

**Differences in survivorship and growth between male and female grasshoppers: Identifying impacts of skewed sex ratios and spider predation**

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## Abstract

I performed a field study on sexually-dimorphic grasshoppers (*Melanoplus borealis*) in the Michigan Upper Peninsula to ascertain whether varying sex ratios and predator abundance would lead to any differences in growth and survival between the sexes. Grasshoppers were placed in cages in an open field in sex ratios of 8:2, 5:5, and 2:8. Wolf spiders (Family Lycosidae) were added to half of the cages. By monitoring survival and body weight over time, I determined if there were any significant differences in survival and growth between the sexes in the face of predation and skewed sex ratios. Females survived better in the presence of spiders, and had higher survival when there were more males and fewer females in the sex ratio. Females also grew at a faster rate and reached a larger size by adulthood. Size proved to be a major factor in survival, confirming previous experiments that showed larger body size equates with resistance to spider predation. Intraspecific and intersex competition was evident when females survived better when males were eaten by spiders. This study explored the survival and growth of a high density of grasshoppers with and without predators and at markedly different sex ratios. Considering the dynamic nature of grasshopper populations and their ability to affect their environments through herbivory, it may be valuable to understand how different circumstances might favor them.

## Introduction

An animal with a short life span, such as a grasshopper, must maximize its food intake and maintain rapid growth in order to reach sexual maturity and reproduce in a small period of time. For a grasshopper that must complete a life cycle in a single season, growth to maturity and successful reproduction means facing many challenges. Numerous different constraints weed out the least fit individuals. Predation is one factor that may affect grasshoppers, but intraspecific competition can play

a major role in grasshopper communities as well (Belovsky 1997). Any morphological differences between individuals could create disparities in competitive abilities. I performed an experiment on the grasshopper *Melanoplus borealis*, a sexually-dimorphic species with larger females than males. I tested for differences in survival and growth by sex at three different male to female ratios with or without predators.

There is a strong trend indicating that the size of a grasshopper has much to do with its likelihood of survival. Oedekoven and Joern (1998) found decreasing mortality for grasshoppers at progressing nymph stages and lowest mortality for adults. Contributing to this trend was the prey selection by spiders. Preferring smaller prey, spiders had significant negative effects on the early nymph stages, but no noticeable effect on adults. Ovadia and Schmitz (2002) described any grasshopper with smaller initial size during instar stages as having inherently lower fitness. Smaller grasshoppers actually face a number of obstacles. Besides being choice prey for spiders, smaller grasshoppers are at higher risk for starvation and must balance time spent foraging for food with time spent avoiding predators. Larger grasshoppers, too, must balance between feeding and hiding from predators, but smaller individuals are under greater pressure to consume food. Because smaller individuals have to spend more time

feeding, they are more likely to encounter a predator (Ovadia and Schmitz 2002).

Larger body size may not only be an advantage in predator-resistance for grasshoppers, but size also affects foraging ability and diet choice. Belovsky (1997) demonstrated that larger-bodied herbivores are capable of surviving on less nutritious plant matter while smaller herbivores require nutrient-dense plants that are more easily digested. The advantage for the smaller individual is that it can survive on less plant mass. One model of diet selectivity states that herbivores will share some plants with herbivores of other body sizes and also have plants they can exclusively utilize (Belovsky 1997). Grasshoppers of different sizes may compete if the larger individuals consume both low quality and the high quality food preferred by smaller individuals (Schoener 1974). If size influences resource consumption and competitive ability, it should also affect survival. For a sexually-dimorphic species, like grasshoppers, survival might be expected to differ between the sexes. Schultz (1981) experimented on a sexually-dimorphic South American grasshopper *Astroma riojanum*. The females of this species are double the size of the males at maturity. Small bird predators preferred early instars to adults, but would not take adult females until every male had been eaten. The

increased handling time involved in consuming the larger females was a deterring factor (Schultz 1981).

If females are significantly larger than males by adulthood in my experiment, I may deduce that they will be better foragers and better competitors in the face of predation. Males' smaller size will limit what types of plants they can eat. Males may have to sacrifice foraging for food in order to avoid predators. Finally, they may have to spend time attracting females with which to mate. To better examine the competition between and within the sexes, I employed three different sex ratios of 8:2, 5:5, and 2:8 (female: male). I hypothesized that females would grow faster and become significantly larger than males. For this reason, I predicted that females would also survive better in the presence of spiders due to their larger size. I hypothesized that increased female density would result in decreased survival and growth for all grasshoppers due to reduced food resources. Finally, I predicted that growth would increase significantly and survival would decrease significantly over time.

### **Materials and Methods**

This experiment was conducted in an old field at the University of Notre Dame's Environmental Research Center in the Michigan Upper

Peninsula from 5/31/2005 and 7/10/2005. The grasshopper species used was *Melanoplus borealis*. The spiders used were wolf spiders of the family Lycosidae.

On the site I constructed 28 aluminum screen enclosures specially-designed to contain and observe grasshoppers (Belovsky and Slade 1993). The cages were 0.36 m<sup>2</sup> at base and stood ca. 1 m tall. The base of each cage was made of aluminum sheet folded and hammered to the screen and driven into the ground a minimum of 3 cm to ensure no immigration or emigration of insects. Each cage was spaced ca. 1 m apart.

Six treatments with four replicates each were assigned to cages with a random number table. Grasshoppers were divided into three sex ratios of 8:2, 5:5, and 2:8 (always stated as female:male). Half of the replicates were given two lycosid spiders. The treatments with grasshoppers were stocked at ca. 300% field density (10 grasshoppers). I calculated field density by using 0.1 m<sup>2</sup> quadrants and estimating the number of grasshoppers in this area.

Spiders were captured by setting pitfall traps in rows ca. 20 cm apart throughout grassy areas on UNDERC property. These were monitored every 24 hours. The grasshoppers were collected by sweeping with insect nets in the grass at my study site. At the time of capture, most grasshoppers were 3<sup>rd</sup> instar nymphs, which are middle to late stage

nymphs. The grasshoppers' weights were recorded on Day 0 before being sorted into the appropriate sex ratios. On a weekly basis all the surviving individuals were collected and weighed to obtain average male and female weights for each cage. Grasshoppers were counted and identified to sex two times a week to measure of survival.

Statistical analysis was performed with SYSTAT 11 (Wilkinson 1990). Two-way ANOVAs were used to determine significant differences in grasshopper survival and growth among treatments.

## **Results**

### *Effects of time on survival and growth*

Grasshopper survival across both sexes decreased significantly over time ( $df = 8$ ,  $F = 59.868$ ,  $p < 0.001$ ). All grasshoppers also grew significantly ( $df = 4$ ,  $F = 48.635$ ,  $p < 0.001$ ) over time.

### *Effects of predation on survival*

Females in all three sex ratios had significantly higher survival in cages with spiders than in cages without spiders (Table 1, Figure 1A-C). Male survival did not differ significantly in cages with or without spiders

for sex ratios of 8:2 and 5:5 (Table 1, Figure 1D-E). For sex ratios of 2:8, males had significantly lower survival without spiders (Figure 1F).

#### *Effects of sex ratio on survival*

Female grasshoppers had higher survival in the ratio of 2:8 than the other two sex ratios in cages with spiders (Table 2, Figure 2A). In the absence of spiders, female survival did not differ among sex ratios (Table 2, Figure 2B). Male survival did not differ significantly among sex ratios either with or without spiders (Table 2, Figure 2C-D). To analyze differences in female versus male survival with and without spiders, male survival in all sex ratios with and without spiders and females without spiders were pooled because they did not differ significantly. Female survival in the 5:5 and 8:2 sex ratios with spiders were pooled, as they were not significantly different.

#### *Effects of sex on survival*

In the absence of spiders, there was no difference in survival between males and females (Table 3, Figure 3A). Females in the sex ratio of 2:8 survived significantly better with spiders present than all other females and all males (Table 3, Figure 3B), which did not differ significantly from each other ( $df = 1$ ,  $F = 0.362$ ,  $p = 0.548$ ).

*Effects of predation on growth*

Due to high grasshopper mortality by the end of the experiment, loss of degrees of freedom prevented statistical analysis from showing any trends between spider predation and grasshopper growth for all males and for females in sex ratios of 2:8 and 5:5 (Figure 4B-F). Females in 8:2 ratios did not grow significantly more with or without spiders ( $df = 1$ ,  $F = 0.024$ ,  $p = 0.878$ , Figure 4A).

*Effects of sex ratio on growth*

High levels of grasshopper mortality over the course of the experiment resulted in inadequate degrees of freedom to calculate a significant difference of growth by sex ratios for all but females in the presence of spiders (Figure 5A), for which there was no significant difference ( $df = 2$ ,  $F=0.046$ ,  $p = 0.955$ ). It appears that growth rates of females without spiders did not differ significantly by sex ratio (Figure 5C). Males with and without spiders did not appear to have different growth (Figure 5B, D).

*Effects of sex on growth*

Sex was a significant factor on the average weights of grasshoppers as females were larger than males (Table 4, Figure 6). The sex\*time interaction was significant, indicating that the rate of growth was greater for females.

**Discussion**

The high survivorship of female grasshoppers in the presence of spider predation compared to survival without spiders may indicate a number of unexpected dynamics at work. Belovsky and Slade (1993) demonstrated that a predator can actually increase the abundance of medium- to large-sized grasshoppers by eliminating smaller grasshoppers that might otherwise have acted as competitors for resources. The fact that females with spiders had higher survival than females in corresponding conditions but without spiders suggests that spiders may indeed have been fostering more ideal conditions for females by removing their competitors (males) while not affecting the females directly. For males, no difference in survivorship was evident except at sex ratios of 2:8, where survival was significantly higher with spiders. Why males were positively affected by spider presence in terms of survival in the 2:8 sex ratios is less clear. If the

competition with females for food is a stronger factor in male survival than predation by spiders, it is possible that the spider presence in the 2:8 ratio cages affected the females' ability to compete as strongly. In other words, the spiders could have been increasing male survival overall by removing females as well as males and decreasing the inter-sex competition which favors females. Rothley et al. (1997) found that grasshoppers will change their behavior in the presence of a spider even if they are not at risk to be killed, so females may have been eating less in the presence of spiders even though they did not seem to be preyed on as much. If this was the case, however, the statistics do not support any negative influence on survival or growth by spiders on females in this sex ratio. Future studies could focus more on why the presence of spiders can increase male survival in a specific sex ratio of 2:8.

The higher survival of females in 2:8 ratios versus the other sex ratios in the presence of spiders may be explained by effects of spiders removing the smaller grasshoppers and creating opportunities for larger individuals to have higher survival. When there were only two females in the cages, intraspecific competition might not have been as intense as with five or eight females, because females ate more and survived longer than males. When no spiders were present, I would have expected the males in the 2:8 sex ratio treatments to survive better because they had fewer

female competitors and no predator. However, if the smaller-bodied males relied on more nutritious plants that were possibly less abundant, their increased initial numbers may have counterbalanced the fact that they were only competing with two females because there could have been food limitation. Comprehensive analysis of the plant composition in the field would have to be undertaken to prove this hypothesis, however.

The females in sex ratio of 8:2 were the only grasshoppers that survived long enough to supply adequate data to test for effects of predation on growth. There was hardly any variance in average weights of these grasshoppers depending on the presence or absence of a spider and the similar nature of the other sex ratios of females and males (Figure 4) indicates that predation had no effect on growth. Grasshoppers have been shown to alter feeding behavior in response to predation level (Schmitz 1997), but if that was the case in this experiment, it did not significantly affect their growth. The wolf spiders used were ground-dwelling predators that might not prevent grasshoppers from feeding on leaves above the ground (Weber 2002).

The high mortality rate also affected my ability to calculate any differences concerning growth by sex ratio. Again, the figures suggest that time was significant for average body size, but that sex ratios did not influence growth (Figure 5). Because there were differences in survival,

the fact that growth did not show any difference by sex ratio could mean the grasshoppers that dies may have been the smaller individuals.

Grasshoppers died throughout the course of the experiment for a variety of reasons. Many contracted a deadly fungus which caused them to climb as high as possible before dying and releasing the spores (Laws, personal communication); others had parasites, while still others died when they became stuck in the aluminum screening. In sum, these outside factors could have had a significant effect on the grasshoppers' survival or growth.

The average body weights of females were significantly greater than males, but the significant time\*sex interaction term demonstrates that the rate of growth was different between sexes. The females grew faster, which indicates that they may have been consuming more resources than males. For males, this would mean that fewer resources were available. In addition, males must spend energy foraging for specific plants that are higher in nutrients, and avoiding predators, and attracting a mate.

Belovsky (1996) showed that females select mates who are the best foragers. These factors could have limited male food intake. Behavioral differences between sexes not observed in this study may also be important to explain differences in growth and survival. Schultz (1981) noticed variation in anti-predator behavior by sex that involved males

jumping away from a predator or sizeable moving object while females were more likely to stay in place. Males may have been easily disturbed and interrupted while feeding in my experiment, resulting in an overall decrease in feeding time compared to females. Further studies on male and female grasshoppers could focus on predator-avoidance behavior as a factor in growth.

It would seem that more females than males would survive to adulthood. If this were true, a number of hypotheses could be made to explain how these grasshoppers function on the population-level. Uneven sex ratios at birth with more male nymphs would be one way to achieve a 50/50 ratio by the time for adults to mate, because males are inferior competitors. On the other hand, 50/50 ratios may not be normal or even optimal for these grasshopper populations. Over thirty more males than females were counted when the sexes were separated in lab after randomly collecting roughly 400 individual grasshoppers in the field. This could mean that lower survival in males is offset by higher numbers during the early stages of life.

For lower grasshopper densities, males and females might not compete. This experiment used 300% field density because smaller numbers of grasshoppers per replicate would put the experiment at higher risk of losing important data should one grasshopper die unexpectedly and

inexplicably. Experimenting with different sex ratios could supply useful knowledge about what could happen if there was a large-scale sex ratio imbalance. Testing at high density could also help predict what the outcome of a population explosion might be. Grasshopper populations are very dynamic, so it is worthwhile to consider how various factors such as density, sex ratio, and predation interact. An ongoing experiment examining future generations in the cages could be a worthwhile endeavor to ascertain more long-term effects of altered sex ratios and predation levels on grasshoppers.

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### Tables and Figures

Sex	Sex ratio (Female:Male)	df	F-ratio	p-value
Females	8:2	1	10.108	0.002
Females	5:5	1	9.836	0.003
Females	2:8	1	9.846	<0.001
Males	8:2	1	1.23	0.272
Males	5:5	1	0.621	0.434
Males	2:8	1	6.811	0.012

Table 1: ANOVA results for effects of spider predation on survival of different sexes by sex ratio.

Sex	Spiders	df	F-ratio	p-value
Females	Present	2	18.57	<0.001
Females	Absent	2	21.932	0.255
Males	Present	2	0.225	0.799
Males	Absent	2	0.004	0.992

Table 2: ANOVA results for effects of sex ratios on survival of different sexes by spider treatment.

Spider	Factor	df	F-ratio	p-value
Present	Time	8	85.129	<0.001
	Sex	1	24.14	<0.001
	Time*Sex	8	2.01	0.047
Absent	Sex	1	1.731	0.190

Table 3: ANOVA results for effects of time and sex on grasshopper survival by presence of spiders

Source	df	F-ratio	p-value
Time	4	48.635	<0.001
Sex	1	180.794	<0.001
Time*Sex	4	9.835	<0.001

Table 4: ANOVA results for effects of sex , time, and time\*sex interaction on average weights of grasshoppers

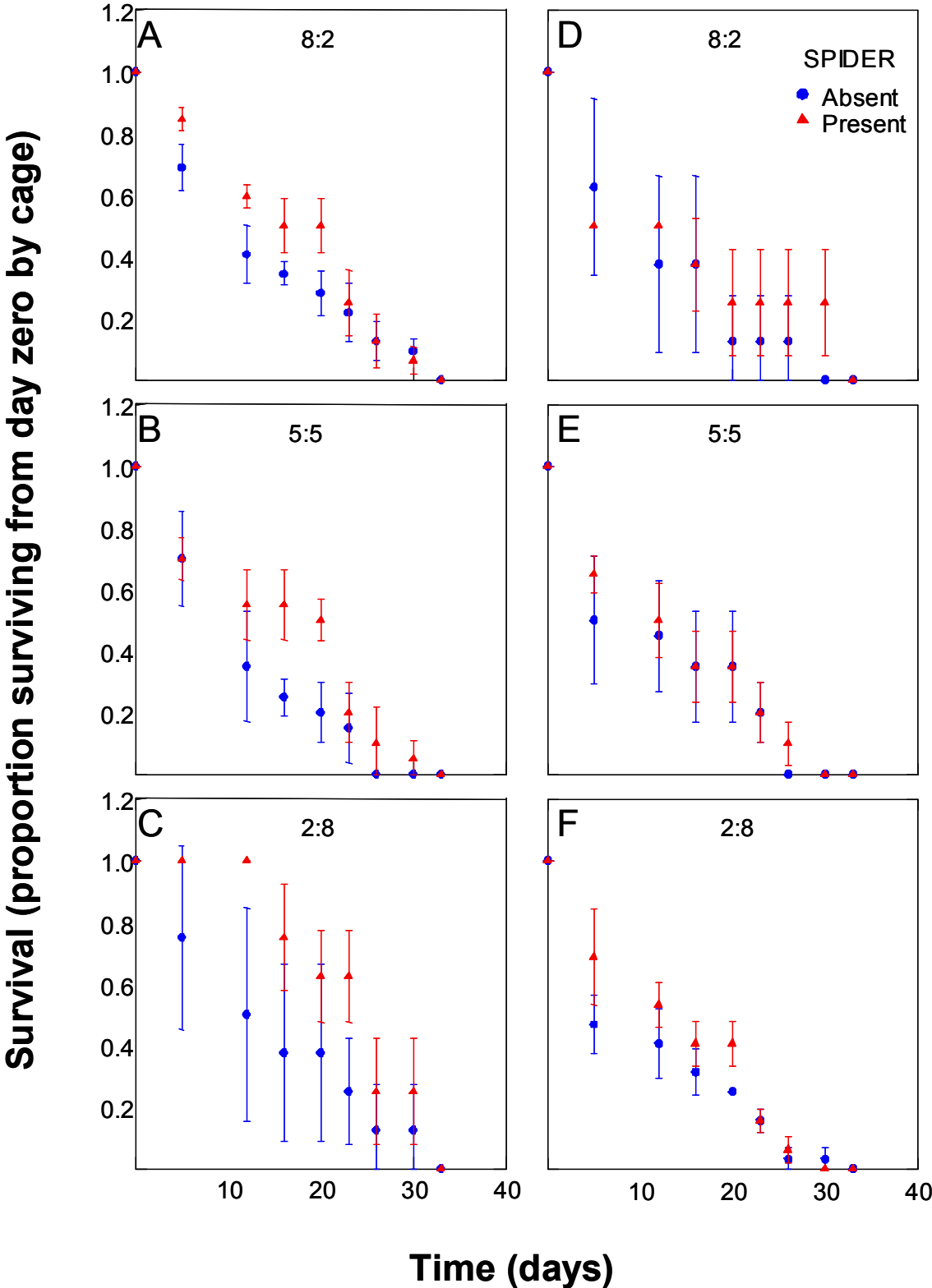


Figure 1: Effects of spider predation on grasshopper survival. Survival as a proportion of individuals surviving is plotted against time in days. The sexes are separated and arranged by sex ratio given as (female:male). Error bars represent standard error.

Survival (proportion surviving from day zero by cage)

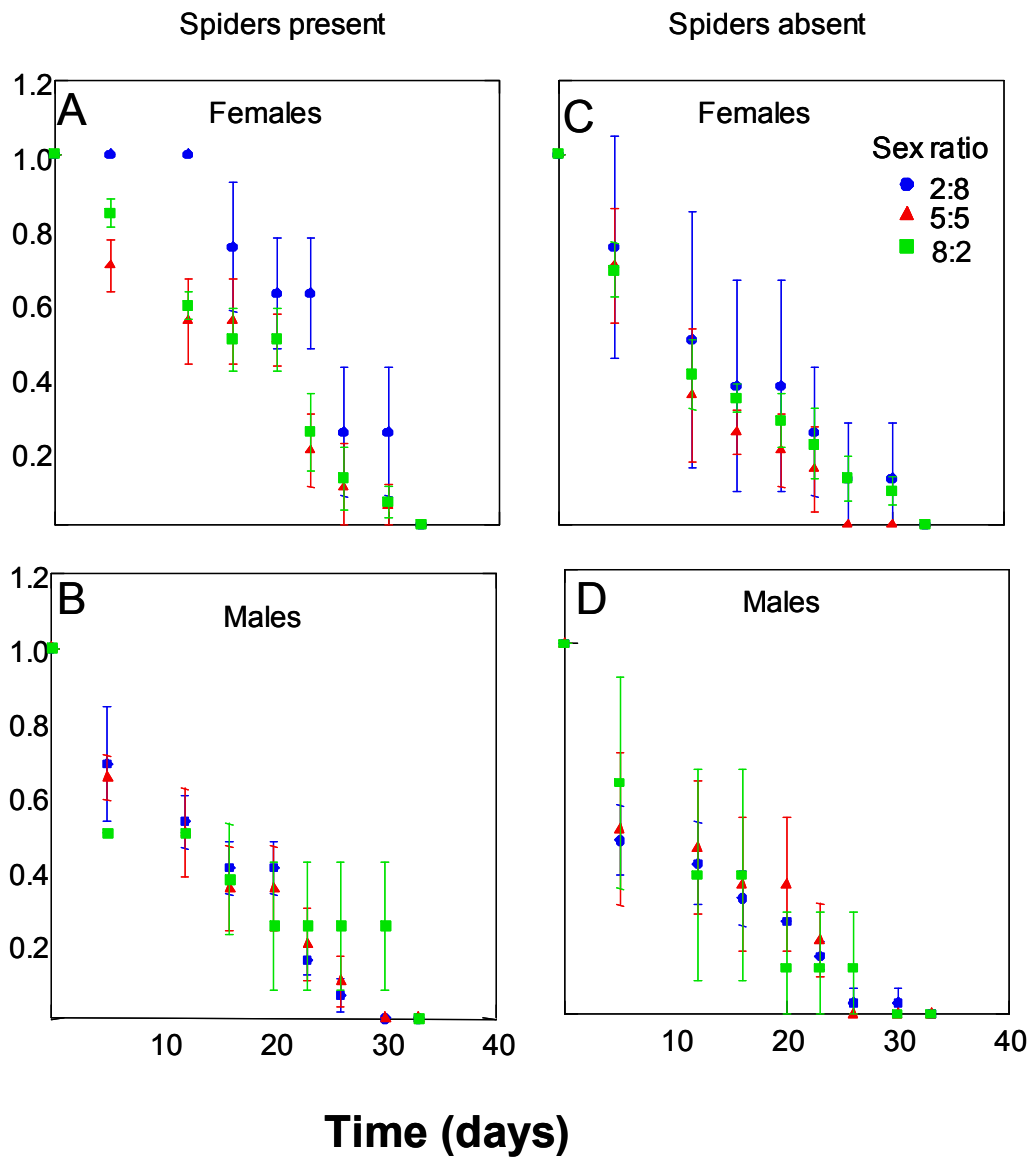


Figure 2: Effects of sex ratio on grasshopper survival. Survival as a proportion of individuals surviving is plotted against time in days. Sex ratios are given as (female:male). The figures are separated by presence or absence of spiders and by sex. Error bars represent standard error.

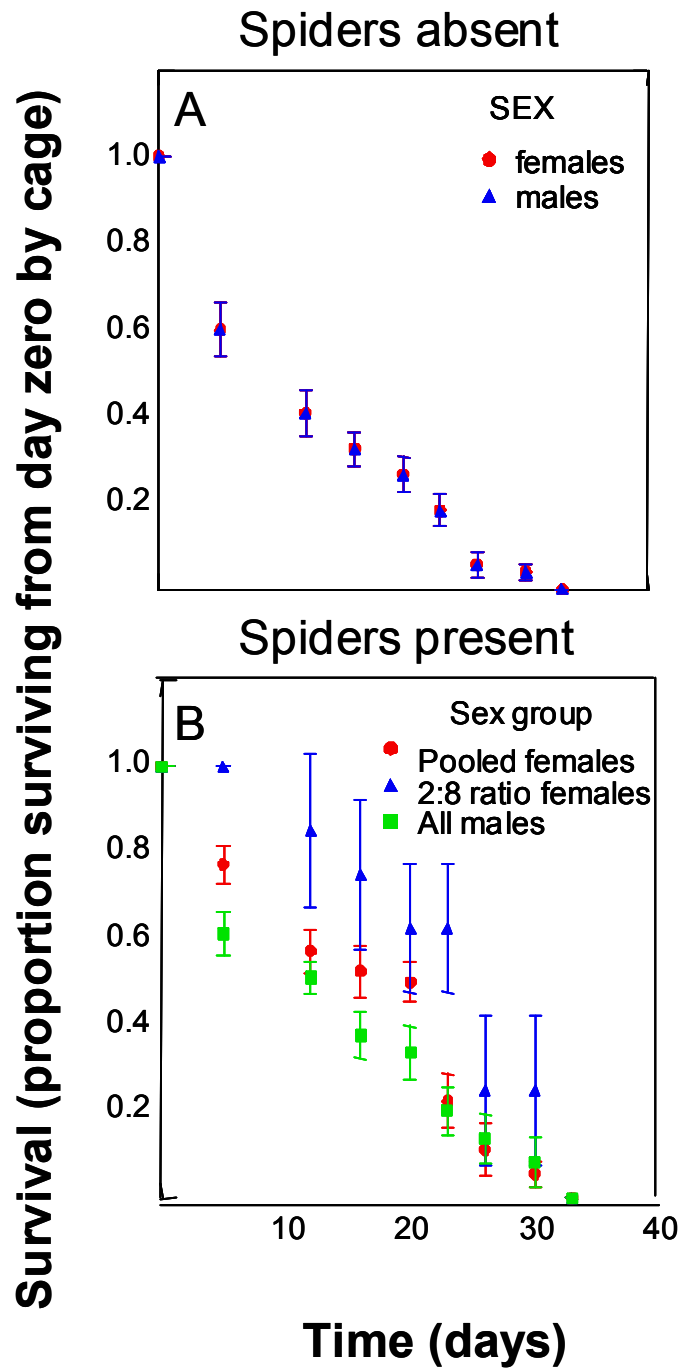


Figure 3: Effects of sex on grasshopper survival. Survival as a proportion of individuals surviving is plotted against time in days. In the absence of spiders, sex ratios are pooled due to lack of significant difference in survival without spiders. With spiders present, females in sex ratios of (female:male) 5:5 and 8:2 are pooled due to no significant difference in survival and are designated as “Pooled females.” Females in cages with sex ratios of 2:8 are designated “2:8 ratio females.” Males are pooled because of no difference in survival with spiders present. Error bars represent standard error.

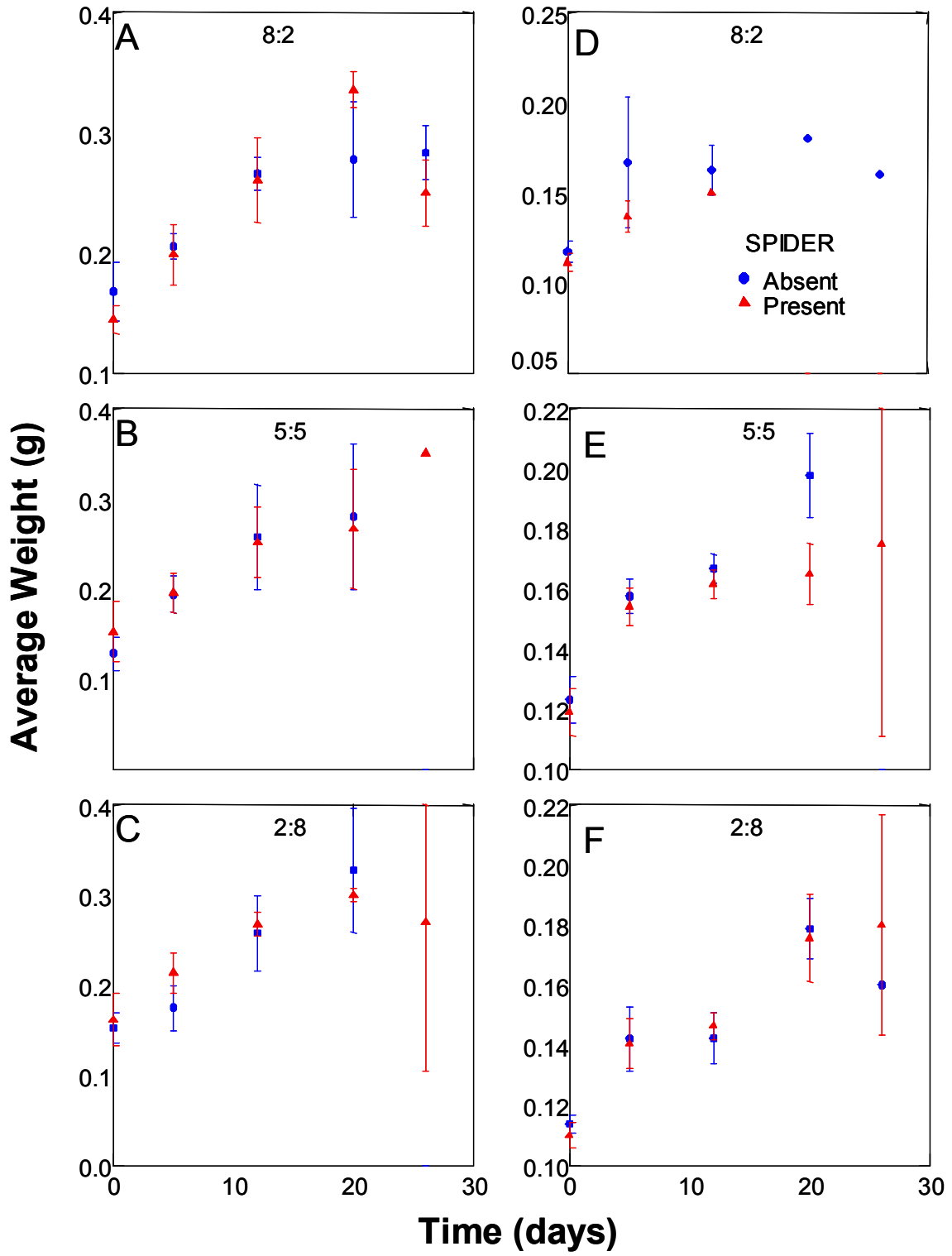


Figure 4: Effects of spider predation on grasshopper growth. Average body weight of grasshoppers in grams is plotted against time in days. The sexes are separated and arranged by sex ratio given as (female:male). Note dissimilar v-axis scales. Error bars represent standard error.

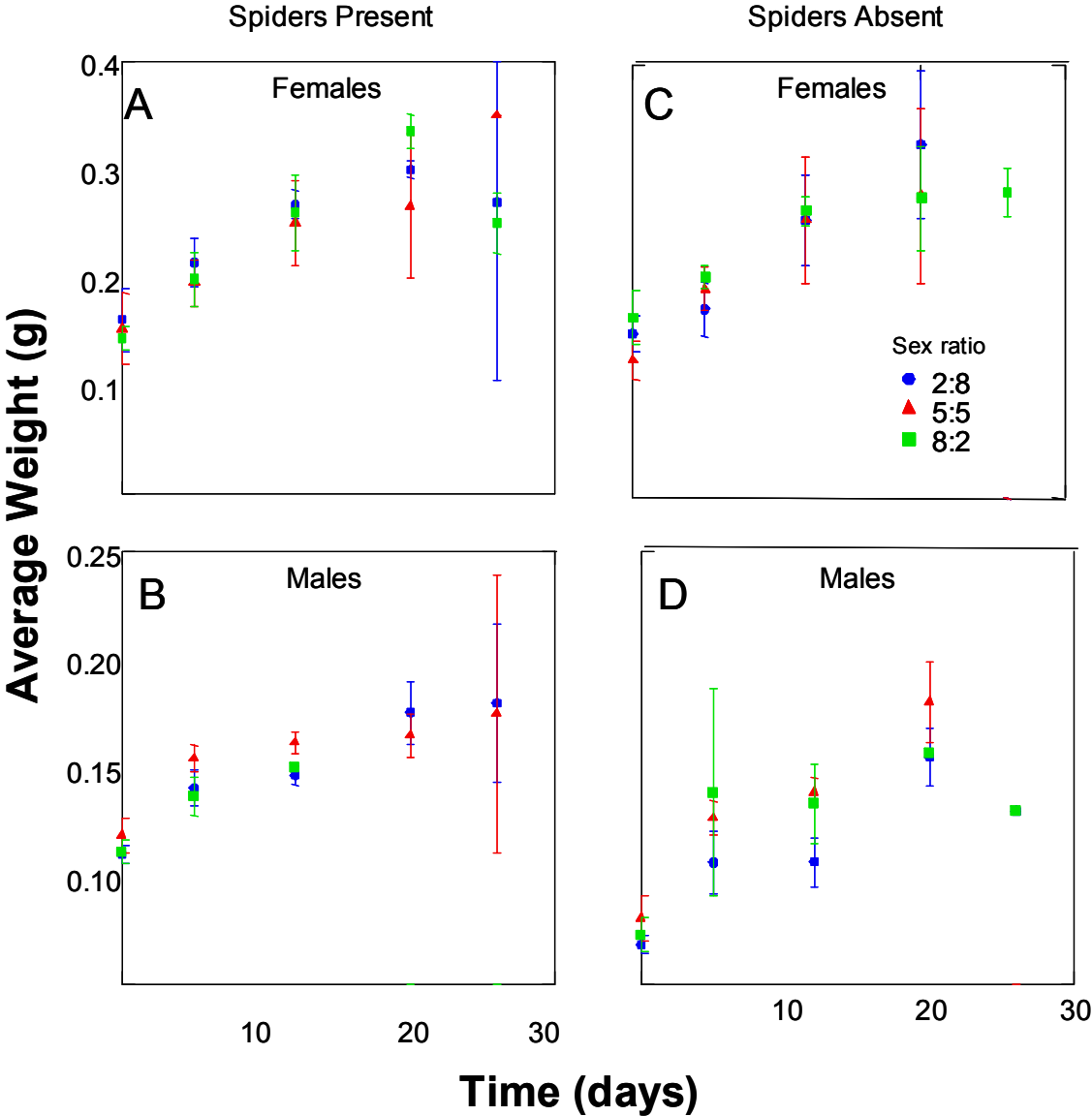


Figure 5: Effects of sex ratio on grasshopper growth. Average body weight of grasshoppers in grams is plotted against time in days. Sex ratios are given as (female:male). The figures are separated by presence or absence of spiders and by sex. Error bars represent standard error.

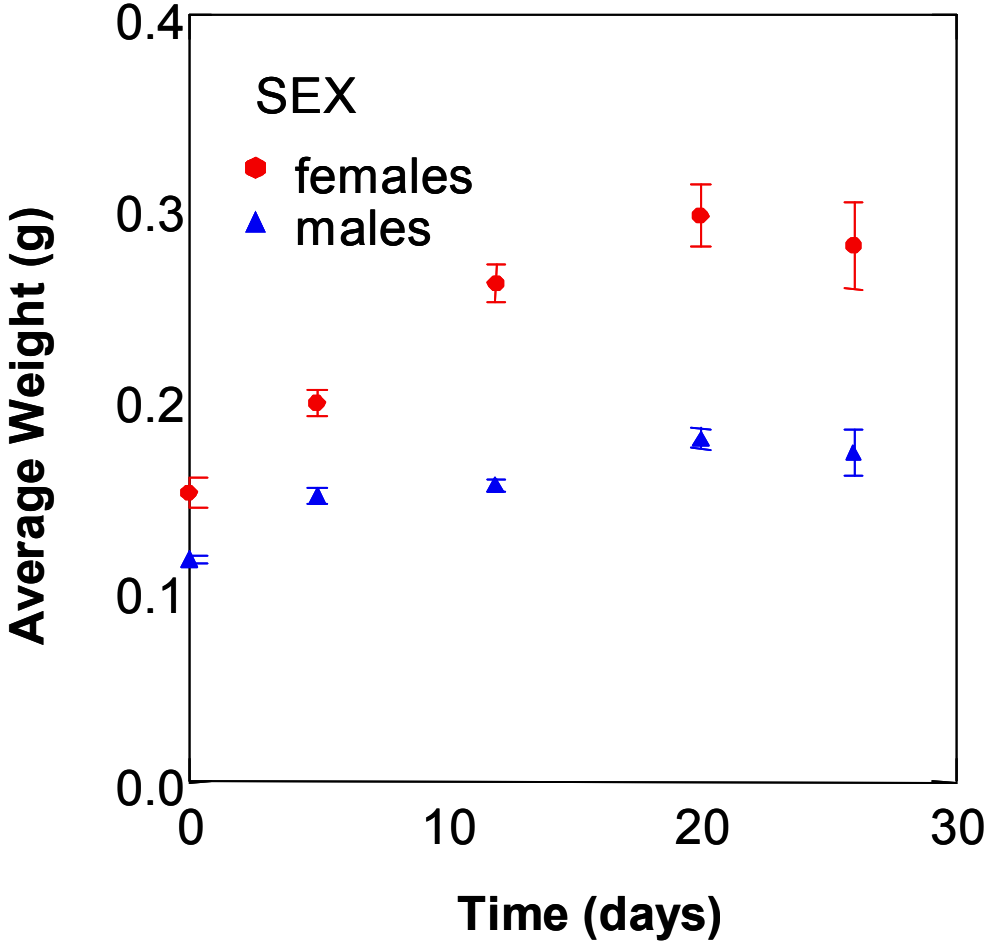


Figure 6: Effects of sex on grasshopper growth. Average body weight of grasshoppers in grams is plotted against time in days. Grasshoppers from all sex ratios and spider treatments are pooled by sex as there was no significant difference in body weights among either. Error bars represent standard error.