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Reproduction Decreases Life Span in the Giant Waterbug (Belostoma flumineum)

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ABSTRACT.—Senescence is the result of age-specific trade-offs among life history traits. Energetic trade-offs among various components of an organism's energy budget can also affect an individual's life span. An increase in reproductive effort, for instance, can result in less energy available for maintenance of body tissues resulting in a shorter life span. We investigated the effects of reproduction on longevity of giant waterbugs (*Belostoma flumineum*). Female giant waterbugs oviposit eggs onto the backs of males which then provide all post-copulatory parental care. The number of reproductions was manipulated in both males and females, and male waterbugs were divided into groups that provided parental care or did not. This allowed us to determine the relative costs of mating versus parental care. Both male and female waterbugs maintained as virgins outlived those that bred. Parental care incurred a greater cost in male waterbugs than the act of mating, but the number of reproductions had no effect on life span suggesting that a single reproductive event is as costly as many. In both males and females the age at first reproduction was significantly positively correlated with age at death.

INTRODUCTION

Senescence, the process by which organisms age and ultimately die, is generally considered to be a product of the decreasing ability of natural selection to remove detrimental genes expressed after an individual has reproduced (Comfort, 1954; Medawar, 1955, 1957; Rose, 1991). Since life span has a direct impact on the lifetime fitness of an organism, it is generally accepted that it will be correlated with other fitness traits. Typically, the suite of fitness traits an organism possesses cannot be maximized concurrently, necessarily resulting in trade-offs among various life history characteristics (Stearns, 1992). Life span, for example, has been shown to be positively correlated with age at first reproduction (Clarke and Maynard Smith, 1961; Wattiaux, 1968; Sokal, 1970; Mertz, 1975; Law, 1979; Rose and Charlesworth, 1980, 1981; Luckinbill *et al.*, 1984; Partridge and Barton, 1993; Zwaan *et al.*, 1995; Sgro and Partridge, 1999; Sgro *et al.*, 2000). Individuals that reproduce early die sooner than individuals that delay reproduction.

Life span is also shown to be negatively affected by increased rates of reproduction (Murdoch, 1966; Loschiavo, 1968; Tinkle *et al.*, 1970; Ricklefs, 1977; Haukioja and Hakala, 1978). This has generally been explained as either a result of increased extrinsic mortality (predation, disease) due to compromising reproductive behaviors or of competing energy requirements. When extrinsic mortality is experimentally removed in laboratory situations, the effect of energetic trade-offs in decreasing life span can be addressed. An organism's energy budget can be divided into four components to include growth, maintenance,

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reproduction and storage (Gadgil and Bossert, 1970; Congdon *et al.*, 1982). Since available energy is finite in many, if not all, cases, when more energy is allocated to one area there is necessarily less available for other compartments. Individuals that invest more energy into reproduction, therefore, have less available energy to maintain their cells and tissues, which can result in a shorter life span. While this relationship has been shown in a variety of organisms, most studies have focused on females (Snell and King, 1977; Law, 1979; Partridge and Farquhar, 1981; Nur, 1984; Clutton-Brock *et al.*, 1988; Fowler and Partridge, 1989; Service, 1989; Prowse and Partridge, 1997; for exceptions *see:* Partridge and Farquhar, 1981; Service, 1989; Prowse and Partridge, 1997). Females tend to have higher levels of parental investment per offspring than males (Trivers, 1972), typically making them a better choice for investigating energetic trade-offs between reproduction and life span. One would predict, however, that increased rates of reproduction would decrease life span in both sexes of organisms in which significant amounts of parental investment is supplied by males.

The giant waterbug, *Belostoma flumineum*, is one of the few species in the animal kingdom that exhibits exclusive post copulatory paternal care and has often been cited as an example of "sex-role reversal" (Smith, 1976; Wittenberger, 1981; Daly and Wilson, 1983; Thornhill and Alcock, 1983; but *see* Kruse, 1990). Female giant waterbugs oviposit eggs onto the back of males, which care for the eggs until they hatch 7–14 d later (Torre Bueno, 1906). Male brooding behavior consists of aerating and cleaning the eggs and is largely accomplished by positioning the body and the developing eggs near the water-air interface and gently stroking the eggs with the legs. This behavior is known to be energetically costly for males, decreases their feeding efficiency and increases their risk of predation under natural conditions (Crowl and Alexander, 1989; Kight *et al.*, 1995).

Since both male and female giant waterbugs provide significant parental investment, with females contributing the eggs and males providing parental care of the eggs, *Belostoma flumineum* is an excellent organism to study the effect of parental investment on life span. While the relationship between reproduction and life span has been investigated in a number of organisms, this is the first study to address the costs of mating and parental care in an organism where all postcopulatory parental care is provided by the male. We addressed four questions relating reproductive behavior and life span: (1) What is the effect of mating on life span in both males and females? (2) What is the effect of mating plus parental care on life span in males? (3) Does the overall cost of reproduction differ between males and females? (4) Is age at first reproduction correlated with life span in both males and females?

MATERIALS AND METHODS

Giant waterbugs were collected with aquatic dip nets as last instar nymphs from three ephemeral ponds in Coles County, Illinois in July and August 1994, 1995 and 1996. The animals were transported to the laboratory in plastic coolers containing water and aquatic vegetation from the ponds. Nymphs were individually separated and kept in 2 liter plastic cylinders containing deionized water and pieces of floating plastic that served as perch sites. Nymphs were fed crickets twice a week and kept at normal summer conditions of 30 C under 14L:10D photoperiod until adult emergence. Day of emergence was recorded as adult age zero. Within 1 wk of emergence each waterbug was sexed by examining the genital plate (Menke, 1960) and individually marked by painting a number on its pronotum using white model airplane paint covered with cyanoacrylate glue.

Experiments on males.—In 1994, 93 male waterbugs were randomly allocated to eight experimental treatments. Ten males were kept individually as virgins for their entire life. In order to control for effects of having multiple waterbugs in a single container, 12 males were randomly paired into six containers and maintained as virgins until death. The remaining

71 males were randomly allocated into one of two reproductive treatments: brood or abort. Males in the brood group were allowed to breed and, subsequently, brood their eggs until hatching. Males in the abort group, on the other hand, had their egg pads removed and, thus, provided no parental care. Males in both breeding treatments were further divided into groups that mated either two, three or five times. Ten males were allocated to each of the breeding treatments, except for the two groups that were required to breed five times. The breed five times and abort treatment had a total of 12 males, while the breed five times and brood group was allocated a total of 19 males. These treatments allowed us to test the differential effect of mating vs. mating followed by parental care, as well as the effect of multiple reproductions on male life span.

Male breeders were placed in groups of 8–10 individuals in 38 liter aquaria approximately 1/3 full of deionized water with plastic perching sites. Each aquarium also contained 15–20 gravid female waterbugs as brood stock. Individual males were checked every 24 h for the presence of egg pads. Egg-laden males were removed from the aquaria and either allowed to brood their clutch until hatching in a 2 liter plastic container or their egg pad was removed and they were immediately replaced into the aquaria. Date of reproduction, total number of eggs brooded, percent hatching success and total brooding time were recorded for each clutch. Once the breeder males of both treatments completed their assigned number of reproductive attempts, they were removed from the aquaria and maintained individually in a 2 liter plastic container until death.

Experiments on females.—In 1995, 47 female waterbugs were randomly allocated to one of four treatment groups. In the first treatment, ten were maintained individually and kept as virgins in 1 liter plastic containers. For the second treatment, ten were maintained as virgins and housed in groups of five in Rubbermaid brand plastic storage containers (PSC) (40.6 × 28.0 × 15.2 cm) to control for group effects on longevity. The remaining females were then allocated to one of two breeding groups such that 12 females were limited to oviposit 200 to 300 eggs (limited breed) and 15 female breeders were allowed to breed continuously (lifetime breed) until death. Each female breeder was housed with four or five male waterbugs in PSC. Females in the "limited breed" group were removed once they reached their assigned reproductive output and placed in PSC with other females. Male brood stock in the female breeding chambers were checked every 24 h for the presence of an egg pad. Egg pads were removed, the number of eggs counted and these males were immediately returned to their breeding chamber.

Experiments on males and females.—In 1996 male and female waterbugs were kept under similar experimental regimes in order to test for differences in the effect of reproduction on life span between the sexes. Both male and female waterbugs were randomly allocated to one of two treatments. Thirty of each sex were maintained as virgins while 18 males and 16 females were allowed to breed continuously until death. Virgins of both sexes were housed as single sex groups of five or six per PSC. Male breeders were kept under the same conditions as in 1994 and brooded all clutches of eggs. Female breeders were also kept under the same conditions as in 1995. Therefore, male and female breeders were exposed to slightly different breeding environments which were necessary in order to accurately determine when mating had occurred and to maximize breeding opportunities.

In all experiments, waterbugs were maintained under the same environmental conditions as described for the nymphs. Water in aquaria was changed weekly while water in PSC and 1 or 2 liter individual containers was changed twice weekly. Waterbugs were fed commercial crickets *ad libitum* and dead/ partially consumed crickets were removed every 24 h.

Statistical tests.—Life spans of individual male and female virgins were compared with virgins maintained as pairs or groups using a Student's *t*-test. In both cases there were no

TABLE 1.—Mean life spans and mean number of eggs carried for entire life by male waterbugs of various reproductive treatments in 1994

Treatment	n	Mean life span (days) ± SD	Mean number of eggs ± SD
Virgin	10	207 ± 47.2	0
Virgin Pair	12	181 ± 59.1	0
Breed 2 Abort	9	178 ± 17.3	163 ± 42.9
Breed 2 Brood	9	151 ± 40.7	145 ± 29.6
Breed 3 Abort	6	184 ± 59.7	194 ± 32.8
Breed 3 Brood	8	156 ± 35.8	207 ± 55.7
Breed 5 Abort	9	170 ± 32.5	365 ± 99.1
Breed 5 Brood	15	163 ± 47.3	372 ± 100.2

significant differences (Table 1), so single and paired virgins were pooled for all other analyses. A one-way analysis of variance (ANOVA) was used to test for differences in the total number of eggs carried among all male breeding groups in order to determine if females behaved differently toward brooders and aborts. Differences in male life span among all treatments in 1994 and female life span in 1995 were analyzed using a one-way ANOVA. Differences between both male and female virgins and lifetime breeders in 1996 were analyzed using a one-tailed Student's *t*-test, as previous studies have shown that virgins typically live longer than breeders. Differences in response between the sexes was analyzed using a two-way ANOVA with interaction (main effects: gender and reproductive treatment) for both reproductive treatments in 1996. Two-way ANOVAs (main effects: year and treatment; year and sex) were used to control for confounding effects among years in order to pool data from similar treatments tested in different years. Significant main effects of all ANOVAs were further analyzed using Tukey's means comparison test. Correlations were used to determine the relationship between the age of first reproduction and life span for all years, sexes and breeding treatments. A correlation was also used to determine the effect of the number of oviposited eggs on female life span. All statistical analyses were performed using general linear models of SAS (1990).

RESULTS

Only male breeders that successfully bred the number of times they were assigned were included in the following analyses. This reduced the sample sizes of every group (Table 1). The number of matings did not affect life span for either males that were allowed to brood their eggs ($F_{2,33} = 0.22$, $P = 0.80$), or in males that had their egg pads removed immediately after mating ($F_{2,21} = 0.28$, $P = 0.76$). The lack of significant differences among these groups allowed us to pool these data into two breeding treatments: male "brooders" and male "aborts." Male virgins, "brooders" and "aborts" in 1994 differed significantly in life span (Table 2, Fig. 1); virgins had the longest mean life span followed by "aborts" and "brooders" respectively. Tukey's means comparison test revealed that male virgins lived significantly longer than male brooders ($P < 0.05$) but neither virgins nor "brooders" differed significantly ($P > 0.05$) from "aborts." This difference in life span was not due to females behaving differently toward male brooders and male aborts, as similar numbers of eggs were oviposited on the backs of males in both breeder groups that mated the same number of times (Table 1).

Male virgins and brooders showed a similar trend in 1996, but the difference between the two groups was not significant (one-tailed $t = 1.40$; $df = 45$; $P = 0.08$). Male life span did not differ significantly between 1994 and 1996 ($F_{1,127} = 0.09$; $P = 0.77$). Since neither the

TABLE 2.—Results of one-way ANOVAs for age at death of male waterbugs that were either maintained as virgins, allowed to breed and have the egg pads removed, or allowed to breed and brood the eggs in 1994 (top) and pooled data from 1994 and 1996 (bottom)

Source	SS	df	MS	F	P
Repro. Trmt.	13,373.40	2	6686.70	3.70	0.03
Error	135,697.30	75	1809.30		
Total	149,070.70				
Repro. Trmt.	19,579.73	2	9789.87	4.43	0.01
Error	278,740.41	126	2212.22		
Total	298,320.14				

number of matings, nor the year of the study, had an effect on life span, male virgins and brooders were pooled by reproductive treatment from both 1994 and 1996. Pooled male brooders lived an average of 158.3 (±44.3) d while pooled male virgins lived an average of 185.1 (±53.9) d. The difference in life span between male brooders and male virgins was significant, while male aborts were intermediate to and not significantly different from either of the other two treatments (Table 2). Male virgins and brooders not only differed in mean life span, but also the maximum life span attained. The maximum observed life span of a male virgin was 301 d while no male breeders lived beyond 269 d.

Successfully breeding female waterbugs was much more difficult than breeding males. As a result, several females in each breeding treatment oviposited a small number of eggs, reducing the sample sizes of both breeding treatments. While females in the "limited breed" treatment had an expressed minimum threshold, we set a minimum threshold of 150 eggs for females in the "lifetime breed" treatment. This ensured that female breeders were meeting some lower limit of parental investment. This limited the analysis to only eight females in the "limited breed" treatment and 13 females in the "lifetime breed" treatment.

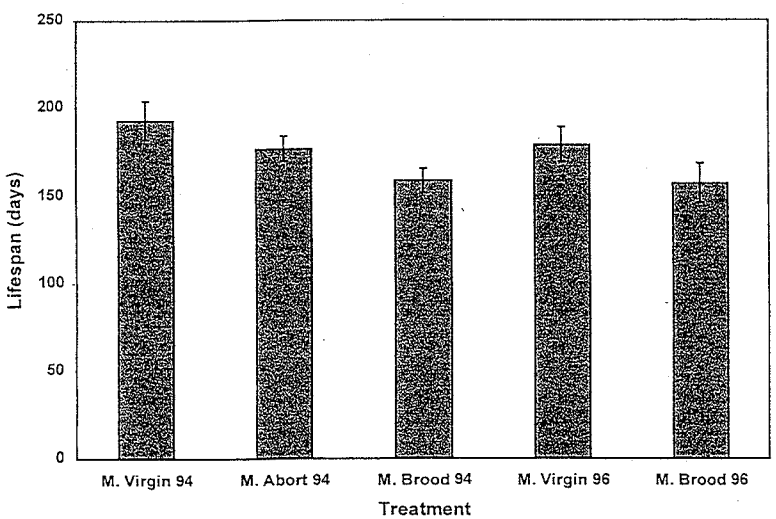

FIG. 1.—Mean age at death (and 95% CI) for male waterbugs pooled by reproductive treatment, regardless of number of reproductive bouts. Data from both 1994 and 1996 are shown.

TABLE 3.—Results of a one-way ANOVA for age at death among female waterbugs that were maintained as virgins, limited breeders (200 and 300 eggs) or lifetime breeders

Source	SS	df	MS	F	P
Repro. Trmt.	3474.61	2	1737.31	1.40	0.26
Error	47,001.88	38	1236.89		
Total	50,476.49				

As observed in males, female virgins had a longer maximum life span than female breeders. The longest life span observed in female virgins was 271 d, while the maximum age of a female breeder was only 226 d. Female waterbugs maintained as virgins have the longest mean life span of the three groups, followed by the "limited breed," and the "lifetime breed" treatments respectively, but no significant difference in life span was observed among the treatments (Table 3, Fig. 2). Interestingly, female breeders did not show a significant negative correlation between total number of eggs oviposited and age at death ($r = -0.13$; 0.51) (Fig. 3). This suggests that all female breeders could be pooled for comparison with virgins. When female breeder treatments from 1995 were pooled the difference between female virgins and breeders was significant (one-tailed $t = 1.75$; $df = 31$; $P = 0.045$); females maintained as virgins lived significantly longer than those that bred.

In 1996 virgin female waterbugs lived significantly longer than female lifetime breeders (one-tailed $t = 3.54$; $df = 44$; $P < 0.001$). Interestingly, female life spans observed in 1995 were significantly shorter than in 1996 ($F_{1,85} = 8.61$; $P = 0.004$). Consequently, year was included as a variable in a 2-way ANOVA to remove any confounding effects before treatments were tested. When females were pooled by treatment across years with year in the model as a covariate, female lifetime breeders had significantly shorter life spans than female virgins (Table 4).

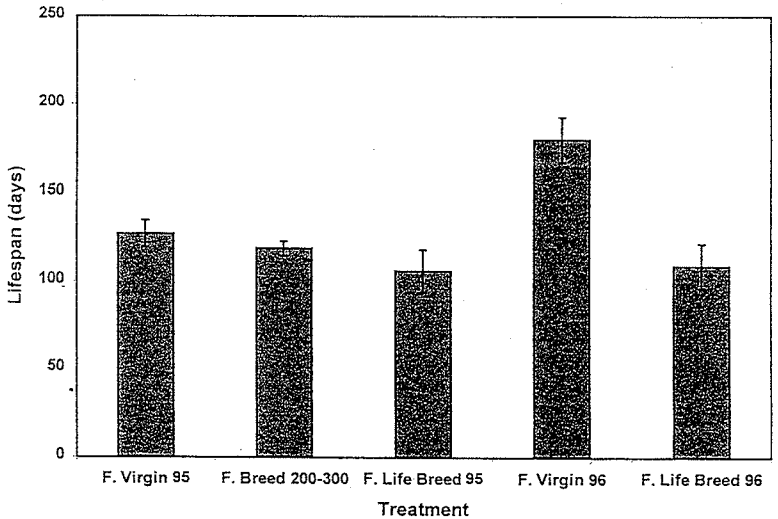

FIG. 2.—Mean age at death (and 95% CI) for female waterbugs of differing reproductive treatments in 1995 and 1996.

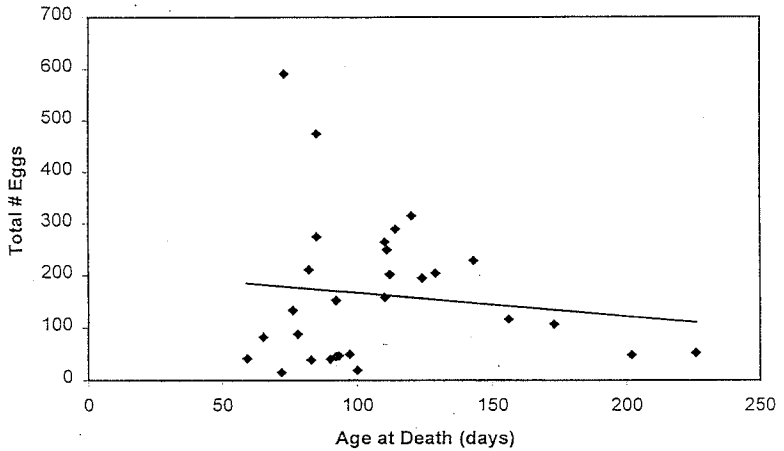

FIG. 3.—Relationship between the number of eggs a female oviposited and age at death. Data shown include females from both 1995 and 1996. A linear best fit trend line is included in the figure

Since females had a significant year effect, comparisons of differences in reproductive cost between males and females were conducted in two ways. First, differences between the sexes and the treatments were analyzed using a two-way ANOVA using only data from 1996. Second, we pooled data from different years and used a pair of two-way ANOVAs (main effects: year and sex) to compare life spans of: (1) male and female virgins and (2) male brooders and female lifetime breeders. In both cases life spans were adjusted for the significant differences in female life span in different years by including year as a covariate in the model. Analysis of the 1996 data revealed a significant interaction between gender and reproductive treatment, suggesting that males and females responded differently to similar breeding regimes (Table 5). While both male and female virgins had similar mean life spans, male brooders lived an average of 48 days longer than female breeders in 1996. Analysis of the pooled data adjusted for the year effect revealed that life spans of male and female virgins did not differ, but female lifetime breeders had significantly shorter life spans than male brooders (Table 6; Fig. 4).

In all breeding treatments age at first reproduction was positively correlated with age at death (Fig. 5). Males that bred early also died early. Male breeders, whether they brooded their eggs or not, showed a significant positive correlation between the date they first

TABLE 4.—Results of a two-way ANOVA comparing pooled female virgins from 1995 and 1996, pooled female lifetime breeders from 1995 and 1996, and female limited breeders from 1995. Year was fixed in the model as a covariate to account for the significant year effect on female life span. Only Type III results are shown

Source	SS	df	MS	F	P
Year	22,824.72	1	22,824.72	7.74	0.007
Repro. Trmt.	45,198.26	2	22,599.13	7.66	<0.001
Error	244,823.70	83	2949.68		
Total	319,402.41	86			

TABLE 5.—Results of a two-way ANOVA of age at death with main effects of reproductive treatment and gender. Both male and female waterbugs were either maintained as virgins or allowed to breed continuously

Source	SS	df	MS	F	P
Repro. Trmt.	52,144.95	1	52,144.95	15.97	0.0001
Sex	11,054.62	1	11,054.62	3.39	0.0690
A × B	14,222.06	1	14,222.06	4.36	0.0397
Error	293,898.10	90	3265.53		
Total	363,016.80				

reproduced and the date they died (brooders: $r = 0.55$; $P < 0.001$; aborts: $r = 0.64$; $P < 0.001$). Female breeders showed a similar relationship ($r = 0.60$; $P < 0.001$).

DISCUSSION

Both male and female waterbugs showed decreased life spans due to reproduction. Breeders of both sexes had shorter mean and maximum life spans than virgins, although the differences were not significant for all treatments. For example, the cost of reproduction in males differed depending on whether the male invested in both mating and parental care or mating without parental care. Males that brooded their clutches had significantly shorter life spans than virgins, but males that had their egg pads removed had mean life spans that were intermediate to and did not differ significantly from either virgins or brooders. This suggests that parental care adds a significant cost to reproduction in giant waterbugs and is at least an additive, if not greater, cost to mating. This supports the hypothesis of an energetic cost to reproduction—additional reproductive activities result in a larger cost.

Since males that provided no parental care had life spans intermediate to, and not significantly different from either virgins or breeders, the relative costs of mating and parental care are not clear. Unfortunately, it is impossible to determine the relative costs of mating and parental care with the sample sizes in the present study. Proportional hazards tests and the calculation of relative survival probabilities require larger sample sizes in order to be effective. The use of waterbugs precludes the acquisition of sample sizes often used in studies involving species of *Drosophila*. Waterbugs typically live in small ephemeral ponds and

TABLE 6.—Results of two-way ANOVAs comparing life spans of pooled female virgins (1995 and 1996) with pooled male virgins (1994 and 1996) (top) and life spans of pooled female lifetime breeders (1995 and 1996) with pooled male brooders (1994 and 1996) (bottom). In both cases year was fixed in the model as a covariate. Only the Type III results are shown

Source	SS	df	MS	F	P
Sex	22.30	1	22.30	0.01	0.934
Year	36,580.86	2	18,290.43	5.66	0.005
Error	313,467.17	97	3231.62		
Total	367,296.04	100			
Sex	19,697.36	1	19,697.36	9.38	0.003
Year	93.59	2	46.79	0.02	0.978
Error	165,859.33	79	2099.49		
Total	214,268.24	82			

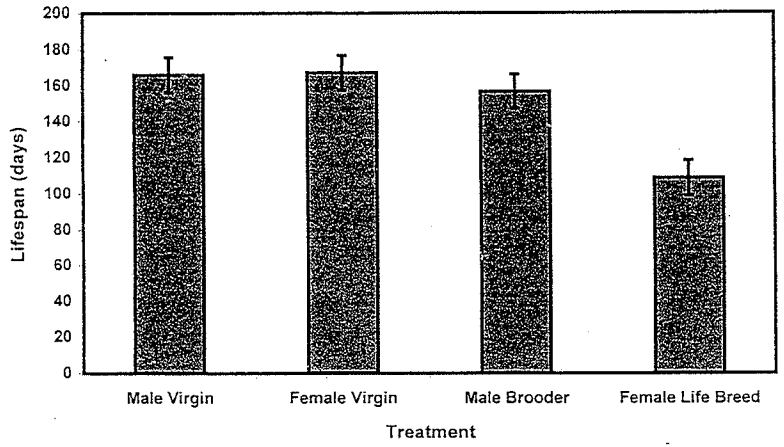

FIG. 4.—Least square mean age at death (±1 SE) (means adjusted for between year variance in life span) for each male and female treatment pooled across years

are often the top aquatic predator. Therefore, their densities are typically low. We have also had very little success raising waterbugs from birth in the laboratory, making it difficult to boost our sample sizes with lab-reared animals. Still, the data clearly show the expected outcome; that parental care increases the cost of reproduction in male waterbugs. Curiously, the increased cost involved with brooding is apparent even in a laboratory situation. In the wild, brooding males have been shown to be slower, making them feed less efficiently and more susceptible to predation (Crowl and Alexander, 1989; Kight *et al.*, 1995). In the laboratory waterbugs experience neither predation risks nor a lack of feeding opportunities. Therefore, the cost of reproduction observed in male brooders is not due to increased behavioral risks associated with brooding.

Female breeders also showed a decrease in life span compared to virgins. Females allowed to breed throughout their adult life in 1996 showed a large decrease in life span relative to virgins. While the relationship was not as strong in 1995, pooling of similar reproductive treatments from both 1995 and 1996 (with year as a covariate) shows that female breeders do not live as long as female virgins. Small sample sizes again hampered our ability to obtain clear results of intermediate breeding groups, like the "limited breed" treatment. Interestingly, even though all postcopulatory parental care is provided by the male, female waterbugs still incur the greater cost of reproduction. This was apparent in both 1996, when males and females were treated similarly, and when comparing data pooled across years. Male and female virgins had similar life spans, but female breeders had significantly shorter life spans than male breeders.

Examples of mating costs in females of many species are quite common, while similar examples in males are fairly rare. Many studies have concentrated only on female costs to reproduction, while those that investigate both sexes or only males have differing results.

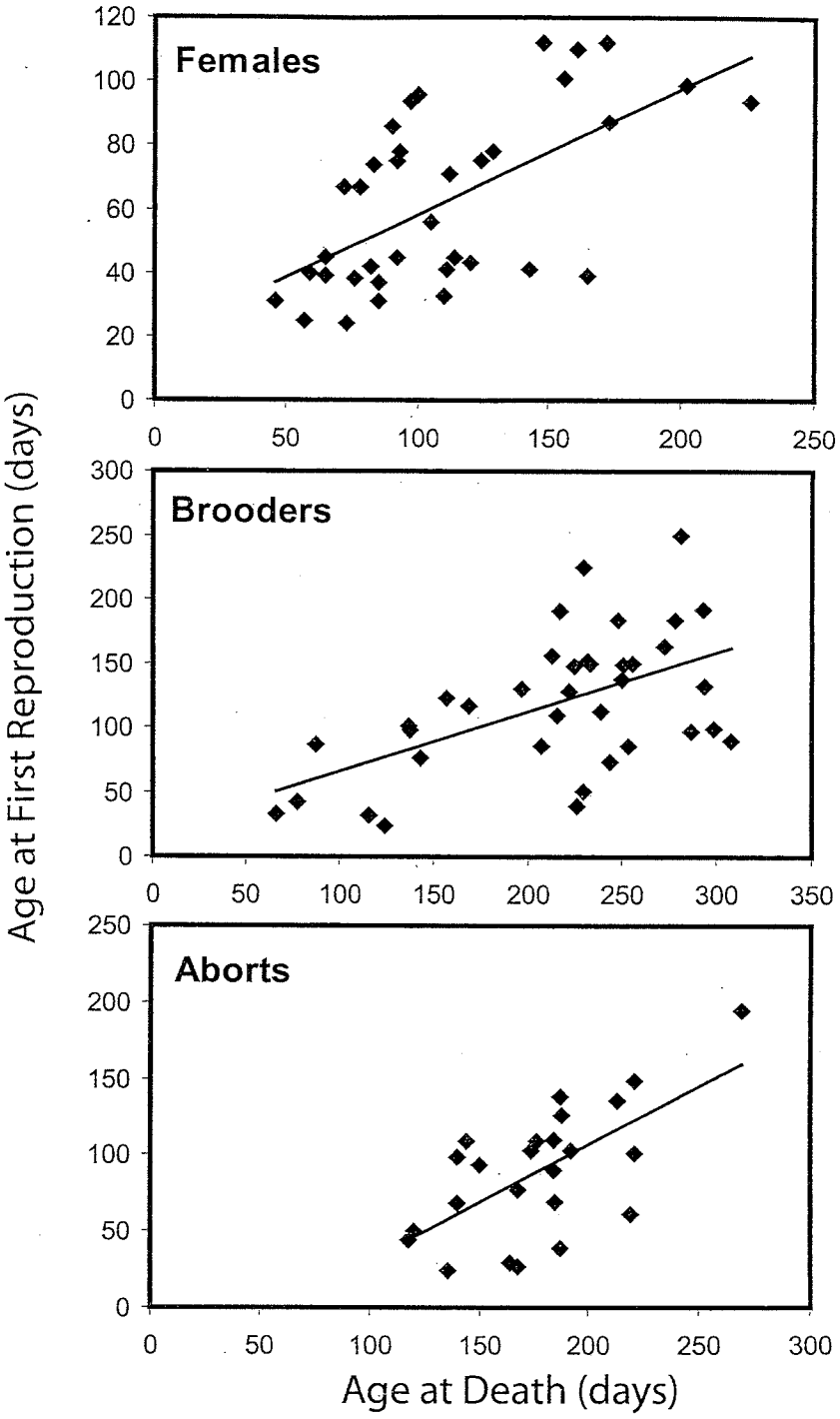

FIG. 5.—The relationship between age at first reproduction and age at death for male brooders, male aborts, and females. The graph of male brooders includes individuals from both 1994 and 1996, while the graph of females includes waterbugs from both 1995 and 1996. Linear best fit trend lines are included in all graphs

Life spans of male virgin and breeder monarch butterflies did not differ (Oberhauser, 1989) while several studies on male *Drosophila melanogaster* have shown decreased longevity due to reproduction (Partridge and Farquhar, 1981; Partridge and Andrews, 1985; Service, 1989; Prowse and Partridge, 1997). In studies that manipulated parental care by increasing and/or decreasing clutch size no significant effect on longevity was observed in either male blue tits (Nur, 1984) or great tits (Pettifor *et al.*, 1988). One aspect that could account for the difference between waterbugs and the aforementioned bird species is that male waterbugs are responsible for all postcopulatory parental care whereas the male blue and great tits both share duties with the female. Therefore, the cost of parental care in male waterbugs is potentially greater than in either bird species.

Whereas many of the results of this study conform to the hypothesis that increased reproductive investment will decrease life span, some of the data appear contradictory. For example, male breeders did not show an increased cost with an increase in the number of reproductive bouts. Whether they mated two, three, five or an unlimited number of times there was no difference in life span among the treatments. Similarly, there was no correlation between the number of eggs a female oviposited and life span. We predicted that life span would decrease with an increase in both the number of reproductive bouts and the number of eggs oviposited since they are indications of larger reproductive investment. While these results are unexpected, the same phenomenon has been observed in several studies of Lepidoptera (Shapiro, 1982; Svard, 1985; Oberhauser, 1989) and Megaloptera (Hayashi, 1993). These results suggest that the first reproduction incurs an intrinsic cost to the organism, but that subsequent reproductive events do not add significantly to the cost.

We suggest three hypotheses that can explain the lack of further reduction of life span by multiple reproductions or greater rates of oogenesis. One potential explanation is that during the first reproductive event, the organism's physiology changes to produce a shift in its energy budget allocating more resources to reproduction. Once this shift has occurred, the organism does not revert to its previous physiological state and further reproductive events do not increase the allocation to reproduction. A second possibility is that our ad lib feeding regime limited the effect of multiple reproductions. In the field, where food resources may be more limiting, multiple reproductions and continued oogenesis might have a greater effect on life span. Finally, it is possible that the mere presence of members of the opposite sex has a negative influence on life span that is not apparent in same sex groupings. This has been suggested in fruit flies (Tatar and Promislow, 1997) and in red-legged grasshoppers (Dean, 1981), where the number of oviposited eggs had no effect on life span but virgins outlived breeders. Each of these hypotheses requires further testing.

Another surprising outcome of the study was the significant difference in female life spans between years. While female breeders did not differ in life span between 1995 and 1996, virgin females in 1996 lived an average of 53 d longer than virgin females in 1995. Neither male breeders nor virgins, however, differed in life span between years. We cannot explain why females lived significantly longer in 1996 than in 1995. Although year to year variability in life span might be due to environmental differences, we do not know why such variability might manifest itself in only one sex. Although we kept some females "virgins," it is important to remember that they continued to produce eggs and, therefore, were committing some energy to "reproduction." It is possible that year to year variation in some environmental variable (*e.g.*, pond temperature, food availability) might affect females more than males.

Timing of reproduction also significantly affected life span in both sexes. Individuals that reproduced early typically had shorter life spans than those that delayed reproduction. A large number of selection experiments have shown this same relationship, suggesting that it

is genetic (*see* Rose, 1991 for a review). Our data also suggest that the correlation is genetically based, and not due to an energetic trade off. This can be best illustrated by the male waterbug data. Both male "brooders" and "aborts" showed a significant positive correlation between age at first reproduction and age at death. Since males that had their eggs aborted did not incur as much of a reproductive cost as males that brooded their eggs, it does not seem plausible for both groups to show a similar correlation if the effect was due to energetics. A genetic correlation between age at first reproduction and age at death seems a better explanation. This suggests that an individual's life span can be concurrently affected by both genetics and rates of reproduction.

Reproduction decreases life span in both male and female waterbugs, although the cost depends on the type of reproductive investment. Male waterbugs that provided parental care suffered a significant cost compared to virgins, whereas mating without parental care had no apparent cost. Increase in the number of reproductive events (males) or the total number of eggs oviposited (females) did not, however, affect life span. Therefore, future work on the effects of reproduction on life span needs to take into account the possibility of different effects of the various categories of reproductive investment, including mate acquisition, mating, parental care and the effect of multiple matings.

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