AVAILABILITY AND NUTRIENT CONTENT OF COMMON ARTHROPOD PREY OF NORTHERN BOBWHITES (*COLINUS VIRGINIANUS*) IN WESTERN OKLAHOMA

By

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Abstract:

Variation in the relative abundance and biomass of arthropods, as well as individual variation in macronutrient and elemental content, have important potential consequences for insectivores. We studied the influence of seasonality and habitat management (i.e. burning and strip disking) on the availability of potential arthropod prey for brooding northern bobwhites (*Colinus virginianus*), and tested variation in macronutrient and elemental content between and within common orders of prey. Burning changed the biomass composition of the arthropod community, but disking did not result in any community-level changes. Burning also increased the total abundance and biomass of arthropods collected compared to the control, but disking did not affect total abundance or biomass. Seasonality exerted a broader influence on arthropods, and total abundance and biomass increased throughout the duration of the sampling period (May-July) at burned/paired control and disked/paired control sites. Ants, which had the highest abundance and biomass of any taxa, appeared to drive these patterns. The response of individual orders to management and seasonality varied in size and direction, though we observed more and stronger effects of seasonality than burning or disking. These results support the idea that burning provides benefits to foraging bobwhite broods through increased total availability of arthropod prey, as well as favorable habitat characteristics (i.e. bare ground, structural heterogeneity). However, large seasonal variation in total arthropod abundance and biomass, as well as that of individual orders, likely influences the relative importance of individual prey items in the bobwhite diet based on the timing of nest initiation and hatching, and temporal shifts are particularly important given variation in nutrient content displayed by arthropod taxa. We found that common orders of prey (Hymenoptera and Coleoptera) had high exoskeleton and low protein content, suggesting that the most available prey are also poor quality. Other orders, like Araneae and Orthoptera, had low exoskeleton and high protein content, suggesting that bobwhite chicks benefit from maintaining high diet diversity. Thus, a better understanding of existing variation in arthropod availability and nutrient content is critical for elucidating the role of prey selection and nutrient uptake in shaping the success of avian insectivores.

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CHAPTER I

SEASONALITY AND HABITAT MANAGEMENT INFLUENCE ARTHROPOD PREY FOR NORTHERN BOBWHITES (*COLINUS VIRGINIANUS*)

Introduction

Arthropods are an important component of terrestrial systems, as a source of food, pollination, and ecosystem services (Kaspari and Joern 1993; Isaacs et al. 2009; Birkhofer et al. 2016). Yet, up to 41% of insects are in decline (Sanchez-Bayo and Wyckhuys 2019). The causes of this decline include habitat loss, use of pesticides, and spread of invasive species (Sanchez-Bayo and Wyckhuys 2019). Many species that depend on insects as a food source face parallel declines in response to reductions in insect abundance and biomass (Allen et al. 1995; Morrow et al. 2015). For example, survival rates of Attwater's prairie chicken (*Tympanuchus cupido attwateri*) broods were reduced by more than half in habitats invaded by red imported fire ants, which had lower abundance and biomass of arthropod prey (Morrow et al. 2015). Additionally, areas with higher neonicotinoid insecticide application are associated with lower abundance of bobwhite quail (Ertl et al. 2018a) and many other grassland birds (Mineau and Palmer 2013). Some studies have failed to find evidence to support toxicity of neonicotinoids to quail, which suggests that the effect could be due to reduced arthropod food availability (Toll 1990; Boatman et al. 2004; Turaga et al. 2015; Gobeli et al. 2017; Ertl et al. 2018b; Bean et al. 2019).

Northern bobwhites (*Colinus virginianus*, hereafter bobwhite), which rely on invertebrate prey at a critical early life stage, continue to decline across their range in the United States (Brennan et al. 1991; Williams et al. 2004; Hernandez et al. 2013). Bobwhites are insectivores for the first 2-10 weeks of life and consume a larger proportion of plant materials after 2-3 weeks (Nestler et al. 1942, Hurst 1972; Eubanks and Dimmick 1974). Chicks must consume energy and protein to quickly gain body mass, build muscle, and grow feathers necessary for flight, predator evasion, and body condition maintenance through cold winter months (Nestler et al. 1942; Hurst 1972; Eubanks and Dimmick 1974; Woodard et al. 1977; Potts 1997).

Habitat management for quail often focuses on creating areas of grasses and shrubs for nesting habitat, shrubs for cover from predation and heat, and forbs to support insect prey important for brooding (Elmore et al. 2017). In addition to having forbs, brooding habitat should have heterogeneous vegetation cover with considerable amounts of bare ground, which allows chicks to move and forage unimpeded (Potts 1986). To accomplish the goal of providing diverse habitats necessary for nesting, protection and brooding; prescribed fire, grazing, and strip-disking (mechanical soil turnover) are often applied to different patches of habitat in the landscape separately or in conjunction.

Prescribed fire has well documented but variable impacts on the arthropod community. In their review, Kral et al. 2017 found that Coleoptera and Orthoptera tended to respond positively in a large proportion of reports, and that Araneae and Lepidoptera tended to respond largely negatively. However, the response of some orders to fire, like Hemiptera and Hymenoptera, was so variable that a clear trend was not apparent. Traits linked to individual species' success in response to fire are mobility, life stage, and feeding guild; with mobile, adult grass eaters and generalists responding the most positively (Evans et al. 1984; Swengel 2001; Engstrom 2010; Branson and Vermeire 2013; Kral et al. 2017). For example, forb eating Orthopterans experienced high mortality and reduced abundance in the post-disturbance assemblage compared to grass eating Orthopterans, likely due to the stable abundance of fire tolerant grasses (Evans 1984). Additionally, variation in fire characteristics (wind speed, fuel load, soil temperature, etc.) may influence the direction and degree of species' response.

The effects of strip disking on arthropods are poorly understood and appear variable in effect size and direction. Several studies report overall increases in both abundance and biomass of arthropods as a result of disking, but relationships between disking and the abundance and biomass of individual invertebrate orders are not well established (Madison et al. 1995; Greenfield 1997; Benson et al. 2007; Dollar et al. 2013). However, linear application of strip disking limits its influence on arthropod communities due to the ability of individuals to move in and out of narrow strips (Hanson et al. 2016).

Seasonality exhibits variable influences on arthropod assemblages in terms of both abundance and biomass (Hurst 1972; Doxon and Carroll 2007; Foye et al. 2015). Arthropods can vary in voltinism, which is the number of generations in a year. While there is a large amount of variability in both the size and direction of the effect between orders of arthropods, many orders experience peaks in abundance and biomass in early-to mid-summer, but some also experience peaks as late as August (Doxon and Carroll 2007; Foye et al. 2015). The size structure of arthropod populations can also shift over the season as individuals mature, which is important since bobwhite chicks may be constrained in the size of prey that they can consume. Bobwhites are known to make multiple reclutching attempts in a given breeding season, and there are important potential consequences for bobwhite chicks depending on the timing of individual clutches (Cox et al. 2012; Brooke et al. 2016). Evidence suggests that clutches from early nesting attempts (April-May) are larger and more successful than late ones (July-August) (Cox et al. 2005; Brooke et al. 2016). It is therefore reasonable that changes in the relative abundance of appropriately sized prey items due to seasonality (i.e. juvenile grasshoppers growing too large to be consumed by bobwhite chicks) may influence total intake, breadth, and nutritional quality of individual diets.

The objectives of this work were to: 1) test the effects of prescribed burning and strip disking on potential bobwhite prey abundance and biomass and 2) test the influence of seasonality on prey abundance and biomass. Both abundance and biomass are important metrics for bobwhite prey because chicks must capture individual prey items, and because the total amount of mass ingested has important implications for growth. We predicted that burning and disking would have a positive effect on arthropod abundance and biomass because of the presence of higher quality forage available to herbivorous arthropods.

Methods

Study Site

The study was conducted at Packsaddle Wildlife Management Area in Ellis County, Oklahoma during the months of May, June, and July 2019. Annual rainfall is 63.5 cm on average. Packsaddle WMA contains a wide variety of soil types including fine sandy loams, loam fine sands, and fine sands (Oklahoma Dept. of Wildlife Conservation and the United States Department of Agriculture). Situated in traditionally productive quail habitat, the 6,475-ha WMA is managed with prescribed fire, strip disking, and cattle grazing. Burning begins in late summer and ceases at the end of March, weather permitting, and strip disking is applied November through April. Common vegetation present at sites includes grasses such as big bluestem, Indian grass, little bluestem, side-oats grama, and buffalo grass, as well as shrubs like shinnery-oak, sagebrush, and sandplum (Oklahoma Dept. of Wildlife Conservation).

Sampling Design

Invertebrate Collection and Identification - Treatment sites were first selected by identifying areas applied with either prescribed fire or strip-disking no more than six months prior to first sampling (May 2019). Specific locations for each plot were selected so that they represented a wide range of habitats available at Packsaddle WMA (i.e. lowland plains, pastures, gulleys/riparian areas, rocky outcroppings) and were placed where an analogous untreated site of the same ecotype was available. To test the effects of prescribed fire on potential arthropod prey of bobwhites, we chose four burned sites and four paired control sites. Burned sites were placed in three different burned areas, which were burned between February 26 and March 18, 2019. The smallest of these burns was 64.75 ha, which only contained one plot. Two larger burns of ~250 and ~325 ha were also used for treatment plots, and the ~250 ha burn contained two plots. Paired control sites were then selected for each treatment site and were located at least 150 m but no more than 500 m from the treatment site in an area of the same ecotype as the paired treatment site.

To test the effects of strip-disking on potential arthropod prey of bobwhite, we chose four strip-disked sites and four paired control sites. Four separate disked areas were used for treatment plots, and these areas were disked in December 2018 and January, February, and March 2019. Disked strips were made using a tractor pulling a disk, and strips were cut 1/4-2" deep depending on soil texture and vegetation. All treatment plots were placed in disked strips that were at least 10 m wide, the largest of which was ~30 m wide. Plots were placed in the strip so that transects ran parallel to the direction of the strip, so that pitfall traps were as far from edges as possible. Paired control sites were then selected for each treatment site and were located at least 150 m but no more than 500 m from the treatment site in an area of the same ecotype as the paired treatment site. One disked site was seeded with sunflowers between the May and June sampling events and was burned between the June and July sampling events. Thus, during July, only 3 disked and paired control sites were active.

Each sampling site contained a 10m transect of 10 pitfall traps at 1-m intervals. Pitfall traps were charged with 100mL of killing solution (10% propylene glycol with a few drops of unscented dish soap) were used to collect invertebrates. Charged pitfall traps did not use any cover and remained open for 48 hours. After collection, invertebrates were sifted out of killing solution and stored in 70% ethanol to preserve samples for identification. Individual invertebrates were identified to their taxonomic order, counted, and measured based on five size classes: <2mm, 2-5mm, 5-10mm, 10-15mm, and >15mm (Foye 2014, Campbell-Kissock 1985). Using the median length from each size class, all abundance data was converted to biomass using the equation from Rogers et al. 1976 ($W = 0.0305*L^{2.62}$).

Abundance and biomass datasets were split so that analyses could be completed on the portion of collected invertebrates that are potential prey items for bobwhite chicks. Because flightlessness, small size, and narrow beak gape constrain bobwhite chicks' prey capture ability to ground-dwelling invertebrates that are 2-10mm long (Foye et al. 2015), only arthropods of the size classes 2-5mm and 5-10mm were included in analyses. Additionally, only prey common in reports of typical bobwhite diets were used in analyses, and inclued *Araneae*, *Coleoptera* (adults and larvae), *Hemiptera*, ground dwelling *Hymenoptera* (i.e. ants), *Lepidoptera* (larvae), and *Orthoptera* (Eubanks and Dimmick 1974; Doxon and Carroll 2010; Butler et al. 2012). These reports list ants, Coleoptera, and Orthoptera as the largest proportion of invertebrate food items in the bobwhite diet, but it is likely that chicks gain nutritional benefits from consuming prey items of diverse orders.

Vegetation and Soil Sampling - Vegetation sampling occurred during all three months at 2 m in a random cardinal direction from three points along each transect of pitfall traps: at the first (1m) cup, between the fifth and sixth cups (halfway point of the transect), and at the last (10m) cup. Estimates of vertical vegetation structure were taken using a Nudds Board, and ground cover was estimated using a 1m^2 Daubenmire frame (Daubenmire 1959; Nudds 1977). Ground cover estimations were grouped by coverage of bare ground, rock, plant litter, grass, forbs, and shrubs, and both measurements used estimation scales of <5%, 5-25%, 25-50%, 50-75%, 75-95%, and >95%.

Three soil cores were taken at each transect at 2m from the first pitfall trap, halfway point, and tenth pitfall trap. Cores were taken using a 2 in diameter, 12 in long soil corer, and cores were separated into top and bottom layers (6 in). Soil samples were stored in plastic bags and frozen until sample processing occurred. Samples were weighed and then dried at 60C for 24 hours. Samples were then weighed, sieved, and sent to the Oklahoma State University Soil Lab for soil organic matter, Nitrogen content, and soil texture profile analysis.

Data Analysis

Each site (treatment and paired control) was treated as the experimental replicate in analyses. Abundance and biomass collected in the 10 pitfall traps at each site were averaged by size class within each order. Then, average abundance and biomass of the 2.1-5.0 and 5.1-10.0mm arthropods were summed to get single abundance and biomass values for each treatment and control plot. JMP ver 15.0.0 (SAS Institute 2019) was used to apply a log(x+1) transformation to abundance and biomass data, and then perform repeated measures ANOVAs to individually test the effect of sampling month and plot type on abundance and biomass of the five most abundant orders, as well as the total abundance and biomass of all orders collected (Table 1).

Statistical Program R was used to conduct non-Metric Multi-Dimensional Scaling (nMDS) to visualize changes in the arthropod community as a result of treatment and sampling month (R Core Team 2013). Package vegan in R was used to conduct Permutational Analysis of Variance (PERMANOVA) tests on abundance and biomass to test for differences in community structure, using both abundance and biomass, in response to treatment and sampling month (Oskanen et al. 2013). PERMANOVA tests were run on all data together (i.e. all months) in a design including sampling month and plot type as fixed effects and site as a random effect. SIMPER analyses were also completed using package vegan in R to detect the contribution of individual orders to community changes (Oskanen et al. 2013).

Also in R, four principal component analyses (PCA) were conducted on vegetation and soil variables, and PC axes from the four analyses were used to create a composite PCA. The PCAs were split up by treatment type (burn or disk), and the four individual PCAs used to create a composite PCA assessed vertical vegetation coverage, ground coverage, soil type (% sand, silt, and clay), and soil nutrients and moisture. ANOVA was used to test for treatment differences in PCA axes. Additionally, ANOVAs were conducted on all individual vegetative and soil covariates to test for differences between treatment and control sites.

Results

Over three months of sampling, a total of 460 pitfall samples were collected, resulting in the identification and measurement of 30,559 individual invertebrates from 16 orders. Of these, 12,899 met the criteria for being potential prey of bobwhite chicks and were included in analyses based on their size (2.1-10mm) and that they were from orders common in in reports of bobwhite diet (Table 1). Of the potential bobwhite prey, Hymenoptera (ants) were the most common (9,232 individuals) and larval Lepidoptera were the least common (13 individuals). Additionally, ants comprised the largest proportion of total biomass collected (56%), and larval Lepidoptera comprised the smallest proportion of total biomass (0.3%) (Table 1).

Community Effects

Abundance - For abundance, the results of the full-season PERMANOVAs showed that neither burning ($p = 0.095$) nor disking ($p = 0.429$) had a significant effect on arthropod community composition (Figure 1A-B). However, the models showed that there were significant effects of time in both sets of study sites (burned; $p = 0.001$, disked; $p = 0.002$) (Figure 1C-D). The nMDS analysis showed that at burned and control sites, there was community overlap in May and June, but July appeared to be more separated in space (Figure 1C). However, at disked and control sites, there was some overlap during all three months (Figure 1D). Ants contributed the most to dissimilarities between months at burned and paired control sites, and the average abundance of ants increased continuously across the sampling season ($p = 0.002$; Table 2). Additionally, Coleoptera adults was the only other significant contributor to changes in abundance over sampling months with up to 70% of the differences between times being attributed to ants and Coleoptera combined ($p = 0.003$; Table 2).

The repeated measures ANOVAs indicated that burning had an overall positive effect on total arthropod abundance ($p = 0.006$; Table 3; Figure 3). Disking did not result in any significant effects on total abundance (Table 3; Figure 3). In terms of season, total abundance significantly increased throughout the duration of the sampling period at burned/paired control and disked/paired control sites (burn p = 0.03; disk p = 0.01; Table 3; Figure 3). In the untransformed data (Figure 4), the effect of time is less apparent than in the log-transformed data used for analysis because there was one disked site in May in which a large number of Coleoptera adults (608) were collected.

Biomass - The full-season PERMANOVAs performed on biomass data indicated that burning had significant effects (p= 0.028) on community composition as measured through biomass (Figure 2A), and disking had no significant effects (p = 0.24; Figure 2B). Community composition as measured by biomass also changed across the sampling months (burn p = 0.001; disk p = 0.001; Figure 2C-D). The nMDS analysis showed large overlap between May and June, and more separation in space for July at burned and control sites (Figure 2C). Disked and control sites, however, showed the most overlap between May and July, though there was some overlap for all months (Figure 2D). The SIMPER analysis indicated that changes in overall arthropod biomass at burned and paired control sites were largely due to changes in ant and Coleoptera adult biomass (Table 5). Changes in overall biomass across sampling months at disked sites were also shaped by changes in ant and Coleoptera adult biomass, but Coleoptera larvae and Araneae also contributed to dissimilarities between months (Table 4).

Repeated measures ANOVAs performed on biomass data indicated that burn treatment resulted in a significant positive effect on total arthropod biomass (p = 0.05; Table 3; Figure 4). However, disking did not significantly affect total arthropod biomass

(Table 3; Figure 4). In terms of season, total arthropod biomass increased throughout the sampling duration at burned and paired control sites (p = 0.004) but not at disked sites (p = 0.6; Table 3; Figure 4).

Individual Order Effects

Abundance - Ant abundance was the only individual group significantly affected by any treatment type. There were higher numbers of ants in burned sites compared to the control (p = 0.0001; Table 3; Figure 4). There was also a significant increase in the number of ants over the season at both burned (p = 0.003) and disked sites (p = 0.003; Table 2; Figure 4). Coleoptera adult abundance peaked in June at both burned/paired control (p = 0.007) and disked/paired control sites (p = 0.01; Table 3; Figure 4). Orthoptera abundance declined throughout the duration of the sampling period at disked/paired control sites (p = 0.02; Table 3; Figure 4).

Biomass - Burning had a positive effect on the biomass of ants (p = 0.002) and a negative effect on Araneae (p= 0.01, Table 3). Disking did not have a significant effect on any other individual order tested (Table 3). Sampling month had significant effects on the biomasses of several orders at burned and disked sites (Table 3; Figure 4). Ant biomass significantly increased throughout the duration of the sampling period at burned/paired control (p = 0.01) and disked/paired control sites (p = 0.009; Table 3). Average Coleoptera adult biomass peaked in June at burned and paired control sites (p = 0.01; Table 3; Figure 4). Additionally, Orthoptera biomass decreased throughout the duration of the sampling period at disked and paired control sites (p = 0.03; Figure 4).

Vegetation and Soil Analysis

Of the four PCAs (vertical vegetation layers 1-12, ground coverage, soil type, and soil nutrients/moisture) performed on burned/paired control and disked/paired control sites, only two axes from the burned dataset displayed any significant effects as a result of treatment (Table 5; Figures 7-8). There was a significant effect of burn treatment on vertical vegetation layer PC1 ($p = 0.009$). Vertical vegetation layer PC1 loaded negatively onto vertical vegetation layers 1-9, which corresponded to control sites having increased vertical vegetation from 0.0 – 0.9 m height. There was also a significant effect of burning on ground coverage PC1 ($p = 0.006$, Table 5). Ground coverage PC1 loaded positively onto bare ground and negatively onto shrub coverage (Table 6), indicating that burned sites had more bare ground and less shrub coverage than control sites.

ANOVAs conducted on individual habitat variables indicated significant effects of treatment for several individual variables. Burned sites had significantly lower vertical coverage in layers 1-8 compared to control sites ($p < 0.05$, Table 7). Burning also significantly impacted ground coverage; burned sites had increased bare ground coverage ($p = 0.0001$), decreased litter coverage ($p = 0.0001$) and decreased shrub coverage ($p = 0.03$) compared to control sites (Table 7). Soil data from burned and control sites were largely unaffected by treatment, but burned sites had higher soil nitrate (NO_3) in the bottom 6” layer than control sites ($p = 0.002$, Table 7).

Disked sites had significantly lower vertical vegetation coverage in only layers 1 and 8 compared to control sites ($p = 0.04$ and $p = 0.04$, Table 7). Ground coverage was also significantly affected by disking; disked plots had increased bare ground coverage (p

= 0.002) and decreased grass coverage (p = 0.0005) compared to control sites (Table 7). Disking also significantly affected a wider array of soil variables from both top and bottom 6” soil layers. Top and bottom layers had elevated levels of silt (p = 0.01 and p = 0.02, respectively) and SOM (p = 0.05 and 0.003) at disked sites compared to control sites (Table 7). The top 6” soil layer had significantly higher concentrations of P (p = 0.004) and K (p = 0.03) at disked sites compared to control sites (Table 7). The bottom 6” soil layer had significantly higher concentrations of soil nitrate (p = 0.0006) and K (p = 0.02), as well as significantly higher N (%) at disked sites (p = 0.05, Table 7).

Discussion

Our results support the hypothesis that burning affects the availability of arthropod prey for bobwhites. But, we did not find support for an effect of disking on arthropod abundance or biomass. While burning did not affect the composition of the arthropod community (i.e., nMDS and PERMANOVA) it did significantly increase the overall abundance and biomass of arthropod prey, especially of ants. We also found significant effects of time on arthropod abundance and biomass at burned and disked sites. In particular, abundance and biomass increased over the season in burned and burn control plots. Burned sites were characterized by lower vertical vegetative structure and shrub ground coverage, and higher bare ground coverage compared to the control. Disking resulted in decreased grass coverage, and increased bare ground coverage and soil nutrient concentrations compared to the control. The results of this work suggested that prescribed burning positively impacted arthropod prey abundance and biomass for bobwhites, and that seasonality also exerted a strong influence on arthropod community composition, abundance, and biomass.

Burning changed the composition of the arthropod community as measured by biomass and positively affected the total abundance and biomass of arthropods. However, these effects were largely driven by the positive effect of burning on the abundance and biomass of ants, which had by far the highest abundance and biomass (Table 1). Ants likely tolerate fire well because their colonies are often located underground and largely safe from being destroyed by fire. However, Araneae biomass decreased in response to fire, which aligns with substantial evidence that Araneae respond among the most poorly to fire (Reed 1997; Engle et al. 2008; Doxon et al. 2011; Kral et al. 2017). The higher abundance of ants in burned areas could have a positive effect on food intake by quail chicks. Although, the effect of burning on ant abundance is relatively low during May when chicks are small and feeding on very small prey such as ants.

Disking did not affect arthropod community composition, total abundance, or total biomass. Additionally, of the five most abundant orders collected in this work, no order experienced significant changes in abundance or biomass as a result of disking. The lack of significant effects of disking on the arthropod community may be a result of the dispersal ability of collected arthropods and the localized nature of the application of strip disking in the present study. Several studies reported local changes in the vegetative structure as a result of disking similar to those found in this work, but report extremely variable effects on the arthropod community (Greenfield 1997; Benson et al. 2007; Dollar et al. 2013). It is likely that the narrowness of the disked area is not sufficient to support separate populations of arthropods and allowed for mixing of arthropod communities with the surrounding vegetation (Ribera et al. 2001; Dziock et al. 2011; Birkhofer et al. 2015). Although, it is possible that strip disking could affect arthropod communities in other locations or if it is applied differently (e.g., large patches as opposed to narrow strips).

Burned sites were characterized by decreased vertical vegetation structure and lateral shrub coverage, as well as increased bare ground coverage. Burning also significantly decreased litter cover, and increased nitrate (PPM) in the bottom 6" soil core. These changes in habitat structure parallel previous evidence of the effects of prescribed burning and the goals of habitat management for brooding bobwhites, particularly in the provision bare ground. Burning creates heterogeneous patches of vegetation necessary for arthropod herbivores, as well as ample amounts of bare ground that bobwhites require to forage unimpeded (Guthery 1997; Doxon and Carroll 2010; Doxon et al. 2011). Thus prescribed fire can be incorporated into management regimes to effectively manage habitats in ways that may increase arthropod forage or bobwhite foraging ability (Guthery 1997; Fuhlendorf et al. 2006; Doxon and Carroll 2010; Doxon et al. 2011).

While disking did not change overall habitat variables in principal component analyses compared to control sites, disking significantly increased bare ground coverage. Additionally, disking decreased grass cover and vertical vegetation coverage in the 0-10cm and 70-80cm high layers. These changes, while localized, are also congruent with the goals of creating quality forage habitat for brooding bobwhites (Guthery 1997). Hence, even though there was no change in arthropod abundance and biomass, it may be easier for quail chicks to forage for arthropods in disked habitats. Furthermore, strip disking may provide brooding quail with a relatively open habitat in the strip in which to forage that is in close proximity to cover that they can use to escape from immediate threats of predators.

Disking also resulted in a suite of changes in both top and bottom soil layers; the top layer experienced increases in SOM (%), P (PPM), K (PPM), and silt (%), and the bottom layer experienced increases in SOM (%), N (%), nitrate (PPM), K (PPM), and silt (%). Thus, even shallow disking (0.25”-2”) may result in changes in nutrient composition and soil type up to 12” below the soil surface. Disked sites were not disked on a yearly basis, and no seeds or fertilizers were spread in disked strips. These changes may have consequences for soil-dwelling arthropods, namely detritivores (i.e. Coleoptera larvae) (Benson et al. 2007; Osborne et al. 2012).

Arthropod community composition changed significantly over the course of the season in ways that could have consequences for quail brooding. Total arthropod abundance and biomass increased over the duration of the sampling period, and the most common arthropod order (i.e. ants) appeared to drive the observed trends. Ants are some of the smallest prey bobwhite chicks consume and, hence, a greater abundance of ants later in the season is most likely to benefit reclutching and not the first clutch of chicks that may progressively turn their attention to larger prey. Orthoptera abundance and biomass decreased throughout the summer at disked and control sites, which suggests that they may be most available to chicks in early breeding (e.g., May) because they are more abundant and of appropriate size (Gillespie and Kemp 1994). Later in the summer, they may be too large for bobwhite chicks to consume and thus unavailable (Gillespie and Kemp 1994). Coleoptera adult abundance and biomass peaked in June at burned and control sites, which suggests that they may become more available as early clutches grow and second clutches hatch. Although, the relative nutritional quality of Coleoptera is unclear since they typically have high indigestible exoskeleton content (Lease and Wolf 2010; Reeves *in prep*).

We found evidence that burning positively influenced the availability of arthropod prey for bobwhites in terms of abundance and biomass, though these effects were small at the beginning of the sampling period, when quail may be brooding their first clutch. Burning also positively influenced vegetative habitat characteristics essential for bobwhite brooding. Cumulative metrics of arthropod availability may be too broad in scope to observe subtle differences in the seasonality of individual orders of arthropod prey, and here we observed positive effects of seasonality on total arthropod abundance and biomass, but variable responses of individual orders. The variability of seasonal influences on individual arthropod orders highlights the importance of understanding how temporal shifts in prey availability affect realized nutrient gains for insectivores. Because there is large variation in macro- and micro-nutrient content within and between orders of potential arthropod prey (Wilder et al. 2013; Wilder et al. 2019; Reeves *in prep*), shifts in availability toward prey with low metabolizable nutrient content (i.e. low protein content, high exoskeleton content) could negatively impact chick growth and survival. Brooding hens and chicks may be particularly sensitive to arthropod community changes later in the summer, as they experience increased thermal stress (Tanner et al. 2017), as well as decreased clutch size and nest survival (Cox et al. 2005; Brooke et al. 2016). Future work should focus on assessing variation in prey availability and nutrient content across the landscape in relation to predation risk, nest initiation timing, and nest success

CHAPTER II

NUTRITIONAL CONTENT OF COMMON ARTHROPOD PREY OF NORTHERN BOBWHITES (*COLINUS VIRGINIANUS*)

Introduction

Arthropods are an essential food source for a wide variety of invertebrates and vertebrates (Uetz et al. 1992; Kaspari and Joern 1993; Durst et al. 2008; Butler et al. 2012). Arthropod prey provide bulk nutrients such as carbohydrates, lipids, and protein that are important as a source of energy and for building body mass (Nestler et al. 1942; Eubanks and Dimmick 1974; Giuliano et al. 1996; Harveson et al. 2004). Generalist predators often consume a diversity of prey that can vary widely in quality. Prey can vary in a variety of nutrients including macronutrients and micronutrients (e.g., trace minerals, dietary essential amino or fatty acids, etc.). Yet, variation in macronutrient content of prey may be of particular interest because macronutrients can vary greatly in abundance among prey species and are required in large quantities by consumers. For example, arthropod bodies can be composed of 10-85% protein and 5-32% lipids by dry mass (Wilder et al. 2013). Past studies have identified particular prey species that are high or low quality due to their nutritional or defensive compound content (Lase and Wolf 2010; Lease and Wolf 2011; Wilder 2011, Razeng and Watson 2014). Yet, less is known about

about consistency or variation within and among arthropod orders in their nutritional content. Consistency of nutritional content within orders of arthropods could form an evolutionary basis through which predators could base prey choice decisions and may allow better understanding of how outbreaks of particular prey affect the nutritional landscape available to predators.

In addition to macronutrients, exoskeleton may also be an important dietary consideration for insectivores. Exoskeleton is often a large component of arthropod bodies and can vary among taxa, with exoskeleton comprising 18-60% of dry mass (Lease and Wolf 2010). It consists largely of chitin (20-50%), with proteins locked within the chitinous matrix during sclerotization (Lease and Wolf 2010). While exoskeleton is largely comprised of carbon, it can also contain significant amounts of nitrogen. Yet, exoskeletal protein, carbon, and nitrogen are largely unavailable to most consumers since they are unable to digest chitin (Bell 1990; Weiser et al. 1997). In addition to affecting digestibility of prey, exoskeleton can affect the measurement of prey nutrient content. For example, a common measure of arthropod nutrient content (i.e., crude protein = 6.25 x total nitrogen) assumes that all nitrogen is available to consumers (Jones 1941; Peoples 1992; Peoples et al. 1994; Razeng and Watson 2014). It is important to consider how the relative proportions of digestible and indigestible arthropod tissues influence prey quality, nutrient availability for predators, and the way that nutrients in prey are measured (Lease and Wolf 2010; Wilder et al. 2013; Wilder et al. 2019).

Insectivorous birds are one type of predator that can encounter a diversity of potential prey. Bobwhites are seasonally insectivorous, and the proportion of arthropods in the bobwhite diet depends on sex and life stage (Eubanks and Dimmick 1974; Doxon and Carroll 2010; Butler et al. 2012; Foye et al. 2015). Brooding hens require large amounts of arthropod-derived protein and energy in order to produce high quality eggs (Giuliano et al. 1996; Harveson et al. 2004), and it is likely that variation in arthropod availability over the course of the breeding season (April-August) influences egg viability, chick condition, and overall hatching success (Giuliano et al. 1996; Harveson et al. 2004; Foye et al. 2015). In addition, chicks are obligate insectivores for the first 2-3 weeks of life, and slowly incorporate more plant foods into their diet as they mature (Eubanks and Dimmick 1974). During the first few weeks, ~94.1% of the chick diet is arthropods (Eubanks and Dimmick 1974), and chicks require 28% dietary protein per day to maintain optimal growth (Nestler et al. 1942). However, chicks' limited body size, lack of flight ability, and small beak gape constrain their prey capture ability to only ground-dwelling arthropods of approximately 2-10 mm in length (Eubanks and Dimmick 1974; Doxon and Carroll 2010; Butler et al. 2012; Foye et al. 2015). Additionally, bobwhites are constrained internally by their relative inability to digest exoskeleton, as they can only digest 6.7% of ingested chitin (Weiser et al. 1997). Variation in community composition of arthropods among habitats and across the season highlight the importance of understanding how variation in macronutrient and exoskeletal content shape potential nutrient gains for insectivores like bobwhites (Butler et al. *In revision*, Reeves et al. *In preparation*).

We collected potential arthropod prey of Northern bobwhites (*Colinus virginianus*; hereafter bobwhite) to: 1) compare prey nutrient content in terms of macronutrients (lipid and protein), exoskeleton, and elementals (C and N) between potential arthropod prey taxa, and 2) test the strength of correlation between elemental C and N and macronutrients (lipids and protein) in potential prey. Exoskeleton is indigestible for many vertebrates, and juveniles must consume large amounts of protein in order to grow quickly and evade predation. Thus, high quality prey items may be those that contain low exoskeleton content and high metabolizable protein content. In addition to comparing mean values for each order, we also tested if taxa differ in how consistent they are in nutrient content (i.e., if variance in nutrient content differs among taxa). We predicted that Araneae and Lepidoptera larvae would have the lowest exoskeleton content and highest metabolizable protein content. Additionally, we predicted that metabolizable elemental content would predict macronutrient content better than total elemental content.

Methods

Study Site

The arthropods used in this study were collected at Packsaddle Wildlife Management Area in Ellis County, Oklahoma during the months of May, June, and July 2019. Annual rainfall is 63.5 cm on average. Packsaddle WMA contains a wide variety of soil types including fine sandy loams, loam fine sands, and fine sands (Oklahoma Dept. of Wildlife Conservation and the United States Department of Agriculture). Situated in traditionally productive quail habitat, the 6,475-ha WMA is managed with prescribed fire, strip disking, and cattle grazing. Burning begins in late summer and ceases at the end of March, weather permitting, and strip disking is applied November through April.

Common vegetation present at sites includes grasses such as big bluestem, Indian grass, little bluestem, side-oats grama, and buffalo grass, as well as shrubs like shinnery-oak, sagebrush, and sandplum (Oklahoma Dept. of Wildlife Conservation).

Invertebrate Collection and Identification

The goal of invertebrate collection for this study was to collect as diverse of a sample of potential bobwhite prey as possible. Invertebrates were collected in three, 5-day sampling periods in May, June, and July 2019 using sweep net, dry pitfall, coverboard, and hand collection techniques. Sweep net samples were collected in burned, strip-disked, and unmanaged areas using 40-m transects, and a total of 20 sweep net samples were collected per sampling period. Collection locations were not evenly distributed across the landscape but were collected in areas of diverse topography and vegetative cover in order to maximize the diversity of potential bobwhite prey collected. Four 1-m square coverboards were deployed in one burned, one disked, and two unmanaged areas. Transects of five dry pitfall traps were placed in one burned, one disked, and two unmanaged areas. Coverboard and dry pitfall trap samples were collected twice daily (morning and evening), and one hour was spent searching for and hand collecting invertebrates daily. All samples were stored in plastic bags and frozen until sorting.

Individual invertebrates were sorted out of plant matter and other debris and were initially sorted based on order and size class. Size classes used were <2mm, 2-5mm, 5-10mm, 10-15mm, and >15mm, and are based on the ability of bobwhites to consume prey items due to the constraint of beak gape (Campbell-Kissock et al. 1985; Foye 2015).

Individuals were then sorted to order and given a morphospecies label based on differences in appearance, and representatives of each morphospecies were pinned in a reference collection. The number of morphospecies per order used in this study was related to sample availability and an attempt to avoid over or underrepresentation of taxa relative to their known biodiversity. We also included larval and adult representatives of taxa when possible, as they could differ in nutrient content. In total, we measured the nutrient content of the following morphospecies: 23 adult Coleoptera, 2 larval Coleoptera, 22 Hemiptera, 3 Hymenoptera (all ants), 14 Orthoptera, 5 larval Lepidoptera, and 5 Araneae.

Nutrient Analyses

Two identical sets of 74 samples (i.e. same morphospecies) were prepared for nutrient extractions by drying samples for 24 hours at 60°C and measuring their dry mass. We sorted out samples of 15-30mg of dry mass, and the number of individuals per sample varied based on the size of available arthropods. For example, some Orthoptera samples were only 1-2 individuals, but ant samples contained as many as 30 individuals. We measured lipid content of arthropods using a gravimetric method with chloroform as a solvent. All dried samples were soaked in chloroform for 72 hours (Wilder et al. 2013). Chloroform was removed and new chloroform was added every 24 hours, and samples were then dried for 24 hours at 60°C (Wilder et al. 2013). Exoskeleton was removed from one set of samples by soaking in 0.1M NaOH to dissolve soft tissue (Lease and Wolf 2010). Samples were first sonicated at 80°C in 0.1M NaOH for 30 min and then allowed to soak for 24 hours. After 24 hours, samples were centrifuged at 10,000 RPM, the NaOH was removed, and fresh NaOH was added. After another 24 hours, samples were centrifuged again and the NaOH was removed, and samples were washed with water and dried at 60°C for 24 hours. The dry weight after soft tissue removal was used as a measure of exoskeleton.

Samples of 2-3mg of ground, lipid extracted arthropod material, as well as one sample of exoskeleton for each order of arthropods, were also prepared for elemental C and N content analysis. Samples were weighed on a microbalance and packaged in tin capsules to be combusted in an Elementar (MODEL #). N content was used to calculate crude protein content by multiplying it by 6.25, and crude protein was calculated as a proportion of both dry and soft tissue mass. Metabolizable mass was considered to be the part of the body that was not exoskeleton.

Protein content of samples was also measured using a variety of chemical assays on each morphospecies that sufficient biomass permitted. Protein was extracted from arthropods by grinding lipid-extracted samples with a #mm steel ball bearing using an oscillating grinder at ##RPM for 3 minutes. Then, 5mg of ground arthropod material was soaked in 0.1M NaOH and sonicated at 80°C for 30 min. 10µg of the supernatant was then plated and used to conduct the Lowry assay and the Bradford Assay according to the kit instructions for microplate assays. Bovine IgG standard solutions were used to create standard curves.

Data Analysis

Statistical program R ver 3.4.2 (R Core Team 2013) was used to conduct one-way ANOVAs and Tukey’s HSD post-hoc analysis to detect differences in lipid, exoskeleton, protein, and elemental content between and within orders of arthropods. Levene's test was used to test for variance homogenization. We also performed Welch's ANOVA and the Games-Howell posthoc test on macronutrient data that had unequal variance between arthropod orders. Linear regression was used to test how well elemental content predicts macronutrient content, and to compare the predictive ability of total and metabolizable measures of elemental content. Additionally, a correlation matrix was calculated to test the ability of total and metabolizable N to predict protein content.

Results

Among- and Within-Order Variation in Content

Exoskeleton Content. We observed wide variation in exoskeleton content across all orders; the lowest average exoskeleton content was 5.60 mg/100mg dry mass (Araneae) and the highest was 31.6 mg/100mg by dry mass (Hymenoptera; Figure 9). Coleoptera adult exoskeleton content was more variable than any other order (Levene's test, $p = 0.05$). Welch's ANOVA, which we conducted due to unequal variances among groups, indicated that exoskeleton content differed significantly between orders of arthropods ($p < 0.001$). Araneae had the lowest mean exoskeleton content (5.60 ± 1.0 mg/100mg; mean ± 1 SE), and Coleoptera adults (25.6 ± 3.10 mg/100mg; $p < 0.05$) and Hymenoptera (31.6 ± 4.61 mg/100mg) had the highest, though Hymenoptera did not differ significantly from any order (Figure 9). The median exoskeleton contents of Hymenoptera and Coleoptera adults were 5-6 times higher than Araneae. Orthoptera

(19.8 ± 2.76 mg/100mg), Hemiptera (15.0 ± 1.57 mg/100mg), and Lepidoptera (11.8 ± 4.13 mg/100mg) had intermediate exoskeleton content (Figure 9), though Orthoptera did not differ from the orders with the highest exoskeleton content and Lepidoptera did not differ from any order.

Lipid Content. There was also wide variation in lipid content across all orders, with average values ranging from 7.36 mg/100mg dry mass (Orthoptera) to 25.6 mg/100mg dry mass (Hymenoptera; Figure 9). Hemiptera lipid content was more variable than any other order (Levene's test; $p < 0.001$). Welch's ANOVA indicated that lipid content differed significantly between orders of arthropods ($p < 0.001$). Hymenoptera (25.6 ± 4.33 mg/100mg) and Hemiptera (22.9 ± 1.61 mg/100mg) had the highest average lipid content (Figure 9). The average lipid content of Hymenoptera and Hemiptera was ~1.5 times that of Coleoptera adults, and more than double Araneae, Lepidoptera, and Orthoptera lipid content (Figure 9). Coleopterans were intermediate (15.7 ± 1.34 mg/100mg), with significantly lower lipid content than Hemiptera and significantly higher lipid content than Orthoptera ($p < 0.05$). Araneae (10.1 ± 0.93 mg/100mg), Lepidoptera (9.06 ± 1.14 mg/100mg), and Orthoptera (7.36 ± 0.64 mg/100mg) had the lowest average lipid content (Figure 9).

Protein Content. The Lowry assay suggested that there was large variation in protein content within and among orders of arthropods, with average values ranging from 26.45 mg/100mg (Coleoptera adult) to 52.04 mg/100mg (Araneae; Figure 9). Levene's test indicated that there were no differences among taxa in variance of protein content measured by the Lowry assay ($p > 0.05$). The average protein content of Araneae was double that of Coleoptera adults and much higher than Hymenoptera (Figure 9). Araneae had the highest protein content (52.04 ± 1.95 mg/100mg), and Coleoptera adults (26.45 ± 1.24 mg/100mg) and Hymenoptera had the lowest (35.01 ± 5.13 mg/100mg; Figure 1). Orthoptera (43.03 ± 1.22 mg/100mg), Lepidoptera (45.88 ± 5.94), and Hemiptera (32.44 ± 1.55 mg/100mg) had intermediate protein content, though Lepidoptera protein content did not differ from Orthoptera or Hemiptera (Figure 9).

The Bradford assay also suggested that there was large variation in protein content within and among orders of arthropods, with average values ranging from 25.88 mg/100mg (Lepidoptera) to 59.52 mg/100mg (Araneae; Figure 9). However, where the Lowry assay produced distinct differences between intermediate and low-protein orders, the Bradford assay placed Orthoptera lower in rank and grouped Orthoptera, Lepidoptera, Coleoptera adults, and Hymenoptera as the lowest in protein content. Levene's test indicated that there were no differences among taxa in variance of protein content measured by the Bradford assay ($p > 0.05$). Araneae had the highest protein content (59.52 ± 2.09 mg/100mg), and Orthoptera (25.88 ± 3.49 mg/100mg), Lepidoptera (39.87 ± 13.54 mg/100mg), Coleoptera adults (26.40 ± 2.04 mg/100mg), and Hymenoptera had the lowest (26.15 ± 4.78 mg/100mg; Figure 9). Hemiptera had intermediate protein content (38.48 ± 1.84 mg/100mg), though it was not significantly different from Hymenoptera (Figure 9).

Total Elemental Content. C and N content also varied within and between orders of arthropods. C content was somewhat less variable than N content. The lowest average total C content observed was 40.9 mg/100mg by dry mass and the highest was 48.6 mg/100mg by dry mass (Figure 10). Levene's test indicated variances in total C were different between orders ($p = 0.05$), and Araneae had the most variable total C content (Figure 10). Welch's ANOVA indicated that total C content differed significantly between orders ($p < 0.001$). Lepidoptera had the lowest average total C content (40.9 ± 0.67 mg/100mg), and Hemiptera (48.2 ± 0.47 mg/100mg), Coleoptera adults (48.6 ± 0.28 mg/100mg), and Hymenoptera (47.6 ± 0.23 mg/100mg) had the highest (Figure 10). Orthoptera had intermediate total C content (44.7 ± 0.44 mg/100mg), and Araneae total C content (43.7 ± 1.20 mg/100mg) was not significantly different from any other order (Figure 10).

The lowest average total N observed was 7.44 mg/100mg by dry mass and the highest was 10.82 mg/100mg by dry mass (Figure 11). Levene's test indicated that there were no differences among taxa in variance of total N ($p > 0.05$). Lepidoptera had the lowest average total N content (7.44 ± 0.47 mg/100mg) and Araneae had the highest (10.82 ± 0.39 mg/100mg; Figure 11). There was a gradient in total N among taxa, with taxa ranked highest to lowest as Araneae, Orthoptera (9.63 ± 0.24 mg/100mg), Hemiptera (9.12 ± 0.20 mg/100mg), Coleoptera adults (8.88 ± 0.13 mg/100mg), Hymenoptera (8.35 ± 0.82 mg/100mg), and Lepidoptera (Figure 11).

Metabolizable Elemental Content. Patterns in metabolizable C content displayed were different than total C, particularly for orders with high exoskeleton content (i.e. Coleoptera adults; Figure 10). The lowest average metabolizable C was 35.84 mg/100mg by dry mass and the highest was 41.28 mg/100mg (Figure 10). Levene's test indicated that variance in metabolizable C differed between orders ($p < 0.05$), and Coleoptera adults had the most variable metabolizable C content (Figure 10). Welch's ANOVA indicated that metabolizable C differed between orders (Figure 10). Hemiptera (41.20 ± 0.76 mg/100mg) and Araneae (41.28 ± 0.91 mg/100mg) had the highest metabolizable C content, and Coleoptera adults (35.84 ± 1.62 mg/100mg) and Orthoptera (36.26 ± 1.28 mg/100mg) had the lowest (Figure 10). Hymenoptera (35.94 ± 1.85 mg/100mg) and Lepidoptera (36.83 ± 1.63 mg/100mg) did not significantly differ from any other order (Figure 10).

When we analyzed metabolizable N (i.e., total N with exoskeleton N removed), the rank of some orders changed (Figure 11). The lowest average metabolizable N observed was 5.26 mg/100mg by dry mass and the highest was 10.15 mg/100mg by dry mass (Figure 11). Levene's test indicated that there were no differences among taxa in variance of metabolizable N ($p > 0.05$). Araneae had the highest average metabolizable N content (10.15 ± 0.32 mg/100mg; Figure 11). The median metabolizable N content of Araneae was approximately double that of the lowest three orders: Lepidoptera, Coleoptera adults, and Hymenoptera (Figure 11). Orthoptera had similar metabolizable N content (8.25 ± 0.35 mg/100mg) to Araneae, but was only significantly higher than Coleoptera adults and Hymenoptera ($p < 0.05$; Figure 11). Hemiptera was intermediate (7.54 ± 0.28 mg/100mg), but was only significantly lower than Araneae and higher than Coleoptera adults ($p < 0.05$; Figure 11). Lepidoptera (6.84 ± 0.55 mg/100mg), Coleoptera adults (6.40 ± 0.30 mg/100mg), and Hymenoptera (5.26 ± 1.10 mg/100mg) had the lowest metabolizable N content (Figure 11).

Elemental and Macronutrient Regression

Relationships Between C and C-containing Compounds. Total C content was positively related to lipid content ($R^2 = 0.29$; $p < 0.001$; Figure 12). However, the low R^2 value suggests there is much unexplained variation (Figure 12). Metabolizable C also displayed a positive linear relationship with lipid content ($R^2 = 0.14$; $p < 0.001$; Figure 12). However, the low R^2 value suggest that total C is a better predictor of lipid content than metabolizable C (Figure 12).

Total C content was also positively related to exoskeleton content ($R^2 = 0.054$; $p = 0.03$; Figure 12). However, total C poorly accounted for variation in the exoskeletal data (Figure 12). Metabolizable C displayed a negative linear relationship with exoskeletal content ($R^2 = 0.71$; $p < 0.001$; Figure 12).

Relationships Between N and Protein. The correlation matrix calculated for N and protein content indicated that total N and metabolizable N were the most strongly correlated ($R^2 = 0.44$; $p < 0.001$; Figure 12). Metabolizable N and the Lowry assay displayed the second strongest correlation ($R^2 = 0.35$; $p < 0.001$; Figure 12), though similar evidence supported the correlation between metabolizable N and the Bradford assay ($R^2 = 0.34$; $p < 0.001$; Figure 12). Both the Lowry and Bradford assays were more strongly correlated with metabolizable N than total N (Figure 12).

Discussion

We observed substantial variation in elemental and macronutrient content within and between orders of Arthropods common in the bobwhite diet. Overall, our results support the hypothesis that arthropod taxa are consistently different from each other in nutrient content. Although, some taxa are more variable in nutrient content than others. Our prediction that Araneae would have the highest protein content and lowest exoskeleton content was supported, though Orthoptera also had high protein content and Lepidoptera also had low exoskeleton content. In contrast, Coleoptera adults and Hymenoptera had the highest exoskeleton content and lowest protein content. Hymenoptera and Hemiptera had the highest lipid content, though they were also the most variable. Large, consistent variation in macronutrient content within and between orders of arthropods underscores how the frequency of individual orders in the diets of predators may influence nutrient intake (Bell 1990; Weiser et al. 1997; Wilder et al. 2019).

Our results show mixed support for the relationships between elements and macronutrients. Our predictions regarding the ability of total and metabolizable C to predict macronutrients were not well supported. Total C was a better predictor of lipid content, and metabolizable C was a better predictor of exoskeleton content, though the relationship was negative. However, our prediction about total and metabolizable N was supported. Metabolizable N predicted protein content measured by both the Bradford and Lowry assays better than total N. These results suggest that elements are related to macronutrient content and potential nutrient intake of insectivores, especially when those elemental measures account for exoskeletal content (Bell 1990; Weiser et al. 1997; Wilder et al. 2019).

Many consumers cannot digest exoskeleton in meaningful quantities, and it is therefore essential to consider how indigestible components of prey influence potential nutrient intake (Weiser et al. 1997; Wilder et al. 2019). Two of the most common arthropod orders in the bobwhite diet, Hymenoptera (31.6 ± 4.61%) and Coleoptera (25.6 ± 3.10%), had the highest mean exoskeleton content of all orders (Doxon and Carroll 2010; Butler et al. 2012). Thus, up to nearly a third of the dry mass of frequently consumed prey is indigestible. Measures that do not account for elements or macronutrients (i.e. Lowry, Bradford, total N) contained in indigestible tissues will result in different conclusions about variation in nutrient content within and between arthropod orders than ones that account for it (i.e. metabolizable N; Wilder et al. *In preparation*). Adult beetles are extremely variable in body form and nutritional composition (Sloggett 2008; McCullough et al. 2015), and we found that Coleoptera exoskeleton content was the most variable of any order. However, Araneae had very low exoskeleton content, suggesting high nutrient availability for consumers because the majority of tissues in individual Araneae are metabolizable. These results suggest that variation in the relative abundance of high (e.g., Coleoptera and Hymenoptera) versus low (e.g., Araneae) exoskeleton prey could have important impacts on overall nutrient intake by bobwhite chicks (Weiser et al. 1997; Butler et al. 2012; Foye 2015; Morrow et al. 2015). Chicks likely gain greater nutritional benefits when consuming prey low in exoskeleton due to increases in assimilation efficiency (Nestler 1942; Peoples et al. 1994; Weiser et al. 1997), but we found that some of the most common bobwhite prey had the lowest metabolizable N/protein content and the highest exoskeleton content (Eubanks and Dimmick 1974; Butler et al. 2012).

Lipid content was also highly variable within and between orders of arthropods. It is likely that observed differences in lipid content and variation within and between orders is a product of the diversity of trophic levels represented by taxa contained therein (Wilder et al. 2013). For example, Coleoptera and Hemiptera are extremely diverse orders that contain detritivores, herbivores, omnivores and carnivores, and these orders exhibited higher variation in lipid content than any other order. Groups that contain only predators, like Araneae, displayed lower and less variable lipid content, but some herbivorous arthropods, such as Lepidoptera and Orthoptera, also displayed low variation and low lipid content. Variation within orders could also result from variation among individuals in their feeding history, sex, developmental stage, and reproductive state (Lease and Wolf 2011). Unlike exoskeleton and protein, lipids are stored in large quantities and rapidly mobilized for energy (Canavoso et al. 2001), and it is likely that we observed significant variation between individual arthropods based on their individual lipid storage reserves.

Though differences observed between orders in the Lowry assay were extremely similar to those observed in metabolizable N, both the Bradford assay and total N ranked Coleoptera and Hymenoptera higher than metabolizable N. It is extremely important to note this distinction because measures of N or protein content that do not account for exoskeleton overestimate protein content available to consumers. Additionally, protein content from Lowry and Bradford assays correlated better with metabolizable N than total N, supporting the accuracy of metabolizable measures of nutrient content (Wilder et al. 2019; Wilder et al. *In preparation*).

Total C content grouped orders into three distinct levels, where metabolizable C produced only two. However, there was much larger within-order variation in metabolizable C, particularly in orders with high and variable exoskeleton content (i.e. Coleoptera). The ability of C to predict macronutrients and indigestible components also differed between total and metabolizable C content. Total C content predicted lipid content better than metabolizable C content, though neither measure of C accounted well for variation in lipid content ($R^2 < 0.3$). Elemental C may not be a good predictor of arthropod lipid content because variation in C content stems from two pools in individual arthropods: lipid and exoskeleton content (Lease and Wolf 2010; Lease and Wolf 2011). However, C was more tightly correlated with exoskeletal content. Total C was a poor predictor of exoskeleton content ($R^2 = 0.054$), but metabolizable C was a strong predictor of exoskeleton ($R^2 = 0.71$). Arthropods that had low exoskeleton content also had high metabolizable C content, suggesting that consumers of arthropods gain more metabolizable energy from prey low in exoskeleton content, particularly predators with limited exoskeletal digestion ability (Bell 1990; Weiser et al. 1997).

Bobwhites may be getting less protein in their diet than one might expect based on the total nitrogen content of prey, which is commonly used to calculate crude protein (i.e., 6.25 x total N; Jones 1941), since some of the nitrogen is bound within the indigestible exoskeleton. Chicks in the field could be ingesting limited amounts of protein even if they consume abundant prey depending on the relative proportions of represented orders in the diet and metabolizable tissues in each individual (Peoples et al.

1994). Protein limitation has detrimental consequences for growth, feather development, flight, reproduction and ultimate survival (Peoples 1992; Peoples et al. 1994; Kaur and Ab 2015). Wild quail may also face limitations in essential amino acids (EAA), especially in the sulfur-containing EAAs (methionine and cysteine), and future work should assess differences in specific amino acid content between common arthropod prey items (Baldini et al. 1953; Scott et al. 1963; Peoples 1992; Peoples et al. 1994). Specifically, Peoples et al. 1994 found that during the breeding season, wild bobwhites that maintained seed dominated diets (<85% arthropods) were limited in all EAAs except arginine, glycine, and serine, and bobwhites that maintained arthropod dominated diets (>85% arthropods) were limited in methionine and cysteine. While much work concerning the specific amino acid requirements of birds is in relation to agricultural production, it is clear that high EAA intake results in more efficient assimilation and is likely important for feather production (Gregg and Rogers 1986; Peoples 1994; Kuar and Ab 2015).

Prey availability and potential nutrient gains are extremely important to consumers, and increased diet diversity benefits consumers through the provision of additional micro- and macronutrients not present in common prey items. Generalist insectivores must optimize both intake and assimilation, and consuming prey high in indigestible content likely decreases overall nutrient intake and could have consequences for growth or survival (Hejl and Verner 1990; Miles 1990; Sakai and Noon 1990; Kaspari and Joern 1993; Morrow et al. 2015). Ongoing declines in grassland arthropods and birds necessitate increased understanding of the interactions that determine the ultimate survival of these species (Brennan 1991; Hernandez et al. 2013; Sanchez-Bayo and

Wyckhuys 2019). In addition, conditions that alter the community composition of arthropods in ways that shift the relative balance of high versus low exoskeleton prey could have consequences for insectivore growth, even if the overall abundance of prey does not change. The provision of diverse communities of arthropod prey is often a secondary goal of habitat management for grassland birds, but it is clear that variation in prey nutrient content has a critical role in the success or failure of avian insectivores (Sotherton et al. 1993; Butler et al. 2012; Morrow et al. 2015).

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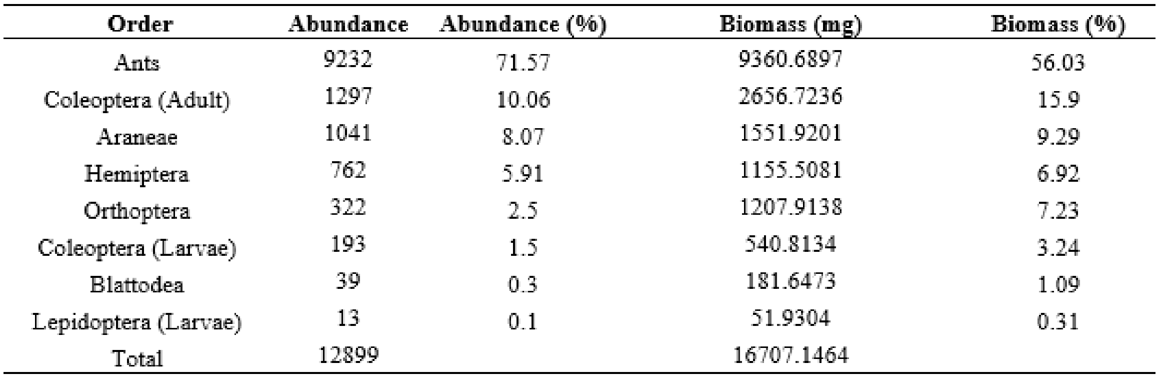
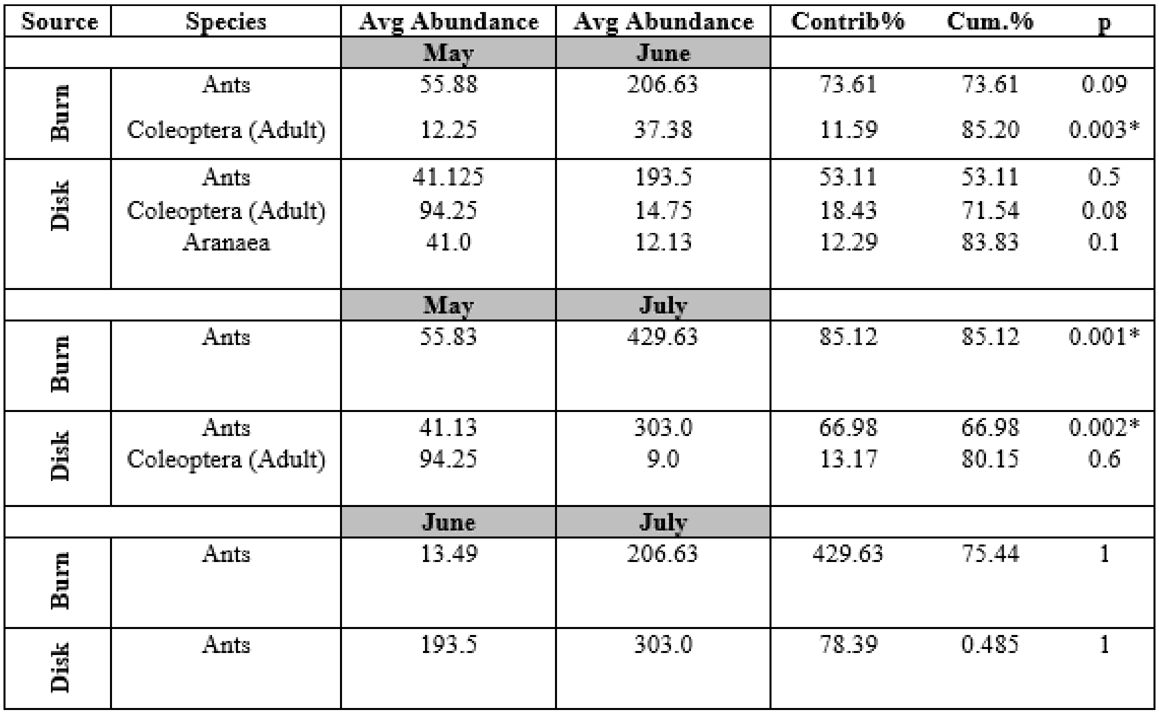
APPENDICES

Table 1. Total and individual order abundance and biomass of potential chick prey data used in analyses. All invertebrates were between 2.0 and 10.0mm in length, and were collected May-July 2019.



Order	Abundance	Abundance (%)	Biomass (mg)	Biomass (%)
Ants	9232	71.57	9360.6897	56.03
Coleoptera (Adult)	1297	10.06	2656.7236	15.9
Araneae	1041	8.07	1551.9201	9.29
Hemiptera	762	5.91	1155.5081	6.92
Orthoptera	322	2.5	1207.9138	7.23
Coleoptera (Larvae)	193	1.5	540.8134	3.24
Blattodea	39	0.3	181.6473	1.09
Lepidoptera (Larvae)	13	0.1	51.9304	0.31
Total	12899		16707.1464	

Table 2. Individual contributions to dissimilarities between sampling months from SIMPER analysis of abundance. Dissimilarities are displayed up to 75% cumulative contribution. Significant tests are marked with (*).

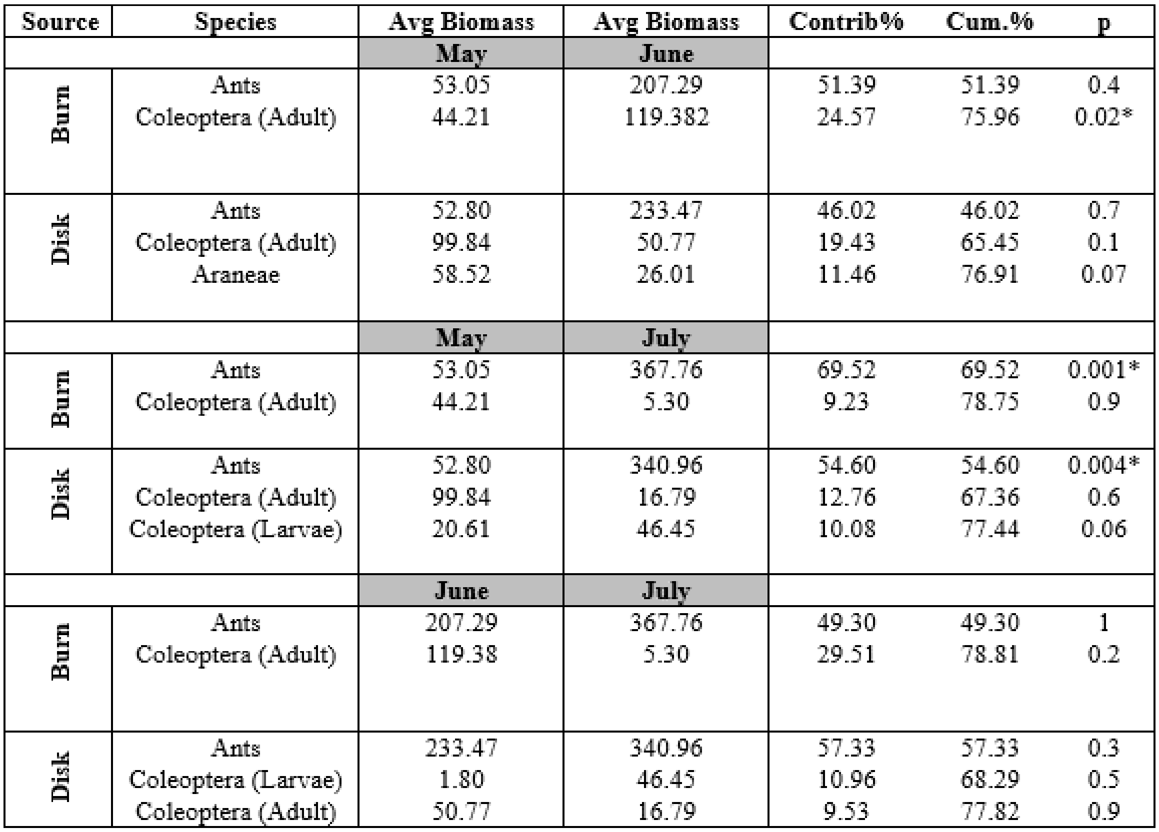


Source	Species	Avg Abundance	Avg Abundance	Contrib%	Cum.%	p
		May	**June**			
Burn	Ants	55.88	206.63	73.61	73.61	0.09
	Coleoptera (Adult)	12.25	37.38	11.59	85.20	0.003*
Disk	Ants	41.125	193.5	53.11	53.11	0.5
	Coleoptera (Adult)	94.25	14.75	18.43	71.54	0.08
	Aranaea	41.0	12.13	12.29	83.83	0.1
		May	**July**			
Burn	Ants	55.83	429.63	85.12	85.12	0.001*
Disk	Ants	41.13	303.0	66.98	66.98	0.002*
	Coleoptera (Adult)	94.25	9.0	13.17	80.15	0.6
		June	**July**			
Burn	Ants	13.49	206.63	429.63	75.44	1
Disk	Ants	193.5	303.0	78.39	0.485	1

Table 3. Results of repeated measures ANOVAs performed on abundance and biomass data. Source indicates the tested effect and the dataset (Burn or Disked). Significant effects are marked with (*).

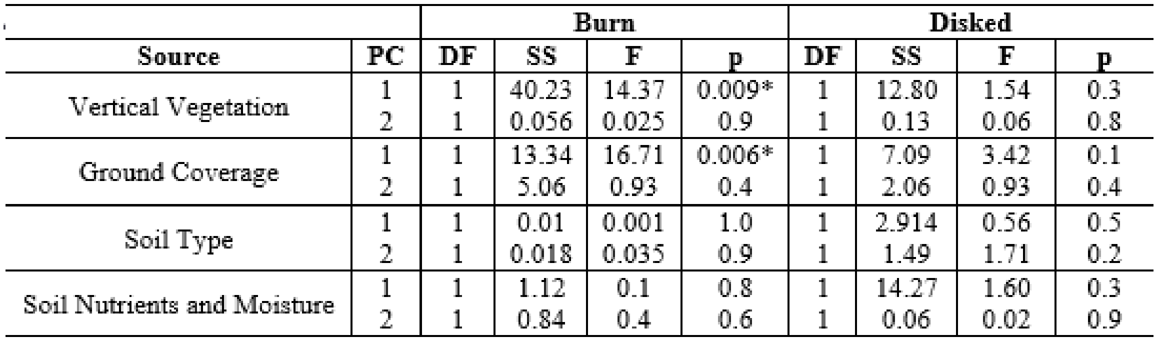
	Abundance					Biomass				
Order	**Source**	**Exact F**	**Num DF**	**Den DF**	**p**	**Source**	**Exact F**	**Num DF**	**Den DF**	**p**
Total	Burn	17.47	1	6	0.006*	Burn	5.80	1	6	0.05*
	Month (Burn)	7.51	2	5	0.03*	Month (Burn)	20.27	2	5	0.004*
	Burn*Month	0.14	2	5	0.9	Burn*Month	0.11	2	5	0.9
	Disked	0.0003	1	4	1.0	Disked	0.31	1	4	0.6
	Month (Disked)	26.19	2	3	0.01*	Month (Disked)	4.08	2	3	0.1
	Disked*Month	1.44	2	3	0.4	Disked*Month	3.88	2	3	0.1
Ants	Burn	31.14	1	6	0.001*	Burn	28.10	1	6	0.002*
	Month (Burn)	23.15	2	5	0.003*	Month (Burn)	13.50	2	5	0.01*
	Burn*Month	0.71	2	5	0.5	Burn*Month	0.59	2	5	0.6
	Disked	2.91	1	4	0.2	Disked	2.63	1	4	0.2
	Month (Disked)	61.10	2	3	0.003*	Month (Disked)	32.99	2	3	0.009*
	Disked*Month	4.40	2	3	0.1	Disked*Month	3.48	2	3	0.2
Coleoptera (adult)	Burn	1.14	1	6	0.3	Burn	0.79	1	6	0.4
	Month (Burn)	16.03	2	5	0.007*	Month (Burn)	11.48	2	5	0.01*
	Burn*Month	0.41	2	5	0.7	Burn*Month	0.25	2	5	0.8
	Disked	26.40	1	4	0.6	Disked	0.53	1	4	0.5
	Month (Disked)	1.9315	2	3	0.3	Month (Disked)	5.20	2	3	0.1
	Disked*Month	6.65	2	3	0.1	Disked*Month	8.07	2	3	0.06
Araneae	Burn	2.90	1	6	0.1	Burn	13.78	1	6	0.01*
	Month (Burn)	0.87	2	5	0.5	Month (Burn)	1.17	2	5	0.4
	Burn*Month	1.85	2	5	0.3	Burn*Month	1.04	2	5	0.4
	Disked	0.041	1	4	0.8	Disked	0.31	1	4	0.6
	Month (Disked)	1.33	2	3	0.4	Month (Disked)	2.31	2	3	0.2
	Disked*Month	0.94	2	3	0.5	Disked*Month	0.76	2	3	0.5
Hemiptera	Burn	4.33	1	6	0.1	Burn	2.61	1	6	0.2
	Month (Burn)	1.25	2	5	0.4	Month (Burn)	1.94	2	5	0.2
	Burn*Month	1.64	2	5	0.3	Burn*Month	1.86	2	5	0.2
	Disked	0.30	1	4	0.6	Disked	0.82	1	4	0.4
	Month (Disked)	0.22	2	3	0.8	Month (Disked)	1.08	2	3	0.4
	Disked*Month	0.60	2	3	0.6	Disked*Month	0.15	2	3	0.9
Orthoptera	Burn	4.88	1	6	0.1	Burn	4.8120	1	6	0.07
	Month (Burn)	1.03	2	5	0.4	Month (Burn)	0.3973	2	5	0.7
	Burn*Month	0.13	2	5	0.9	Burn*Month	0.1470	2	5	0.9
	Disked	0.99	1	4	0.4	Disked	2.09	1	4	0.2
	Month (Disked)	16.69	2	3	0.02*	Month (Disked)	14.06	2	3	0.03*
	Disked*Month	0.82	2	3	0.5	Disked*Month	3.97	2	3	0.1

Table 4. Individual contributions to dissimilarities between sampling months from SIMPER analysis of biomass. Dissimilarities are displayed up to 75% cumulative contribution. Significant tests are marked with (*).



Source	Species	Avg Biomass	Avg Biomass	Contrib%	Cum.%	p
		May	**June**			
Burn	Ants	53.05	207.29	51.39	51.39	0.4
	Coleoptera (Adult)	44.21	119.382	24.57	75.96	0.02*
Disk	Ants	52.80	233.47	46.02	46.02	0.7
	Coleoptera (Adult)	99.84	50.77	19.43	65.45	0.1
	Araneae	58.52	26.01	11.46	76.91	0.07
		May	**July**			
Burn	Ants	53.05	367.76	69.52	69.52	0.001*
	Coleoptera (Adult)	44.21	5.30	9.23	78.75	0.9
Disk	Ants	52.80	340.96	54.60	54.60	0.004*
	Coleoptera (Adult)	99.84	16.79	12.76	67.36	0.6
	Coleoptera (Larvae)	20.61	46.45	10.08	77.44	0.06
		June	**July**			
Burn	Ants	207.29	367.76	49.30	49.30	1
	Coleoptera (Adult)	119.38	5.30	29.51	78.81	0.2
Disk	Ants	233.47	340.96	57.33	57.33	0.3
	Coleoptera (Larvae)	1.80	46.45	10.96	68.29	0.5
	Coleoptera (Adult)	50.77	16.79	9.53	77.82	0.9

Table 5. Results of ANOVAs conducted on principal components of four PCAs of vegetative and soil habitat covariates. Source denotes PCAs corresponding to principal components. The covariates in each PCA include vertical vegetation layers 1-12, ground coverage covariates (shrub, litter, grass, forb, rock, and bare ground), soil type (% sand, silt, and clay), and soil nutrients, moisture, and infiltration rate).



		Burn				Disked			
Source	**PC**	**DF**	**SS**	**F**	**p**	**DF**	**SS**	**F**	**p**
Vertical Vegetation	1	1	40.23	14.37	0.009*	1	12.80	1.54	0.3
	2	1	0.056	0.025	0.9	1	0.13	0.06	0.8
Ground Coverage	1	1	13.34	16.71	0.006*	1	7.09	3.42	0.1
	2	1	5.06	0.93	0.4	1	2.06	0.93	0.4
Soil Type	1	1	0.01	0.001	1.0	1	2.914	0.56	0.5
	2	1	0.018	0.035	0.9	1	1.49	1.71	0.2
Soil Nutrients and Moisture	1	1	1.12	0.1	0.8	1	14.27	1.60	0.3
	2	1	0.84	0.4	0.6	1	0.06	0.02	0.9

Table 6. Loadings of vegetation and soil habitat covariates from PCAs performed separately on burned/control and disked/control sites, which were used to create a composite PCA. Only two PCs are displayed per analysis, and proportions of variance are displayed respective to source analyses. P-values are reported from ANOVAs testing the effect of treatment on PC axes, and significant effects are marked with (*).

	Burn		**Disk**	
PCA 1	**PC1**	**PC2**	**PC1**	**PC2**
Vertical Layer 1	-0.3258014	0.14351709	-0.3016145	0.16158631
Vertical Layer 2	-0.3309417	-0.01759746	-0.326115	0.13619513
Vertical Layer 3	-0.345257	-0.02372032	-0.3115163	0.26476638
Vertical Layer 4	-0.342676	0.02752246	-0.3168803	0.22344059
Vertical Layer 5	-0.3394979	-0.01495814	-0.3256181	0.07719732
Vertical Layer 6	-0.3325352	-0.07694672	-0.3217662	0.16733827
Vertical Layer 7	-0.3247938	-0.09748458	-0.3259898	0.12580435
Vertical Layer 8	-0.2944414	-0.07559618	-0.3199424	0.04335909
Vertical Layer 9	-0.1706514	-0.51851798	-0.2669307	-0.46269806
Vertical Layer 10	-0.1650702	-0.39913785	-0.2406002	-0.53364598
Vertical Layer 11	0.1914503	-0.51392536	-0.2406002	-0.53364598
Vertical Layer 12	0.1914503	-0.51392536	-	-
Proportion of Variance	67.89	16.07	81.50	15.29
p (treatment)	0.009*	0.9	0.3	0.8
PCA 2	**PC1**	**PC2**	**PC1**	**PC2**
Rock Cover	0.2854185	0.3899455	-	-
Bare Ground	0.4595594	0.3977447	-0.5468248	0.2567346
Forb Cover	0.3323131	-0.5231208	-0.4128213	-0.1540699
Grass Cover	0.1439193	-0.5326257	0.3169737	-0.7219978
Litter Cover	-0.5514905	-0.2051692	0.5153381	0.1098193
Shrub Cover	-0.5215888	0.3005026	0.4056052	0.6140103
Proportion of Variance	43.16	36.59	55.85	23.33
p (treatment)	0.006*	0.4	0.1	0.4
PCA 3	**PC1**	**PC2**	**PC1**	**PC2**
Sand (top)	0.4103129	-0.45378392	-0.4400337	-0.2033388
Silt (top)	-0.3998022	0.54965582	0.4094581	0.3833998
Clay (top)	-0.419443	0.06928466	0.4416664	-0.1179078
Sand (bottom)	0.4117367	0.44123777	-0.4266045	0.3209252
Silt (bottom)	-0.3992925	-0.5313263	0.397018	0.4335639
Clay (bottom)	-0.4085431	-0.10079613	0.3225376	-0.7118883
Proportion of Variance	89.61	7.56	81.72	15.97
p (treatment)	0.98	0.9	0.5	0.2
PCA 4	**PC1**	**PC2**	**PC1**	**PC2**
Infiltration Rate	0.1953084	-0.47973235	-0.14023426	-0.457421211
Soil Moisture (top)	-0.2991311	0.04832492	0.30246991	0.078412026
Soil Moisture (bottom)	-0.2818332	0.01981496	0.26663961	-0.078164645
pH (top)	-0.2257929	-0.43283143	-0.24566968	0.272317204
NO_3 (PPM) (top)	-0.1602021	0.26937089	0.31008281	0.055314041
P (PPM) (top)	-0.172391	-0.22550906	0.28616615	-0.158896395
K (PPM) (top)	-0.3096017	-0.10048408	0.31066479	0.128754734
SOM (%) (top)	-0.2969882	0.07409624	0.20493193	0.364797466
N (%) (top)	-0.3014842	0.11834455	0.2868041	0.23049194
pH (bottom)	-0.2262519	-0.44378071	-0.16165169	0.429557712
NO_3 (PPM) (bottom)	-0.2602691	0.26939495	0.30323751	0.008454459
P (PPM) (bottom)	-0.2288394	-0.33055257	-0.03368347	-0.482137065
K (PPM) (bottom)	-0.2459163	-0.09474019	0.30521165	-0.053636446
SOM (%) (bottom)	-0.30442	0.11436192	0.25159032	-0.105121544
N (%) (bottom)	-0.2952759	0.16107089	0.28795249	-0.205637888
Proportion of Variance	65.20	13.19	64.72	15.65
p (treatment)	0.8	0.6	0.3	0.9

Table 7. Vegetation and soil covariates from burned and disked sites. Means of treatment sites are marked with $\bar{x}$ **(T)** and control site means are marked with $\bar{x}$ **(C)**. Results from ANOVAs testing the effect of treatment are displayed, and significant results are marked with (*).

	Burn						**Disk**					
Covariate	**$\bar{x}$ (T)**	**$\bar{x}$ (C)**	**DF**	**SS**	**F Ratio**	**p**	**$\bar{x}$ (T)**	**$\bar{x}$ (C)**	**DF**	**SS**	**F Ratio**	**p**
Vertical Layer 1 (%)	59.76	93.54	1	6848.44	25.87	0.0001*	49.55	73.48	1	3152.02	4.95	0.04*
Vertical Layer 2 (%)	40.68	76.46	1	7681.79	14.09	0.001*	32.73	57.65	1	3416.70	3.42	0.08
Vertical Layer 3 (%)	21.08	62.92	1	10503.65	21.41	0.0001*	21.36	39.39	1	1788.1.96	1.69	0.2
Vertical Layer 4 (%)	12.22	52.50	1	9733.80	23.32	0.0001*	13.71	28.48	1	1200.28	1.74	0.2
Vertical Layer 5 (%)	5.10	38.47	1	6680.56	32.32	0.0001*	7.88	19.51	1	742.76	2.09	0.2
Vertical Layer 6 (%)	2.57	28.61	1	4069.01	17.43	0.0004*	6.97	17.29	1	585.99	2.43	0.1
Vertical Layer 7 (%)	0.62	16.81	1	1570.86	7.51	0.01*	2.95	10.76	1	334.88	3.08	0.09
Vertical Layer 8 (%)	0.49	11.60	1	740.74	5.10	0.03*	0.61	5.98	1	159.12	4.92	0.04*
Vertical Layer 9 (%)	0.49	2.43	1	22.69	1.25	0.3	0.00	1.21	1	8.08	3.49	0.08
Vertical Layer 10 (%)	0.07	1.81	1	18.08	1.00	0.3	0.00	0.53	1	1.55	1.37	0.3
Vertical Layer 11 (%)	0.42	0.00	1	1.04	1.00	0.3	0.00	0.08	1	0.032	1.00	0.3
Vertical Layer 12 (%)	0.42	0.00	1	1.04	1.00	0.3	0.00	0.00	1	0	-	-
Bare Ground (%)	63.00	16.94	1	12728.60	59.94	0.0001*	67.80	21.59	1	11745.58	12.52	0.002*
Rock Cover (%)	1.53	0.00	1	14.00	1.76	0.2	0.00	0.00	1	0	-	-
Forb Cover (%)	8.37	5.28	1	57.30	0.58	0.4	12.88	8.11	1	125.28	0.9916	0.3
Grass Cover (%)	26.06	28.53	1	36.57	0.096	0.8	6.52	28.67	1	2700.64	17.32	0.0005*
Litter Cover (%)	6.98	54.93	1	13796.01	108.90	0.0001*	27.80	54.92	1	4045.58	4.63	0.4
Shrub Cover (%)	11.93	27.78	1	1507.47	5.64	0.03*	3.18	8.88	1	178.74	1.10	0.3
Infiltration Rate (cm/0.25 hr)	7.98	8.73	1	3.38	0.083	0.8	12.95	17.62	1	119.62	1.82	0.2
Top 6" Soil Core												
pH	7.19	7.28	1	0.042	0.083	0.8	6.54	6.91	1	0.75	2.95	0.1
Moisture (%)	9.17	10.22	1	0.00067	0.55	0.5	9.83	7.90	1	0.0020	2.01	0.2
SOM (%)	1.28	1.05	1	0.32	0.68	0.5	1.06	0.85	1	0.24	4.58	0.04*
N (%)	0.088	0.069	1	0.0022	0.87	0.4	0.062	0.53	1	0.00040	1.54	0.2
NO_3 (PPM)	14.54	13.50	1	26.04	0.39	0.5	35.36	26.39	1	442.51	1.89	0.2
P (PPM)	6.33	8.00	1	66.67	0.85	0.4	19.64	11.42	1	370.91	10.61	0.004*
K (PPM)	114.75	113.54	1	35.04	0.0033	0.9	272.06	175.55	1	51233.46	5.23	0.03*
Sand (%)	76.58	78.36	1	18.90	0.054	0.8	85.39	89.22	1	80.44	4.10	0.06
Silt (%)	16.79	14.38	1	34.80	0.16	0.7	9.48	6.42	1	51.52	7.24	0.01*
Clay (%)	6.68	7.32	1	2.41	0.15	0.7	5.15	4.41	1	3.01	0.85	0.4
Bottom 6" Soil Core												
pH	7.42	7.27	1	0.13	0.34	0.6	6.74	6.77	1	0.0061	0.037	0.8
Moisture (%)	9.56	9.64	1	3.73e-6	0.0034	0.9	0.086	8.40	1	2.58e-5	0.062	0.8
SOM (%)	0.97	0.60	1	0.84	3.26	0.08	0.56	0.39	1	0.16	12.00	0.002*
N (%)	0.061	0.046	1	0.0013	1.88	0.2	0.041	0.033	1	0.00034	4.35	0.05*
NO_3 (PPM)	8.08	6.63	1	51.04	12.40	0.002*	18.48	12.39	1	204.05	16.37	0.0006*
P (PPM)	2.63	2.29	1	2.67	0.13	0.7	4.00	2.00	1	22.00	1.50	0.2
K (PPM)	93.54	103.29	1	2281.50	0.76	0.4	197.67	146.70	1	14288.50	6.33	0.02*
Sand (%)	78.25	78.25	1	0.00	0.00	1.00	85.58	87.55	1	21.27	0.55	0.5
Silt (%)	14.87	14.41	1	1.28	0.011	0.9	8.14	5.32	1	43.68	6.34	0.02*
Clay (%)	7.41	7.41	1	3.75e-19	0.00	1.00	6.35	7.19	1	3.82	0.18	0.7

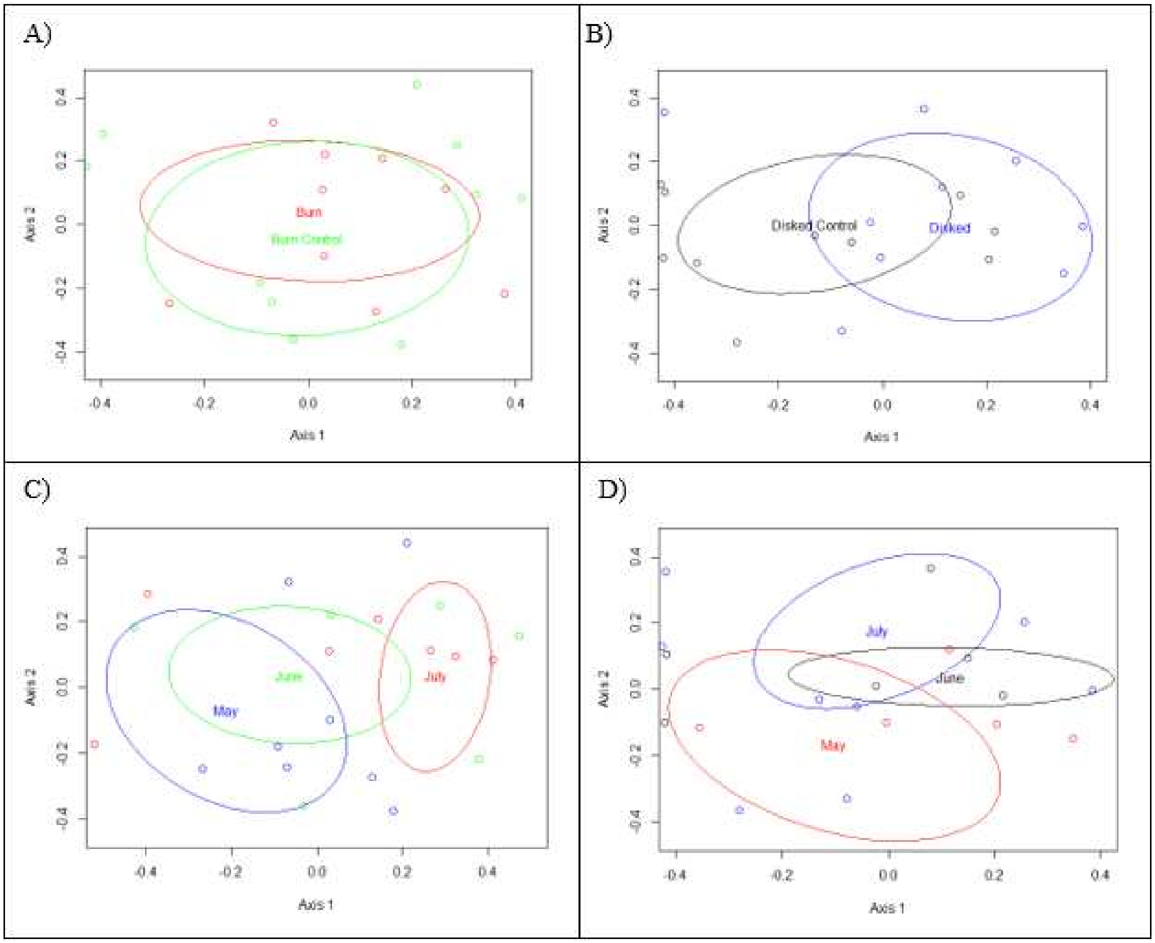


Figure 1. nMDS ordination of abundance of potential bobwhite prey across all sampling months. Ellipses represent community centroids of A) treatment differences in burned and paired control sites (2D stress = 0.1713008, PERMANOVA p = 0.095), B) treatment differences in disked and paired control sites (2D stress = 0.1897308, PERMANOVA p = 0.429), C) sampling period differences in burned and paired control sites (2D stress = 0.1713008, PERMANOVA p = 0.002), and D) sampling period differences in disked and paired control sites (2D stress = 0.1897308, PERMANOVA p = 0.001).

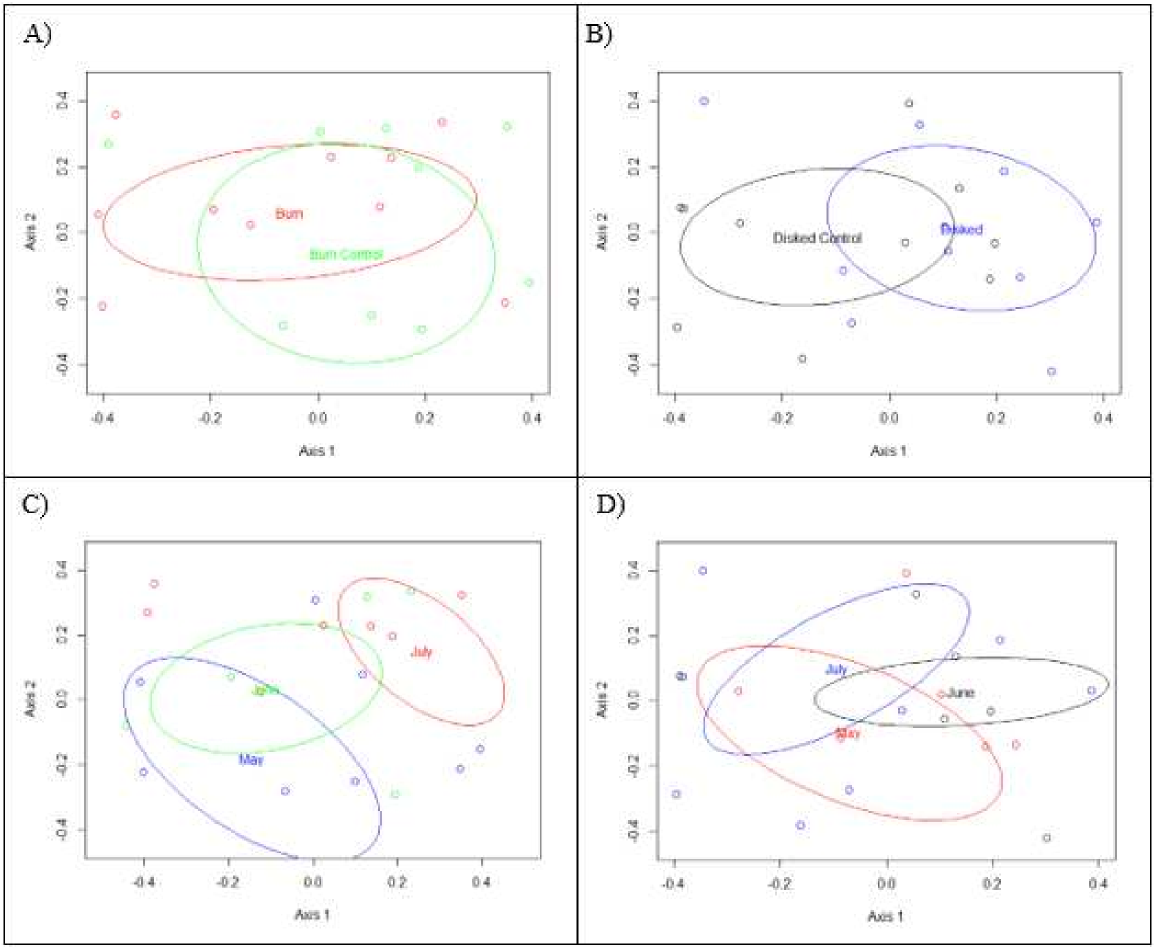


Figure 2. nMDS ordination of biomass of potential bobwhite prey across all sampling months. Ellipses represent community centroids of A) treatment differences in burned and paired control sites (2D stress = 0.1697498, PERMANOVA p = 0.028), B) treatment differences in disked and paired control sites (2D stress = 0.1935342, PERMANOVA p = 0.24), C) sampling period differences in burned and paired control sites (2D stress = 0.1697498, PERMANOVA p = 0.001), and D) sampling period differences in disked and paired control sites (2D stress = 0.1935342, PERMANOVA p = 0.001).

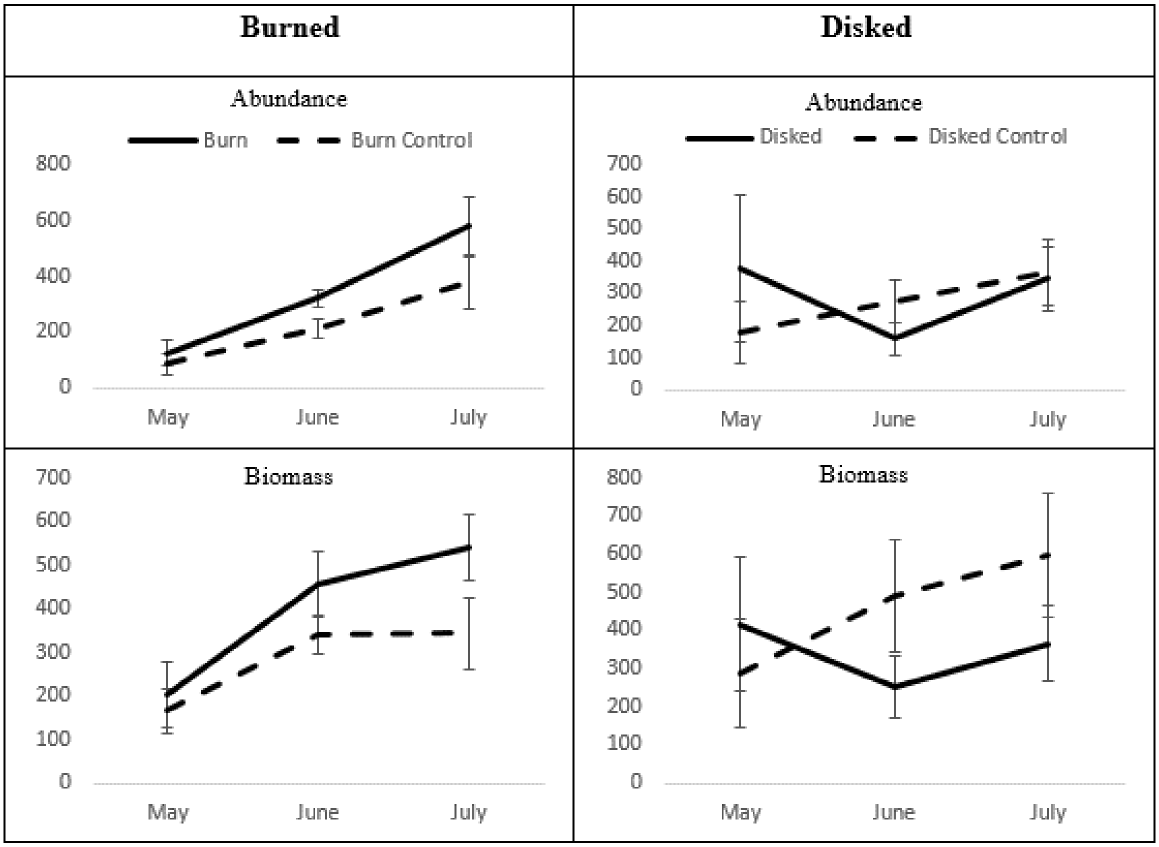


Figure 3. Average abundance (individuals/site) and biomass (mg/site) of all arthropods collected at burned/paired control and disked/paired control sites.

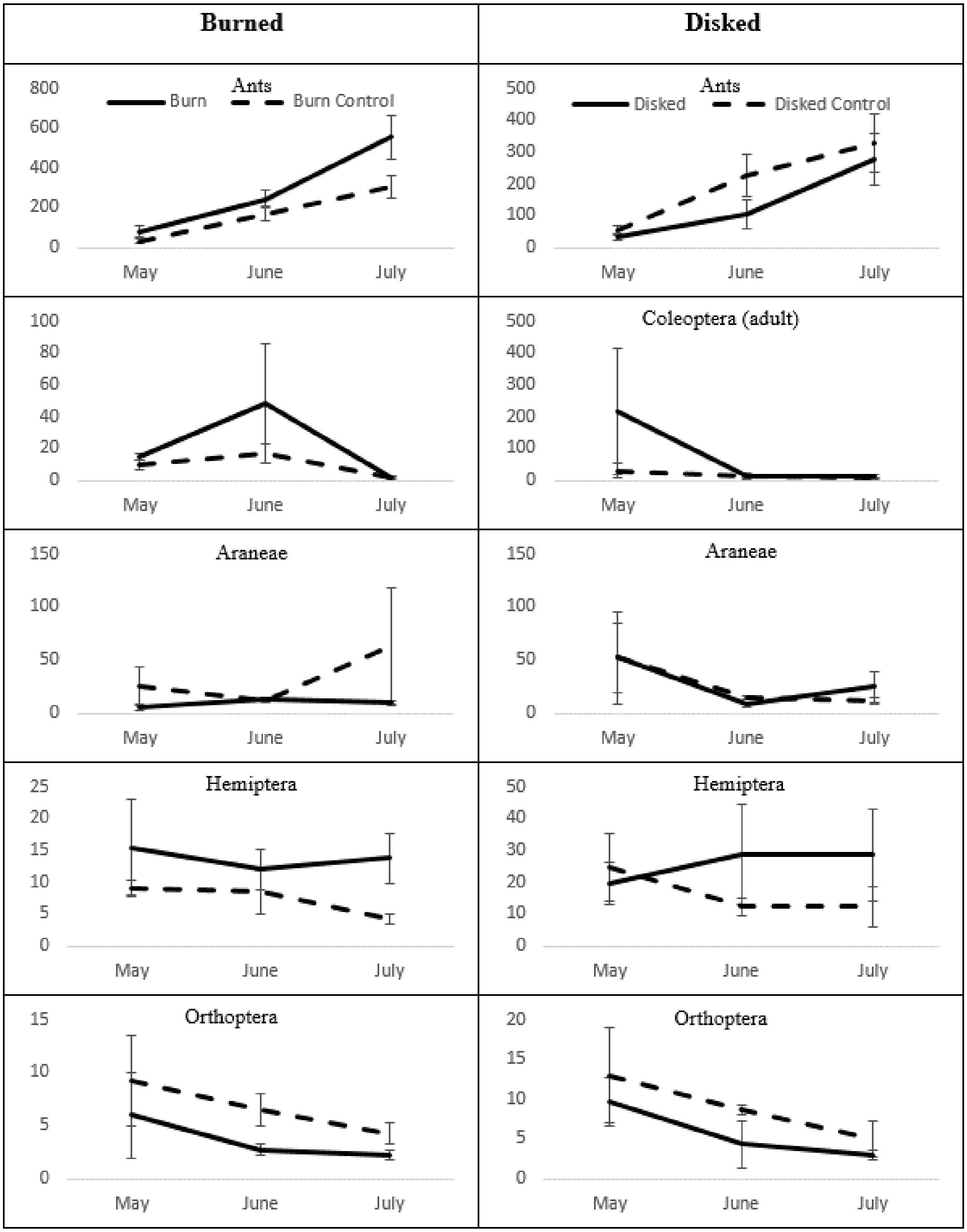


Figure 4. Average abundance of the five most abundant orders from burned and disked datasets. The five orders are listed from most to least abundant. Solid lines represent data from treatment sites, and dashed lines represent data from control sites.

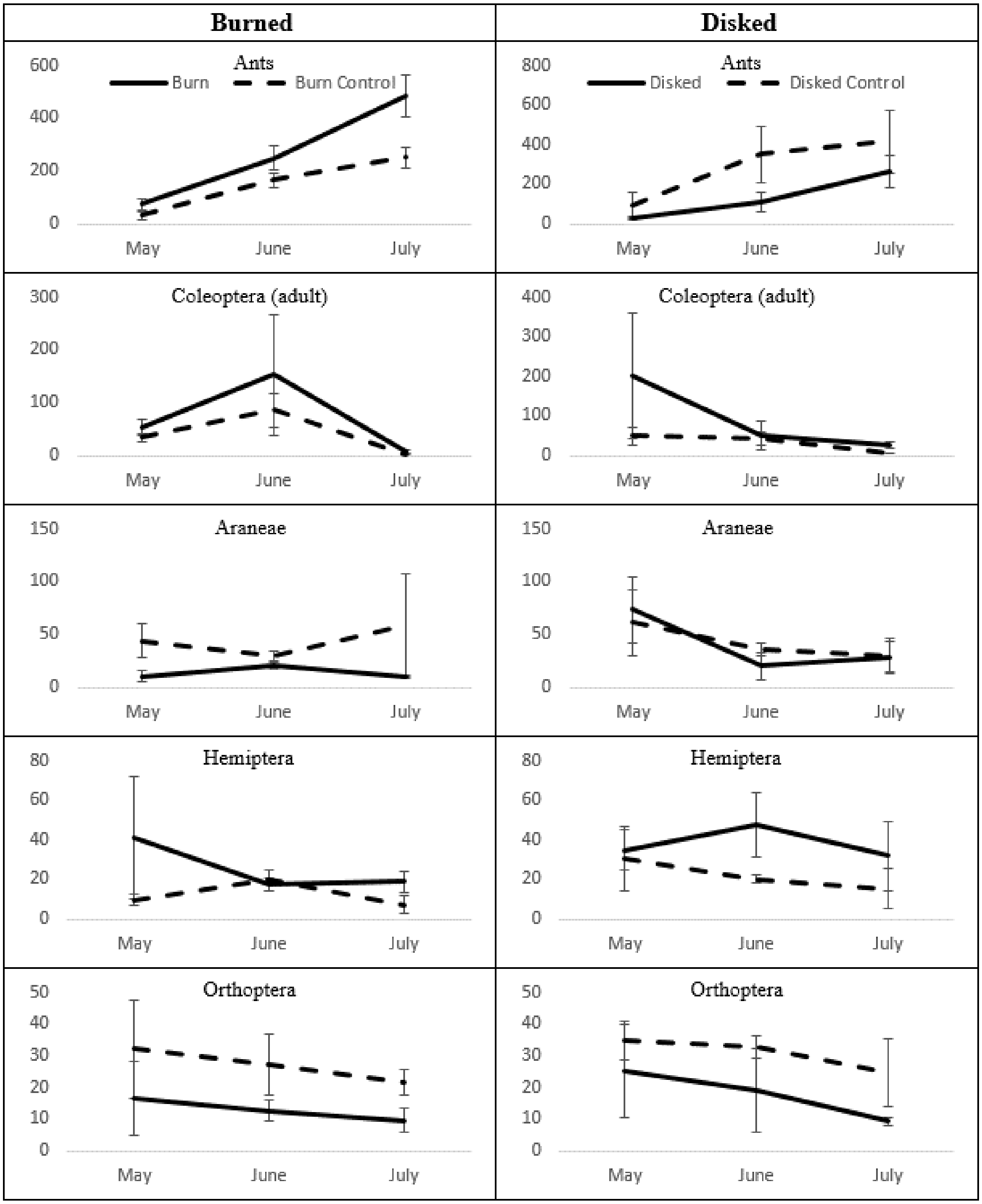


Figure 5. Average biomass (mg) of the five most abundant orders from burned and disked datasets. The five orders are listed from most to least abundant. Solid lines represent data from treatment sites, and dashed lines represent data from control sites.

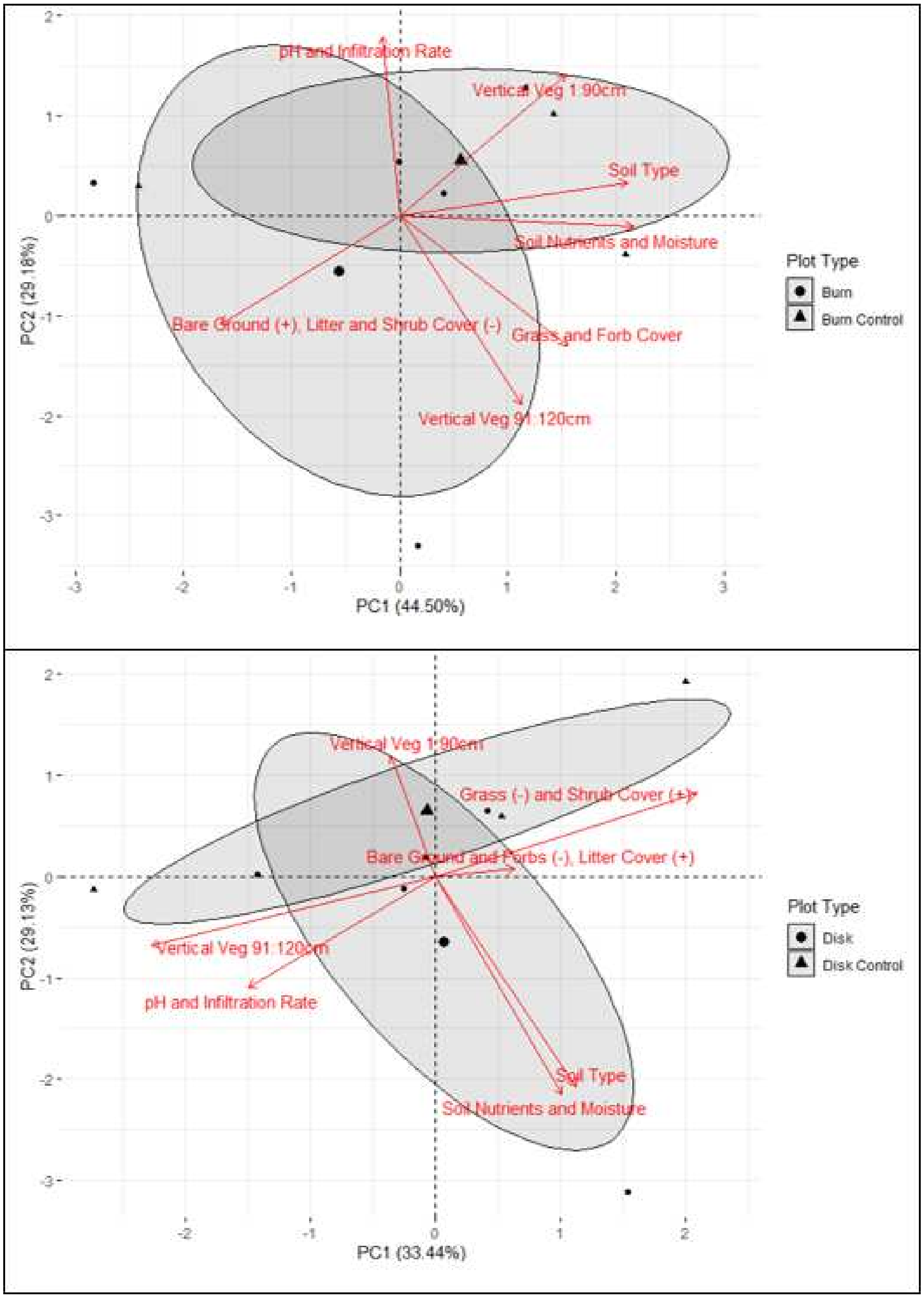


Figure 6. Principal component analysis of seven PC axes from four PCAs of vegetation and soil habitat covariate data. Where present, (+) and (-) indicate positive or negative trends relative to the direction of the eigenvector. Else, covariates all maintain positive trends with the direction of the eigenvector.

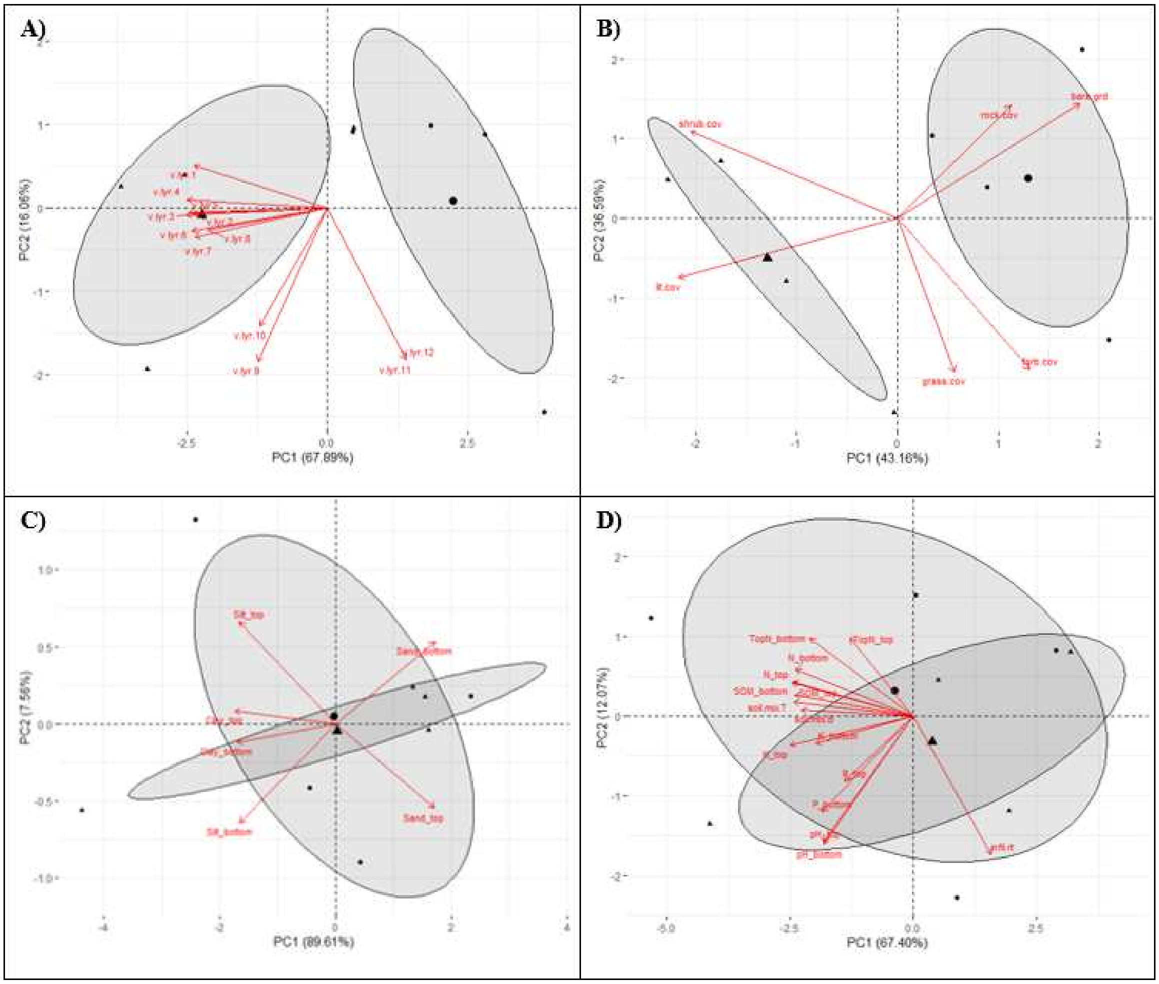


Figure 7. Principal component analyses of vegetative and soil habitat covariates from burned and control sites. Data from burned sites are marked with a closed circle, and data from control sites are marked with a closed triangle. The covariates in each PCA include **A)** vertical layers 1-12, **B)** ground coverage covariates (shrub, litter, grass, forb, rock, and bare ground), **C)** soil type (% sand, silt, and clay), and **D)** soil nutrients, moisture, and infiltration rate.

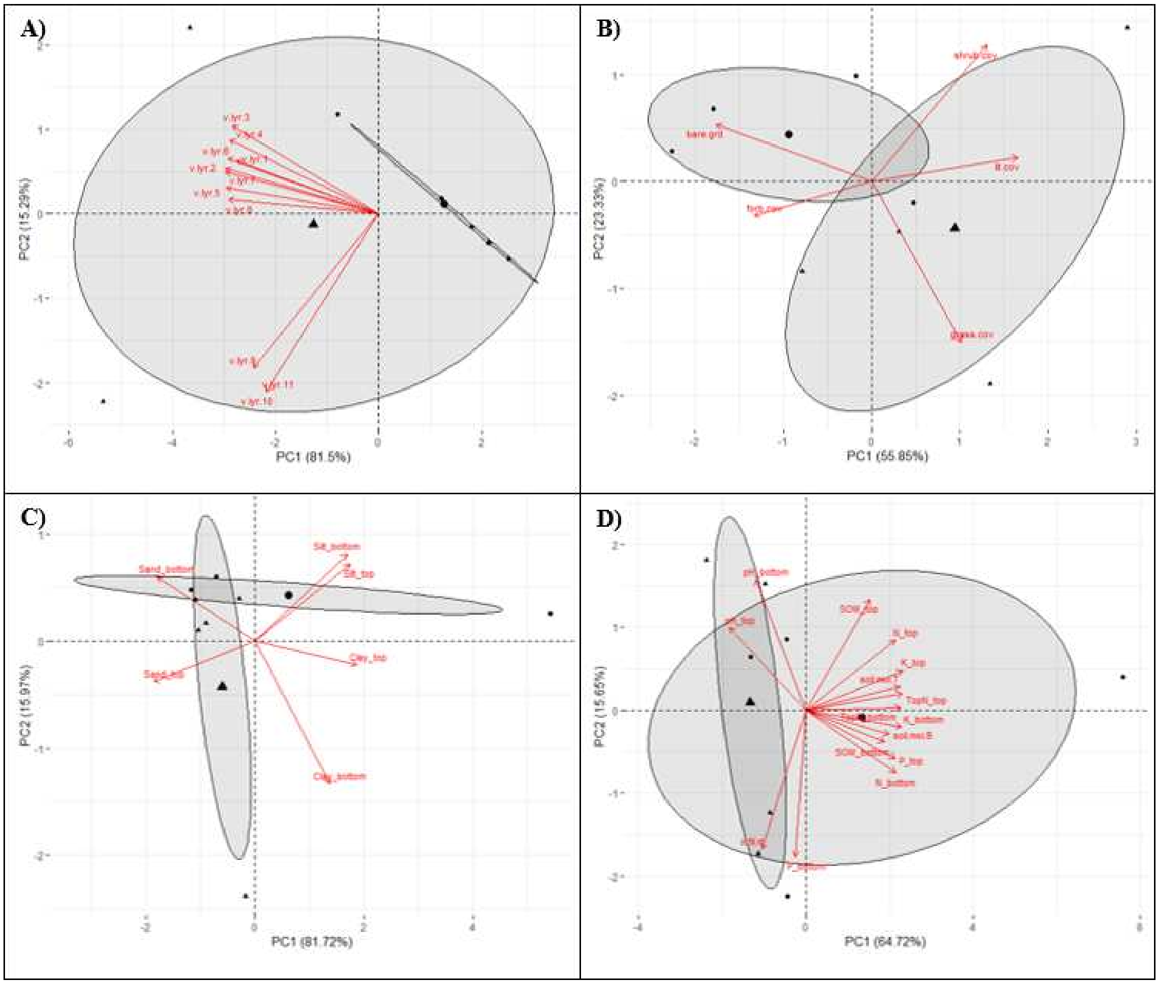


Figure 8. Principal component analyses of vegetative and soil habitat covariates from disked and control sites. Data from burned sites are marked with a closed circle, and data from control sites are marked with a closed triangle. The covariates in each PCA include **A)** vertical layers 1-12, **B)** ground coverage covariates (shrub, litter, grass, forb, rock, and bare ground), **C)** soil type (% sand, silt, and clay), and **D)** soil nutrients, moisture, and infiltration rate.

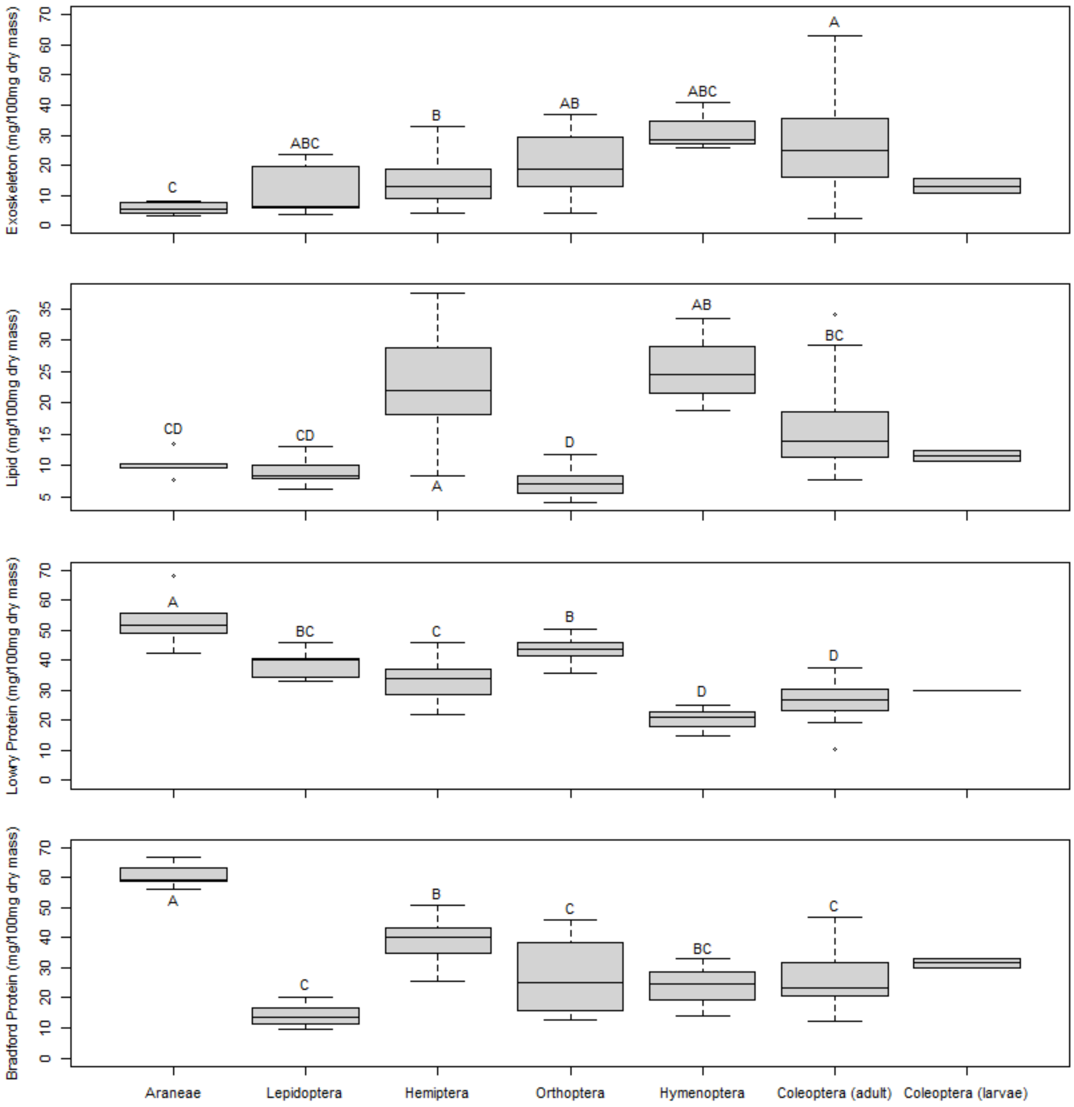


Figure 9. Indigestible (exoskeleton) and macronutrient (lipid and protein) content of 74 arthropods as a proportion of total dry mass (mg/100mg dry mass). Protein content was measured by the Lowry and Bradford assays. Orders not connected by the same letter are significantly different ($p < 0.05$). Coleoptera (larvae) data are presented but were not included in analyses.

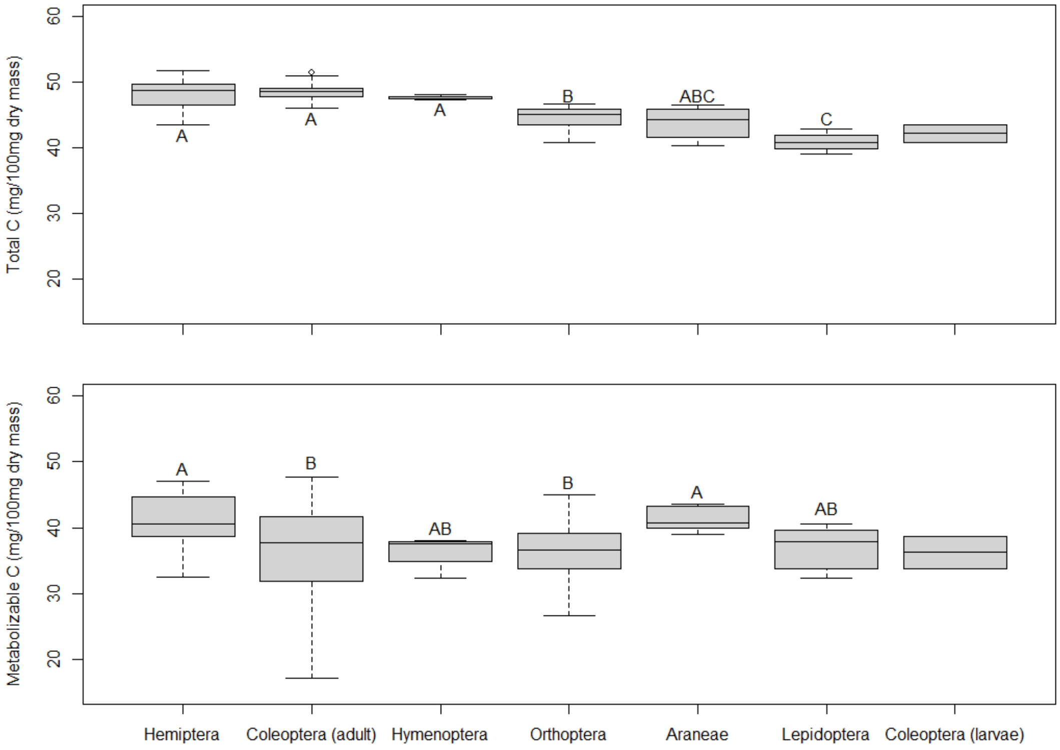


Figure 10. Total and metabolizable C content of 74 arthropods as a proportion of dry mass. Orders not connected by the same letter are significantly different ($p < 0.05$). Coleoptera (larvae) data are presented but were not included in analyses.

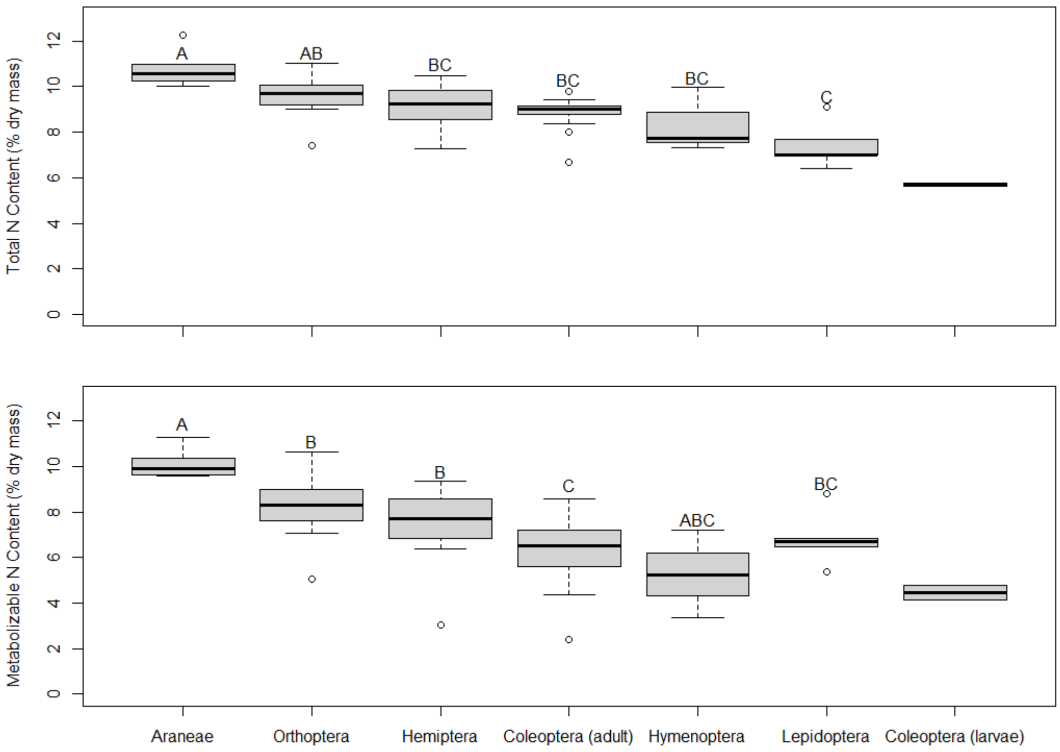


Figure 11. Total and metabolizable N content of 74 arthropods as a proportion of dry mass. Orders not connected by the same letter are significantly different ($p < 0.05$). Coleoptera (larvae) data are presented but were not included in analyses.

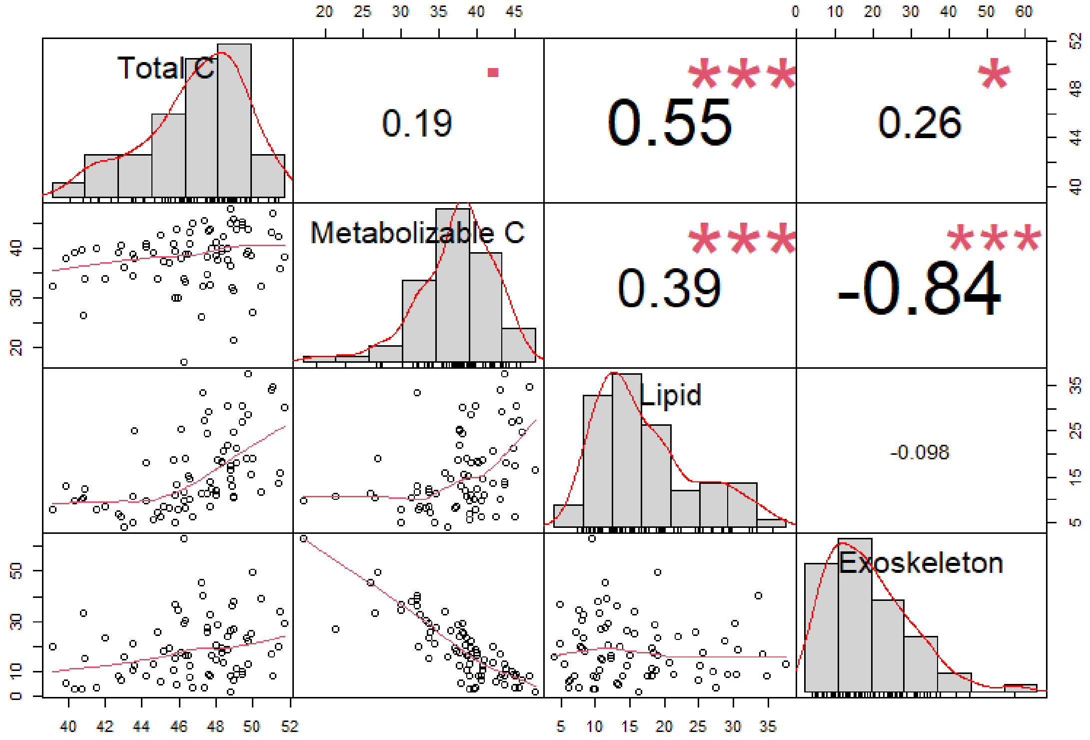


Figure 12. Correlation matrix of total and metabolizable C content with lipid and exoskeleton content of 74 arthropods. Histograms display distributions of C, lipid, and exoskeleton content, and asterisks indicate level of significance associated with correlation coefficients: * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001.

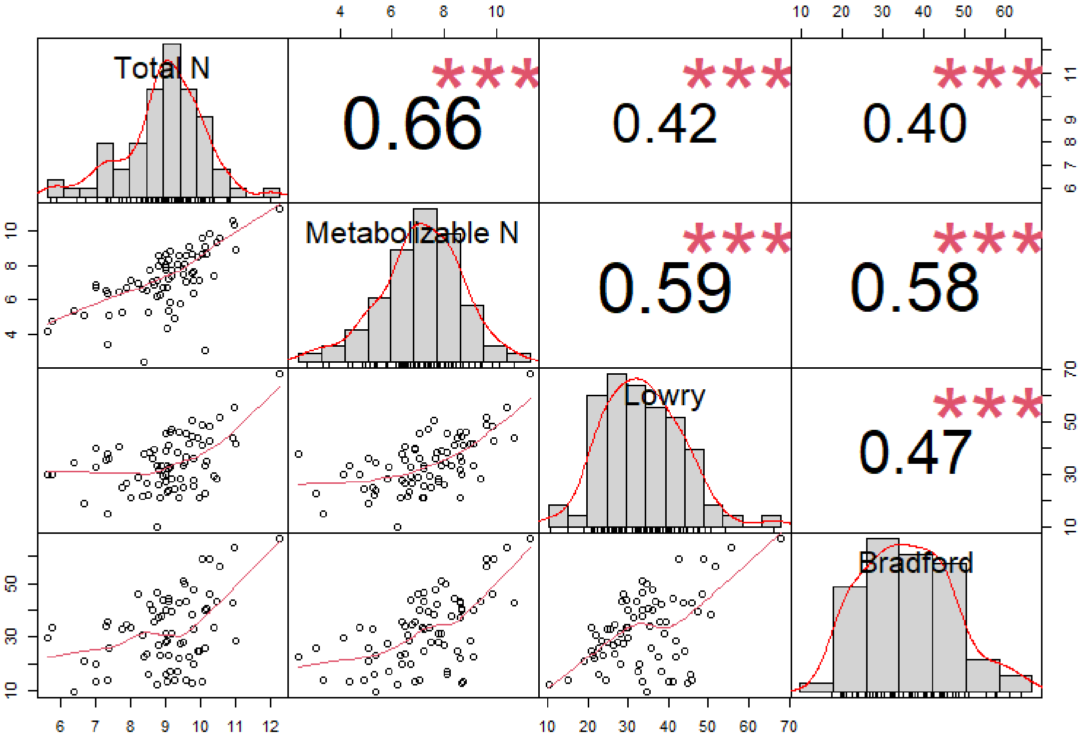


Figure 13. Correlation matrix of total N, metabolizable N, and protein content measured by the Lowry and Bradford assays. Histograms display distributions of N or protein content measured by each assay, and asterisks indicate level of significance associated with correlation coefficients: * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001.

VITA

Jacob Tyler Reeves

Candidate for the Degree of

Master of Science

Thesis: AVAILABILITY AND NUTRIENT CONTENT OF COMMON ARTHROPOD PREY OF NORTHERN BOBWHITES (*COLINUS VIRGINIANUS*) IN WESTERN OKLAHOMA

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