with constant access to a full diet and females, delaying female access for 20 days when access to a full diet was constant improved the life expectancy of males by 9.20 days ($t = 2.38$, $P = 0.020$) (Fig. 3), whereas delaying only a full diet when female access was constant and delaying access to both a full diet and females for 20 days did not significantly affect the life expectancy of males ($t = 1.30$, $P = 0.199$ and $t = -1.96$, $P = 0.107$, respectively) (Fig. 3).

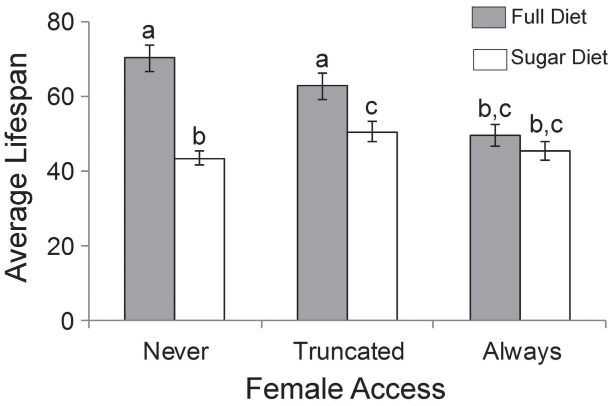

Fig. 2. The mean ± SE lifespan (days) of the male Mexican fruit fly *Anastrepha ludens* provided either a full diet (3 : 1 sugar to yeast protein) or a sugar-only diet, whereas female access was prevented (never), only provided until age 20 days (truncated) or was constant from eclosion until death (always). Means with different lowercase letters represent significant differences ($P < 0.05$) among treatments, as determined via linear regression and subsequent *t*-tests.

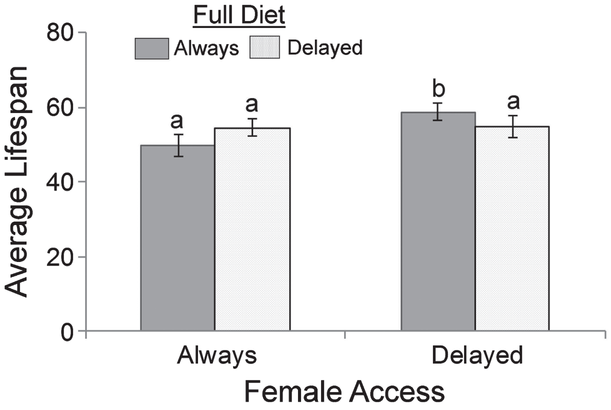

Fig. 3. The mean ± SE lifespan (days) of the male Mexican fruit fly *Anastrepha ludens* provided full diet (3 : 1 sugar to protein derived yeast) at eclosion (always), or at age 21 days (delayed), prior to which only sugar was provided, when females were provided beginning at eclosion (always) or beginning at age 21 days (delayed). Means with different lowercase letters represent significant differences ($P < 0.05$) among treatments, as determined via linear regression and subsequent t-tests.

Diet and age-specific reproduction

Male insemination success was dependent on age and shown to behave as a quadratic function ($t = -10.86$, $P < 0.001$) (Table 1). Figure 4 demonstrates how insemination success first

Table 1. The estimated effect of each diet factor (level) and the covariate age on the mean ± SE proportion of male Mexican fruit flies *Anastrepha ludens* successfully to inseminate females.

Variable	Estimate	*t*-value	*P*
Full diet (intercept)	0.242 ± 0.065	3.705	0.001
Diet (level)			
Sugar only	−0.123 ± 0.053	−2.313	0.026
Delayed full diet	−0.139 ± 0.053	−2.604	0.013
Covariates			
Age	0.039 ± 0.004	10.255	<0.001
Age squared	−0.001 ± 0.000	−10.863	<0.001

The estimate shows how the diet affects insemination success relative to the intercept (full diet), with the *t*-values and *P*-values calculated from two tail *t*-tests. Age squared shows the quadratic effect of age on insemination success (Fig. 4).

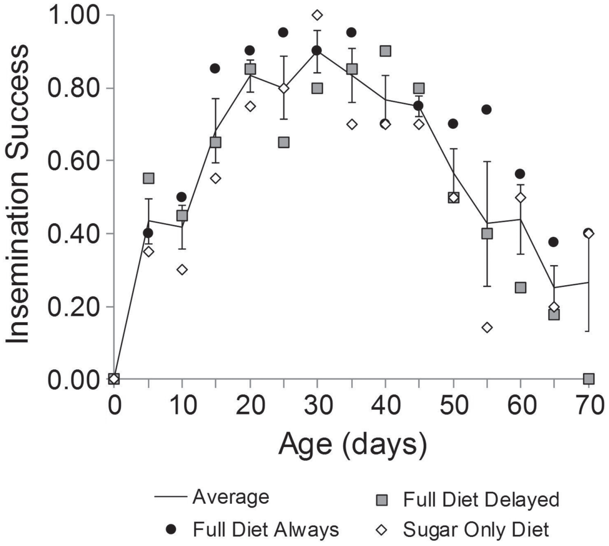

Fig. 4. Age-specific insemination success of the male Mexican fruit fly *Anastrepha ludens* measured as the proportion of females to lay eggs that produced larvae, when a full diet was provided from eclsoion until death (full diet always), when it was delayed until age 21 days, prior to which a sugar diet was provided (full diet delayed), and when only a sugar diet was provided (sugar diet). The line is the mean proportion of males to exhibit successful insemination across all diets at each age, with error bars representing the SEM at each age.

increased with age and then decreased after approximately day 30. A two-piece linear function with a change point at day 30 was also tested, although both models resulted in the same conclusion for the treatment effects (diet and female access), so that only the quadratic fitting is reported. The diet treatments were found to have a significant effect on mean insemination success ($F_{2,40} = 4.07$, $P = 0.024$), with both delayed full diet and sugar diets reducing mean insemination success compared with a constant full diet ($t = -2.31$, $P = 0.025$; $t = -2.60$, $P = 0.012$, respectively) (Table 1). However, there was no difference in the insemination success of males provided a sugar diet and those that experienced a 20-day delay in access to a full diet ($t = 0.04$, $P = 0.966$). The interaction of age and diet was not significant, so that the effect of age on reproductive ability was not influenced by the dietary conditions.

Discussion

Female access reduces the life expectancy of the male Mexican fruit fly *Anastrepha ludens*, when fed a full diet, by 30%, which is consistent with the cost of male reproduction reported in other insects (Kotiaho & Simmons, 2003; Martin & Hosken, 2004; Papadopoulos, *et al.*, 2010). This reproductive cost is affected by the timing and duration of female availability, such that truncated and delayed female access improves male life expectancy compared with when female access is constant. On average, Mexican fruit fly males are not expected to be sexually mature until age 10 days (Pereira *et al.*, 2013) and reproductive success does not appear to peak until after age 20 days. Therefore, truncated female access likely improves the life expectancy of males by reducing their opportunities to mate. Similarly, delaying female access lessens its cost on male life expectancy because reproduction is postponed until the age when reproductive ability appears to be declining. Therefore, delaying reproduction limits the opportunity for males to mate until they are older and less likely to copulate.

A sugar diet is detrimental to the lifespan of male Mexican fruit flies, reducing the life expectancy by 40% compared with unpaired males fed a full diet. Unexpectedly, the life expectancies of paired and unpaired males fed sugar diet are not different. Initially, this result appears to suggest that males are avoiding the cost of female access when a poor quality diet is available, supporting the assumptions of optimal resource allocation models (Perrin & Sibly, 1993). However, sugar-fed males still mate when provided females, albeit at reduced success. If a sugar diet prevents the cost of female access, the life expectancy of males with truncated female access should be the same as those of paired and unpaired males. Instead, truncated female access increases the life expectancy of sugar-fed males. It is unclear why truncated female access extends the lifespan of the sugar-fed males, although prior female exposure may reduce male reproductive effort later in life, as observed in the tephritid, *Ceratitis capitata* (Liedo, *et al.*, 2002). It is unlikely that sugar-fed males are avoiding the cost of reproduction. They still inseminate females and their lifespan appears affected by prior female access. Instead, a sugar diet acts as a limiting factor on survival, as observed in some other insect species (Judge *et al.*, 2008; Harwood *et al.*, 2013). Therefore, dietary conditions have a stronger influence on male Mexican fruit fly survival than female access.

In contrast to the effect of dietary timing in female tephritids (Carey *et al.*, 1998), delaying access to full diet does not improve the life expectancy of male Mexican fruit flies. Additionally, there is no improvement in male life expectancy when both female access and a full diet are delayed. Consequently, a sugar diet at eclosion nullifies the improvement in life expectancy associated with delaying female access.

As observed previously, the reproductive ability of male Mexican fruit flies is influenced by diet (Liedo *et al.*, 2013; Pereira *et al.*, 2013). Although the nutrients in the full diet are not required for successful insemination, they are required to maximize lifetime copulation success. Any period of sugar-only diet reduces the overall insemination success of males. This reduction in insemination success may result from a decrease in pheromone production (Liedo *et al.*, 2013), which is needed to initiate copulation. Additionally, the sugar diet may weaken the males in some way, making them less likely to copulate. The loss of reproductive success as a result of sugar diet cannot be reversed when a full diet is provided at age 20 days. Therefore, the lack of appropriate nutrients early in life constrains the lifetime mating ability of males.

The effect of age on reproductive ability does not vary among diet types. Regardless of dietary treatment, males demonstrate three distinct age-specific reproductive periods corresponding to those observed in female insects (Novoseltsev *et al.*, 2003, 2004). The first is the period of reproductive onset, from age 0–20 days, when the males began to mature. Next, reproductive maturity is reached between ages 25 and 30 days, as demonstrated by the plateau of reproductive success when the highest levels of insemination success are reached. Finally, the period of maturity ends with the onset of reproductive senescence at 30 days, when insemination success begins to decline. Physiologically controlled reproductive senescence is well documented in females from various species (Austad, 2010; Haaga *et al.*, 2010), although sexual selection theory and experimental data suggest that male reproductive performance should increase with age (Williams, 1966; Bonduriansky *et al.*, 2008; Maklakov *et al.*, 2009). In contrast to these predictions, reproductive senescence in the male Mexican fruit fly begins when almost 80% of the males are still alive. Male tephritids are reported to decrease reproductive effort in a response to prior reproductive success and age (Liedo *et al.*, 2002; Lopez-Guillen *et al.*, 2008) and the willingness of the female tephritid *C. capitata* to mate with males is observed to be negatively correlated with male age (Papanastasiou *et al.*, 2011). Nevertheless, these changes in behaviour may be linked to a physiological decline in reproductive ability as a result of senescence, and would therefore be mutually affecting. Further investigation is required to isolate the effects of each on age-specific reproduction.

Based on these results, male Mexican fruit flies do not gain a reproductive advantage by avoiding reproductive effort when dietary protein and females are unavailable. The males are still able to reproduce successfully in the absence of a protein source, even though the poor dietary conditions shorten their life expectancy and constrain life time reproductive ability. Additionally, any delay in reproductive effort is expected to result in a loss of reproductive opportunity associated with ageing, so that the males cannot gain a fitness benefit through delaying reproduction and extending the lifespan. Therefore, it can be expected that male Mexican fruit flies in their natural environment will attempt to attract and copulate with females regardless of the nutritional conditions encountered because delaying reproduction decreases their fitness. Moreover, the possibility of male reproductive senescence, in which male reproductive ability is affected by both natural lifespan and the onset of senescence, challenges the hypotheses of the male disposable soma theory, in which male reproductive effort should increase with age (Williams, 1966).

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