

## Greater Mating Success of Middle-Aged Females of *Drosophila ananassae*

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**Madegowda Prathibha and Mysore Siddaiah Krishna (2010)** Greater mating success of middle-aged females of *Drosophila ananassae*. *Zoological Studies* 49(6): 806-815. Out bred population of *Drosophila ananassae* established from progenies of 150 isofemale lines collected at Mysore, India was used to study how female age influences mating success, mating latency, courtship activities, copulation duration, fecundity, ovariole number and female wing length. It was noted that middle-aged females had significantly greater mating success, and mated faster, and males showed significantly greater intensities of courtship activities, i.e. tapping, scissoring, vibrating, licking toward middle-aged females compared to younger and older females, and copulated longer than with younger and older females. It was also noted that middle-aged females had significantly greater fecundity and ovariole numbers than younger and older females. However, no significant variation in female wing length was found among females of different age classes. Therefore, we hypothesized that in *D. ananassae*, middle aged females were more eager to mate than were younger or older females. Thus, these studies on *D. ananassae* suggest that middle-age females had greater mating success and fitness than younger and older females. <http://zoolstud.sinica.edu.tw/Journals/49.6/806.pdf>

**Key words:** *Drosophila ananassae*, Female age, Male mate preference, Ovariole number, Wing length.

Theoretical models and empirical studies of mate choice have largely concentrated on females, as they are often the selective sex that chooses from among males (reviewed by Milinski 2001). Despite the female-biased empirical evidence in the literature, males are also likely to demonstrate mate choice under some conditions (Dewsbury 1982). Male mate choice is expected in systems where males allocate valuable resources to parental investment, in response to variations in female quality, or where the costs of mate searching and/or assessment are low (Bounduriansky 2001). Furthermore, assuming the costs of male mate choice are not too great (Altmann 1997), it would benefit males to exercise mate choice: 1) if male reproductive success is limited by more factors than simply the number of female mates, and 2)

if females differ in quality or, more specifically, in their reproductive potential (Byrne and Rice 2006). Both of the preceding criteria need to be in place so that male mate selectivity can be evolutionarily advantageous. If all females in a male's pool of potential mates have equal reproductive potential, males should not preferentially mate with one over another, as maximizing only the number of female mates would give males the highest reproductive pay off (Bateman 1948). If females differ in their reproductive potential, males might exercise some degree of mate choice. Therefore, males must operate under time constraints, as well as possibly dwindling energy or sperm reserves, or both. Males that exercise mate selectivity might therefore have a reproductive advantage by wisely allocating their time, sperm, and energy. This is possible with

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females (Andersson 1994) that provide them with the greatest gain in reproductive success.

Nowadays, it is becoming increasingly apparent that in many species, males have a high cost of reproduction (mating) due to costs arising from factors such as energetically expensive courtship displays (Judge and Brooks 2001) and the productions of ejaculates (Dewsbury 1982, Galvani and Johnstone 1998). If the cost of mating is low for males, in the currency of time lost and/or resources consumed, then low levels of male mate discrimination are predicted (Engqvist and Sauer 2000, Kokko and Johnstone 2002). Individuals that are selective concerning mating partners are likely to lose mating opportunities and energy in searching for more-attractive suitors (Bonduriansky 2001). For this behavior to be adaptive, these individuals have to benefit one way or another. On the one hand, benefits may come in the form of direct enhancement of survival or fecundity (Burley 1977), as selection favors mating preferences towards mates that are more fertile (Avent et al. 2008), provide superior resources, offer more parental care, or otherwise help to reduce reproductive costs. On the other hand, selective mating may be adaptive as a consequence of indirect benefits (Somashekar and Krishna 2010), and offspring may inherit genes that promote their survival or reproduction (Andersson 1994). Specifically, mate choice may lead to production of offspring with genotypes that increase viability or that make them more attractive to members of the opposite sex.

In general, mate choice is less common in males, being reported in only 58 insect species, distributed among 11 orders and 37 families (Bonduriansky 2001). There are now growing numbers of observations of male choice seen in a wide range of taxa including insects (Bonduriansky 2001, Byrne and Rice 2006), birds (Jones and Hunter 1993), and fish (Amundsen and Forsgren 2001). Those studies suggest that male mate choice is predicted to be adaptive when variance in female fitness is large and males experience costs of mating such that they cannot inseminate all females encountered (Burley 1977, Parker 1983, Owens and Thompson 1994, Johnstone et al. 1996, Kokko and Monaghan 2001). However, the empirical evidence is limited.

Characters used by males to select females are generally virginity, and her size, age, and gravid status (see Bonduriansky 2001). The most-obvious character influencing the reproductive

value of a female is her fecundity (Bonduriansky 2001). When mating opportunities are constrained, males that show a preference for more-fecund females will directly benefit by increasing the number of offspring they produce (Katvala and Kaitala 2001). The most-compelling studies of male choice suggest that female mating success is often associated with traits that are correlated with female fecundity (Bonduriansky 2001, Byrne and Rice 2006), while in others, mate assessment may occur through display traits such as coloration, pheromones, or ornamental and morphological features (Amundsen 2000, Chenoweth and Blows 2003, Lebas et al. 2003). However, models of the evolution of male choice suggest that male choice tends to break down when males target arbitrary female traits rather than those that reliably signal fecundity (Kokko and Johnstone 2002, Chenoweth et al. 2006, Servedio and Lande 2006). Therefore, male preference for female traits may be an indirect way of assessing female fecundity. Thus, there is a need to understand how male choice is related to such traits.

The fruitfly provides unique opportunities to test the predictions of male mate choice models. The status of *Drosophila* as one of the most important model genetic organism of the early 21st century is a consequence of the vision of early researchers who chose the fruitfly to study courtship behaviour. Those early evolutionary biologists could easily maintain *Drosophila* in the laboratory, and they also recognized that the elaborate and complex courtship display was an ideal system to study aspects of sexual selection, i.e., to test predictions of male mate choice models.

For this purpose, *D. ananassae* was selected as the experimental model because of its following characteristics. It is a cosmopolitan domestic species belonging to the *melanogaster* group of the *ananassae* subgroup and the *ananassae* species complex (Bock and Wheeler 1972). This species occupies a unique status in the entire *Drosophila* genus due to certain peculiarities in its genetic behavior (Singh 1985a b). An absence of male crossing-over, a high level of inversion polymorphism, and high mutability are features which make it useful for certain genetic studies. The influence of male age on mating success and offspring fitness has not been studied.

## MATERIALS AND METHODS

Outbred stock of *D. ananassae* established from progenies of 150 naturally inseminated isofemale lines collected at domestic localities of Mysore, Karnataka, India was used. Progeny produced by each of the above isofemale lines were mixed together and redistributed to 20 different culture bottles. These stocks were cultured using 40 flies (20 males and 20 females) per quarter pint milk bottles (250 ml) containing wheat cream agar medium and were maintained at  $21 \pm 1^\circ\text{C}$  at a relative humidity of 70% using a 12: 12 h light: dark cycle. This procedure was continued for 3 generations to allow flies to acclimatize to the laboratory. At the 4th generation, synchronized eggs ( $\pm 30$  min) were collected from parental stocks (5-6 d old) using Delcour's (1969) procedure. Eggs (100) were seeded in a vial containing wheat cream agar medium. When adults emerged, virgin females and unmated males were isolated within 3 h of eclosion and were aspirated into a new vial containing wheat cream agar medium. These flies were aged as required for the experiment. In order to provide uniform environmental conditions for females of different age classes, female flies collected first were assigned to 32-33 d (older); females flies collected next were assigned to 17-18 d (middle-aged). Following this, female flies collected were assigned to 2-3 d (younger). Before beginning the experiment, developmental times of flies collected at different times were also tested, and the results indicated no significant variations. These females of different age classes were kept in groups of 4 flies each in culture vials containing wheat cream agar medium and were transferred to a new vial containing wheat cream agar medium once a week until they were used in the experiment. Male flies were aged for 5-6 d. These flies were also maintained using the above-described laboratory conditions until they were used in the experiment.

### The influence of female age on male mating preferences

To study the influence of female age on male mating preferences, 2 females (younger vs. middle-aged, younger vs. older, or middle-aged vs. older) and a 5-6 d-old male were aspirated into an Elens-Wattiaux mating chamber (1964). Indian ink was painted on the thorax of one of the females. The effect of paint was tested before commencing the experiment by painting young flies in 1 trial and

middle-aged/older females in an alternate trial and allowing them to mate. In 27 of 50 trials, middle-aged females mated, and in the remaining 23 of 50 trials older females mated ( $\chi^2 = 0.32$ ;  $d.f. = 1$ ;  $p > 0.05$ ). Results showed insignificant differences suggesting that painting had no influence on the performance of the flies. Each pair was observed for 1 h. When mating occurred, the copulating pair was aspirated out of the mating chamber and placed in a new vial containing wheat cream agar medium. In total, 50 trials were conducted for each combination of female ages. A Chi-square analysis was carried out to examine male mate choice data.

### The influence of female age on mating activities and female fecundity

A male with a female (younger, middle-aged, or older) were aspirated into an Elens-Wattiaux mating chamber (1964), and observed for 1 h. Mating latency (time between introduction of the male and female together in the mating chamber and initiation of copulation by the pair) and copulation duration (time between initiation and termination of copulation by the pair) were recorded. We also quantified courtship acts such as tapping, scissoring, vibrating, licking, circling, ignoring, extruding, and decamping following the procedures of Hegde and Krishna (1997).

During tapping, the male initiates courtship with a foreleg motion, partially extends and simultaneously elevates 1 or both forelegs, and then strikes downward; thus, bringing the ventral surface of the tarsus into contact with the partner. During scissoring, a courting male, during the interval between wing vibrations, sometimes opens and closes both wings with a scissor-like movement. During vibrating, the wing movement of males involves expanding 1 wing laterally from a resting position and then rapidly moving 1 or both wings up and down. During licking, a courting male positions himself close behind the female, extends his proboscis, and licks her genitalia. During circling, the male, after posturing at the side or rear of a non-receptive female, faces her as he moves. Sometimes, he moves to face her and then retraces his path to the rear, while at other times, he moves completely about her in a full circle. During ignoring, a non-receptive female when courted sometimes simply continues with whatever activity she is engaged in and obviously ignores the male's actions. During extruding, a non-receptive female presses her vaginal plates

together, contracts certain of the abdominal muscles, and apparently relaxes other muscles. During decamping, a non-receptive female often attempts to escape by running, jumping, or flying away from the courting male.

The behaviors of the male and female were simultaneously recorded but separately by 2 observers for 1 h; the number of pairs that mated was also recorded. Soon after mating, the mated female was transferred to an individual fresh vial containing wheat cream agar medium and evaluated once every 24 h to study fecundity, and this continued for 16 d. The total number of eggs laid by each female was recorded. In total, 50 trials were carried out for each of the 3 female age classes. One-way analysis of variance (ANOVA) followed by Tukey's honest post-hoc test was carried out on mating latency, courtship activities, copulation duration, and fecundity data using SPSS vers. 10.1 software (SPSS, Chicago, IL, USA).

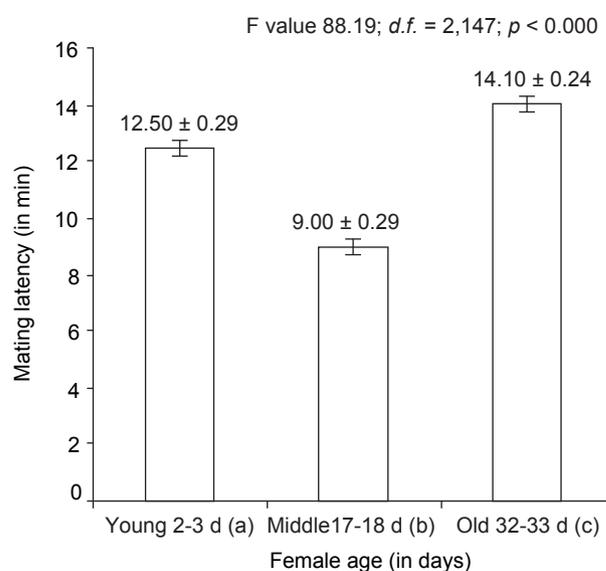
#### The influence of female age on the number of ovarioles and wing length

Virgin younger, middle-aged, and older females were individually sacrificed to count the number of ovarioles and determine the female wing length following the procedures of Krishna and Hegde (1997). To count the number of ovarioles, each female was dissected in a drop of physiological saline using a binocular stereomicroscope; ovarioles of the left ovary were separated from one another with the help of fine needles. The number of ovarioles in each female was counted. From the same female, wing length was also measured using a 100x [microscope] following the procedures of Hegde and Krishna (1997). The mean ovariole number and female wing length data were also subjected to one-way ANOVA followed by Tukey's honest post-hoc test. In total, 50 trials were separately conducted for each of the 3 female age classes.

## RESULTS

Males generally chose to mate with middle-aged females more frequently than younger or older females (Table 1). Middle-aged female success in crosses involving younger and middle-aged females was 32 ( $n = 50$ ); middle-aged female success in crosses involving older and middle-aged females was 34 ( $n = 50$ ). Younger female success in crosses involving younger and older females was 30 ( $n = 50$ ).

The mean mating latency of females mated to males of different age classes is provided in figure 1. Males mated to middle-aged females took a shorter time to initiate mating, while males mated to older females took a longer time to initiate mating. One-way ANOVA followed by Tukey's honest post-hoc test carried out on the mean mating latency data showed significant variations in the mean mating latency among males mated to



**Fig. 1.** The influence of female age on the mating latency of *Drosophila ananassae*. Different letters in brackets indicate a significant variation by Tukey's test.

**Table 1.** The influence of female age on the mating success of *Drosophila ananassae* in a female choice experiment

Male (5-6 d)	Female				Female				Female			
	Younger	Older	$\chi^2$ value	$p$ value	Younger	Middle-aged	$\chi^2$ value	$p$ value	Middle-aged	Older	$\chi^2$ value	$p$ value
No.	30	20	2	>0.05	18	32	3.92	<0.05	34	16	6.48	<0.01
%	60%	40%			36%	64%			68%	36%		

females of different age classes. Tukey's honest post-hoc test showed that the mean mating latency of middle-aged females was significantly less than those of younger and older females. However, the mating latency of older females was found to be insignificantly greater than younger females but significantly greater than middle-aged females.

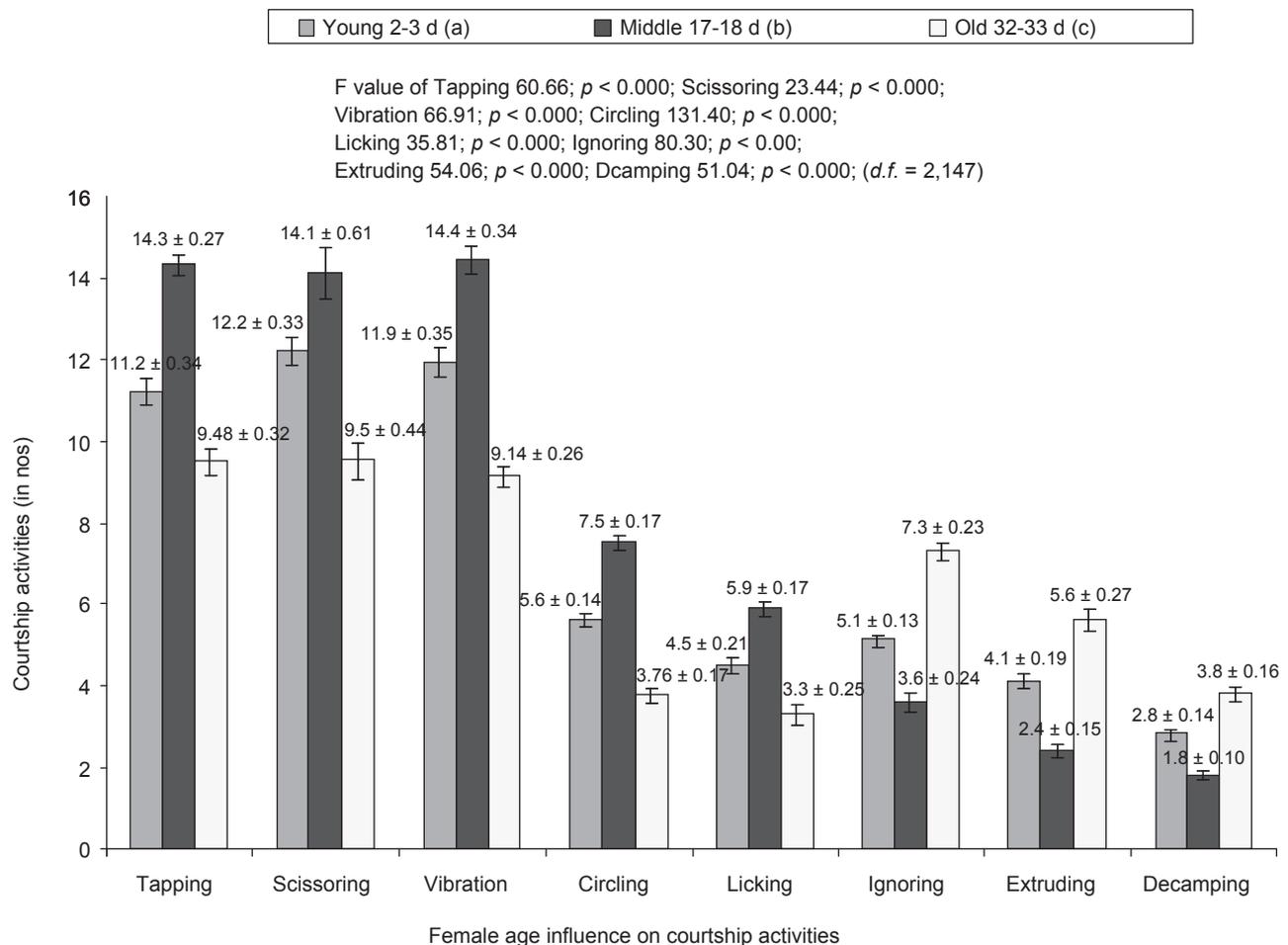
Figure 2 shows that in *D. ananassae*, males showed significantly greater courtship activities such as tapping, scissoring, vibrating, circling, and licking with middle-aged females compared to younger and older females. On the other hand, middle-aged females showed fewer rejection responses toward males such as ignoring, extruding, and decamping than younger and older females. One-way ANOVA followed by Tukey's honest post-hoc test carried out on mean courtship activities showed significant variations in courtship activities among different female age classes.

Figure 3 shows the average copulation dura-

tions of males mated to females of different age classes. Males mated to middle-aged females copulated longer compared to males copulating with younger and older females. Copulation duration data subjected to one-way ANOVA followed by Tukey's honest post-hoc test showed significant variations in copulation durations among females of different age classes.

The mean fecundities of younger, middle-aged, and older females of *D. ananassae* are given in figure 4. It was noted that middle-aged females had the highest mean fecundity while older females had the least mean fecundity. One-way ANOVA followed by Tukey's honest post-hoc test showed significant differences in mean fecundity among females of different age classes; Tukey's honest post-hoc test showed that middle-aged females had significantly greater fecundity compared to younger and older females.

Figure 5 shows the mean number of ovarioles

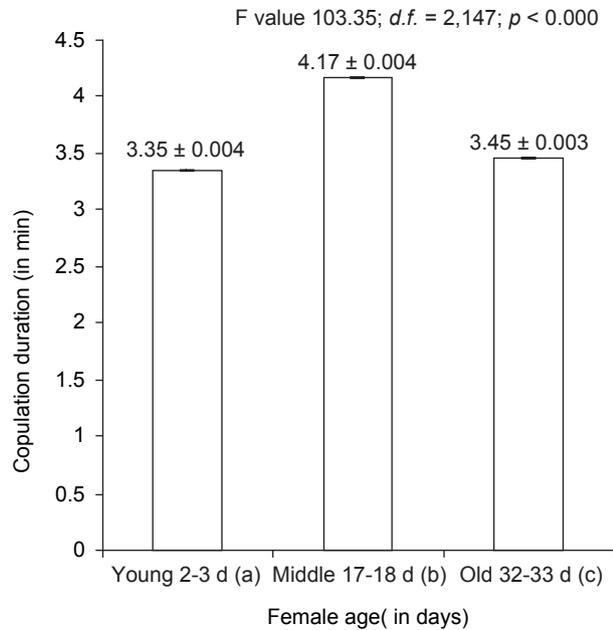


**Fig. 2.** The influence of female age on mating activities of *Drosophila ananassae*. Different letters in brackets indicate a significant variation by Tukey's test.

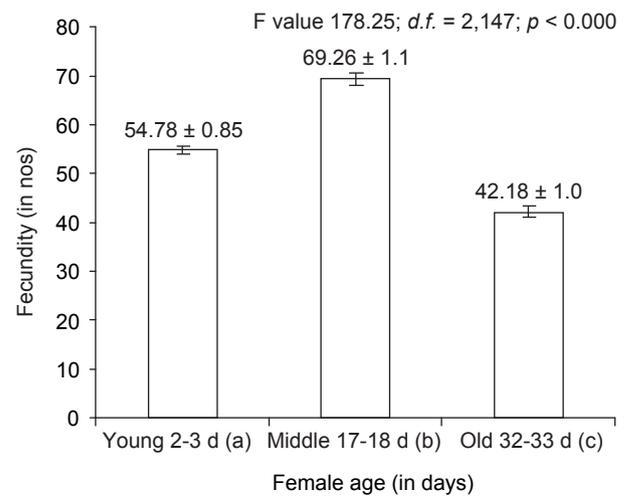
of younger, middle-aged, and older females of *D. ananassae*. The highest mean number of ovarioles was found in middle-aged female, while the least mean number of ovarioles was found in older females. The mean number of ovarioles data subjected to one-way ANOVA followed by Tukey's honest post-hoc test showed significant variations

in the mean numbers of ovarioles among females of different age classes. Tukey's honest post-hoc test also showed that middle-aged females had a significantly greater mean number of ovarioles compared to younger and older females.

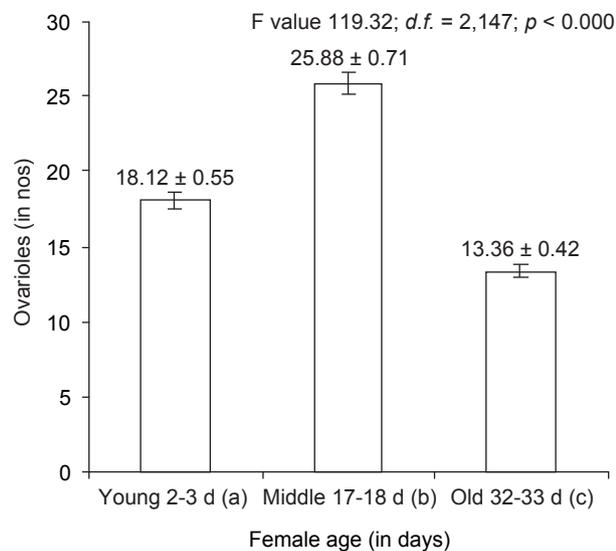
The mean female wing lengths of younger, middle-aged, and older females of *D. ananassae*



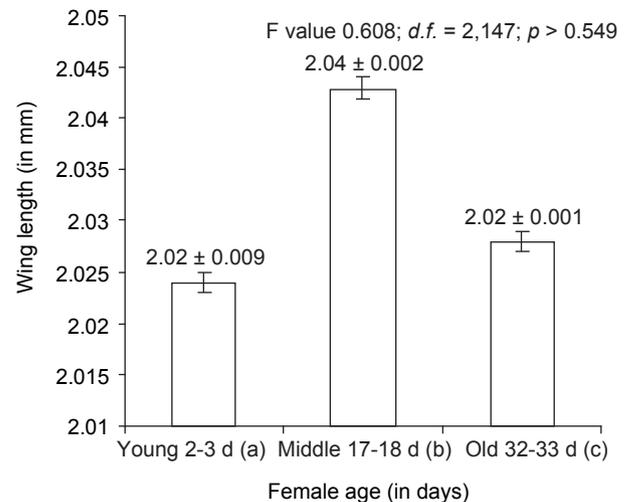
**Fig. 3.** The influence of female age on the copulation duration of *Drosophila ananassae*. Different letters in brackets indicate a significant variation by Tukey's test.



**Fig. 4.** The influence of female age on the fecundity of *Drosophila ananassae*. Different letters in brackets indicate a significant variation by Tukey's test.



**Fig. 5.** The influence of female age on ovariole numbers of *Drosophila ananassae*. Different letters in brackets indicate a significant variation by Tukey's test.



**Fig. 6.** The influence of female age on the wing length of *Drosophila ananassae*. The same letters in brackets indicates an insignificant variation by Tukey's test.

are given in figure 6. It was noted that differences in mean female wing lengths of different age classes were insignificant.

## DISCUSSION

Restrictions in mating opportunities of males may arise for various reasons (for a review, see Clutton-Brock and Parker 1992). Males of *Drosophila* do not show parental care, and males only contribute sperm and components of the ejaculate to the courted female (Somashekar and Krishna 2010). In *Drosophila*, the high cost of reproduction is due to costs arising from such factors as energetically expensive courtship displays, the production of ejaculates, and time lost during different courtship displays (Bonduriansky 2001). It is assumed that in *Drosophila*, males exercise mate choice because 1) reproductive success of males of *Drosophila* is limited by more factors than simply the number of females mated, and 2) females also differ in quality, i.e., fecundity. These 2 criteria need to be in place for male *Drosophila* mate selectivity to be evolutionarily advantageous (Bateman 1948). Table 1 reveals that males of *D. ananassae* prefer to mate with middle-aged females more frequently than younger and older females, suggesting that males of *D. ananassae* exercise mate choice to obtain direct benefits in the form of greater fecundity. Thus, it appears that female age is an important determinant of male mate choice. In other words, males of *D. ananassae* do not show the same levels of interest in females of different age classes they encounter. This confirms earlier studies of the existence of male mate choice for females in other insects (Bonduriansky 2001). Male mate choice was also found for female characters. Gowaty et al. (2003), while working on *D. melanogaster*, also pointed out that males of *Drosophila* do not show the same level of interest in all females they encounter, and provided evidence that males have also evolved to selectively mate. Therefore, these studies suggest that male preference for female traits may be an indirect way of assessing female fitness.

Mating behavioral studies in *Drosophila* have assumed that females control mating success, i.e., whether mating takes place and with whom (Speith 1952). Female mate choice not only involves the female preference for males but also involves male-male competition (Hegde and Krishna 1997, Avent et al. 2008, Somashekar and

Krishna 2010). Those studies suggested that male-male competition can reinforce female mate preference rather than operating in an antagonistic fashion (Moore and Moore 1999). Even with male mate choice, it is difficult to separate among male choice, female-female competition, and differences in female motivations to mate (Byrne and Rice 2006). Therefore, we can hypothesize that in *D. ananassae*, middle-aged females are more eager to mate than younger or older females. This agrees with earlier studies of sexual selection in different species of *Drosophila* (Speith 1952, Manning 1961, Hegde and Krishna 1997, Byrne and Rice 2006).

Studies on mating behavior in *Drosophila* suggest that male mating success not only depends on male preferences, but successful copulation also requires female receptivity (Speith 1952). In *Drosophila*, sexually mature females show a range of behaviors to thwart unwanted advances of courting males, such as decamping, wing flicking, kicking, and ovipositor extrusion (Speith 1952), while immature females do not show such rejection behaviors. This is because newly emerged (immature) females do not perform any of these rejection behaviors (Manning 1961). The cuticles of immature females have not yet hardened, their wings are folded, and they move slowly. In *D. ananassae*, it was noted that females were unreceptive on the day of eclosion for up to 36 h; thereafter, females were receptive, and they were found to be receptive for up to 32 d. This supports the work of Manning (1965) who while working on *Drosophila*, also found that most females are unreceptive on the day of eclosion. They are highly receptive between 2 and 20 d, after which there is a general decline in receptivity. Those studies suggest the existence of species-specific differences in female receptivity. In the present study, the different age classes used were all virgins and were found to be receptive. Therefore male preference for middle-aged females could not be accounted for by differences in female life history.

In addition to the above characters, the rearing of females of different age classes in groups before they were exposed to males is an important factor that accounts for the experience of female interactions on female mating success (Svetec and Ferveur 2005). It was noted that in the present study, females were kept in groups of 4 females per vial separately for each of the 3 female age classes. Therefore, the observed greater mating success of middle-aged females

in our study is unlikely due to females being kept with other females longer; instead, it was an effect of age. Thus, these studies on *D. ananassae* suggest that there are many other potential cues that males may use when making a choice between females of different age classes.

Earlier studies on mating behaviors of *Drosophila* suggested that male activity and female receptivity are important for successful mating in *Drosophila* (Manning 1961, Spieth 1968). In *Drosophila*, mating latency to courtship or copulation is a good estimate of sexual receptivity of females and sexual activity of males (Spieth and Ringo 1983). During this period, the male fly performs various courtship acts such as tapping, scissoring, vibrating, and circling to increase the receptivity of females (Spieth 1968, Hegde and Krishna 1997). Figure 1 reveals that middle-aged females took a shorter time to initiate copulation compared to younger and older females, suggesting an influence of female age on mating latency. As speed is the reverse of time, flies which took more time were slow maters while those which took less time were fast maters. This suggests that in *D. ananassae*, middle-aged females were fast maters while older females were slow maters. This supports age influencing mating activities as was reported in *D. pseudoobscura* (Noor 1997). Since female receptivity is also related to the time of initiation of copulation, middle-aged females were more receptive than younger and older females of *D. ananassae*.

We also quantified male and female courtship activities, such as tapping, scissoring, vibrating, circling, licking, ignoring, extruding, and decamping in single female trials (no-choice method). It was noted that males of *D. ananassae* showed greater courtship activities toward middle-aged females than toward younger and older females, suggesting an influence of female age on male courtship activities in *D. ananassae* (Fig. 2). This supports earlier studies that age and other environmental factors influence courtship activities in different species of *Drosophila* (Spieth 1952, 1968, Hegde 1979, Hegde and Krishna 1997, Noor 1997). Through these courtship activities, males of *Drosophila* better convey chemical, auditory, and visual signals to middle-aged females and more quickly try to convince middle-aged females to mate than younger and older females. This agrees with earlier studies of *Drosophila* that males which perform greater courtship activities are better mates and obtain greater mating success than those males which do not show high levels of

courtship activities (Hegde and Krishna 1997).

Mating behavior involves male and female courtship activities which culminate in initiation of copulation (Spiess 1970). The duration of copulation, that is the time elapsed between initiation and termination of copulation, varies in different species of *Drosophila*. It varies from 30 s in *D. muller* to more than 1 h in some species (Spieth 1952). During copulation, sperm from the male is transferred to the female reproductive tract, and therefore the duration of copulation has a lot of significance in an animal's life. The duration of copulation is known to be influenced by genotype, environmental factors, size, age, etc. Figure 3 reveals that middle-aged females copulated longer than younger and older females. This suggests an influence of female age on copulation duration. An increased copulation duration increases the number of ejaculations, and it is advantageous for males with a limited number of mating opportunities during their lifespan (Hegde and Krishnamurthy 1979). Hence in *D. ananassae*, middle-aged females had greater reproductive potential as they copulated longer compared to younger and older females.

One theory suggests that when males seek direct fecundity benefits, they should discriminate among potential mating partners on the basis of traits which are reliable indicators of fecundity (Fitzpatrick et al. 1995, Servedio and Lande 2006). Models of the evolution of male choice suggest that male choice tends to break down when males target arbitrary female traits rather than those that reliably signal fecundity (Kokko and Johnstone 2002, Chenoweth et al. 2006).

Figure 4 shows that middle-aged females had significantly greater fecundity compared to younger and older females, suggesting that females of the same species show variations in reproductive potential across age. This confirms earlier work suggesting that female age is also one of the traits known to influence female fecundity, such as that of Bonduriansky (2001), in working on the evolution of male mate choice in insects who also found an influence of female age on female fecundity.

Since the number of ovarioles is positively correlated with fecundity, we sacrificed females of different age classes to study variations in the number of ovarioles if any at different female ages. Figure 5 shows that middle-aged females had a significantly greater number of ovarioles than younger and older females, and follows a pattern of fecundity across female age. This again

confirms earlier studies of the influence of female age on reproductive success in other insects (Bonduriansky 2001). From our results, it was also noted that in *D. ananassae*, middle-aged females had a significantly greater number of ovarioles and higher fecundity compared to younger and older females. Therefore, it is advantageous for males to mate with middle-aged females compared to younger and older females. However, it is not known why older female had fewer ovarioles than younger and middle-aged females. We do not know whether they reabsorb them as the females age.

Studies in insects also found a positive correlation between female size and the number of ovarioles (Branquart and Hemptinne 2000). Even in *Drosophila*, studies of Robertson (1957) found a positive correlation between female size and the number of ovarioles. Therefore, in the present study, flies which were sacrificed to study the ovariole number were also used to measure wing length to understand relationships among female age, wing length, and ovariole number. It was found that there was an insignificant difference in the mean female wing length among females of different age classes (Fig. 6). This suggests that female age has no influence on female body size, but has a significant influence on ovariole number. These studies suggest that females of *D. ananassae* differ in reproductive potential, i.e., fecundity and ovariole number across different female age classes, but they did not significantly differ in body size across the different female age classes. Therefore, one would expect that males of *D. ananassae* might exercise some degree of mate choice because of more factors that put an upper limit on male reproductive success. For this behaviour to be adaptive, these individuals are expected to benefit by enhanced survival or fecundity. Therefore, it is important that males carefully select females to increase their fitness. The benefits may come in the form of direct enhancement of survival or indirect benefits in the form of fecundity (Trivers 1972). Thus, these studies on *D. ananassae* suggest that middle-aged females have greater mating success and fitness characters than younger and older females.

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