

THE EFFECTS OF AGE ON REPRODUCTION IN A CITRUS ROOT WEEVIL DIAPREPES
ABBREVIATUS

by
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ABSTRACT

Understanding the factors influencing mate choice is a major focus of sexual selection. Many factors are potentially involved, including age of the individual. The good genes model and the youth advantage model both make predictions about the effect of age on mate choice. Under the good genes model older mates would be the more preferable due to their proven high survivability. The “youth advantage” model, predicts that young to intermediate age males would be more advantageous as mates because of a decrease in sperm quality and the possibility of increased germ-line mutations in older animals. I examined the effects of age on behavioral and physiological factors in *Diaprepes abbreviatus* experimentally. Both males and females were found to be the least optimal as mates during the intermediate stage of their lives, with preferences for young and old age classes. Females had higher fertilization rates when young and fertilization steadily declined with age, consistent with the youth advantage model. Males overall had higher fertilization rate and procured matings faster when they were older, which was in accordance with the good genes model, though experience could also play a role in this result. These data here suggest that in *D. abbreviatus* age may play an important role in mate choice decisions.

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CHAPTER 1: INTRODUCTION

Sexual selection theory helps explain sex differences in morphology, physiology, and behavior in many species (Andersson 1994). Individuals may choose mates based on characteristics that show potential benefits, such as size, previous mating success, parasite loads, and age (Andersson 1994; Krebs and Davies 1993). The age of an individual can play a major role in mate choice (Trivers 1972; Jones *et al.* 2007). Two models that predict the influence of age on mate choice are the good genes model, and the “youth advantage” model, as it is referred to here (Trivers 1972; Hanson and Price 1995; Beck and Powell 2000). The good genes model, also called the viability indicator model, predicts that females should choose older males because they exhibit higher genetic quality by their increased ability to survive longer (Trivers 1972; Manning 1985; Kirkpatrick 1987). Several studies have noted the preference for older males by females (Zuk 1988; Grahn and Vonschantz 1994; Enstrom 1993; Price 1984), including a simulation model developed by Kokko and Lindstrom (1996) that showed females preferred older males under varying ecological conditions.

The youth advantage model predicts that females should not choose older males because these males may have reduced sperm viability resulting in fewer progeny and an increase in potentially deleterious mutations (Hansen and Price 1995 and 1999; Beck and Powell 2000). In ladybird beetles (*Coccinella septempunctata*) and in hide beetles (*Dermestes maculatus*) males of intermediate ages were able to fertilize more eggs than older or younger individuals (Jones *et al.* 2007; Strivastava and Omkar 2004). Female ladybird beetle fecundity was independent of male age, but male age influenced egg viability yielding significantly higher viability when at an

intermediate age and better quality progeny when they were of a young to intermediate age (Pervez *et al.* 2004; Strivastava and Omkar 2004). Therefore in these species, females that preferentially mated with intermediate-aged males gained direct fertilization benefits (Jones *et al.* 2000; Jones and Elgar 2004).

In species where female fecundity and egg quality can change over time, and a male's success is limited by female reproductive potential, male mate choice can also occur (Thornhill and Alcock 1983; Simmons *et al.* 1994; Santolamazza-Carbone *et al.* 2007; Opit and Throne 2007). Many males prefer to mate with virgin females because unmated females may have higher potential fecundity and egg viability (Simmons 2001; Bonduriansky 2001). However, a study of the ladybird beetle revealed that females of intermediate age had higher fecundity than older or younger females (Pervez *et al.* 2004). Older females also can possess qualities that males may choose e.g. higher proportion of mature eggs and increased receptivity (Bonduriansky 2001).

Diaprepes abbreviatus (L.) (Coleoptera: Curculionidae), a neotropical root weevil, is a destructive, invasive species that is a major pest on citrus, as well as many other plant species (Woodruff 1985, 1964). Females and males are promiscuous and mate often (Harari *et al.* 2003). When mating, males used stroking behaviors to influence postcopulatory success with the female and to reduce female movement before the male has finished copulating (Sirot *et al.* 2007). Males also exhibit extensive postcopulatory mate guarding, perhaps to ensure paternity because last sperm precedence occurs in this species (Harari *et al.* 2003). Observations in size assortment trials have shown that males exhibit active choice on female size, preferring larger females, and

females are more receptive to larger males (Harari *et al.* 1999). Females also show preference for males that exhibit satisfactorily rapid stroking rates during copulation (Sirot *et al.* 2007).

However, not all the patterns of mate choice in this species are explained by body size and it remains untested whether age is another factor in determining mate choice (Harari *et al.* 1999).

The long life, short dispersal distance, high reproductive rate, evidence of mate choice, and overlapping of multiple generations makes this species a good model for observing the effects of age on reproduction (Knapp *et al.* 2001; Harari *et al.* 1999).

Hypothesis and Predictions

Diaprepes abbreviatus have long life spans and a high reproductive rate which could lead to mutation accumulation, decreased gamete quantity and quality, and physical degradation in older individuals. Due to these factors I hypothesize that this species will follow the youth advantage model, where younger individuals will be favored as mates. If *D. abbreviatus* follows this model then I predict the following:

Hypothesis 1: If age reduces the mating attractiveness of females, then I predict males will less readily mate with older females.

Hypothesis 2: If age reduces the reproductive success of females, then I predict: a) egg mass size will decrease in older females and b) egg viability will decrease in older females.

Hypothesis 3: If age reduces the mating attractiveness of males, then I predict that females will less readily mate with older males.

Hypothesis 4: If age reduces the reproductive success of males, then I predict older males will fertilize fewer eggs.

In addition to assessing the youth advantage model, these data allowed me to assess several classic hypotheses regarding life history evolution in *D. abbreviatus*. Specifically, I examined the potential for early-age reproductive effort to influence both late-age reproductive effort and life span.

Biology of Study Organism

Originating from Puerto Rico, *D. abbreviatus* was first discovered in Florida in 1964 in an Apopka citrus nursery and has since spread through much of the state (Woodruff 1964; Lapointe *et al.* 2007). Large, adult weevils are 10mm-19mm in length with several color morphologies ranging from gray to yellow to green to orange with black markings (Woodruff 1964). Egg masses are laid between two leaves and sealed. Eggs hatch within 7-10 days, and larvae fall to the ground and burrow into the soil where they feed on plant roots, completing 8 to 10 instars over several months before pupation (Wolcott 1936; Beavers 1982). A vertical pupation chamber is formed by positioning itself with the head upward and spinning to compact the soils walls (Wolcott 1936). The larvae stays within the pupation chamber for anywhere between 9-26 days. During this time the larvae grows appendages, eyes, wings and other adult features. The adult sheds the pupae skin and its exoskeleton hardens. The adult has been noted to stay in the pupal chamber 11-126 days after it is seemingly mature. Once the adult is ready to emerge it digs its way out of the ground with the assistance of mandibular appendages, which break off during this journey (Wolcott 1936). After emergence, individuals initially disperse less

than 45m away and usually settle on a nearby plant, and in some places accumulate in dense aggregations of reproductively active adults (Beavers and Selhime 1978; Nigg *et al.* 2001; Sirot and Lapointe 2008). Adult weevils are long-lived relative to other insect species, with females living a mean of 147 days and males a mean of 135 days after emergence (Beavers 1982). Both males and females become reproductively active 7-10 days after emergence from the soil (Beavers 1982; Wolcott 1936). Females lay egg masses frequently, with some individuals laying daily (Wolcott 1936). Over her lifetime a female weevil can lay over 5,000 eggs, depositing 70 eggs or more at one time (Wolcott 1936; Beavers 1982).

CHAPTER 2: MATERIALS AND METHODS

Housing of Insects

I obtained 20 male and 25 female newly emerged *D. abbreviatus* from populations reared at the USDA Horticultural Research Laboratory in Fort Pierce, Florida. I kept the males and females separately in 35cm x 15cm x 15cm wire mesh cages, until reaching 3 weeks of age. I placed mating pairs in 8cm x 4cm x 8cm clear, plastic mating containers. During mating the temperature and relative humidity were recorded. The temperature ranged between 25.1 °C- 32.3 °C and the relative humidity ranged between 29% - 73%, depending on the time of day, weather and month. After mating, I housed the individuals alone in 20cm x 20cm x 10cm wire mesh cages which were placed in a screened outdoor structure to maintain a natural light cycle and weather conditions. I collected the behavioral data, female physiological data, and the first part of the male physiological data occurred during the mating season of *D. abbreviatus* (May – December). I provided citrus leaves (*Citrus macrophylla*) and organic greenbeans as a food supply and water was provided through wet cotton wicks. I taped the wax paper (3cm x 10cm) to the side of the cage as an oviposition substrate for the females (Harari *et al.* 2003; Sirot and Lapointe 2008).

Mating

Effects of age on male reproduction

I used 18 three-week-old males as the experimental males and twenty 3-week-old females were used as mates. Previous research has found that body size is an important trait in mate choice, (there is a preference for large mates), although male size does not seem to affect the number of offspring fertilized or offspring produced (Harari *et al.* 1999). To avoid size preference I used individuals with elytra lengths ≥ 11 mm in females and ≥ 10 mm in males, size ranges considered large (Harari *et al.* 1999).

I provided each male with a randomly selected, 3-week-old virgin female for copulation. I placed each mating pair in an observation container and allowed them to mate. Using a DXG-580V Compact 1080p HD camcorder, DXG (City of Industry, CA) I recorded the behaviors of both the male and female during the first hour of precopulation and copulation interactions. If copulation did not occur during the allotted time, I visually monitored the pair for up to 12 hours by checking the pair every 15 minutes to see if they were mating. If mating did not occur within the visual monitoring period, I left the individuals together over night. In the morning if no evidence of mating was evident, those individuals were excluded from the experiment. Evidence of mating in males included observed copulation or mate guarding. Males were only additionally excluded if the female produced no fertilized eggs, indicating that a mating had not occurred. After copulation was completed, I separated the individuals and placed them on their own in a cage.

To assess attractiveness, I recorded behaviors during precopulation and copulation. During precopulation I recorded if the female opened her genital aperture. During copulation I

recorded if she attempted to end copulation by fleeing, falling to the ground or vigorously shaking the mounted male (Harari *et al.* 2003).

After mating, I housed the females individually and provided fresh oviposition substrate, (wax paper). I checked the females' cages daily for egg masses; egg masses were removed as they were deposited and replaced with fresh oviposition substrate. I placed the egg masses in plastic bags misted with distilled deionized water and stored them in an incubator at 26°C (Lapointe 2001). After 5 days, I counted the total number of eggs and the number of fertilized eggs (identified by a brown coloration) using a Stereozoom S6E stereomicroscope with a L2 cold light illuminator (Leica, Sydney, Australia) (Harrari *et al.* 2003). I collected the egg masses until the female stopped laying fertilized eggs.

The males were mated every 2 weeks to a new virgin 3 week old female for 8 mating events. I used the same procedure and collected the same data for each occurrence.

Effects of age on female reproduction

To test the effects of age on female fecundity, I used 25 three-week-old females with elytra lengths ≥ 11 mm. I allowed each female to copulate with one 3-week-old male that had an elytron length of ≥ 10 mm. I placed each mating pair in an observation container and allowed them to mate. I recorded the behavior of both the male and female for the first hour for precopulation and copulation behaviors. If copulation did not occur during the allotted time, I visually monitored the pair for up to 12 hours by checking the pair every 15 minutes to see if they were mating. If mating did not occur within the visual monitoring period, I left the individuals together over night. In the morning if no evidence of mating was evident, those

individuals were excluded from the experiment. Evidence of mating in females included observed copulation. After copulation was completed, I separated the individuals and placed them on their own in a cage.

Once the copulating pair had separated, I removed them and placed them in individual cages. To assess mate attractiveness, I recorded if and at what time the male mounted the female with his aedeagus extended during precopulation and during copulation if he removed the aedeagus and/or dismounted the female.

After mating, I placed females in an individual cage and checked daily for egg masses. I removed the egg masses as they were deposited and replaced with fresh oviposition substrate. I placed egg masses in a plastic container misted with distilled deionized water and placed in an incubator at 26°C (Lapointe 2001). After 5 days I counted the total number of eggs and the number of fertilized eggs.

The same females were mated to new 3 weeks old virgin males every 2 weeks for 8 mating events. I repeated the same procedure and collected the same data for each individual during each occurrence.

Data analysis

Life history Trade-offs

To determine if early reproductive effort influences life span, (i.e. a trade-off between survival and reproduction), I examined the correlation between early-age reproductive effort and age at death using the multivariate model procedure in JMP version 8.0 (SAS Institute Inc., Cary,

NC, USA). As stated, I measured several components of reproductive success at week 3, these variables were: average egg mass, total egg mass, total fertilization, average fertilization proportion, and latency to mate. The data were analyzed both parametrically, using Pearson product-moment correlations, and non-parametrically, using Spearman's *rho*.

I also explored the potential for individuals to trade-off between current and future reproduction. To this end, I examined the relationship between reproductive success variables at week 3 (early-age) and week 17 (late-age). I only included individuals that survived through week 17 in these analyses.

Youth Advantage Model

To assess the youth advantage model, I analyzed the effects of age, as a continuous variable, on reproduction success with ANOVA in JMP. I included body size as a covariate, along with the interaction between body size and age, in all analysis. If I found either to be non-significant, it was removed from the model. The P-value, F- statistics and degrees of freedom were reported.

Due to the small sample size, I further explored the effects of age on reproduction by collapsing the data it into age classes, young (3-7 weeks), intermediate (9-13 weeks) and old (15-17 weeks), and analyzed for change between life stages. Body size and the age class-body size interaction term were included in all analysis. If either was found to be non-significant, it was removed from the model. The P-value, F- statistics and degrees of freedom were reported.

I analyzed the latency to mate data as binary data due to the extremes values. This was because most latency values occurred after 7 hours (and thus were not observed after this time)

or within times of less than 1 hour. Values under 7 hours were coded as 1 and the values over 7 hours were coded as 0. When age was examined as a discrete variable, the binary score was averaged within each life stage (young, intermediate, and old) for each individual. I reported the chi square, P-value and degrees of freedom for the binary data. A significance level of 0.05 was set for all analysis.

CHAPTER 3: RESULTS

I mated both males and females in two week intervals, starting at 3 weeks in age, for 8 events. Due to death of some individuals during the experimental period only 13 of the 25 females and 9 of the 18 males contributed to all 8 mating events, but all were included in these analyses unless otherwise noted. The reproductive success variables examined for the females were average fertilization proportion, total number of fertilized eggs, average egg mass size, and total number of eggs. The success factors examined for the males were average proportion of fertilized eggs and total number of fertilized eggs.

Life History Trade-offs

To test if early reproductive effort traded-off with life span, I examined the correlation between reproductive effort at week 3 and age at death. No significant relationships were found between any reproductive effort variables and age at death for both males and females (all $P > 0.40$). In addition, body size was not significantly associated with reproductive success or age at death.

To test whether there was a trade-off between early and late reproductive effort, I examined the correlation between reproductive effort at week 3 and week 17. I only included individuals that lived through the week 17 event in these analyses (females: $n = 13$; males: $n = 9$). Again no significant associations were found between any of the reproductive effort variables (all $P > 0.10$) or between body size and reproductive effort.

Youth Advantage Model

To explore if this species follows the youth advantage model, I analyzed the influence of age on mate attractiveness and reproductive success. Using ANOVA, I explored age as a continuous variable with body size included as a covariate, as well as the interaction between age and body size. I found that female age was significantly associated with the proportion of eggs fertilized (Figure 1; $F_{1,149} = 24.88$, $P < 0.001$); with younger females producing a greater number of fertilized eggs and fertilization declining with age. Additionally, I found that male age was associated with total number of eggs fertilized where males fertilized more eggs as they got older (Figure 2; $F_{1,99} = 6.11$, $P = 0.02$). Male latency to gain a mate was marginally associated with age, with older males mating faster (Figure 3; $\chi^2 = 3.35$, $P_1 = 0.07$).

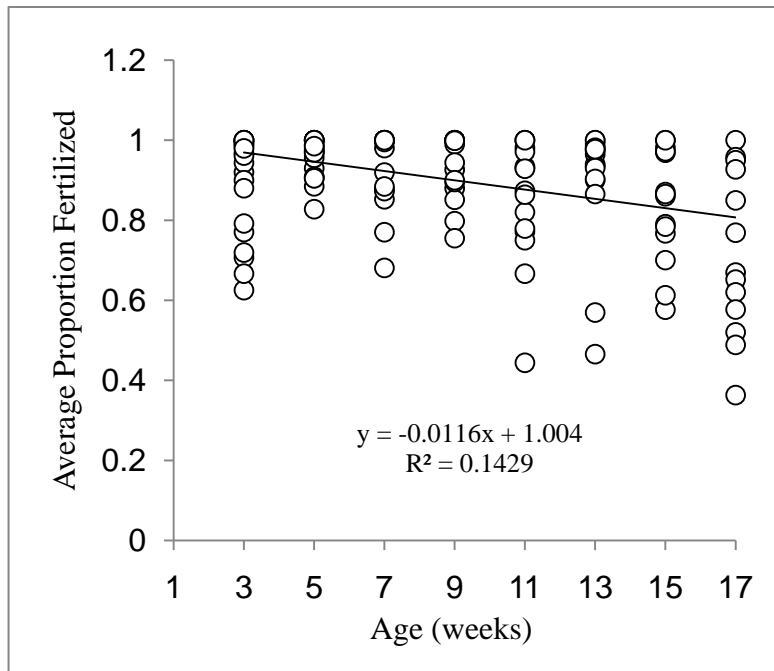


Figure 1- Average proportion of fertilized eggs over lifespan of female *D. abbreviatus*

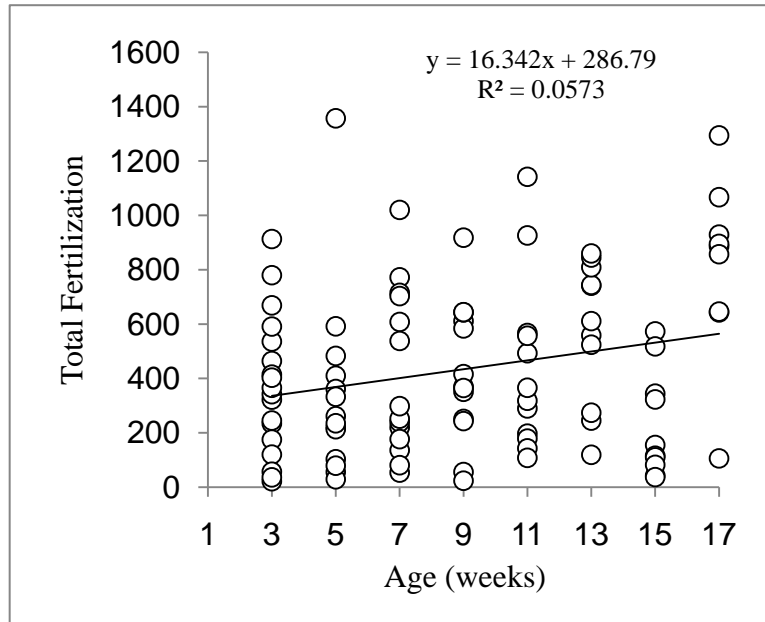


Figure 2- Total number of fertilized eggs over lifespan of male *D. abbreviatus*

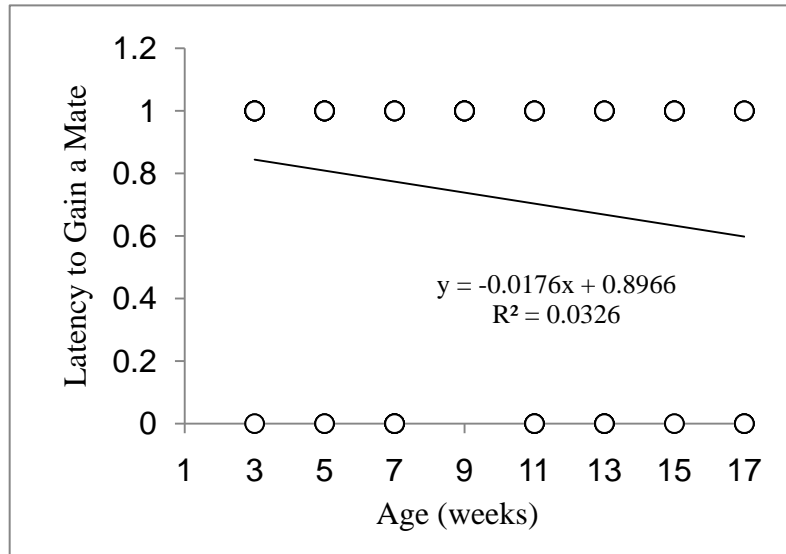


Figure 3- Latency to gain a mate over the lifespan of male *D. abbreviatus*

I further explored the effect of age as a discrete variable on reproduction by dividing the populations into 3 age classes, young (3-7 weeks), intermediate (9-13 weeks), and old (11-17 weeks). Multiple observations within each age class were averaged for each individual. I found that, again, a female's age was significantly associated with the proportion of fertilized eggs; with younger females fertilizing a greater proportion of eggs and it declining with age (Figure 4; $F_{2,55} = 5.12$, $P = 0.01$). Furthermore, I found female latency to gain a mate was significantly associated with female age, with the intermediate class exhibiting a significantly greater mating latency than the other two classes (Figure 5; $F_{2,55} = 7.19$, $P = 0.001$). With regard to the males, age was marginally associated with the proportion of eggs fertilized, with the intermediate aged males exhibiting the lowest number of eggs fertilized (Figure 6; $F_{2,39} = 3.13$, $P = 0.06$).

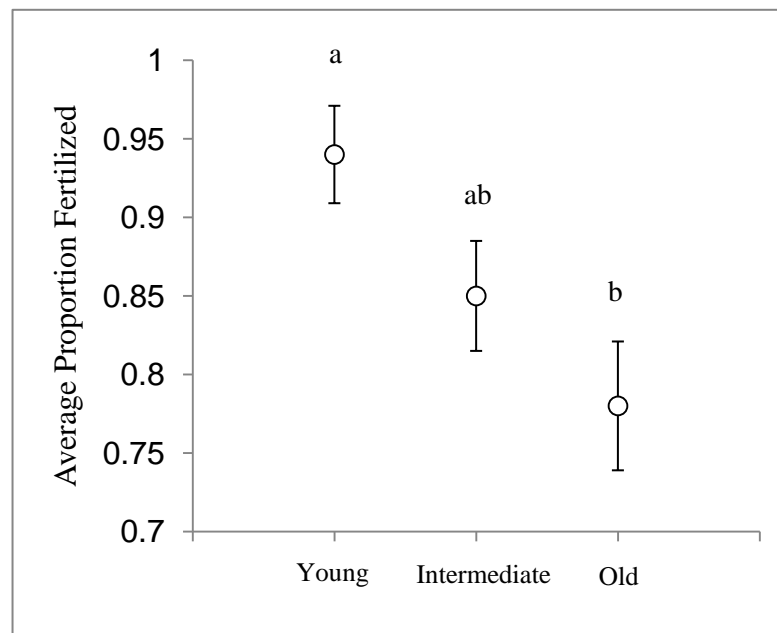


Figure 4- Average proportion of fertilized eggs among the age classes in female *D. abbreviatus*

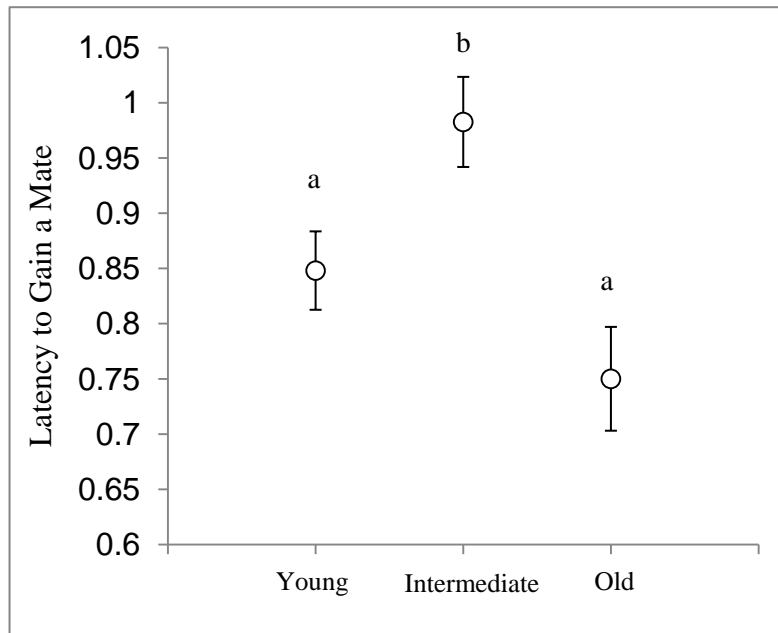


Figure 5- Latency to gain a mate of each age class in female *D. abbreviatus*

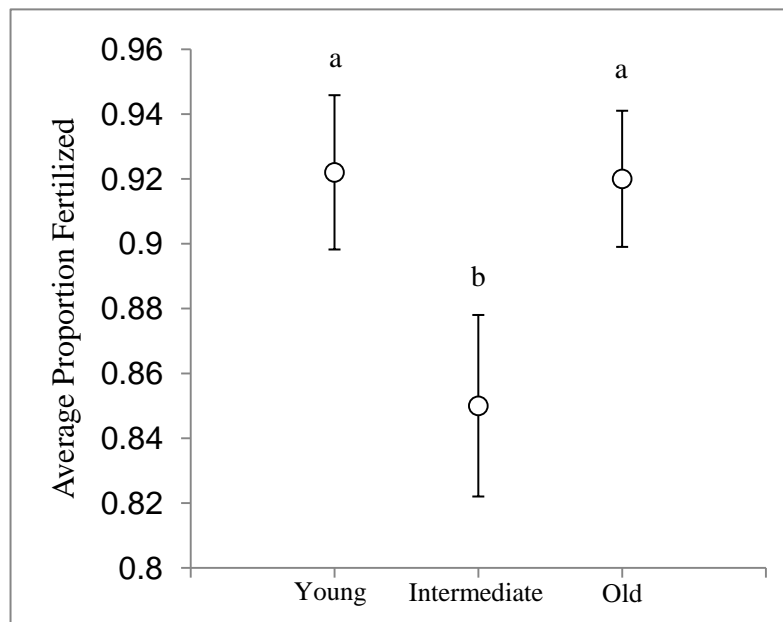


Figure 6- Average proportion of fertilized eggs among the age classes of male *D. abbreviatus*

CHAPTER 4: DISCUSSION

When making mating decisions, both males and females are apt to be choosy about their mates in species where both sexes contribute resources to the offspring and there is little parental care (Bondurainsky 2001). This is typically seen in system where search costs are low and both sexes vary in quality (Trivers 1972; Kokko and Johnstone 2002). An individual must use any cues they can to determine who is a good mate, and age can be an important cues. In *Diaprepes abbreviatus* individual quality can vary in terms of body size and individuals appear to choose mates based on body size. However, my data also suggests that age may have an effect on an individual's mate choice.

Two models of mate choice are evaluated here in association with *Diaprepes*: the good genes model and the youth advantage model. The good genes model suggests that individuals should prefer older mates due to proven survivability and other advantageous characteristics that may come with experience and maturity. The youth advantage model suggests that young to intermediate aged individuals should be preferable due to low potential mutation load and increased gamete quality or quantity. I hypothesized that this species would follow the youth advantage model. This model was chosen due to the long life span of the species that could lead to increased mutation load over time, the frequency of mating and egg laying that could potentially lead to faster depletion of gametes and increased physical degradation. With this I predicted that I would find that females would have decreased egg mass size, decreased fertilization rates, and decreased mate attraction as they aged. I also predicted that males would have decreased fertilization rates and mate attraction as they aged.

The cues for mate choice by males are not as widely evaluated and understood as they are with female mate choice, especially in accordance with age (Bonduransky 2001). I found that old and young females gained matings faster than intermediates. Age preference has been found in other species. For instance onion flies (*Delia antique*) were found to prefer older females as mates. This was thought to be due to variance in female quality as young females lacked mature eggs (McDonald and Borden 1996). This is not so in other insect species. For example, two species of *Drosophila* were found to prefer young mates to older ones (Cook and Cook 1975; Polak *et al.* 1998). The preference for younger mates was also noted in bush crickets (*Requena verticalis*) (Simmon *et al.* 1994). When considering the two models with respect to attractiveness, *D. abbreviatus* does not seem to adhere strictly to either. Both older and younger individuals procured mates significantly faster than the intermediates, but with no statistically significant difference in time between the young and old age classes. Therefore, I did not find evidence supporting my first hypothesis that stated that females would attract mates less readily as they became older.

Female *D. abbreviatus* did not show a difference in egg mass size with age, but there was a decline in egg fertilization with age. I found that the old age class fertilized significantly fewer eggs than the young. Mate choice by males seems to be more prevalent in a promiscuous species where there is a variation in mate quality, such as *D. abbreviatus*, and a key factor can be female fecundity (Bonduransky 2001; Gwynne 1991). In many species young females potentially have the most eggs, but older females tend to produce a higher number of eggs that are ready for fertilization. This has been noted in the seed beetle (*Acanthoscelides obtectus*) where younger females produced fewer eggs than older females and fertility was higher in older females

(Maklakov *et al.* 2007). In many other insect species, the intermediate lifestage has been noted to lay the most eggs and be the most successful in fertilization. This pattern was observed in seven-spotted ladybird beetles (*Coccinella septempunctata*) where intermediate aged females laid the most eggs (Omkar and Richmond 2004). Similarly increased success of the intermediate stage of life was also seen in the parthenium beetle (*Zygogramma bicolorata*), where intermediate females had higher fecundity than other life stages due to having a higher number of mature ova (Omkar *et al.* 2010). These data shows some support for the youth advantage model, and my 2nd hypothesis, with respect to egg fertilization, where young females were fertilizing more eggs and egg fertilization steadily declined with age.

Diaprepes males exhibited a marginally significant success in gaining a mate when they were older. This could lend support to the good genes age model which predicts that the older males are more desirable mates due to high survivability, which can be a signal of a good quality mate (Trivers 1972; Manning 1985; Kokko and Lindstrom 1996). The youth advantage model would have predicted the opposite to have been true, and has been seen in other beetle species (Hansen and Price 1995; Beck and Powell 2000). Aging was found to reduce male persistence and ability to mate in the *Callosobruchus maculatus* beetle, where older males typically failed to mate with virgin females and may have been actively selected against by them (Fricke and Maklakov 2007). In hide beetles (*Dermestes maculatus*) intermediate males secured more mating than young or old males, as well as passing more sperm than younger males and more viable sperm than older males (Hale 2008). Additionally, female sandflies have been noted to refuse to mate with older males (Jones *et al.* 2000). Attractiveness may be affected by age for *D. abbreviatus* males. This is in contradiction to my 3rd hypothesis prediction that males would less

readily gain mates as they became older; therefore, I did not find evidence to support my 3rd hypothesis.

Proportion of eggs fertilized was found to be marginally associated with male age. Intermediate males exhibited the lowest proportion of egg fertilization, with no difference between young and old males. But, older males were found to have higher total fertilization rates. This is the opposite of what has been seen in other species. Males at an intermediate age were found to be the optimal mates in ladybird beetles (*Propylea dissecta*) as they had better progeny viability at this stage (Omkar and Richmond 2004). Jones *et al.* (2007) also found intermediate males to greater sperm success than young or old individuals. When considering fertilization rate and the mate choice models, the adherence to one model in particular is not clear cut in *Diaprepes* and the results do not show solid support for my 4th hypothesis. Young males had higher fertilization rates than intermediate males. This could be support for the youth advantage model. Males did have better total fertilization rates as they were older than at an intermediate age, but this may not be strictly a physiological indicator. Every time an individual mates experience is gained. It has been shown in a previous study that male *Diaprepes* utilize stroking techniques during precopulation and during copulation (Sirot et al. 2007). It is possible that the increase in fertilization could be due to the increase in stroking experience with each mating. These two factors, age and experience, cannot be teased apart to assess the contribution of each to the results.

CHAPTER 5: CONCLUSION

In both male and female *D. abbreviatus*, the overall trend seems to indicate that intermediate aged individuals are the least optimal mates. These data provide some support for youth advantage model in females, considering that they had a lower latency to gain a mate than the intermediate aged females. Thus, they may be viewed as more attractive by potential mates. Furthermore, young females tended to produce the higher proportion of fertilized eggs.

In contrast, the data provide mixed results for the good genes model in males, considering that the older males tended to produce high “total fertilization” than their younger counterparts, as well as tended to have a lower mating latency (i.e. their female mates may have found them more attractive). However, both young and old males tended to exhibit greater average fertilization compared to their intermediate counterparts. Also, experience could be playing a role in the older male’s success in gaining mates more quickly, and perhaps even the higher fertilization observed, and the contribution of this factor to the results cannot be determined.

There may be many other factors controlling the success of certain ages over others, including food intake. In other beetle species a decrease in food intake with age caused a decrease in egg production and fertilization (Dixon and Aragwala 2002). Other factors that should be considered are changes in the quality and quantity of sperm with age, and the ability of males to successfully transfer that sperm (Jones *et al.* 2007; Jones and Elgar 2004; Radwan 2003). Behaviorally, male *Diaprepes* has been observed to utilize stroking techniques during courting and mating (Sirot *et al.* 2007). The relationship between these behaviors and age of the males performing them was not assessed here, but may lead to the differential mating attraction

success. Also, another important factor to consider is progeny viability (Hansen and Price 1998; Jones *et al.* 2000). I only looked at egg fertilization in correlation with age, but viability and quality of the progeny with regard to age of the mating pair was not assessed.

Mate choice and mating success can be influenced by several factors. In *D. abbreviatus* size has been documented as an element important to this species. My observations suggest that concerning mate choice decisions, age is also a factor.

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