

The effect of competition and predation on resource allocation in *Camnula pellucida*

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Abstract

Predation and competition regularly affect grasshoppers by reducing foraging activity or reducing the amount of available resources. These interactions limit the amount of resources an herbivore can obtain through time and space. Consequently, predation and competition have direct effects on survival, growth, reproduction, and other life history traits. Grasshoppers strive to maximize resource intake and reduce the costs of foraging, but how do they balance the selective pressures? Using field experiments on the National Bison Range I stocked grasshoppers in four different treatments which ranged between low and high densities and those exposed to predation within density treatments. Grasshopper performance was measured by calculating survival, growth measurements, and reproductive output. Predation was found to slightly affect grasshopper survival, but was not significant in the other measures. Density-dependent food limitation is the primary constraint on the grasshoppers. Those in low density treatments consistently outperformed those in high density treatments

Introduction

Ecological theory states that organisms are subject to various ecological tradeoffs throughout their life. These tradeoffs ultimately determine the adaptive potential of the organisms: morphology, pigment, defense, reproductive output, growth, longevity, adaption to novel environments (Agrawal et al. 2010). However, fitness-enhancing traits cannot all be improved at the same time, organisms must make exchanges according to competing demands from internal and external factors. For example, reproduction involves a tradeoff between the size of offspring and the total number of offspring or litters per year, in which limiting resources cannot be allocated simultaneously to two functional traits (Agrawal et al. 2010). Tradeoffs among external factors, such as defense, is seen in the goldenrod gall fly larvae that are protected

from parasitoid wasps in larger galls but the larger galls are more easily found and predated upon by birds (Agrawal et al. 2010). Tradeoffs occur because a finite amount of available resources are divided among several functions throughout the body (Agrawal et al. 2010). Likewise, animals have a finite amount of time/space to forage for resources, thus optimal foraging theory refers to the idea that animals will strive to maximize energy intake and minimize costs (Sinervo 1997). Animals face numerous costs during foraging 1) temporal costs—the time it takes to find and digest food, 2) energetic costs—the energy expended during foraging and processing, 3) cognitive costs—which involves the process of learning and memorizing the location of food sources, 4) exogenous costs –predation risk, competitive interactions, and weather (Sinervo 1997). The challenge, then, is to determine how animals balance selective pressures (Rothley et al. 1997). Optimal foraging states that the major constraint among herbivore dynamics lies in the discrepancy between allocation demands and the availability of nutritious resources (Hawlena & Schmitz 2010). As a result, fitness-enhancing traits such as development, fecundity, and survivorship are heavily dependent on plant choice (Joern 1979; Sinervo 1997). Predation risk and competitive interactions alter foraging activity which ultimately effects growth, reproductive output, and survivorship. In this study I am going to focus on the interaction among predation from hunting spiders and intraspecific competition and thier effects on morphological, reproductive, and survivorship outcomes in Clear-winged grasshoppers, *Camnula pellucida*.

Predation can have significant effects on prey (Hawlena & Schmitz 2010; Schmitz et al 2004; Schmitz 1998; Pitt 1999; Schmitz 2008; Oedekoven & Joern 2000; Joern et al. 2006; Rothley et al 2007). Grasshoppers are vulnerable to various predators throughout their lifecycle including spiders, lizards, small mammals, and birds (Danner & joern 2004; Pitt 1999). For instance, grasshopper nymphs and early instar stages are primarily predated upon by spiders, but

as they increase in size become less susceptible. (Danner & Joern 2004). Predators can influence herbivore prey both directly and indirectly. Predators directly forage on prey which reduces overall density. Through field experiments, Schmitz (1998) found that predation spider treatments reduced grasshopper nymph density when compared to no-predator treatments; however, there was no significant effect on adult grasshoppers. Predators can also effect prey indirectly without actually capturing and consuming. Presence of predators activate behavioral shifts towards increased vigilance, reduced foraging activity and habitat selection (Pitt 1999; Joern et al. 2006; Schmitz et al. 2004; Schmitz 2008; Hawlena & Schmitz 2010). Rothley et al. (1997) found that diet generalist grasshoppers, *M. femurrubrum*, will alter its diet from primarily grasses to primarily forbs in response to predation risk (Schmitz 1998). In all cases, grasshoppers will choose an average diet that favors vigilance over energy maximization (Rothley et al. 1997). Consequently, predation can have significant effects on grasshopper growth, reproductive output, and survivorship. Predator-prey interactions involve coevolutionary adaptations that reduce the prey's chances of encountering a predator and increases the chances that the predator finds its prey (Joern et al. 2006). Antipredator behavior can have implications for fitness. Prey must balance the benefits of behavior to reduce predation that also reduces resource intake (Pitt 1999). Predation risk exposes prey to stress, which triggers metabolic processes to heighten vigilance, consequently stress increases nutrient demands as well (Hawlena & Schmitz 2010). Prey will not increase foraging time under predation risk instead they compensate by allocating resources from reproduction and growth to maximize survivorship (Hawlena & Schmitz 2010). Overall, avoiding predation results in prey making alternative food choices that may involve less handling time but also may be less nutritious or harder to digest—a tradeoff between resource allocation and predation avoidance.

Competitive interactions have similar effects on grasshopper development. While predation can reduce the time spent feeding or induce shifts in diet choice, competition reduces the amount of available resources. Individuals in the same species or cohort are not equally able to obtain resources (Oedekoven & Joern 2000). Stronger individuals may force lesser individuals to depend on less nutritious food sources. Less nutritious food could increase the time needed to develop to reproductive maturity. Allocation costs are accentuated under competitive or stressful conditions because of limited food resources (Schmitz 1998; Oedekoven & Joern 2000). Schmitz et al. (2004) noted that individuals which require a longer time to develop may have lower fitness because of the initial size disadvantage and the time lost to reproduce. Belovsky and Slade (1995) found that grasshopper survival and reproduction primarily responded to density-dependent food limitation in both experimental and field populations. Resource abundance declined relative to grasshopper requirements. Consequently, more hatchlings were produced than could be supported under the highest available resources in the next growing season. Since competition is an important factor on the Bison Range, we may observe that predation will not significantly affect grasshopper populations. Rather, predation may increase fitness due to competitive release (Chase et al. 2002). Predation can reduce densities of competing consumers, resulting in an increase in resources available to the population.

Using field experiments in the Palouse Prairie of the National Bison Range in Montana, I studied how predation risk combined with intraspecific competition influenced development, fecundity, and survival of *Camnula pellucida*. Four different enclosure treatments including high or low densities of grasshoppers and those with or without spiders to elucidate the interactions. These experiments will help determine whether available resources are the limiting factors for *C. pellucida* on the Bison Range, or if there are ample resources and the grasshoppers are choosing

to allocate their resources to maximize fitness. Given prior knowledge of the effects of predation risk and food availability (Oedekoven & Joern 2000), I predict that grasshoppers will respond negatively in enclosures with high densities and predation risk. Those in enclosures without predation and stocked in low densities will respond positively. As seen in experiments conducted by Schmitz (1999), I predict that the grasshoppers stocked in high densities without predators and those in low densities with predators will compensate accordingly so that no negative effects will not manifest during adult stages. Overall, grasshoppers stocked in low densities without predators will perform better than those stocked in low densities with predators or those in high densities without predators, which will perform better than grasshoppers stocked in high densities with predators. Specifically, I predicted that:

1. Within predator treatments, high density treatments will perform worse than low density treatments due to competition for resources. Overall, predation negatively affects survivorship, increases the time needed to develop to sexual maturity from trait-mediated effects which decreases growth and fecundity.
2. Within density treatments, survival will be lower in treatments with predators compared to those without predators.
3. Within density treatments, growth and fecundity will decrease in treatments with predators due to trait-mediated effects.

Methods

Study Site

I conducted field experiments during the summer of 2014 during late June to late July at the National Bison Range, a site located in the Palouse Prairies of Moiese, Montana. This site is an open vegetation structure composed of bunch grass prairies dominated by grasses (70-96% of dry mass in various years); *Poa pratensis* and *Elymus smithii* are the most abundant grasses, while *Achillea millefolium* and *Aster falcatus* are the most abundant forbs (Belovsky & Slade 1993).

Camnula pellucida are among the 15 different species of grasshoppers (Orthoptera, Acrididae), in which *M. femurrubrum* and *M. sanguinipes* were the most abundant. Average densities of grasshoppers varies between 2-12 adults m², and nymph densities range from 7-120 individuals m² in earlier summer months (Belovsky & Slade 1993). Spiders, those in families Aranedae, Lycosidae, and Clubionidae, are the most common grasshopper predators. Adult grasshoppers are mainly predated upon by birds including western meadowlark (*Sturnella neglecta*), the grasshopper sparrow (*Ammodrammus savannarum*) and kingbird species (*Tyrannus spp.*) All grasshoppers were caught using sweep nets and those within the 2nd-3rd instar stages were stocked to allow for spider predation.

Cage Design

Grasshoppers were contained in 64 field cages (0.66m wide x 0.66m deep x .0.80m tall; =0.40m² basal area) similar to those used by Danner & Joern (2004) and Oedekoven & Joern (1998). All grasshoppers, spiders, and other insects (those that were detectable) were removed from the cages before burying the aluminum flashing 20 cm into the ground (Danner & Joern 2004). Cages were placed over suitable areas dominated by *Poa pratensis* and *Elymus smithii* among other forbs. The cages were constructed using 30 cm tall aluminum flashing at the base with 1mm window screening attached to all sides. This design restricts access of other insects in

or out of the enclosures. 16 cages of each type were constructed which produces 4 replicates during the experiment.

Experimental Conditions

32 (half) of the enclosures were stocked with low density of grasshoppers (2 males: 3 females) while the other half was stocked with a high densities of grasshoppers (4 males: 6 females). This produces 13 grasshoppers m^2 in low densities and 25 grasshoppers m^2 in high density treatments. Skewed sex ratios were used to ensure reproduction during the experiment. Hunting spiders including wolf spiders, oblong running crab spiders, and crab spiders were stocked in 16 of the low density enclosures and 16 of the high density enclosures. Spiders were captured using pitfall traps and visual encounter surveys during night and day. Stockings were randomly assigned.

Grasshopper performance

Density counts were conducted once a week to calculate survival. Growth was recorded for every surviving grasshopper at the end of the experimental period. Growth was assessed by measuring body mass, hind femur length, and pronotum length. Previous research has studied the effects of competition and predation on grasshopper fecundity, but it failed to observe the interaction between timing and the allocation of resources among different treatments. Reproduction will be assessed by removing a replicate of 16 enclosures every 4 days after the initial period of growth. Staggering removal will elucidate whether females are modifying allocation based on time, predation, competition, and available forage. At the conclusion of each experimental period all females were captured and immediately frozen for at least 24 hours to preserve for dissecting. Reproductive output will be calculated by dissecting and counting the

number of functional ovarioles, nonfunctional ovarioles, follicular relicts, and reabsorption bodies. A .1 m² plot was clipped and removed from each enclosure. Clippings were separated into grasses and forbs and then dried at 150 degrees Celsius for two days before weighing.

Statistical Analysis

All statistical tests were conducted using SYSTAT. ANCOVA was used to determine any interaction between density, predation, and the weeks in which the grasshoppers were removed. General Linear Models were used to assess the effects of density, predation, and time on vegetation biomass, growth, survival, and reproduction. Regressions determined any significance between morphological measurements.

Results

Vegetation Biomass

Grass biomass from enclosure clippings is shown in Fig 1. Only grass biomass is considered from the data because forb biomass was not significant related to grasshopper survival or the week that the experimental grasshoppers were removed from the enclosures. Grass biomass significantly decreased as time goes on from grasshoppers foraging and becoming brown for both low and high densities ($p=0.02$; $p=0.003$ respectively).

Survivorship

Differences were observed in survival among the predator treatments (Fig. 2). Grasshoppers stocked in enclosures without predators exhibited greater proportional survival. The amount of grass biomass did not significantly affect survivorship, however the presence of

predators did significantly affect both density treatments (low density, $p=.01$; high density, $p=.008$). It is interesting that predators seemed to have a stronger influence within high density treatments.

Growth

Growth of female grasshoppers was significantly higher in low density treatments ($p=0.009$). However, female hind femur length did not exhibit similar correlations even though a regression between female mass and femur length showed a tight fit ($p<0.001$) (Fig. 3). Growth was not significantly related to predator presence or amount of available biomass in the enclosures.

Reproductive Output

Only four of the experimental grasshopper females produced pods during the research period, so reproductive performance was measured using the proportion of females that had functional ovarioles as well as the average number of functional and nonfunctional ovarioles per enclosure. There is a significant increase in the proportion of females with functional ovarioles stocked in low density treatments ($p=0.005$) (Fig. 3). Additionally, low density treatments exhibit a gradual increase in functional ovarioles as time continues, whereas high density treatments did not continually increase over time. Proportional functionality nor the average number of functional ovarioles was significantly correlated between predator treatments. Proportional functionality was not significantly affected by the presence of predators or the amount of grass biomass, however there is a significant increase in the number of functional ovarioles as females grow larger ($p<0.001$).

Discussion

Balancing the costs of foraging while attempting to maximize resource intake is an important dynamic that determines the structure of various animal communities (Belovsky & Slade 1995; Danner & Joern 2003; Hawlena & Schmitz 2010; Oedekoven & Joern 2000). Foraging activity is regularly altered by competition for limited resources and predation through trait-mediated effects. These trophic interactions have direct consequences for an organism's evolutionary path (Agrawal et al. 2010; Danner & Joern 2003; Schmitz et al. 2004). Experiments involving predator-prey interactions consistently demonstrate that both direct and indirect interactions alter herbivore foraging activity and efficiency (Chase 1996; Danner & Joern 2003; Schmitz 1998). Predators induce behavioral shifts that reduce foraging activity and increase vigilance; consequently, negatively affecting allocation towards growth, survival, and reproduction. However, the field experiments conducted over the summer on the National Bison Range support previous findings that the local populations of grasshoppers respond significantly to density-dependent resource limitation rather than predation risk (Belovsky & Slade 1995; Chase 1996). Competition in a food limited environment is the primary mechanism that structures the local communities, which is supported by my results. Grass biomass decreased over the experimental period, except when the first replicate of enclosures were removed. One theory to explain this deviation from the expected results is the summer rains during July. 2013 received .09 inches of rain during the month and there was .24 inches of rain in July in 2014, which may have caused an increase in the density of vegetative biomass (Farmer's Almanac). As a result, growth, survival, nor reproduction directly correlated with the amount of available grass biomass. However, several significant differences were observed between low and high density populations. Figure 1 illustrates during the beginning of the experiment more grass biomass was

clipped in treatments with predators relative to no predator treatments. This trend indicates a trophic cascade, but it soon disappears as resources are depleted and competition becomes more important (Chase, 1996). Additionally, the amount of grass biomass was similar in both low and high density enclosures when the last replicate was removed. This occurrence indicates that the grasshoppers are food limited. If more food was available we would expect grass biomass to be lower in high density treatments from a higher number of grasshoppers foraging. Subsequently, grasshoppers in the high density treatments have less access to food per capita; each individual has less to forage on. Therefore, we see negative effects on growth, survival and reproduction between density treatments.

Females stocked in low density treatments were significantly larger due to more available resources per individual. Larger body size can have several implications for fitness. Although survival was not significantly correlated within density treatments, predator presence was found to effect survival. Furthermore, effects of predators is exacerbated in high density treatments. Predation in high density treatments seems to be additive whereas it is compensatory in low density treatment. Additional stress from predation risk trait-mediated effects compounded with competition for food may reduce the probability of survival. Reduced foraging activity to avoid predation risk, a type of trait-mediated effect, provides insight on the reduced survival in predator treatments (Danner & Joern 2003). In an attempt to maximize survival, grasshoppers spend less time feeding which limits the intake of resources that can be allocated to other functions in the body. As grasshoppers become bigger they are less sensitive to predation from spiders; however, contradictory to results found by Danner and Joern (2003), there was no indication that the grasshoppers increased growth rate to counteract predation risk. Nor did grasshoppers with access to more resources in low density treatments exhibit increase in growth

rate relative to predator treatments. These results compare with those of Ovadia and Schmitz (2002) where they found predation did not affect growth of *Melanoplus femurrubrum*. Similar to *M. femurrubrum*, *C. pellucida* is a diet generalists that will alter their diet from primarily grasses to primarily forbs in the presence of spiders. *Ageneotettix deorum*, the species sampled by Danner & Joern (2003) is a grass specialist. They are not able to shift their diet to forbs in order to satisfy nutrient demands.

Significant outcomes in reproduction were produced within density treatments. Similar to survival and growth, reproduction is tightly linked with competition. Typically, reproductive performance is measured by counting the number of follicular relicts versus reabsorption bodies. However, only a small sample of females in this experiment produced pods during the nine week period which would not present a reliable platform to analyze reproduction. We resorted to measuring the average number of functional ovarioles for each enclosure (Fig. 4) and calculating the proportion of females in each enclosure (Fig. 5). The number of functional ovarioles and the proportion of functional females was significantly higher in low density treatments and increases as time continues relative to high density treatments. This can be explained because female mass is a good indication of the probability of having functional ovarioles. Larger females are going to produce more functional ovarioles. Additionally, low density treatments produced larger females; subsequently, low density treatments produced a higher proportion of females with functional ovarioles. This can be attributed to the increase in resources per capita in low density enclosures. The proportion of females with functional ovarioles increases linearly throughout the experiment, however there is no data to support whether this accounts for adjusted allocation rather than normal development. No significant correlations occurred within high density treatments, but some interesting trends arise in that data (Fig. 4 & Fig. 5). We see that high

density treatments generally start producing functional ovarioles first even though they produced smaller females. Could this be a response to the added stress set on by competition?

Additionally, low density treatments tend to increase over time, but the proportion of functional females in high density treatments is much more unstable. The average number of functional ovarioles does not seem to increase over time, but remains constant instead. This suggests that stress induced from predation risk or the competitive interactions inhibited reproduction to a small degree.

This study provides insight into trophic cascade dynamics and determining whether top-down or bottom-up forces are the primary mechanisms structuring natural communities (Chase 1996; Danner & Joern 2003, 2004; Schmitz et al. 2004) Predation and trait-mediated effects from predation risk have the potential to influence herbivores. Nevertheless, I provide support that density-dependent and bottom-up forces are the primary constraints for *Camnilla pellucida* on the Bison Range. It may be the total number of stressors encountered by an organism rather than the type of stress. The effects of predators was much stronger in high density enclosures where those grasshoppers were subject to intraspecific competition. Moreover, competition further reduces the limited available resources that can be allocated for various functions. Food limitation is the primary constraint on grasshopper fitness on the National Bison Range.

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Figures and Tables

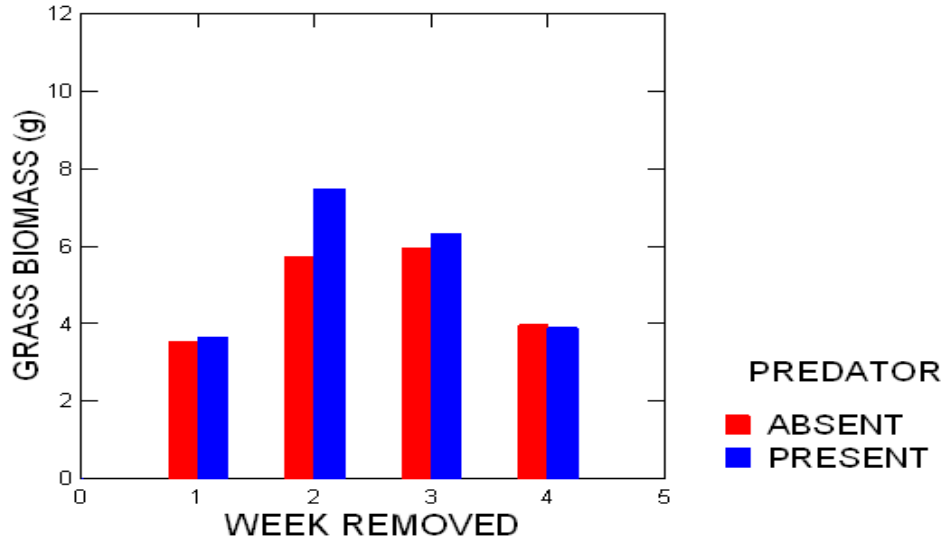


Figure 1: Bar chart illustrating the removal of grass biomass over time after the second replicate was removed. Grass biomass is significantly related to the week removed ($p=.02$) but not significantly related to predator or density treatments.

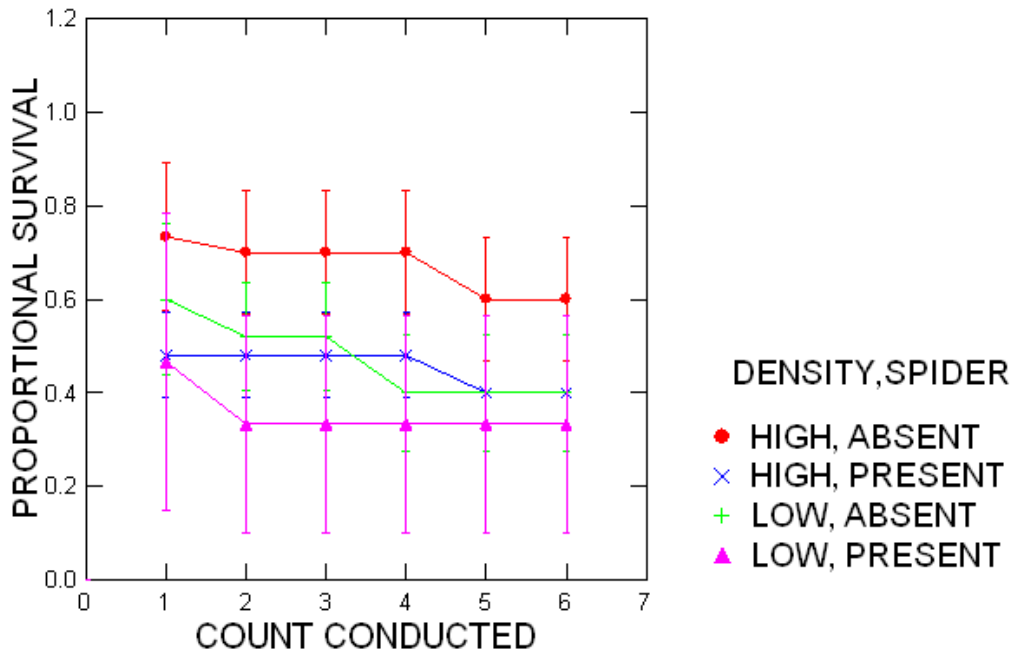


Figure 2: Proportional survival of the last replicate removed from the experiment. No predator treatments significantly survived better than those exposed to predation. ($p=.0006$)

Confidence Interval and Prediction Interval

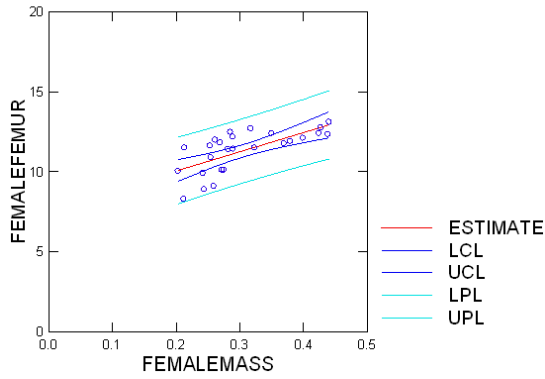


Figure 3: Linear regression showing the relationship between female mass and female femur length ($p=.0007$; $r^2=.319$)

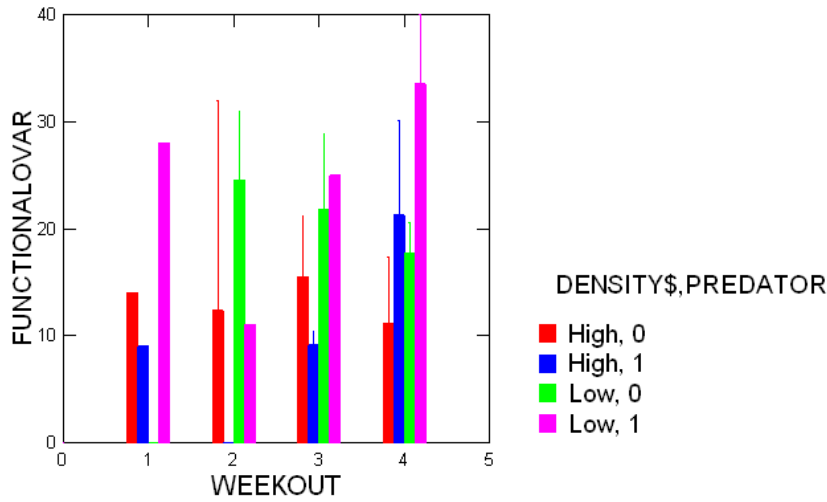


Figure 4: Bar chart illustrating the average number of functional ovaries between different treatments over time.

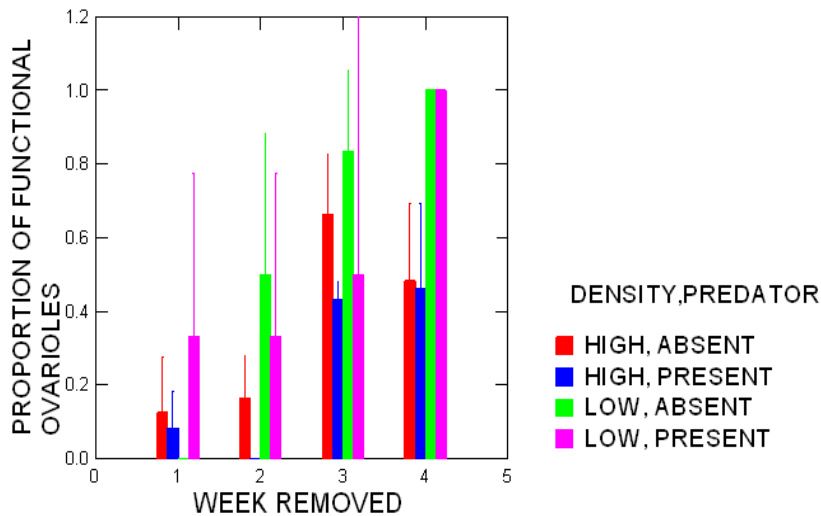


Figure 5: Bar chart illustrates the proportion of females in each treatment that had functional ovarioles. Low densities significantly outperformed high density treatments ($p=.005$)

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