Brood Habitat and Invertebrate Biomass of the Greater Prairie Chicken (*Tympanuchus cupido pinnatus*) in Northwestern Minnesota

By

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ABSTRACT

This study assessed the influence of terrestrial invertebrate abundance and vegetation characteristics on northwest Minnesota greater prairie chicken brood success. Radio telemetry was used to determine movements of greater prairie chicken hens and their broods. Invertebrate abundance indices were collected using a sweep net and vegetation data were recorded with overhead and dot-board photographs. Invertebrates were dried, sorted by size and order, and weighed and counted. Vegetation was classified according to life form and height was measured. Greater prairie chicken broods appear to use those habitats most readily available with increased invertebrate resources. Invertebrate biomass was not related to the occurrence of uncultivated forbs which averaged < 17% in Minnesota habitats where greater prairie chicken broods were located. Relatively undisturbed grasslands produce sufficient invertebrate resources to fledge greater prairie chicken chicks. However, location data and invertebrate-habitat indices suggest increased brood success would be likely with improved habitat placement/availability and irregular disturbance regimes that produce beneficial mixed grass/forb vegetation attractive to both greater prairie chicken broods and their invertebrate prey.

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INTRODUCTION

Native solely to the United States of America, pinnated grouse (*Tympanuchus* spp.) numbers have been decreasing over the last century (Silvy et al. 2004, Johnsgard 2002, Johnson et al. 2011). Several limiting factors including a reduction in the quantity and quality of grassland habitat, loss of open space, reduced nesting success, and poor chick survival have contributed to the decline, extirpation, and extinction of pinnated grouse conspecifics – Greater prairie chicken (*Tympanuchus cupido pinnatus*), Attwater's prairie chicken (*Tympanuchus cupido atwattri*), and Heath Hen (*Tympanuchus cupido cupido*), and the congeneric Lesser prairie chicken (*Tympanuchus pallidicinctus*) (Toepfer 2003, 2009, Morrow et al. 1996, Vodehnal and Haufler 2008, Silvy et al. 2004).

Although populations have declined approximately 80% in the last three decades, the greater prairie chicken (hereafter GPC) retains the greatest range of all pinnated grouse (Storch 2007, Rich et al. 2004, Johnsgard 2002, Westemeier and Gough 1999). GPC is red-listed by the International Union for the Conservation of Nature as vulnerable (BirdLife 2012). It is a Partners in Flight Watch List species, and the Minnesota Department of Natural Resources has listed GPC as a species of Special Concern since 1984 (Partners in Flight 2012, Anonymous 2012*a*). At the time of this study, relatively stable GPC populations exist in northeast Colorado, Nebraska, Minnesota and South Dakota (Vodehnal and Haufler 2008, Svedarsky et al. 2000, Norton 2005, Robb and Schroeder 2005, Toepfer 2007).

Problem Statement

Early grouse biologists believed that species numbers were determined by breeding success, indexed by the autumn juvenile:adult bird ratio (King 1937 and Bump 1947 *in* Bergerud 1988). Decades of subsequent research on galliforme population size generally support this concept whereby species numbers are ultimately determined by fluctuations in fledgling success, defined here as chick survival to brood break-up and dispersal, and reproductive success where young-of-the-year outnumber the adults in a population (Bergerud 1988). Consequently, nesting success and early chick survival are critical factors in population sustainability (Bergerud 1988, Blank et al. 1967, Wisdom and Mills 1997, Toepfer 2003, Hannon and Martin 2006), which means that nesting and brood rearing habitat must facilitate a high number of hatched nests and fledged chicks (Hamerstrom et al. 1957, Kirsch 1974, Bergerud 1988). Fledgling success depends on the interplay of numerous extrinsic factors; in particular, predation, exposure to the elements and food supply (Bergerud 1988). A number of studies have challenged the direct link between weather and chick mortality, and predation may also be insufficient in explaining high mortality rates in several galliforme species (*see* Bergerud 1988). It would seem that many grouse biologists hypothesize inadequate food supplies as the greatest cause of chick mortality, evidenced by the high number of brood studies that measure the abundance of invertebrates which have proven to be the staple of young grouse subsistence (Bergerud 1988, Ford et al. 1938, Loughrey and Stinson 1955, Jones 1963, Kobriger 1965, Southwood and Cross 1969, Peterson 1970, Hurst 1972, Potts 1970, Kastdalen and Wegge 1984, Green 1984, Erikstad 1985, Hill 1985, Rands 1985, Savory 1989, Burger et al. 1993, Drut et al. 1994, Madison et al. 1995, Baines et al. 1996, Panek 1997, Griffin et al. 1997, Park 2001, Jamison et al. 2002, Pratt et al. 2003, Hagen et al. 2005, Doxon and Carroll 2007, Morrow et al. 2010, Gregg and Crawford 2009). It might also be assumed that plentiful food resources could increase chick robustness towards exposure and predation attempts (Woodard et al. 1977, Moreby 2004) making invertebrate availability the "pacemaker" of fledgling success (Bergerud 1988).

Early GPC diet analysis of chicks 9-10 weeks of age showed invertebrate material to make up 39.5% of crop contents, but it was thought that very young chicks probably consumed only invertebrate matter (Yeatter 1943). Jones (1963) examined faecal droppings and found invertebrates made up 97% of the total foods consumed by GPC broods in Oklahoma, and forb communities were associated with higher invertebrate populations. In South Dakota, Renhowe (1968) combined sharp-tailed grouse and greater prairie chicken data to show that the crops of chicks up to 13 weeks contain mostly invertebrate material, usually at ≥ 90%. Analyzing faecal samples, Rumble et al. (1988) reported that in the first several weeks of life, arthropods made up over 80% of the diet of juvenile GPC in North Dakota.

Many studies have documented GPC brood rearing habitat (Jones 1963, Svedarsky 1979, Newell 1987, Toepfer 1988, Golner 1997, Keenlance 1998, Ryan et al. 1998, Norton 2005, McNew 2010, Matthews et al. 2011, Anderson 2012) but few have investigated invertebrate abundance within the habitat (Jones 1963, Pratt et al. 2003). More research is needed with regards to the role and potential impact of invertebrates on GPC brood survival, and the grassland management practices and programs that create habitat structures which maintain invertebrate populations necessary for fledging success

(Svedarsky 1979, Peterson and Silvy 1996, Toepfer 2003, Hagen et al. 2005, Robb and Schroeder 2005).

Research in Texas on the endangered Attwater's prairie chicken (APC) suggests that inadequate invertebrate availability due to poor quality brood habitat may be a critical limiting factor with regards to chick survival and the ability to sustain APC numbers in the wild (Peterson and Silvy 1996, Griffin et al. 1997, USFWS 2010). The APC recovery team has suggested that additional applied research into such questions should be carried out using non-endangered wild GPC populations (USFWS 2010). For several decades the GPC population in northwestern Minnesota has been studied and results are being used as baseline data for APC research (Pratt et al. 2003, J. Toepfer per. comm.). This dual species approach has already been used to compare reproductive success between APC and GPC populations (Peterson and Silvy 1996), and is consistent with other studies on endangered wildlife which use surrogate species to augment and/or compare information (Powell et al. 1985, Collar et al. 1992).

Objectives

This research was conducted in northwest Minnesota from April 8, 2009 to September 8, 2009. I sought to determine which northern prairie habitats produce invertebrate abundance and composition conducive to GPC fledgling success. The objectives of this study were to (1) document the variations in invertebrate abundance (indexed as biomass and number of invertebrates) and composition (indexed as Order) in habitat classes (vegetation type and disturbance regime) used by successful and unsuccessful GPC brood hens, and (2) identify the land use practices and programs that provide habitats where GPC brood rearing may be most successful.

LITERATURE REVIEW

This literature review begins with a description of greater prairie chicken brood habitat, followed by a review of grouse research addressing the relationship between brood success and invertebrate abundance. The relationship between brood range size and invertebrate abundance is mentioned. A note is made with regard to the prevalent emphasis on forbs in brood habitat. In the next section I discuss the role of habitat in producing invertebrate-rich vegetation conducive to brood productivity. Burning, grazing and mowing management regimes and their impact on invertebrate populations are reviewed and the importance of heterogeneous vegetation is highlighted. Last, the impacts of the federal Conservation Reserve Program (CRP) are discussed with regard to both prairie grouse and invertebrate populations. Suggestions to improve the management of CRP are mentioned. These subjects speak to the relationships between grouse broods and their invertebrate prey, broods and brood habitat, habitat and invertebrate characteristics, and the management regimes that impact them all.

Greater Prairie Chicken Brood Habitat

Critical to population sustainability, GPC nest success and brood survival rely on quality habitat. In most modern prairie landscapes of large fields and croplands, nest and brood habitat are comparatively different (Svedarsky et al. 2003). Nesting habitat is described as dense, medium height grasses (often residual cover from the previous year) that provide protection from weather elements and conceal the hen from potential threats while allowing unobstructed views and escape routes from predators (Bergerud and Gratson 1988, Kates 2006, Svedarsky et al. 2003, Johnson et al. 2011). Brood rearing habitat should also shelter from the elements and predators, but must facilitate chick movement at ground level and, most importantly, provide an adequate amount of invertebrates for early sustenance (Bergerud and Gratson 1988, Kates 2006, Svedarsky et al. 2003, Johnson et al. 2011).

Initial insights into GPC brood rearing habitat showed hens with broods (hereafter broods) in Oklahoma moving from dense nesting habitat into disturbed vegetation (predominantly cultivated pastures) in search of invertebrates in forb-dominated habitats of short weeds with pockets of taller weeds for loafing cover (Jones 1963). Svedarsky (1979) completed the first comprehensive work on spring and summer female GPC ecology with a substantial component on brood ecology in Minnesota. He also found that broods moved from undisturbed brome (*Bromus inermis*) and redtop (*Agrostis stononifera*) nesting sites to grassland habitats disturbed by burning and haying, as well as disturbed and undisturbed alfalfa (*Medicago staiva*) fields. Cropland was avoided. Young broods (< 2 weeks) moved extensively, presumably in search of quality habitat. 68.8% of young brood locations were in disturbed habitats which increased to 78% for older broods (> 2 weeks). Two week old broods moved an average distance of 983.2 m from the nest, and at four weeks broods had moved an average distance of 1580 m. Movements were greater in burned brome and undisturbed bluestem (*Andropogon gerardi*) and sweet clover (*Melilotus alba*), and less in grazed and burned bluestem, indicating a preference for disturbed bluestem habitats. Alfalfa was also used extensively and the author noted he saw more invertebrates in alfalfa fields and recently burned sites. Successful brood home range size averaged 82.6 ha compared to 133.8 ha for broodless females.

In North Dakota, Newell (1987) found GPC broods most often used alfalfa (41% of locations) and planted prairie hay (37.9% of locations) habitats. Cash crops and pastures with cattle present were avoided by both broods and broodless females. Both broods and nonbrood hens used disturbed habitats of at least 40 ha with vegetative heights 25-50 cm the majority of the time. Newell (1987) found habitat use was influenced by vegetation height which was determined by land use practices. Therefore, habitat use was thought to be determined by habitat disturbance regime first and community type second. The intensive use area of brood home ranges averaged 40.4 ha compared to 85.8 ha for broodless females. Hens that nested later in the season had broods with smaller home range sizes because advanced vegetative growth provided more suitable brood habitat, thereby decreasing movements and increasing survival rates.

In Wisconsin, Toepfer (1988) presented more evidence that newly hatched GPC chicks move from undisturbed residual vegetation to less dense cover in search of food and increased mobility. Broods were found in habitats undisturbed during the season of use, although the sites had been disturbed within the previous two years. Broods were described as using “disturbed regrowth” which provided superior height, minimal residual vegetation and probably increased invertebrate abundance, particularly in two month old spring burns. 95% of brood locations were in grass or mixed grass/forb (mostly *Solidago*) habitats or the edge between them. Therefore, non-grass habitats were thought to be relatively unimportant and higher forb quantities may have decreased chick mobility. Vegetation height at 64.9% of brood locations was 26-50 cm and was created by taller grass species including brome (*Bromus inermis*), timothy (*Phleum pretense*) and quackgrass (*Agropyron repens*), though, since species were different among study areas, the author indicated that vegetation structure and form were more important for brood use than species composition. The average brood home range was 253 ha.

Also working in Wisconsin, Golner (1997) reported results in support of Toepfer (1988) where he found 77% of GPC brood locations to be in grass and grass/forb habitat types. Broods avoided habitats disturbed the year of use and selected habitats infrequently disturbed (4-6 years since the last disturbance), and disturbed with specific management techniques (i.e. burning and grazing), suggesting disturbance methods are important in the selection of brood habitat. 71% of brood locations were in habitats grazed 4 years prior to use. 40% of brood locations were in habitats 3 and 5 years after burning. Broods showed little use for mowed habitats or habitat treated with herbicides, regardless of time since last disturbance. Broods used hay, oats, and corn that were cultivated the year of study and also farmed fields left idle for ≥ 6 years. The average home range size of successful broods was 90 ha. The seasonal (pre-nesting, nesting, brood, post-brood) average home range for hens that raised successful broods was 173 ha, versus those with unsuccessful broods at 19 ha.

Keenlance (1998) reported similar GPC brood habitat selection results to Toepfer (1988) and Golner (1997) where broods showed a preference for grass, grass/forb and forb/grass cover types while avoiding forb, forb/shrub, wooded and agricultural sites. Selected habitat types were disturbed 1, 3 and 4 years prior to brood use. Habitats disturbed the same year as data collection were avoided. Nonbrood rearing hens also selected grass/forb and grass habitat types but were found in these areas the same year they had been disturbed, as well as 1, 5 and 6 years since disturbance. They were found to avoid agricultural, wooded and forb/shrub sites and areas disturbed 3 years prior to data collection.

Macro-habitat analysis in Missouri showed that in contiguous grassland landscapes with large blocks of habitat, 55.8% of GPC brood locations were in native prairie, 28.3% in mixed grass pastures and only 16% were in agricultural fields (Ryan et al. 1998). The inverse was true in mosaic landscapes of smaller grassland tracts where 68.1% of brood locations were in scattered the agricultural plots, 23.4% in mixed grass pastures and 11.7% in native prairie. Brood movement was much higher in the prairie mosaic landscape where average home range size was 379 ha, compared to 219 ha in the contiguous landscape.

Studying both sharp-tailed grouse and greater prairie chicken in South Dakota, Norton et al. (2010) found GPC broods used flat, lowland landscapes (< 0.5% slope) and selected habitats dominated by western wheatgrass (*Pascopyrum smithii*), Japanese brome (*Bromus japonicas*), green needlegrass (*Nassella viridula*) and mixed forbs. It was thought these vegetation communities, in particular when interspersed, offered suitable invertebrate abundance and increased chick mobility. Both species seemed to avoid monotypic smooth brome habitats which the authors felt likely provided few invertebrates and little overhead cover from predators due to cattle grazing. Vegetation visual obstruction height at GPC brood sites averaged ≥ 26 cm.

Most recently, comprehensive reports on GPC ecology in core GPC range have included components on brood habitat. In eastern Kansas, McNew (2010) reported higher survival rates for broods in grasslands fragmented by cultivation, but practicing longer burning rotations and moderate cattle grazing. Contiguous grasslands with annual spring burns and early intensive grazing showed poor reproduction. This is in contrast to Ryan et al. (1998) who suggested contiguous grassland blocks support increased GPC productivity, thereby highlighting the importance of land use patterns and grassland disturbance regimes and their impact on suitable brood rearing habitat. Young broods moved from unburned nesting sites to habitats burned in the spring of the year of use where the authors documented an increase in bare ground and forbs (McNew et al. 2011*b*). Similar to Svedarsky (1979), the average distance between nest locations and two week old broods was 871 m, suggesting undisturbed nesting habitat should occur < 1 km from disturbed brood habitat.

Unlike previous studies that documented broods occupying disturbed habitats, Matthews et al. (2011) found that broods in southeastern Nebraska selected undisturbed cool season CRP grasslands (29% of locations) more often than disturbed rangelands (27% of locations), possibly due to vegetation structure altered by intense cattle grazing. They avoided cropland (7% of locations). Like McNew et al. (2011*b*), selected brood locations showed more bare ground and forbs present. The average vertical obstruction reading at brood locations was 24 cm. Most notably, Matthews et al. (2011) did not associate brood survival with habitat use, but found it to be a function of hatch date and brood age where survival decreased with progressing hatch dates and increased with brood age. The authors suggested this non-association with land cover could be due to the way the habitat was measured, or because all cover types used were equally poor brood habitat. High chick mortality caused by high predation rates (Schole et al. 2011) made it difficult to discern the effects of habitat on brood survival. Poor quality, fragmented habitats have been linked to increased predation pressure (*see* Schroeder and Baydack 2001, McNew 2010).

In the Sandhills of north central Nebraska, Anderson (2012) found GPC broods chose habitats according to availability on the landscape, with most locations in upland sites which are grazed considerably. The average visual obstruction reading recorded at brood locations was the lowest among those previously reported at 6.92 cm. Models used in analysis showed vertical obstruction reading and litter depth (average 0.06 cm) as the strong predictors in brood habitat selection. Litter depth also had the strongest effect on daily brood survival where greater litter depth meant taller cover for concealment from predators. Unlike most other studies, Anderson (2012) did not find a significant relationship between brood habitat selection and the presence of forbs, though forbs were identified as important in the daily brood survival model.

GPC brood habitat is frequently described as disturbed, forb-dominated vegetation and although it is often assumed GPC broods select for these habitat characteristics in search of sufficient invertebrate numbers, only Jones (1963) in Oklahoma has sampled the vegetation looking for associations between invertebrate availability and habitat type at GPC brood locations.

Brood-Invertebrate Literature

The importance of invertebrates in the diet of galliforme chicks lies in their nutrient content. They provide approximately four times the amount of protein as compared to plant food, of which 70-90% is highly digestible vs. the 24-48% digestibility of protein in plants (Savory 1989). Invertebrate protein also provides more vitamins and amino acids that are essential to the development of muscle and feathers (Savory 1989, Woodard et al. 1977, Moreby 2004), thereby reducing the time for chicks to fledge and enhancing their ability to avoid predators (Woodard et al. 1977, Moreby 2004).

Partridge and other grouse species

The majority of research on young galliforme-invertebrate dynamics has been carried out in Western European countries where the duration of grouse studies is longer than those carried out in North America (Potts and Robertson 1994, Sotherton 2000). One of the first studies was completed by Ford et al. in 1938 on grey (Hungarian) partridge in Great Britain where crop examination revealed the subsistence of chicks less than 2 weeks of age to be almost exclusively invertebrate fauna, particularly weevil larvae (*Phytonomus* larvae), fleas (*Sminthurus viridis*), aphids (Aphididae) and ant cocoons (Formicoidea cocoons). Within the 3rd week of life, their diet evolved to include only plant material. It was hypothesized that chicks ate invertebrates in part because of their early-age pecking habits. This practice was suggested again by Riley and Davis (1993) where lesser prairie chicken brood foraging sites were identified by signs of pecking and scratching. Because the invertebrates found to be most abundant in the partridge chicks' crops were those commonly found in the habitat from which the specimens were taken, Ford et al. (1938) concluded that the birds likely chose their habitat first and then ate those invertebrates that were most abundant and easiest to catch.

Numerous partridge ecology studies have followed the lead of Ford et al. (1938). Cross (1966) concurred that young partridge chicks feed largely on invertebrates and co-published results (Southwood and Cross 1969) showing that chick survival rate is not density dependent, but contingent upon invertebrate abundance more than any other limiting factor (i.e. weather and/or predators), and that invertebrate size, numbers and biomass vary across different habitat types. Grasslands hold higher invertebrate numbers and biomass compared to agricultural fields, and cereal crops treated with herbicides show even fewer invertebrate numbers, thereby explaining the significant declines in partridge population numbers (Southwood and Cross 1969). Like Ford et al. (1938), Southwood and Cross (1969) analyzed chick crops and also found that young partridge chicks feed on those invertebrates most abundant and readily available for consumption.

Throughout the 1970s, G.R. Potts built upon these findings and continued detailed research into the effects of herbicides, insecticides and other modernized farming techniques on heavily utilized partridge brood cereal habitats (1970, 1971, 1978, 1980). He found partridge chick survival was adversely affected by decreased invertebrate availability caused by the increased use of herbicides and insecticides in cereal crops (1971, 1978). Green (1984) published results substantiating Potts findings and further compared partridge chick diets in different habitats by analyzing faecal samples. Rands (1985, 1986) reported that average brood size increased alongside increasing invertebrate abundance and smaller home range size. Partridge broods in Poland utilized habitats with higher invertebrate populations which in turn were dependent on habitat size and cover (Panek 1997). Dahlgren (1990) found that partridge chick survival was correlated to egg volume which was, in turn, determined by the amount of invertebrate protein consumed by egg-laying hens. He also found that once hatched, a partridge chick’s final growth weight (measured at 17 weeks) was dependent upon the protein components of their juvenile diet. Thus, partridge chick survival was likely affected by both the amount of invertebrate protein in egg-laying hen diets and the post-hatch consumption of invertebrates by chicks themselves (Dahlgren 1990).

Most recently, Borg and Toft (2000) found that young partridge chick survival increased when more than one species of invertebrate was made available for consumption and that greater invertebrate diversity may be more important than simply an increase in invertebrate abundance. Their findings support those of Krebs and Avery (1984) who saw increased chick survival rates when more than one prey species was made available for consumption, indicating that invertebrate quality may be just as important as abundance when evaluating habitats for insectivores (Borg and Toft 2000).

Corroborating the pioneering findings of Ford et al. (1938), studies on greater prairie chicken, ring-necked pheasant, sharp-tailed grouse, sage grouse, northern bobwhite quail, black grouse and capercaillie, have shown high amounts of invertebrate material in the crops and faecal samples of young chicks with continual declines in animal matter as they age (Schwartz 1945, Loughrey and Stinson 1955, Kobriger 1965, Peterson 1970, Pepper 1972, Hurst 1972, Kastdalen and Wegge 1984, Rumble et al. 1988). Moreover, there is no shortage of studies documenting the role of invertebrates in the growth and survival of various grouse species (Southwood and Cross 1969, Potts 1970, 1971, 1978, 1980, Green 1984, Rands 1985, 1986, Hill 1985, Jorgenson and Blix 1985, Erikstad 1985, Johnson and Boyce 1990, Drut et al. 1994, Panek 1997, Park et al. 2001, Gregg and Crawford 2009). Jorgensen and Blix (1985) supported Southwood and Cross' 1969 partridge study when their laboratory study of willow ptarmigan chicks confirmed invertebrate availability as the primary limiting factor in brood survival, and temperature per se was of little consequence. Conversely, Erikstad (1985) felt that weather (temperature and precipitation) influenced invertebrate availability, foraging time and food intake, thereby affecting willow ptarmigan chick survival. Hill (1985) found that pheasant chick survival rates were correlated ($p = 0.01$) with increased invertebrate abundance, and believed that, overall, food supply determined the movement of broods and the habitats they chose, as opposed to habitat first determining brood location as suggested by Ford et al. (1938). Johnson and Boyce (1990) correlated ($p < 0.02$) the survival of captive sage grouse under 21 days old with invertebrate quantity. In Oregon, long term productivity estimates of sage grouse (indexed by chick numbers) were in accordance with measured forb and invertebrate consumption (Drut et al. 1994). Growth rates and survival increased for red grouse chicks in Scotland in habitats with greater invertebrate abundance (Park et al. 2001). Lepidoptera availability has been associated with brood survival for Nevada and Oregon greater sage-grouse broods (Gregg and Crawford 2009). It has even been shown that certain grouse species have temporally adapted hatch dates and brood-rearing activities to times when preferred invertebrates are at their maximum availability (Baines et al. 1996).

Brood Range Size

Several studies on different galliforme species have shown that the movement of broods increases as invertebrate availability decreases (Southwood and Cross 1969, Erikstad 1985, Hill 1985, Rands 1986, Bergerud and Gratson 1988, Drut et al. 1994, Park et al. 2001). Increased brood movement further correlates to decreased growth rates and increased chick mortality (Green 1984, Erikstad 1985, Rands 1986, Hill 1985, Bergerud and Gratson 1988, Park 2001) presumably due to high energy costs and increased exposure to predators (Baines et al. 1996, Svedarsky et al. 2003).

Prairie chickens

Efficacious research on the prairie chicken-invertebrate dynamic has been minimal thus far. The link between invertebrate consumption and prairie chicken brood survival can be inferred based on many of the above publications, and, as populations steadily decline, the role of invertebrates in brood habitat becomes increasingly important. Perhaps because it has been a candidate for listing under the Endangered Species Act since 1998, the lesser prairie chicken (LPC) is the congeneric to have received the most attention in regards to brood diet and productivity. In the sandy mixed prairie of south eastern New Mexico, Davis et al. (1980) found 100% invertebrate material in the crops of chicks 1-4 weeks old; the same measurement recorded for chicks 5-10 weeks old was 99.3%. Subsequently, the same study identified LPC brood foraging habitat to be dominated by shrubs and suggested its utilization was related to invertebrate abundance (Riley and Davis 1993). In south western Kansas, Jamison et al. (2002) were able to correlate invertebrate abundance in sand sagebrush habitat with an increase in forbs. This study area was comprised of fragments of native sand sagebrush prairie rangeland vegetated primarily by sand sagebrush (*Artemisia filifolia*), gramas (*Bouteloua* spp.), bluestem grasses (*Andropogon* spp.) and forbs of ragweed (*Ambrosia* spp.), sunflowers (*Helianthus* spp.) and Russian thistle (*Salsola iberica*) (Jamison et al. 2002). Although, like Hill (1985), they believed it likely broods chose use areas based on invertebrate numbers, they could not statistically discern whether broods selected for invertebrate biomass or forb abundance.

Across the same LPC study area surveyed by Jamison et al. (2002), Hagen et al. (2005) demonstrated that lesser prairie chicken broods likely select for invertebrate abundance first, and habitat second. Furthermore, vertical obstruction readings in various brood and non-brood habitats suggested that vegetation structure (i.e. vertical density) was more important to brood usage than vegetation type, corroborating observations made by Hamerstrom et al. in 1957 where vegetative characteristics played the dominant role in prairie chicken habitat selection. This is also true of invertebrate distribution and abundance which is determined by vegetative structure and complexity (Murkin et al. 1994). Thus, vegetation structure has the potential to influence both invertebrate abundance and prairie chicken habitat usage.

Research on GPC brood diet and habitat remains restricted to Jones (1963) and Rumble et al. (1988) whom reported that GPC broods forage for invertebrates in areas of tall vegetative cover with forbs, but no association is made to brood success.

Initial efforts towards Attwater's prairie chicken (APC) recovery determined that poor reproductive success was the primary reason for population declines, but researchers were unsure if numbers had decreased due to poor nesting success and/or a decrease in chick survival rates (Peterson and Silvy 1996). Griffin et al. (1997) were able to establish a relationship between APC population declines and a decrease in invertebrate abundance and hypothesized that the combined effects of insectivorous cattle egrets (*Ardea ibis*), destructive red imported fire ants (*Solenopsis invicta*), and the increased use of insecticides were factors responsible for fewer invertebrates. Such theories may soon find support in recent preliminary findings that show an increase in invertebrate abundance at study sites where fire ants have been targeted with chemical controls (Morrow et al. 2010). Recent extreme droughts throughout APC range may also have increased invertebrate numbers while decreasing fire ant activity (Morrow et al. 2010). This is in contrast to earlier hypotheses that suggested drought would decrease plant growth and negatively impact invertebrate abundance (Peterson and Silvy 1994).

The federal Attwater's Prairie Chicken Recovery Plan outlines several objectives including a goal to increase chick survival rates in support of wild population management (USFWS 2010). Limiting factors thought to influence brood survival are broken into three categories: physiological (genes, disease), behaviour (maladaptive parental behaviour), and habitat quality (invertebrate availability, impact of imported red fire ants) (USFWS 2010). Research to address these effects is underway. So as not to negatively impact already fragile APC populations, some studies are being conducted on other non-endangered prairie chicken populations. Pratt et al. (2003) reported similar biomass between Minnesota GPC invertebrate samples and Texas APC invertebrate samples collected at brood sites. However, Minnesota had a significantly higher number of invertebrates, indicating that in Minnesota, GPC brood habitat produced smaller invertebrates while larger invertebrates could be found in Texas APC vegetation. The difference in invertebrate size between study areas could prove important as Davis et al. (1980) suggested that LPC chicks selected smaller invertebrates because they were not able to consume larger grasshoppers. In a captive feeding study, Whitmore et al. (1986) observed young pheasant chicks chose invertebrates partially based on consumable size and Hurst (1972) found northern bobwhite chicks selected invertebrates less than 8mm long and weighing under 0.005g.

Forbs and Legumes

As is common to habitat-invertebrate research, many studies speak specifically to positive relationships between uncultivated forb quantity and invertebrate abundance (Jones 1963, Southwood and Cross 1969, Hill 1985, Burger et al. 1993, Drut et al. 1994, Jamison et al. 2002, Hagen et al. 2005). The overall benefit of forbs is perhaps best evidenced by their near ubiquitous presence in the management recommendations of grouse brood-habitat studies (Hurst 1972, Kirsch 1974, Whitmore et al. 1986, Jackson et al. 1987, Burger et al. 1993, Golner 1997, Keenlance 1998, Riley et al. 1998, Jamison et al. 2002, Hagan et al. 2004, Rodgers 2005, Norton et al. 2010, Anderson 2012), and many consider it rather common knowledge that the presence of forbs in the vegetative landscape will increase the invertebrate populations young grouse depend on (Rodgers 2005). Of note, some leguminous forbs such as alfalfa (*Medicago sativa*) (cultivated) and sweet clover (*Melilotus alba*) (uncultivated), while diversifying stand structure and supporting invertebrates, also effect soil quality by fixing nitrogen, releasing deep micronutrients, providing pollen (an important food resource for many invertebrates), and increasing plant biomass (Rodgers 2005, Burger et al. 1993, Koricheva et al. 2000). Still, other cultivated leguminous forbs such as soybeans (*Glycine max*) seem to hold very little invertebrate biomass and this is perhaps why many studies show GPC broods avoid cropland habitats (Svedarsky 1979, Newell 1987, Keenlance 1998, Matthews et al. 2011). Remarkably, some studies have shown GPC brood habitat selection *for* soybean and other cultivated crops such as corn (*Zea mays*) (Ryan et al. 1998, Emery 2009), indicating the important role of landscape scale habitat availability in GPC range. More research is needed on the type of forb(s) thought to attract invertebrate prey and predators.

Habitat-Invertebrate Literature

Habitat-invertebrate management for broods

Much of the literature on galliforme brood dietary resources examines the vegetation composition and habitat management regimes that maintain invertebrates on the landscape (Madison et al. 1995 (northern bobwhite), Panek 1997 (grey partridge), Svedarsky et al. 2003 (GPC), Hagen et al. 2005 (LPC), Doxon and Carroll 2010 (ring-necked pheasant and northern bobwhite) and Rhodes et al. 2010 (greater sage grouse)). In Kentucky, Madison et al. (1995) presumed good northern bobwhite habitat to contain mostly forb vegetation hosting high invertebrate abundance with adequate bare ground. They found that subsequent to the initial burn, fall disking provided the best brood rearing habitat for the following year, while the use of herbicides provided the best habitat by the third year. Studying the grey partridge in Poland, Panek (1997) found more broods utilized small (< 10 acres) agricultural fields where high invertebrate abundance was associated with diverse crop mosaics and decreased pesticide usage as compared to large fields where high quality cover was compromised by pesticides and homogeneity. In Kansas, Hagen et al. (2005) suggested LPC brood rearing habitat be composed of 43-60% grass, 24-43% shrub and 13-26% forb for optimum invertebrate populations. Also in Kansas, Doxon and Carroll (2010) found that ring-necked pheasant and northern bobwhite chicks foraged with the least impediment in native vegetation which included Maximilian sunflower (*Helianthus maximiliani*), purple prairie clover (*Dalea lasiathera*), prairie coneflower (*Raliba columnifera*) and Illinois bundleflower (*Desmanthus illinoensis*). Untreated weedy winter wheat (*Triticum aestivum*) fields also provided sufficient mobility and invertebrate populations. Advocating for more ground level open space, light disking and burning were recommended management techniques in Kansas CRP fields. Studying fire ecology in Wyoming sage grouse habitat, Rhodes et al. (2010) found cover was approximately 50% less after burning due to sage brush loss. Forb quality and abundance did not increase after fire and Hymenoptera (ant) populations decreased following burning, possibly due to insufficient precipitation (Arenz and Joern 1996), confirming that fire is a poor management technique in sagebrush steppe ecosystems (Rhodes et al. 2010).

Habitat management for invertebrates

Prairie landscape management practices influence invertebrate abundance and diversity (Arenz and Joern 1996) and, by association, the sustainability of many insectivorous wildlife populations. The evolutionary history of prairie landscapes shows the symbiotic relationship of grasslands and disturbance elements, specifically, natural and First Nations ignited fires and bison grazing (Kirsch 1974, Vodehnal and Haufler 2008). Thus, it is likely that many invertebrate species, and, in turn, prairie birds are well adapted to these types of historical disturbances and/or techniques that mimic their results (Van Amburg et al. 1981, Tester and Marshall 1962, Samson et al. 2003, Rodgers 2005, Fuhlendorf et al. 2006). Therefore, in order to grow resilient, diverse, fertile grassland ecosystems, natural and/or human-engineered imitations of evolutionary periodic disturbances remain necessary to remove excess accumulated litter, precipitate nutrient cycling and inhibit woody species invasion (Rodgers 2005, Farrand et al. 2007), thereby fostering grassland invertebrate forage and their grouse predators.

The most notable disturbance techniques administered across prairie grasslands include burning (sometimes in conjunction with disking), mowing, grazing and, more infrequently, herbicides. A complex set of factors help determine which method will likely be the most beneficial to birds and their invertebrate prey including, the regional location (specifically latitude) of the site which influences weather/precipitation and phenology, site disturbance history, site size, technique intensity, frequency, and timing, as well as the species' under consideration (Leopold 1933, Vickery et al. 2001, Svedarksy et al. 2003, Farrand et al. 2007). The short term and long term impacts of the method used must also be considered since the frequency of mowing and grazing techniques on conservation lands is generally limited (Farrand et al. 2007). In Minnesota, each of these techniques should be carried out no more than once every three years on CRP (Conservation Reserve Program) designated lands (Anonymous 2012*c*). Generalizations are employed for practical purposes, but it must be remembered that the prairies are a complex ecosystem where different bird and invertebrate species will show unique responses to various management techniques which tend to change across the geographic range of the species' (Van Amburg et al. 1981, Warren et al. 1987, Swengel 2001, Jonas et al. 2002, Atkinson et al. 2005, Farrand et al. 2007).

Burning

As an ancient prairie disturbance type, fire is considered a natural biological control and is commonly used in grassland management regimes (Kirsch 1974). However, modern burning techniques often mimic evolutionary processes inadequately with too frequent or infrequent (fire suppression) burns as well as inappropriate timing. In Minnesota, managers tend to burn grassland habitats in the spring during vegetative regrowth and when many birds are nesting, not in the summer as was historically common (J. Toepfer pers. comm.). As one would expect, the results of burning are mixed and occur relative to many variables in the habitat at the time of study. Information on how fire affects grassland invertebrate populations is lacking (Branson 2005).

Extensive research on invertebrate-disturbance relationships was carried out in Britain throughout the seventies (Morris and Lakhani 1979, Morris 1979, 1981*a*, 1981*b*, Morris and Plant 1983). Among his findings, Morris (2000) termed the effects of fire on habitat structure as "catastrophic" because not only did it reduce vegetative height, it also removed most litter. Yet, his preliminary findings showed little change in Hemiptera abundance even though species richness and diversity decreased. Halvorsen and Anderson (1979) reported insignificant increases in invertebrate biomass on burned plots in June, July, August and October in central Wisconsin. In Kansas tallgrass prairie, Evans (1988) noted that forb abundance correlated to forb-feeding Orthoptera abundance ($p > 0.05$), highlighting that infrequent burns (> 3 years) produced an increase in grasshopper species richness. Tester and Marshall (1961) reported Orthoptera abundance on Minnesota remnant tallgrass prairie as relative to the amount of litter remaining after the burn, where minimal litter showed few grasshoppers and moderate litter cover increased grasshopper abundance. Conversely, Coleoptera populations were found to be associated with sparse litter and were highest in burned plots one year following disturbance. Nearby on tallgrass prairie in Clay County, Minnesota, Van Amburg et al. (1981) added to numerous studies that detail how various invertebrate species, usually grouped by Order, will respond differently to fire management (*see* Siemann et al. 1997). Overall, eleven taxa increased with burning, including Lepidoptera, wasps, plant hopper

Homoptera, mites, Coleoptera and some Diptera species; ten taxa increased with no burning including ticks, ants, Orthoptera and two Diptera families; and seventy-five taxa showed no response, in particular, Hemiptera (Van Amburg et al. 1981). A study in oak savanna just north of Minneapolis found burning initially decreased invertebrate richness and abundance, especially Homoptera and Lepidoptera, but the frequency of fire showed no effect on long-term invertebrate abundance indicating that, overall, burning has little impact on invertebrate populations (Siemann et al. 1997). Similarly in North Dakota, Branson (2005) found grasshopper densities decreased subsequent to a fall wildfire, but the reduction was temporary and populations rebounded the following year.

Summarizing the literature up until 1987, Warren et al. (1987) wrote that, overall, burning modifies habitat to the benefit of most arthropod populations. The effects of fire on invertebrate populations are dependent on several factors including the invertebrate species involved in the disturbance, the fire characteristics, size and timing relative to the invertebrate life stage, post-burn weather and the degree of habitat re-structuring. Fire effectively removes standing vegetation and litter, often altering vegetation structure while making things drier. In doing so, the destructive disturbance increases invertebrate exposure to predation and influences emigration and immigration to the site; as the flora returns, so do the invertebrates. Perhaps post-burn habitats look attractive to invertebrates because the vegetation has had a reprieve from insect predators (Swengel 2001).

In their discussion on prairie invertebrates, Arenz and Joern (1996) emphasized that grassland disturbance techniques, like burning, establish heterogeneous plant communities which augment invertebrate diversity. However, they note fire can be overly destructive if the climate is too dry for proper vegetative regrowth. Even ancient tallgrass prairies required three to six years for recovery post-burn. Likewise, high frequency fires can decrease plant diversity (especially forbs) generally decreasing invertebrate populations. Spring prairie burns in particular can be hard on invertebrates emerging from dormancy (Arenz and Joern 1996). Therefore, the key to fire management is a mosaic/patchwork burn pattern that leaves 25-50% of the plant community as refuge for invertebrates during the burn, and adjacent populations from which immigration can commence post-burn. Invertebrate abundance initially decreases immediately following a burn, and population rebounds depend on their access to vegetative regrowth (Swengel 2001). The ability of invertebrates to recolonize a burn site is the most important factor in invertebrate abundance post-disturbance (Swengel 2001), consequently, 100% burns can endanger many species (Arenz and Joern 1996). Patch-burn mosaics through fields and over landscapes can foster various flora and fauna successional stages simultaneously, successfully sustaining and rejuvenating grassland ecosystems at the same time (Arenz and Joern 1996, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Farrand et al. 2007, Engle et al. 2008).

The use of fire as a management tool is further augmented by its nominal cost and the unlikely possibility invertebrates will establish genetic resistance to it as they can with chemical treatments, since they evolved with fire (Warren et al. 1987). Also, burning concurrently suppresses woody invasive plants and increases the productivity of desirable grasses while recycling nutrients from dead vegetation (Warren et al. 1987).

Grazing

As a management tool, grazing shares many characteristics with burning. Like fire, grazing frequency and intensity must balance between total consumption with no residual, and minimal disturbance resulting in dense vegetative stands of little use to most wildlife. Grazing also shares historical significance with fire by means of nomadic bison. Modern fenced ranching has made current grazing methods more complex since frequency, intensity, timing, and the species used (cattle, sheep, etc.) can vary almost indefinitely (Tester and Marshall 1961, Morris 2000, Ryan et al. 2006, Farrand et al. 2007). And yet it is the most widely used grassland management tool in Britain and North America (Morris 2000, Krausman et al. 2009) likely due to its ability to satisfy both agricultural demands and grassland management needs.

A number of studies have considered the effects of grazing on GPC populations and generally conclude that GPC can tolerate light to moderate livestock grazing (Rice and Carter 1982, Manske et al. 1988, Eng et al. 1988, Fredrickson 1996, Ryan et al. 2006), some recommending its use in combination with rotational fire regimes (ie. patch-burn grazing) that increase plant heterogeneity (Robbins et al. 2002, McNew et al. 2012). Recent rangeland management in core GPC habitat has seen populations tumble alongside annual spring burns combined with early intense grazing (Robbins et al. 2002, Svedarsky et al. 2003, McNew 2010). Rodgers (2005) suggested that short, intense grazing periods outside of nest and brood rearing season creates more productive grasslands via cattle treading than does low-density long-term stocking rates. On the Fort Pierre National Grassland in South Dakota, where the highest GPC brood survival rate has been recorded, researchers recommend rest-rotation grazing that has created grassland mosaics conducive to all GPC life stages (Norton 2005). Yet, overall, there remains a dearth of information with regard to the effects of experimental grazing regimes on nest success and brood survival for most grouse species. And, as with fire, there are even fewer studies examining the effects of grazing on the forb and invertebrate communities that sustain grouse production (Morris 2000, Krausman et al. 2011).

A number of recent European studies concur that invertebrate abundance is negatively affected as grazing intensity increases. Preliminary results by Morris (2000) indicate Hemiptera abundance increases subsequent to grazing cessation. Assessing grasshopper populations, O'Neill et al. (2003) found most Orthoptera species in highest abundance on ungrazed pastures and on grazed pastures 4-6 weeks after livestock were removed. Buckingham et al. (2006) and Dennis et al. (2008) reported invertebrate biomass and avian usage highest in ungrazed pastures and those with decreased grazing pressure. Vickery et al. (2001) felt light stocking and moderate grazing combined with small amounts of organic fertilizer would encourage vegetation heterogeneity and increase invertebrate abundance. Eschen et al. (2012) found that light early grazing fostered invertebrate abundance, but early cessation increased cover and litter to undesirable volumes where vegetation heterogeneity declined, likely impeding bird foraging.

Light, late season grazing outside perennial regrowth periods was linked to increased plant productivity and abundant invertebrate populations early on in North America (Smith 1940), and light, rotational grazing is still considered a beneficial disturbance type best used over large landscapes across the American Midwest (Arenz and Joern 1996). Initial studies showed Orthoptera (*Acridiae*) thriving in heavily grazed pastures in Oklahoma (Smith (1940), while low intensity grazing had no effect on Orthoptera populations in northwest Minnesota (Tester and Marshall 1961). Analyzing Orthoptera species response in South Dakota, Quinn and Walgenbach (1990) associated Orthoptera species richness with grass richness and cover where higher populations of mixed-forb and certain grass-feeding Orthoptera were found in ungrazed pastures with tall grass, and grass-obligate Orthoptera populations increased in grazed, short grass pastures. Fire frequency in Kansas did not impact Orthoptera species richness or diversity, but the heterogeneous habitat structure created by grazing significantly increased Orthoptera species richness and abundance, although the presence of forbs had no effect (Joern 2005). Researching grazing effects on pest management in Montana, Onsager (2000) reported decreases in Orthoptera populations with twice-over rotational grazing regimes, a method that coordinates rotational grazing with grass growth stages that foster vegetative productivity. Conversely in North Dakota**,** Branson and Sword (2010) observed Orthoptera density, diversity and species richness increased using twice-over rotational and patch-burn grazing regimes. Indeed, many recent studies (Arenz and Joern 1996, Fuhlendorf and Engle 2004, Fuhlendorf et al. 2006, Farrand et al. 2007, Engle et al. 2008) have begun to recommend patch-burn grazing systems that create a shifting mosaic of heterogeneous vegetation structure and composition, correlating to increased invertebrate biomass and abundance (Engle et al. 2008) and avian diversity (Fuhlendorf et al. 2006).

As with burning and mowing, grazing decreases overall vegetation, but it also generates additional impacts that should be highlighted. Most notably, vegetation composition and structure are further diversified by means of livestock treading, dung and selective palates that can influence the nutritional quality of vegetative regrowth (Arenz and Joern 1996, Morris 2000). Overall, grazing has the biggest impact on above ground invertebrates (Arenz and Joern 1996), and although response to various treatments can be species specific (Swengel 2001), there is evidence that the majority of invertebrates benefit from less intense grazing regimes.

Mowing

Unlike burning and grazing, mowing is not a natural disturbance type and its use has no evolutionary basis from which to be measured. Yet, it is the most common management technique practiced by landowners on grassland conservation easements in the United States (Farrand et al. 2007). As a popular management tool, the effects of mowing on grassland bird populations have received much attention, especially the negative impacts of mowing on nest success (*see* Farrand et al. 2007). Yet there exists very little information on vegetative and invertebrate responses to mowing.

The dramatic effects of mowing on vegetation tend to be short lived (< 1 year) because, ultimately, reduced height and accumulated litter contribute to increased grass succession and productivity (McCoy et al. 2001). However, Dykes (2005) found mowing reduced forb abundance in Tennessee, and Rooney and Leach (2010) reported decreased plant species density in southeast Wisconsin prairies subsequent to decades of mowing in the early 1900s.

Analysis of invertebrate fauna in Britain showed response to mowing was species specific (Southwood and van Emden 1967). Plant-eating insect populations were higher in cut grass and predacious and decay-eating insects were more numerous in uncut grass.

Overall, mowing increased invertebrate density, but decreased abundance and biomass with smaller insects observed in mowed habitat (Southwood and van Emden 1967). Species within the Order Homoptera responded differently to mowing on a tallgrass prairie in Kansas where one species (*Cieadetta calliope*) preferred burned sites over mowing and the other (*Tibicen aurifera*) failed to appear after burning, and showed no response to mowing (Callaham et al. 2002). In northwestern Minnesota, Orthoptera populations were shown to increase subsequent to mowing, probably due to the increased litter present (Tester and Marshall 1961). In Kansas, Jonas et al. (2002) also noted species specific responses to mowing but determined that, overall, uncut, structurally complex fields with few exotic plant species hosted more invertebrates then did annually mowed native prairie. Dramatic declines were reported in Vermont when mowing decreased invertebrate biomass 36-82% as compared to uncut fields which saw invertebrate biomass increase over the course of Savannah Sparrow nesting season (Zalik and Strong 2008). In Switzerland, comparisons between frequently cut sites (2-3 times over the season beginning in May) and infrequently cut sites (1-2 times over the season beginning in July) showed the majority of invertebrate species were negatively impacted by intensively managed regimes (Giulio et al. 2001). In the Netherlands, Schekkerman and Beintema (2007) also found invertebrate abundance to be significantly higher in uncut fields. Humbert et al. (2009) analyzed the effects of mowing on invertebrates using wax invertebrate models and live caterpillars. They found that mower conditioners (machines that further cut and mulch grass to augment drying) more than doubled invertebrate mortality and ground dwelling invertebrates were significantly affected by tractor wheels. They also noted that large invertebrates were more vulnerable during mowing than small invertebrates. Because no vegetative cutting techniques are damage-free, the authors recommend there be areas left uncut during disturbance for invertebrate refuge, much like patch-burn techniques. Unfortunately, the method itself is generally non-selective. Without manager manipulation, mowers tend to cut all vegetation to the same uniform height, negatively impacting habitat heterogeneity (Arenz and Joern 1996, Morris 2000).

As with fire and grazing, the effects of mowing are dependent on frequency, intensity and timing. And, like burning, the initial impacts of mowing tend to be catastrophic (Morris 2000). Invertebrate numbers decrease substantially immediately following mowing, although less so than after fire (Swengel 2001). In addition to dramatic height reductions, mowing reduces or destroys other potentially useful landscape features such as ant and rodent mounds. Invertebrate mortality is accrued both directly and indirectly via casualties and habitat loss. And although response is species specific, the majority of invertebrates decline in abundance and diversity with decreased vegetative height. However, cutting can promote healthy invertebrate responses if done outside critical growth stages. If the species are still developing, mowing will kill the insects either directly or by destroying needed vegetative structure for various life stages (Arenz and Joern 1996). Just as with all disturbance techniques, patchy, rotational regimes that alternate frequency, intensity and timing, can improve conditions for invertebrate survival (Morris 2000).

Avian growth and survival rates can be influenced by low invertebrate biomass common to recently mowed fields, initiating longer foraging times and increased energy usage (Southwood and van Emden 1967, Schekkerman and Beintema 2007, Zalik and Strong 2008). The results of mowing (Farrand et al. 2007) further indicate brood rearing habitat would likely be impacted by decreased vegetative height, increasing chick exposure to predators; fewer forbs indicating less invertebrate forage; and increased litter accumulations hampering chick mobility.

Invertebrate response to different management techniques is complex. Generally, most species show fewer negative effects when disturbance frequency is reduced (Morris 2000). However, it is clear that invertebrates can and do respond positively to appropriate management techniques when they are targeted to specific habitat characteristics and the invertebrate species being managed (Arenz and Joern 1996, Swengel 2001).

Importance of Heterogeneity

The chief variable tying together all management practices, regardless of technique, is the heterogeneous nature of the vegetation they create. Murkin et al. (1994) advises that invertebrate distribution and abundance are determined by vegetative structure and complexity, and many grouse and passerine studies have concluded that structurally homogenous habitats decrease invertebrate and/or bird abundance (Southwood and Cross 1969, Baines et al. 1996, Evans 1988, Arenz and Joern 1996, Panek 1997, Siemann 1998, Knops et al. 1999, Morris 2000, Koricheva et al. 2000, Vickery et al. 2001, Giulio et al. 2001, Fuhlendorf and Engle 2004, Atkinson et al. 2005, Hagen et al. 2005, Buckingham et al. 2006, Fuhlendorf et al. 2006, Engle et al. 2008, Boyd et al. 2011). Boyd et al. (2011) defined heterogeneity as “the interspersion of various successional stages (or states) of the same general habitat type.” The authors suggest habitat heterogeneity be not simply a factor to consider, but a principle concept guiding disturbance management decisions.

Grassland Management: The Conservation Reserve Program

Grassland conservation easements that protect prairie acres have become essential management tools for both non-profit wildlife agencies (Pheasants Forever, Ducks Unlimited, Delta Waterfowl) and state and federal agencies (State Department of Natural Resources (DNR), Fish and Wildlife departments and Game agencies, United States Fish and Wildlife Service (USFWS), United States Department of Agriculture (USDA) (Anonymous 2011). The Conservation Reserve Program (CRP) was one of several programs written into the USDA Farm Bill of 1985. At the time, surplus crops were decreasing farmer profits. To reduce crop production and prevent soil erosion while maintaining farmer incomes, agricultural producers entered into decade(s) long contracts with the federal government where they were paid to plant resource conserving cover vegetation. The resulting grasslands, trees and riparian buffers improve, among other things, surface and groundwater quality, carbon sequestration, soil preservation, and wildlife habitat (Licht 1997, Barbarika 2009). The program has been amended four times since 1985 in an effort to improve its overall environmental contributions. In 1996, the Federal Agriculture Improvement and Reform Act established CRP benefits specific to wildlife and declared them equal with soil erosion and water quality benefits (Barbarika 2009). So far, all amendments have extended enrollment authority, thereby prolonging the life of the program.

The majority of avian-CRP studies have reported an increase in birds alongside the increase in federal reserve grassland habitat (Johnson and Schwartz 1993*a*, 1993*b*, Reynolds et al. 1994, Best et al. 1997, Farrand and Ryan 2005), but the response has fluctuated over time, dependent on location, seed mixtures planted, subsequent land management and the bird species being studied (Johnson and Schwartz 1993*a*, Rodgers 2005, Farrand and Ryan 2005). In North and South Dakota, waterfowl nest success increased alongside CRP plantings (Reynolds et al. 1994). As well, various passerine species have markedly improved their populations following CRP implementation in the North and Central Plains (Johnson and Schwartz 1993*a*, 1993*b*, Best et al. 1997). Naturally, CRP has benefitted some avian species more than others, but it can be difficult to predict the variables that influence non-response. For example, in the Midwest, grasshopper sparrows (*Ammodramus savannarum*) and dickcissels (*Spiza americana*) are reported to be among the most abundant species in CRP fields (Best et al. 1997), yet, further north, although densities have improved, their population trends continued to decrease post-CRP (Johnson and Schwartz 1993*b*), perhaps due to change in their South American wintering habitat (Reynolds et al. 1994). However, the benefits of CRP to breeding habitats are still expected to contribute to a reverse in these declines (Johnson and Schwartz 1993*a*, 1993*b*).

CRP and prairie grouse

In his review of Federal Conservation Programs (seven through USDA and five through USFWS), Riley (2004) asserted that prairie grouse populations have responded only to the USDA Conservation Reserve Program, and various state representatives have made similar assessments (*see* Nomsen 2005). Prairie grouse respond well to large blocks of undisturbed grassland (Johnson et al. 2011) and CRP is the largest of all Federal Conservation Reserve Programs where most fields are left idle, especially during nesting and brood rearing season (Riley 2004, Farrand et al. 2007). Following GPC population increases in several states post-CRP, the USFWS State of the Birds 2009 report considered the Federal Reserve program a “Reason for Hope” for GPC (North American Bird Conservation Initiative 2009). Positive GPC responses have been most notable in the Central and Northern Prairie regions while other, mainly southern populations have shown little variation or have continued to decline (Rodgers and Hoffman 2005, McLachlan et al. 2007). In Nebraska and Kansas, the beneficial contribution of CRP to GPC populations is overall moderate and estimated to have increased the population by 10-15% (Rodgers and Hoffman 2005, McLachlan et al. 2007). GPC populations increased with moderate expansion in response to CRP in both North and South Dakota as well (Rodgers and Hoffman 2005). The most northern GPC populations in western Minnesota have increased significantly with moderate range expansion, despite forb reductions in smooth brome monocultures (Toepfer 2003, Rodgers and Hoffman 2005).

CRP and invertebrates

Research specific to invertebrate populations in CRP easements is lacking. Assessing northern bobwhite brood habitat in north central Missouri, Burger et al. (1993) discovered high invertebrate abundance and biomass in CRP sites with red clover (*Trifolium pretense*) mixtures and noted the benefits of increased forb/legume forage for insects. As the season progressed, invertebrate numbers decreased and were lowest in early August. They also found few invertebrates in farmed soybean fields. Opposing findings are presented in Hull et al. (1996) whom did not find the invertebrate-forb relationship they were testing for, nor any significant relationship between invertebrates and songbird abundance. Habitat deficiencies and invertebrate collection methodologies were thought responsible. Evaluating the impact of site age, Millenbah (1993) reported invertebrate abundance was highest in young CRP fields (1-2 years old) and began to decrease after three years. In Texas, McIntyre and Thompson (2003) examined the invertebrate abundance in CRP plots of various plantings and phases of disturbance, as well as native prairie. Invertebrate diversity and abundance were highest at the native prairie site due to vegetation heterogeneity. But, invertebrate richness and abundance were found to be the same across all CRP types and in volumes sufficient for grassland bird usage.

Management of CRP

Many CRP fields across the Midwest retain the initial homogenous nature of early, less expensive CRP plantings (Rodgers and Hoffman 2005, Boyd et al. 2011) and common disturbance regimes have sometimes proven inadequate as productive wildlife habitat (Rodgers 2005). Deficient seed mixtures with ineffective management techniques can lead to excess litter accumulation, woody vegetation encroachment and the encouragement of tree planting (Rodgers 2005, Bidwell and Engle 2005).

The Farm Security and Rural Investment Act (2002 CRP amendment) prescribed an increase in the diversity of seeds planted, including more native species, and included mandates for periodic habitat disturbance outside of peak nesting seasons (Farrand et al. 2007). With heterogeneous landscapes the goal, several recommendations to improve current CRP conditions have been made. Since the benefits of habitat management are specific to location and species (Farrand et al. 2007), Bidwell and Engle (2005) have suggested targeting ecologically based approaches to site specific characteristics. This means that, prior to planting and disturbance, managers should determine regional native vegetation, the needs of indicator species studied and the habitats required for them to complete their life cycles.

To improve the overall value of grasslands for prairie grouse, recommendations integrate the planting of mixed, multi-species seed, including the use of beneficial non-invasive exotic species like alfalfa; easements established near or adjacent to existing grassland blocks; and more effective and safe disturbance regimes that improve plant productivity and increase forb abundance, while reducing litter accumulation and combating woody encroachment (Rodgers and Hoffman 2005, Rodgers 2005). The use of exotic, non-invasive vegetation as a surrogate for native flora is thought appropriate if the species augment habitat height and structure (Samson et al. 2003, Rodgers and Hoffman 2005).

As a grassland obligate species, GPC require open prairie for all life cycle stages, incorporating the need for short stands (booming ground), dense stands (nesting and roosting), and moderately dense vegetation that leaves room for increased mobility (brood rearing). It is thought successional heights between 30 and 75cm, or “shin-to-thigh high” (Rodgers and Hoffman 2005) would provide for all GPC phases of development. Grassland disturbance regimes that create heterogeneous patchy mosaics across the landscape are likely to provide superior predator protection and food resources (Bergerud and Gratson 1988), and will sustain multiple species better than homogenous ecosystems (Samson et al. 2003, Farrand et al. 2007). The relative distance between plots should also be taken into consideration. Especially evident in northwestern Minnesota, grouse have done best where CRP has been planted alongside blocks and within mosaics of preexisting grassland (Rodgers 2005) and agriculture, creating the vast expanses required for significant population growth (Hamerstrom et al. 1957).

Summary

Invertebrate abundance is influenced by vegetation structure and composition which is, in turn, dependent on habitat management regimes (Vickery et al. 2001). Together, these factors have made a significant positive impact on many prairie grouse populations (Rodgers 2005). There is a need to understand invertebrate-habitat associations important to GPC broods, and how grassland management practices affect these habitats (Svedarsky et al. 2003, Robb and Schroeder 2005). Ultimately, grouse brood habitat management is about achieving desired vegetative structures in local habitats that will increase invertebrate quality and abundance and provide cover without impairing chick mobility.

METHODOLOGY

This chapter begins with a description of the study area and a note on prairie invertebrates. Next, methods for GPC capture and radio collaring are discussed. This is followed by a description of vegetation and invertebrate sampling. The final section describes how the data was analyzed and looks at the following relationships: brood range size relative to invertebrate biomass; brood and permanent transect types relative to invertebrate abundance and composition; brood types relative to habitat characteristics and their relationship to invertebrate abundance; and permanent transect types (habitat management regimes) relative to invertebrate abundance and composition. These relationships illustrate invertebrate abundance and composition in vegetation types used by successful and unsuccessful GPC broods, and identify the management practices that impact them all.

Study Area

This study was carried out in the present day northern extent of United States greater prairie chicken distribution and remnant tallgrass prairie habitat in northwest Minnesota. Though recent genetic evidence suggests historical GPC distribution may have extended from central Minnesota through to Alberta, Canada, most believe pre-settlement Minnesota GPC populations were relegated to the southern edge of the state before they acquired more northern ranges (Ross et al. 2006, Kohn et al. 2008, Svedarsky et al. 1999, Partch 1973). Populations may have followed settlement and agriculture northward and by 1900, abundant GPC occurred across most of Minnesota, but for the far northeast and north central regions (Svedarsky et al. 1999, Anonymous 2012*a*).

Increasing croplands, fire suppression and forest encroachment initiated decreasing population trends and by the 1960s, most Minnesota GPC were relegated to about 1295 km^2 in the northwest corner of the state, occupying the remnant beach ridges of Glacial Lake Agassiz where sandy soils and glacial till prevented cultivation (Hamerstrom and Hamerstrom 1961, Svedarsky et al. 1999).

Forty years later, it is estimated that 13,383 GPC range over approximately 10,000 km^2 of northwest Minnesota, mostly in Polk, Norman, Clay and Wilkin counties (Rich et al. 2004, Larson and Bailey 2007). Coinciding with Minnesota's ecological boundaries, these counties fall within the Red River Prairie Subsection (15,987 km^2) of the Prairie Parkland Ecological Province (Anonymous 2006*a* and Anonymous 2006*b*) (Figure 1). The dominant landform is the large lake plain left behind by the southernmost lobe of ancient Glacial Lake Agassiz (Anonymous 2009). Remnant tallgrass prairie habitat (< 1% remains) can be found along dry, gravely beach ridges and sand dunes (Anonymous 2009). Approximately half of these remnants are currently protected as prairie preserves (Anonymous 2006*b*). Topography is level to gently rolling with many channelized rivers and streams and early spring flooding is common (Anonymous 2009, G. Huschle per. comm.). Clay, silt and sand lake sediments make up the Mollisols type soil fertilizing row crops which cover 89% of the area's landscape (Anonymous 2009, Anonymous 2006*b*). Most of the land is privately owned (97.4%) and the remaining 2.6% is owned publicly (Anonymous 2006*b*). The public land base includes numerous state Wildlife Management Areas and Scientific & Natural Areas, federal Waterfowl Production Areas and national wildlife refuges (Anonymous 2006*a*).

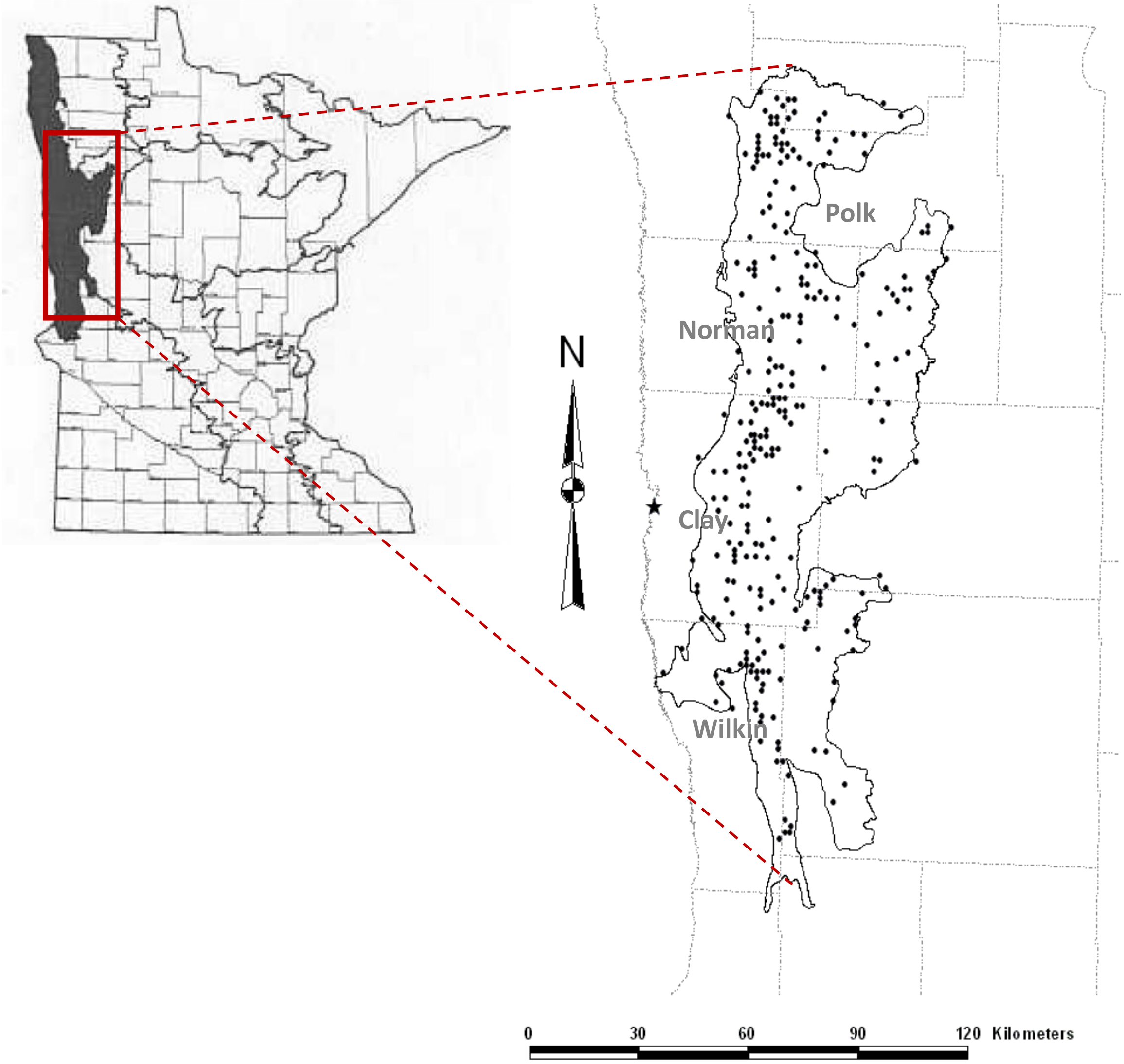

Figure 1. Minnesota greater prairie chicken range in the Red River Valley Prairie section of the Prairie Parkland Ecological Province. Taken from Larson and Bailey 2007 and The Citizens' Advisory Committee 2002.

Within this ecological setting, the study area centres on Norman and Clay Counties where the average summer temperature is approximately 19.4°C and the average yearly precipitation reaches 57.2 centimetres (Anonymous 2009) (Figure 2). In 2009, the study area’s average temperature from June through August was 24.2^{o}C and the average precipitation through the same time period was 8.3 centimetres (Anonymous 2012*b*). Agricultural fields of wheat (*Triticum aestivum*), soybeans (*Glycine max*), corn (*Zea mays*), sugar beets (*Beta vulgaris*) and sunflowers (*Helianthus annuus*) comprise much of the land cover, interspersed with pasturelands, various grassland types and scattered woodlots and treed windrows. Most privately owned grassland tracts are planted with cool season grasses, especially smooth brome (*Bromus inermis*), and relatively undisturbed native prairie sites are composed of both native and exotic plant species such as big blue stem (*Andropogon gerardi*) and Kentucky blue grass (*Poa pratensis*), respectively.

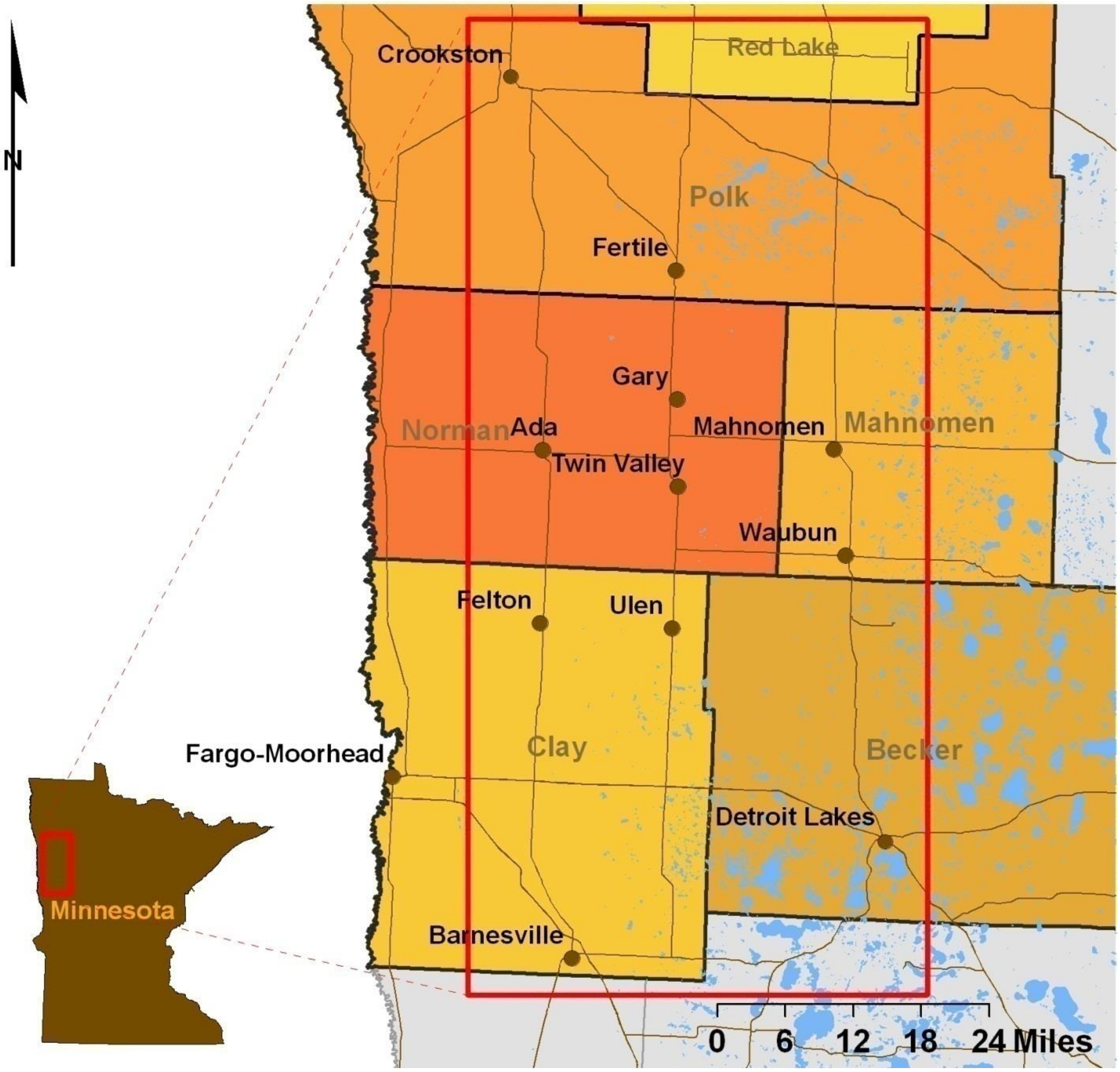

Figure 2. Study area in northwestern Minnesota. Field seasons are centered out of Ada, Minnesota.

The decades-long establishment of beach-ridge grassland landscapes in northwestern Minnesota by the USDA Conservation Reserve Program (CRP) has created GPC habitat and local populations increased dramatically as a result (Toepfer 2003, 2007, Rodgers and Hoffman 2005, Anonymous 2006*a*). Initial CRP plantings consisted mostly of smooth brome and alfalfa (*Medicago sativa*) with heights of approximately 50-70cm, but succession pushed out most alfalfa leaving many smooth brome monocultures (Rodgers and Hoffman 2005), some mixed with timothy (*Phleum pretense*) and quack grass (*Agropyron repens*). Disturbance is minimal with mowing for Canada thistle (*Cirsium arvense*) control and infrequent herbicide usage being most common (Toepfer 2003). CRP cumulative enrollment in Norman and Clay Counties peaked in 1993-1994 with 24,988 hectares and 17,995 hectares respectively (42,983 hectares combined). Expiring contracts and declining re-enrollment left 2009 CRP cumulative enrollment at 20,071 hectares and 14,500 hectares in Norman and Clay Counties, respectively (34,571 hectares combined) (Barbarika 2009). The Nature Conservancy, Minnesota DNR management areas (Wildlife Management Areas and Scientific and Natural Areas), and USDA management lands (Wetland Reserve Program) have also contributed to the formation and maintenance of Minnesota grasslands and GPC habitat (Toepfer 2003, 2007, Anonymous 2006*a*).

Prairie invertebrates

North American prairie invertebrates are poorly studied and only about half have been described (Arnez and Joern 1996). The current list of species is dominated by the Orders Coleoptera, Diptera, Hymenoptera and Lepidoptera (Arnez and Joern 1996). Invertebrate diversity decreases at more northern latitudes, and a small sample of Orders indicate approximately 20-24% distribution of grassland insect diversity occurs in Minnesota (Arenz and Joern 1996). Threats to grassland invertebrate populations are not unlike those of most vertebrate species and include habitat loss, degradation and fragmentation, invasive species competition, pollution and, as non-charasmatic microfauna, human apathy (Arenz and Joern 1996).

Capture and Radio Telemetry

This project was part of an ongoing long-term GPC ecology study by the Society Tympanuchus Cupido Pinnatus, Ltd. (STCP) where GPC have been trapped on booming grounds, radio-collared and followed in northwestern Minnesota since 1992 (*see* Toepfer 2003). Approximately one hundred birds were radio-collared and available for research.

In April 2009, adult and immature GPC were captured on booming grounds using wire lead walk-in traps (Toepfer 1988) (Figure 3). Through the summer, brood chicks were located with the brood hen and caught using a long handled net while night lighting. Cocks and hens were fitted with a closed-loop radio collar mounted on a herculite bib weighing an average of 18 grams (Toepfer 2003). Chicks received a short whip radio, also mounted on a herculite bib weighing approximately 6 grams (Toepfer 2003) (Figure 4). Radioed chicks were recaptured at > 10 weeks and fitted with adult closed-loop radio collars. Whip antenna radios were not used long term as they have been shown to hit birds' wings during flight, possibly influencing their willingness to fly (Marks and Saab Marks 1987). All birds received a uniquely numbered metal leg band.

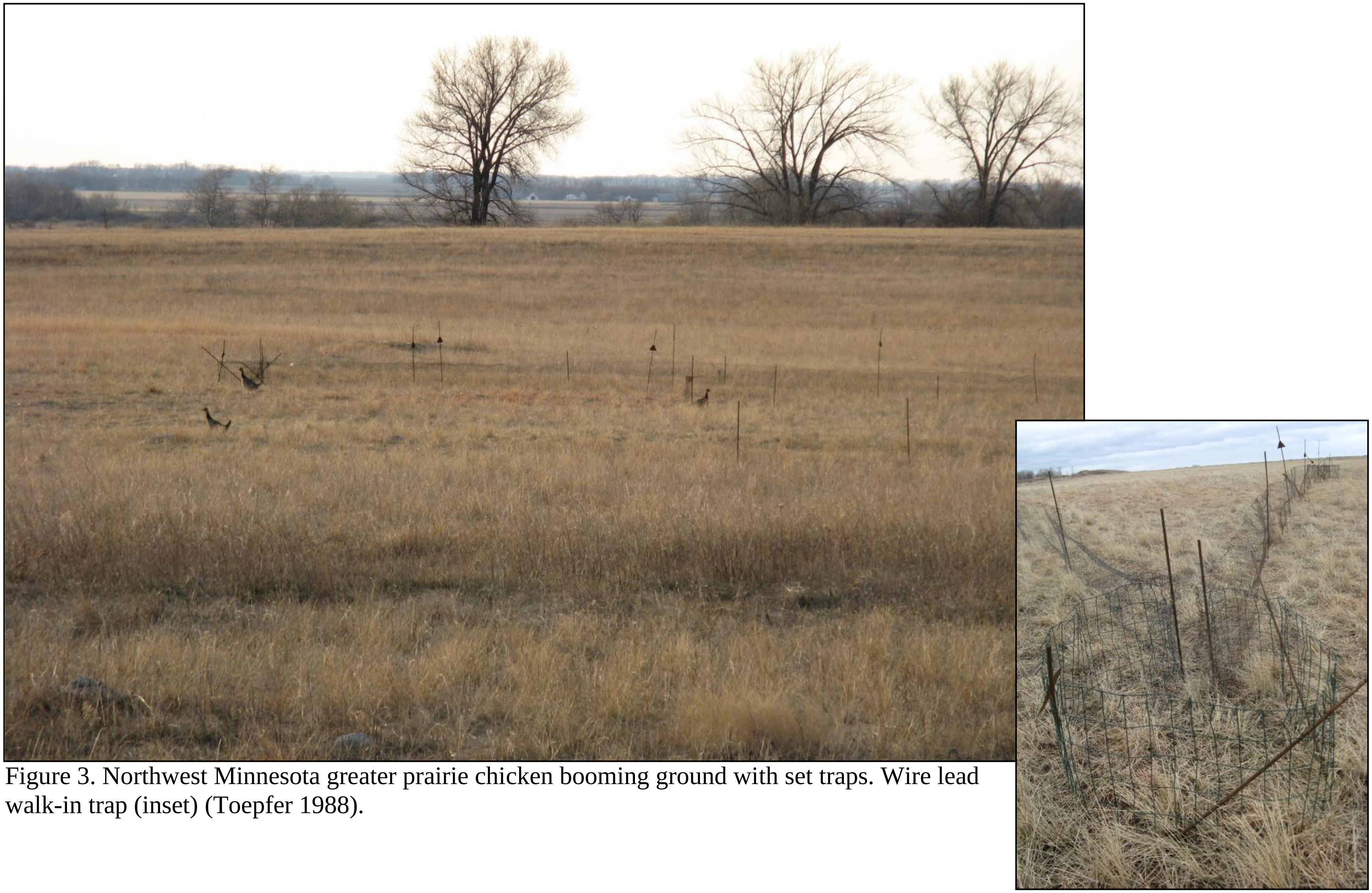

Figure 3. Northwest Minnesota greater prairie chicken booming ground with set traps. Wire lead walk-in trap (inset) (Toepfer 1988).

Figure 4. Greater prairie chicken chick fitted with 6 gram short whip radio, mounted on a herculite bib (Toepfer 2003).

An effort was made to locate each radio-marked GPC hen with a brood (hereafter brood) every day or every other day or, unless missing, at minimum once per week. A single 5-element, 3.5 meter vehicle-mounted antenna connected to an Advanced Telemetry Systems scanning receiver 148-151 MHz was used. Attached to the antenna mast was a pointer that showed the angle from which the signal was being received along a rose compass fixed to the ceiling of the vehicle. Brood locations were triangulated from two or three permanent landmarks, such as intersections and field entries, recognizable on 1:10,000 aerial ortho-photos obtained from the Minnesota DNR Data Deli. Global Positioning System (Garmin eTrex Handheld GPS) way points recorded the location of broods that were circled using a 3-element hand-held Yagi antenna. On June 2nd and July 31st we attempted to locate missing birds in an airplane with five-element antennas mounted to each strut.

Hens with successfully hatched nests (identified by shell remains) were assumed to have broods until flush counts indicated otherwise, deeming them nonbrood hens or unsuccessful broods. An effort was made to walk in on and circle radio-marked hens with potential broods at least once per week. Broods were circled within 15 yards using a hand-held antenna and their location marked with a handheld GPS device. Some brood locations could not be sampled on a regular basis due to lack of access on private properties and/or inability to locate the brood(s) for an extended period of time. At approximately 4 weeks after hatch, hens believed to be brooding were flushed and the number of chicks observed recorded. Broods were then flushed periodically throughout the study to verify chick survival numbers. Hens were considered to have successfully fledged chick(s) if at least one chick from their brood was alive at the six week mark, or, when the study period ended. Young prairie chicken chicks have been shown to survive in the absence of a brooding hen after six weeks of age (McNew et al. 2011*a*, J. Toepfer per. comm.).

Brood Range Size

Triangulated brood locations were hand-plotted in ArcMap (Esri ArcGIS) using an on-screen protractor (Markus Bader Ruler) on 1:10,000 FSA 2003-2004 colour ortho-photos of the study area downloaded from the Minnesota DNR Data Deli. Circled brood locations recorded with GPS way points were transferred into ArcMap. In this study, brood range was defined as the area in which the hen and her brooding chicks live, feed, travel and rest. Each brood range size was calculated in ArcMap using Hawth's Tools by connecting the outer perimeter of location points and the area within the resulting minimum convex polygon (MCP) measured. This range only indicates the extent of the brood's occurrence across the study area (Burgman and Fox 2003).

Vegetation Sampling

Macro-scale land cover categories (grassland, pastureland, agriculture and edge), habitat types (grass, forb, shrub, tree, wetland, agriculture, anthropogenic feature and combinations of these), disturbance types (undisturbed, previously mowed, high top mowed, moderately grazed, grazed, burned and plowed), and temporal disturbance regimes (time since last disturbance: 0-6 months, 7-12 months, 12+ months) were visually identified from ortho-photos and ground-truthed at all successful (n = 700) and unsuccessful (n = 134) brood locations. To account for telemetry error, habitat was classified as edge when a triangulated location was within 50 meters of a different habitat type, disturbance type or other anthropogenic boundary. Location points were also classified according to CRP and non-CRP lands, and land ownership (private, state, federal or The Nature Conservancy).

Micro-scale data on vegetation were collected at nearly all circled brood locations and established permanent reference transects. Permanent reference transects provided estimates of habitat-specific vegetation and invertebrate availability, and offered data with which to compare brood location transects. 20 permanent transects representing 13 habitat types and management regimes were chosen within the study area (Table 1). One permanent transect was initially high top mowed CRP habitat, but was mowed below 15 cm on July 18th; data were collected at this site three times subsequent to mowing and were included in combined permanent transect calculations, but not in individual permanent transect type calculations. At most circled brood and permanent transect locations, micro-scale data on vegetation type, height, effective height and obstruction category were documented.

Table 1. Northwest Minnesota permanent transect habitat types, 2009.

Permanent Transect	Disturbance	No. of Sites
Old CRP	Undisturbed ≥ 10 years	2
New CRP	Undisturbed ≥ 5 years	2
High Top Mowed CRP	Mowed ≥ 15 cm within the last two years	2
Previously Mowed CRP	Mowed ≤ 15 cm within the last two years	2
Recently Mowed CRP	Mowed ≤ 15 cm in 2009	1
Grazed Pasture	Grazed 2009	1
Moderately Grazed Pasture	Moderately Grazed 2009	1
Undisturbed Pasture	Undisturbed 2009	1
Native Prairie	Undisturbed ≥ 1 year	3
Burned Native Prairie	Burned 2009	2
Alfalfa Hayfield	Mowed 2009	1
Soybean	Plowed 2009	1
Wheat	Plowed 2009	1

At 1 metre intervals along each brood and permanent transect, 5 over-head digital photographs were taken at 1 metre above the ground for canopy coverage analysis. Because vegetative characteristics appear to be more important than species composition during prairie chicken habitat selection (Hamerstrom et al. 1957, Jones 1963, Toepfer and Eng 1988, Eng et al. 1988, Hagen et al. 2005), over-head photos taken at each transect location were used to determine the percentage of canopy cover by vegetative life-form (Daubenmire 1959, Jones 1963, Toepfer 1988). Using SamplePoint (Booth et al. 2006), per cent canopy cover of each over-head image was calculated by categorizing 100 equally spaced points into six life-form categories: grass, forb, shrub, soil, litter and other, totalling 500 classifications per transect. These life form percentages were then categorized into vegetation type as follows: Grass = ≥ 80% Grass; Forb = ≥ 80% Forb; Grass/Forb = 50-79% Grass and 0-50% Forb, or 50-79% Forb and 0-50% Grass.

Agriculture was ubiquitous as the planted seed type and categorized according to crop (alfalfa, soybean, wheat, and fallow field).

At 1 metre intervals along each brood and permanent transect, 4 photos were taken of a 0.5 metre^2 dot-board staked vertically behind vegetation to record height (the highest point of vegetation measured on dot-board profile), effective height (the point below which all dots are obscured by vegetation) and obstruction category (the dominant vegetation life form providing visual obstruction) (Newell 1987, Toepfer 2003). Vegetation height and effective height were measured in ArcMap. Each image was aligned within a standardized template. Lines measuring height and effective height were hand-drawn at 5 equally spaced intervals along the dot-board, totalling 20 height and 20 effective height measurements per transect. Height and effective height of each transect was averaged from the 4 images taken at each location. Obstruction categories noted during effective height measurements were categorized as grass, forb, legume, other, grass/forb, forb/grass, grass/legume, legume/grass, grass/other, other/grass, forb/other, other/forb, soybeans, wheat and no vegetation. Obstruction categories with more than one classification (e.g. grass/forb) indicate that both types of vegetation were present providing visual obstruction; the former at quantities $\geq$ 60% and the latter at quantities $\leq$ 40%. For additional reference, a 1 minute 360° panoramic video surveying the landscape surrounding each brood location was also recorded.

Invertebrate Sampling

Many historic galliforme invertebrate studies involved the collection of birds to dissect and analyze crop/gizzard contents, and/or the analysis of faecal droppings.

However, it has been questioned how taxonomically inclusive these methods are, and whether or not soft-bodied invertebrates can be detected after being ingested and/or passed (Moreby 2004). Ford et al. (1938) found some insects – flies and small bugs in particular – to be too mangled for accurate identification, even at the crop level of analysis. Conversely, Dalke (1935) and Swanson (1940), while acknowledging the thoroughness of digestion, felt that nearly all material eaten by gallinaceous birds would leave recognizable remnants in faecal matter and as such could produce qualitative results as frequency per cent, thereby making the collection of birds unnecessary. Faecal analysis continues to be the preferred method of diet analysis for most bird species (Moreby 2004). Other food-selection studies have used feeding trials (Johnson and Boyce 1990), neck collars (Moreby and Stoate 2000) and human imprinted chicks (Doxon and Carroll 2010). Less invasive methods of collecting data for terrestrial invertebrate-habitat studies include pitfall traps, vacuum/suction traps and, as in this study, sweep nets (Murkin et al. 1994).

Although vegetative height and structure can affect sampling efficacy, sweeping is the most common technique used by ornithologists to collect invertebrates from herbaceous vegetation as it can provide a large amount of material with minimal effort (Cooper and Whitmore 1990, Murkin et al. 1994). All invertebrate sampling methods show bias with regard to species caught and sweep net samples tend to be dominated by heavier, active invertebrates that reside on and within vegetation stands (Cooper and Whitmore 1990). Southwood and Cross (1969) reported larger sample sizes using sweep nets but found the results were comparable with vacuum samples. They also observed that invertebrates found in the habitat compared well to crop content analysis.

Conversely, Renhowe (1968) wrote that sweep net samples did not collect everything found in grouse crops, specifically certain ground-dwelling Orthoptera and Coleoptera species. Savory (1977) noted that the invertebrate specimens found in the crops of red grouse chicks were more similar to the samples collected with sweep nets than to those from pitfall traps, suggesting the chicks collected insects off of above ground vegetation more than along the ground. Other studies have indicated many birds forage near the ground and in low vegetation (Jackson et al. 1987, Svedarsky et al. 2003). Comparing two common invertebrate collection methods, Randel et al. (2006) captured similar Orders using both vacuum and sweep net techniques; however vacuum samples contained fewer insects and invertebrate biomass was lower. Doxon et al. (2011) found Diptera, Homoptera and Hymenoptera were most abundant in vacuum samples while Homoptera, Orthoptera and Araneae dominated sweep net samples. Order richness was similar between the two techniques, but the average size of individual insects (4.5 mm) and overall biomass of sweep netted invertebrates was greater (Doxon et al. 2011).

The biases of sampling methods should be fairly constant, but sweep methods fall short of providing accurate data on all taxa available to foraging birds (Cooper and Whitmore 1990). Sweep netting was used in this study to alleviate brood disturbance, and so that results could be compared to other pinnated grouse studies using the same technique (USFWS 2010), and because it is sufficient to demonstrate the indices sought.

Temperature and weather can affect invertebrate activity and vertical movement on vegetation and the efficacy of samples may be altered in unfavourable conditions (Hughs 1955, Murkin et al. 1994). Studying red grouse chicks, Savory (1989) noted that, due to temperature, there were fewer invertebrates caught with a sweep net before noon, and the highest abundance and biomass collected occurred between 12:00-18:00 hours. He found that most invertebrates were caught when the temperature was between 10-15^{o}C; however, wind and light precipitation had no effect on the number of invertebrates caught. During this study, most invertebrate sampling took place between 13:00 and 19:00 hours when the weather was fair.

Data on invertebrates were collected in the same way at circled brood locations (n = 140) and established permanent transects (n = 93). Above ground invertebrate samples were collected at the time the broods were located using a sweep net along a randomly chosen transect, either from where the brood flushed, or, to avoid disturbance, within approximately 15 yards of their signaled location. Time spent at brood locations was minimal in an effort not to impact chick survival. Permanent reference transect sampling took place biweekly. The sweep net was constructed of canvas, measured 38 centimetres in diameter and was attached to a 1 metre wooden pole by a steel ring. One sweep was one 180° arc through the vegetation. Each transect consisted of 25 moderately fast sweeps at a constant walking pace. Net contents were emptied into a 4 litre plastic bag and frozen until processed. Although some weight loss occurs, freezing is a common invertebrate preservation technique (Murkin et al. 1994).

Precocial chicks tend to have a diverse invertebrate diet, and most birds can adapt to normal fluctuations in invertebrate food selection, making invertebrate availability more important than specific species preference or presence (Jones 1963, Moreby 2004). Moreover, many invertebrate characteristics contribute to predator selection including size, life stage, palatability, colour, and movement (Cooper and Whitmore 1990). Still, a comparatively large number of studies place emphasis on Orthoptera and/or Coleoptera populations (Tester and Marshall 1961, Evans 1988, Chambers and Samways 1998, Jonas et al. 2002, McIntyre and Thompson 2003). Notably, when examining the effects of different grassland habitats and management techniques, Jonas et al. (2002) found Coleoptera to be a better overall indicator with more consistent species response across disturbance patterns, as compared to highly variable responses from various Orthoptera species. Yet, grasshoppers are thought to be the preferred invertebrate for most birds, and species from both Orders are the most abundant insects on the prairie landscape and across most GPC range (Smith 1940, *see* Tester and Marshall 1962, Hull et al. 1996, McIntyre and Thompson 2003). Several studies have suggested species in the Orders Coleoptera, Homoptera, Hemiptera, Diptera and Orthoptera compose the preferred diet of various galliforme chicks (*see* Burger et al. 1993). Yeatter (1943) and Jones (1963) found Coleoptera and Orthoptera species dominated the invertebrate diet of GPC chicks based on crop and faecal samples, respectively.

In this study, all invertebrates were sorted to taxonomic Order and then pooled into the following six Orders: Coleoptera, Diptera, Hemiptera, Homoptera, Orthoptera, and Other.[1] Invertebrates pooled under Other included Acarina, Araneida, Neuroptera, Hymenoptera, Lepidoptera, Odonata as well as snails and centipedes. While determining Order, invertebrates were also separated according to size. Insects 3 to 5.9 mm were categorized as small and those 6 mm and larger were categorized as big. In each sample, invertebrates 2.9 mm and smaller were pooled together and weighed regardless of Order, but not counted. Perhaps due to their inconspicuous nature, Whitmore et al. (1986) found

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[1] Although Homoptera is no longer recognized as a taxonomically distinct order, its suborders Auchenorrhyncha and Sternorrhyncha having been subsumed into the Order Hemiptera, it was used in this study to maintain compatibility with previous and concurrent comparative pinnated grouse studies.

that, even when abundant, pheasant chicks did not ingest invertebrates < 3 mm and, if chosen, would provide only limited biomass/nutrition per capture. In their study, invertebrates > 6 mm were considered large, and insects such as grasshopper nymphs, honey bees and sizeable flies were classified as very large and were included in analysis since chicks were often seen dissecting such substantial insects prior to ingesting them. Studying the distribution of invertebrates in black grouse and capercaillie brood habitat, Baines et al. (1996) also omitted invertebrates < 2 mm from their data sets.

Each size-classified Order was oven-dried at 60°C for 90 hours, counted, and weighed to the nearest ten-thousandth (0.0001) gram using an electronic balance. Dry weight is considered a more accurate measurement because, relative to the specimen's size, the amount of moisture in each live invertebrate can vary (Murkin et al. 1994). Due to the nature of the technique, sweep net samples can only estimate indices of relative invertebrate abundance and not absolute abundance (total invertebrate population) (Cooper and Whitmore 1990). Therefore this study indexed relative invertebrate abundance by the number of individuals tallied and their dry biomass (Pratt et al. 2003). Relative invertebrate composition was measured as the proportion of Orders per sample (Burger et al. 1993).

Time Intervals

Galliforme chick mortality rates are high and caused by the interplay of multiple factors including, but not limited to, predation, exposure to the elements and food resources (Dobson et al. 1988, Bergerud 1988, Schole et al. 2011). Generally, the first 20 days are considered the most critical during rapid growth and the development of thermoregulation abilities (Dobson et al. 1988), and many studies indicate that invertebrate consumption and chick mortality are highest through the first 2-3 weeks post hatch (Bergerud 1988, Savory 1989, Hannon and Martin 2006).

In his partridge studies, Potts (1980) determined that partridge chicks feed almost exclusively on invertebrate material during the first 2-3 weeks (21 days) of life. A feeding trial experiment demonstrated that sage grouse chicks < 20 days old require invertebrates for survival and development, and chicks > 20 days old achieve optimum development when invertebrate availability is maintained (Johnson and Boyce 1990). Survival analysis of wild sage grouse hatchlings supports the fact that most sage grouse chicks perish within the first 3 weeks (21 days) of life (Gregg et al. 2007). A number of studies have indicated that many galliforme chicks feed on invertebrates through the first six weeks (42 days) post hatch (*see* Burger et al. 1993, Savory 1989). In Nebraska, Kobriger (1965) reported juvenile sharp-tailed grouse (*Tympanuchus phasianellus*) diets were composed of > 80% invertebrate material until 6 weeks when they slowly began switching to plants which became 92% of their diet by 12 weeks of age. Renhowe (1968) also found > 90% invertebrate material in the combined crops of South Dakota sharp-tailed grouse and GPC up to 13 weeks of age. In New Mexico, Davis et al. (1980) found only invertebrate food in the diets of LPC chicks 1-4 weeks old, and still at 5-10 weeks of age, invertebrates made up 99.3% of the LPC juvenile diet. In fact, when comparing brood food studies of 21 different gallinaceous species, Savory (1989) noted that only the two *Tympanuchus* species (sharp-tailed grouse and LPC) both continued to consume noticeably high amounts of invertebrate food (> 50%) up to 8 weeks of age. In North Dakota, Rumble et al. (1988) reported GPC brood diets containing > 80% invertebrate material through the summer months of June, July and August, confirming the distinctively long term consumption of substantial invertebrate quantities by young *Tympanuchus* species. Paralleling this fact, Toepfer (2003) reported GPC hens lose the majority of their chicks during the first four weeks post hatch and survival increases significantly after 6 weeks.

In this study, comparisons were made between successful brood, unsuccessful brood and permanent reference transects at approximately 2 week intervals from shortly after hatch through to 10 weeks, depending on hatch date, totalling five time intervals over the study period: Interval One = June 14 – June 30; Interval Two = July 1 – July 11; Interval Three = July 12 – July 25; Interval Four = July 26 – August 8; Interval Five = August 9 – End of Study.

Analysis

A total of 834 locations from successful (*n* = 700) and unsuccessful (*n* = 134) brood sites were used in macro-habitat analysis (land cover, CRP versus non-CRP, ownership, and general habitat type). A total of 140 locations from successful (n = 114) and unsuccessful broods (n = 26) were used in micro-habitat analysis (vegetation type, disturbance type, and temporal disturbance regime). In order to compare invertebrate biomass with vegetation type, 13 transects required micro-scale vegetation type be assumed from macro-habitat analysis (as opposed to determined using canopy coverage data). Although disturbance type and temporal disturbance regime data were collected at macro-scale levels, they are organized alongside vegetative micro-habitat data due to the invertebrate analyses performed on them. Micro-habitat analysis involving vegetation height, effective height and obstruction category used a total of 179 locations from successful (n = 90) and unsuccessful broods (n = 16) and permanent transects (n = 73). Tables and figures indicate the number of samples used in a specific calculation.

I did not analyze brood habitat selection versus availability. The focal data of this study were collected at site-specific brood locations, while traditional use-availability studies occur at the landscape scale (Garshelis 2000). Moreover, although use-availability studies are able to establish habitat selection, they are unable to test habitat importance or suitability relative to the fitness of the species' using it (Garshelis 2000). In fact, studies using site-specific data tend to draw stronger inferences of habitat selection than do use-availability studies, although measures of population growth are generally required to further assess their effects on population sustainability (Garshelis 2000).

Through field observations, Toepfer (1988) suggested GPC habitat use centres around three variables: daily needs, current environmental conditions, and the proximity of cover types within a familiar area. Particularly within the first few weeks of life when chick mobility is most limited, familiar habitat neighbouring the hen's nest location appears to be a strong determinant for brood location. In this sense, circumstance may be a better indicator of brood habitat selection than a land cover map of the study area. In this study, broods were assumed to have "selected" accommodating habitats that were present within their mobile limit.

A total of 233 locations from successful brood (*n* = 114), unsuccessful brood (*n* = 26) and permanent transects (*n* = 93) were used in invertebrate analyses. Calculations involving invertebrate Order did not include the biomass of insects < 2 mm, as these insects were not sorted to Order but pooled and weighed together regardless of Order. Calculations involving the number of invertebrates also did not include insects < 2 mm, since these insects were not counted but simply pooled together and biomass weighed. All other invertebrate calculations included insects categorized as < 2 mm. The mean number of invertebrate samples taken per successful brood was 5.7 (range 2-11). The mean number of invertebrate samples taken per unsuccessful brood was 3.7 (range 2-5). The mean number of invertebrate samples taken per permanent transect type was 7.2 (range 3-16).

A statistics tutor was consulted. All statistical tests were performed using IBM SPSS Statistics.

Brood Range Size and Movement

Brood range size was calculated for successful broods with ≥ 24 location points (*n* = 19). One successful brood only had 14 location points and was excluded from brood range calculations. To avoid sacrificing data, unsuccessful brood home range size was calculated for broods with ≥ 17 location points (*n* = 5). Two unsuccessful broods only had 7 and 13 location points, respectively, and were excluded from brood range calculations. The average number of location points used to calculate successful brood MCP was 36 (range 24 – 56, *n* = 19). The average number of location points used to calculate unsuccessful brood MCP was 23 (range 17 – 37, *n* = 5).

A t-test was used to compare the average MCP of successful broods (*n* = 19) to the average MCP of unsuccessful broods (*n* = 5).

The mean distance to nest by brood age for successful and unsuccessful broods was compared using descriptive statistics.

The mean MCP of successful broods relative to the mean invertebrate biomass of those broods was determined using only successful broods that were tracked for 13 weeks and had at least 5 insect transect sweeps ($n = 6$). A linear regression was used to evaluate the relationship between mean invertebrate biomass and brood range size.

Brood and Permanent Transect Type in Relation to Invertebrate Characteristics

All calculations analyzing invertebrate characteristics (biomass, number, size or Order) were done using 114 successful brood transects, 26 unsuccessful brood transects and 93 permanent transects.

One-way ANOVA supplemented with Tukey's honest significant difference (HSD) mean comparison tests were used to detect differences between successful brood, unsuccessful brood and combined permanent transects by comparing mean biomass, mean number of invertebrates, mean biomass by invertebrate size, and mean biomass by invertebrate Order. The size of invertebrates at successful broods, unsuccessful broods and combined permanent transects were shown with descriptive statistics. Descriptive statistics were also used to illustrate invertebrate composition (number and per cent by Order) associated with successful brood, unsuccessful brood and combined permanent transects. A 2x4 ANOVA was used to compare invertebrate biomass and number across brood age between successful and unsuccessful broods. Descriptive statistics were used to evaluate mean invertebrate biomass across five established time intervals between successful brood, unsuccessful brood and combined permanent transects. To illustrate variation within brood samples, mean invertebrate biomass and invertebrate numbers were also averaged across individual broods.

Brood Type in Relation to Habitat Characteristics

A total of 834 locations from successful (*n* = 700) and unsuccessful (*n* = 134) brood sites were used in macro-habitat analysis. Descriptive statistics were used to evaluate differences between successful and unsuccessful brood use of land cover type, CRP lands vs. non-CRP lands, and land ownership. Macro-scale habitat use was compared using chi-square tests.

Micro-habitat calculations involving invertebrate characteristics (biomass, number, size or Order) were done using 114 successful brood transects, 26 unsuccessful brood transects and 93 permanent transect types. Successful and unsuccessful brood use of micro-scale vegetation type was compared using chi-square tests. Next, the influence of these two factors (brood type and vegetation type use) and their interaction on invertebrate biomass was evaluated using a two-way ANOVA. A t-test was used to compare invertebrate biomass in grass and grass/forb vegetation types at combined brood locations. The relationship between forb occurrence and invertebrate abundance was tested with a linear regression. Invertebrate composition among forb types (alfalfa, soybeans, and percentage of uncultivated forbs) was discussed using descriptive statistics. Vegetation causing visual obstruction was shown in a table and observed species are listed. Brood use and invertebrate biomass of disturbance types and temporal disturbance regimes were illustrated using descriptive statistics.

Micro-habitat calculations involving vegetation height, effective height and obstruction category were done using 90 successful brood transects, 16 unsuccessful brood transects and 73 permanent transect types. All height data had corresponding invertebrate data which were used in some effective height calculations. Vegetation height and effective height were compared between successful brood, unsuccessful brood and combined permanent transects using descriptive statistics. The effective height of vegetation across brood age and between successful and unsuccessful broods was also evaluated with descriptive statistics. Vegetation effective height was then divided into four height classes according to the height of a standing prairie chicken (Table 2). Successful and unsuccessful brood use of vegetative effective height classes and the invertebrate biomass within them were illustrated with descriptive statistics. The proportion of effective height categories in various disturbance types where successful GPC broods were located were also compared using descriptive statistics.

Table 2. Northwest Minnesota vegetation effective height classes, 2009 (adapted from Toepfer 1988).

Effective Height Class	Height (cm)	Height (on GPC)
I	0-8	Up to belly of bird
II	9-25	Up to eye of bird
III	26-50	Above bird's head
IV	> 50	n/a

Permanent Transect Type in Relation to Invertebrate Characteristics

Permanent transect calculations involving invertebrate characteristics (biomass, number or Order) were done using 90 permanent transect samples representing 12 habitat types and management regimes. These 12 transects were combined into 8 categories for permanent transect type analyses (Table 3). Graphs detailing invertebrate biomass (Appendix 1), number of invertebrates (Appendix 2), and invertebrate biomass by Order (Appendix 3) in uncombined permanent transect habitat types can be found in the Appendices.

Table 3. Northwest Minnesota combined permanent transect habitat types, 2009.

Permanent Transect	Combined Permanent Transect Type	No. of Sites
Old CRP New CRP	Undisturbed CRP	4
High Top Mowed CRP Previously Mowed CRP	Previously Mowed CRP	4
Grazed Pasture Moderately Grazed Pasture	Grazed Pasture	2
Undisturbed Pasture	Undisturbed Pasture	1
Native Prairie	Native Prairie	3
Burned Native Prairie	Burned Native Prairie	2
Alfalfa Hayfield	Alfalfa	1
Soybean Wheat	Row Crops	2

One-way ANOVA supplemented with Tukey's honest significant difference (HSD) mean comparison tests were used to detect differences between permanent transect types for mean biomass and mean number of invertebrates. Descriptive statistics were used to illustrate mean biomass by invertebrate Order and invertebrate composition (number and percent by Order) associated with each permanent transect. All permanent transects were combined (*n* = 93) and descriptive statistics were used to evaluate mean invertebrate biomass by Order across the five established time intervals.

RESULTS

The results of this study reveal relationships between GPC broods and invertebrate and habitat characteristics. In this chapter, the first section presents the nest and fledging success of Minnesota GPC hens with broods. The second section looks at brood range size and its relationship to invertebrate biomass, and how brood movement changes over time. The final section presents analysis of relationships between invertebrate abundance and composition, and habitat variables across successful and unsuccessful broods and permanent transects types.

Nests and Fledging

A total of 121 GPC nests were located in 2009 and nest success was 50.4% (61/121). Immature hens in their first reproductive year showed higher nest success than adult hens; 56.4% (22/39) and 47.6% (39/82), respectively. The required travel distance to locate certain broods was logistically impractical. Therefore, data for this study were collected for only 27 of the 61 broods known to have hatched. Fledgling success for this study was 32.8% (20/61). Of the 20 successful broods, the total number of confirmed chicks fledged was 56. The mean number of chicks fledged per hen was 2.9 (range 1 - 6).

I followed and collected data on 20 successful broods (hens with at least 1 chick after six weeks) and 7 unsuccessful broods (hens that lost all chicks before six weeks). Four successful broods lost their brood hen before the end of the season. In one of these broods, five chicks were radio-collared before the hen was killed at seven weeks post hatch, enabling data collection to continue on the brood through the rest of the field season. All five chicks were alive when the field season ended, September 8th. This incident supports observations made in other prairie chicken studies where chicks have survived without a brood hen once they are at least six weeks old (McNew 2011*a*, J. Toepfer per. comm.). The other three successful broods retained their brood hen to at least six weeks and data were collected until the death of the hen. Therefore, these four broods were counted as successful, even in the absence of a brood hen at the end of the study.

Brood, Permanent Transect, Invertebrate and Habitat Relationships

Brood Range Size and Movement

Mean brood range size was larger for successful broods than unsuccessful broods, but not significantly so (p = 0.206) (Table 4) (see also Appendix 4).

Table 4. Mean brood range size (ha) of successful and unsuccessful GPC broods, northwest Minnesota June 3 – September 8, 2009.

	Successful Broods[a] $n = 19$	Unsuccessful Broods[b] $n = 5$	p - Value
Range Size (ha)	199.6	129.2	0.206

[a] Broods with ≥ 24 location points.
[b] Broods with ≥ 17 location points.

The mean distance to nest for successful broods aged 0-2 weeks was 536.8 m. The mean distance to nest for unsuccessful broods aged 0-2 weeks was slightly larger, at 551.4 m. This difference increased over time and brood distance to nest was comparatively larger for unsuccessful broods than successful broods at 3-4 and 5-6 weeks of age. At 7+ weeks, unsuccessful brood distance to nest did not change, while successful brood distance to nest continued to increase (Figure 5).

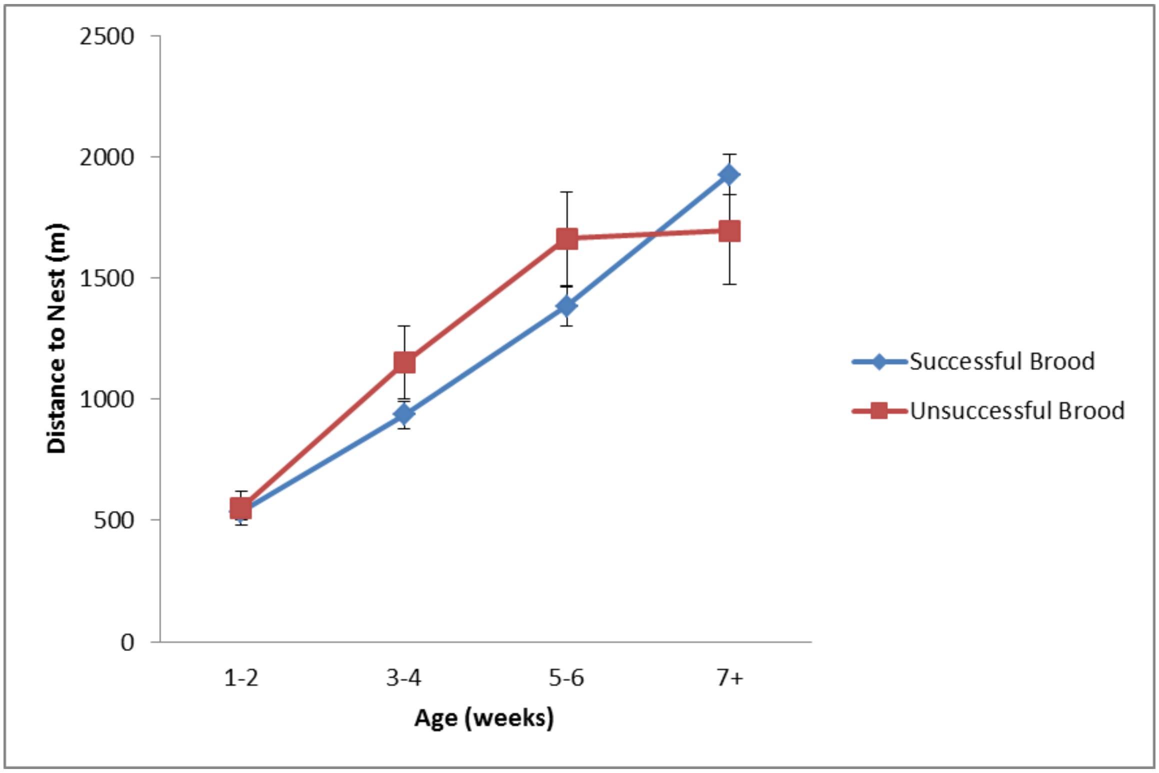


Figure 5. Mean distance to nest (m) by age (weeks) of successful and unsuccessful GPC broods, northwest Minnesota June 14 – September 8, 2009.

Among successful broods, there was a general trend towards larger brood range size when invertebrate biomass within that brood range was low, however a linear regression showed no significance ($n = 7$, $p = 0.890$). Successful broods ($n = 7$) included in this calculation were tracked for 13 weeks and had ≥ 5 invertebrate transect sweeps. One of these broods was found to be an outlier where range size was small relative to minimal invertebrate biomass. The location of this brood on the landscape may indicate its anomaly. The nest was located in a plot of CRP approximately 32 hectares in size, and right on the border of expansive agricultural fields. The plot of mixed grass/forb CRP was surrounded by soybeans on four sides and an active gravel pit directly 0.8 km east may have acted as an additional barrier to initial movement (Appendix 5). This brood was located once in soybeans at 2 weeks of age but was not located in them again until 5 weeks of age when they began using soybeans almost exclusively. Therefore, brood 2 was removed from the calculation. The regression slope became negative indicating overall brood range size (*n* = 6) increased with decreased invertebrate biomass, but remained non-significant (*p* = 0.667) (Figure 6).

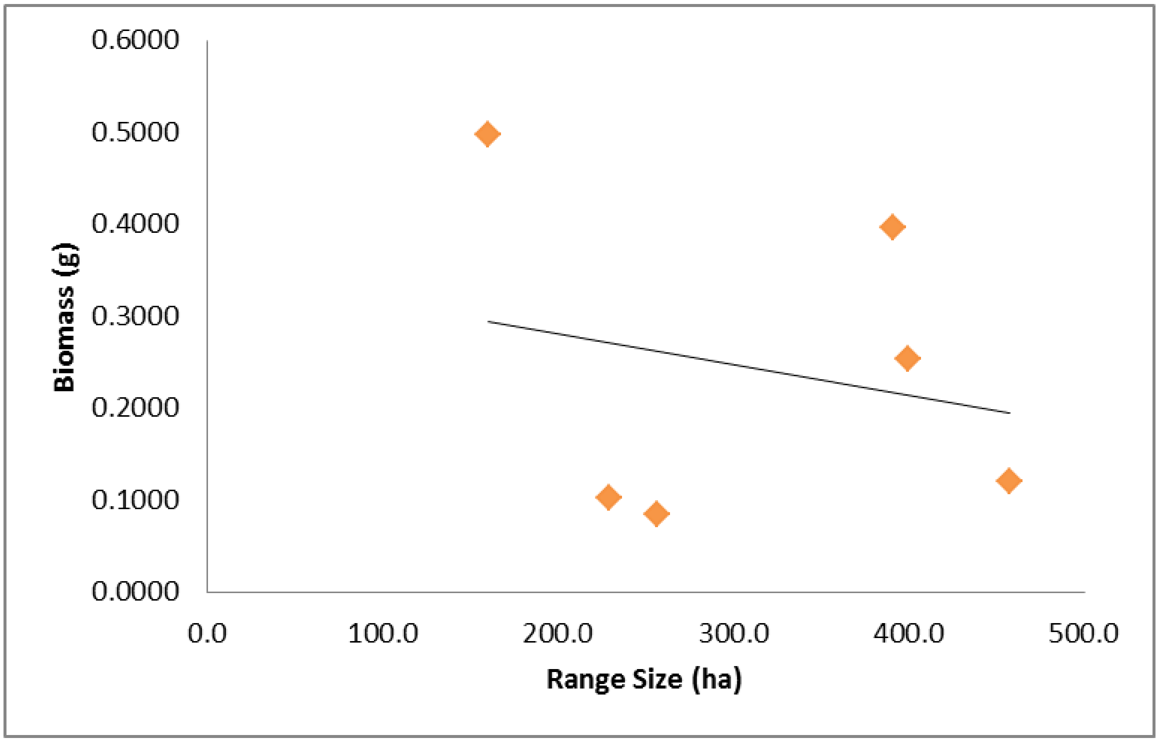


Figure 6. Linear regression for mean brood range size (ha) of successful GPC broods (*n* = 6) relative to mean invertebrate biomass, northwest Minnesota June 3 – September 8, 2009. All broods were tracked for 13 weeks and had ≥ 5 invertebrate transect sweeps.

Brood and Permanent Transect Type in Relation to Invertebrate Characteristics

Greater prairie chicken hens that fledged chicks were more likely to be found in habitats where invertebrate abundance (indexed as biomass and number of insects) was higher. Mean invertebrate biomass was significantly different across samples (one-way ANOVA, $p = 0.001$) (Figure 7). Tukey's HSD showed mean invertebrate biomass was significantly higher for successful broods than unsuccessful broods ($p = 0.029$) and also significantly higher for successful broods over permanent transects ($p = 0.001$). There was no significant difference shown between unsuccessful broods and permanent transects ($p = 0.957$).

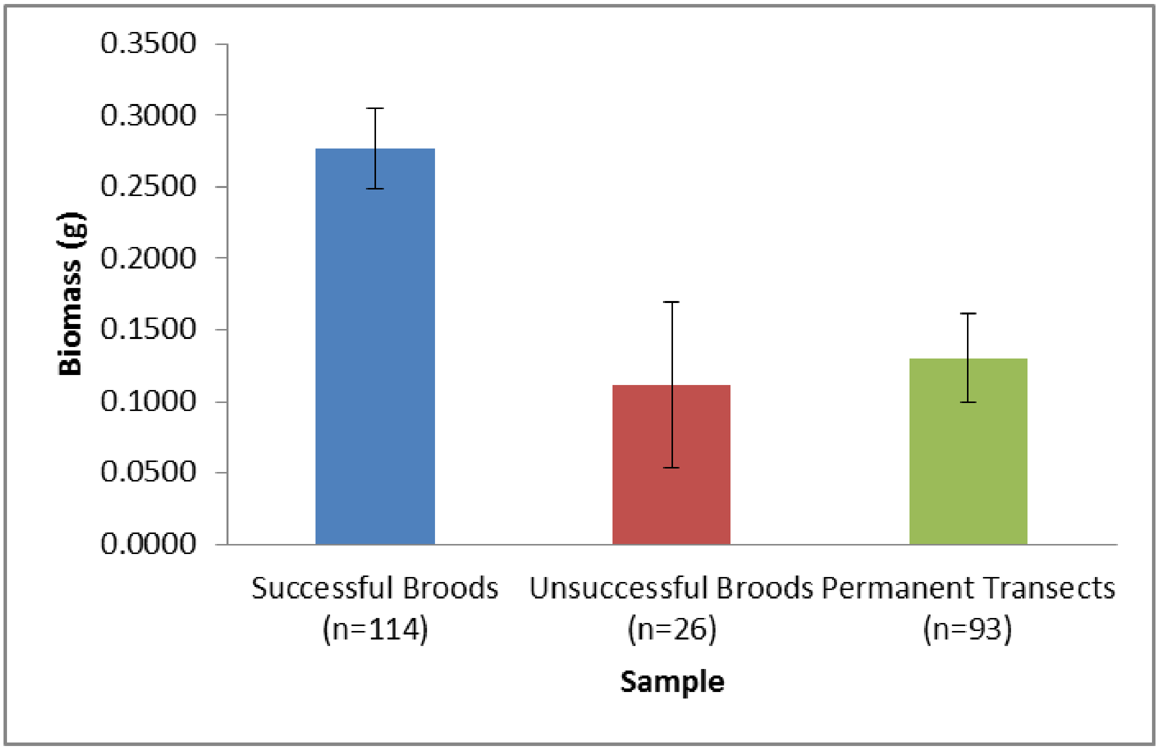


Figure 7. Mean invertebrate biomass (dry mass in grams) at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

The mean number of invertebrates was also significantly different across samples (one-way ANOVA, *p* = 0.005) (Figure 8). Tukey's HSD showed the mean number of invertebrates was significantly higher for successful broods than permanent transects (*p* = 0.006). No significant difference was found between successful and unsuccessful broods (*p* = 0.119). Likewise, there was no significant difference between unsuccessful broods and permanent transects (*p* = 1.000).

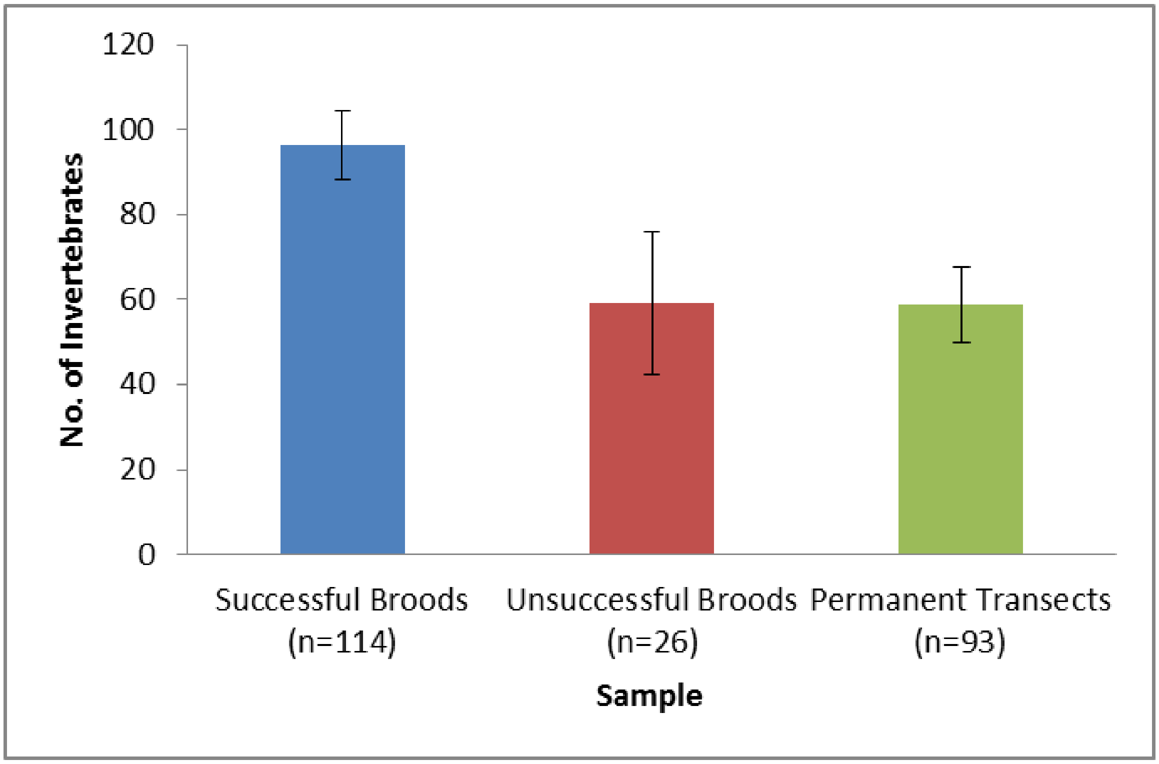


Figure 8. Mean number of invertebrates at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Successful GPC broods occupied areas where mean invertebrate biomass of insects larger than 6 mm was higher (Figure 9). One-way ANOVA detected significance between samples > 6 mm ($p = 0.003$). Tukey's HSD showed mean biomass of invertebrates > 6 mm was significantly higher for successful broods than unsuccessful broods ($p = 0.039$), and also significantly higher for successful broods over permanent transects ($p = 0.009$). No significant difference was found between unsuccessful brood and permanent transects ($p = 0.860$). No significant differences were shown between samples smaller than 6 mm ($p = 0.112$) or samples smaller than 2 mm ($p = 0.153$).

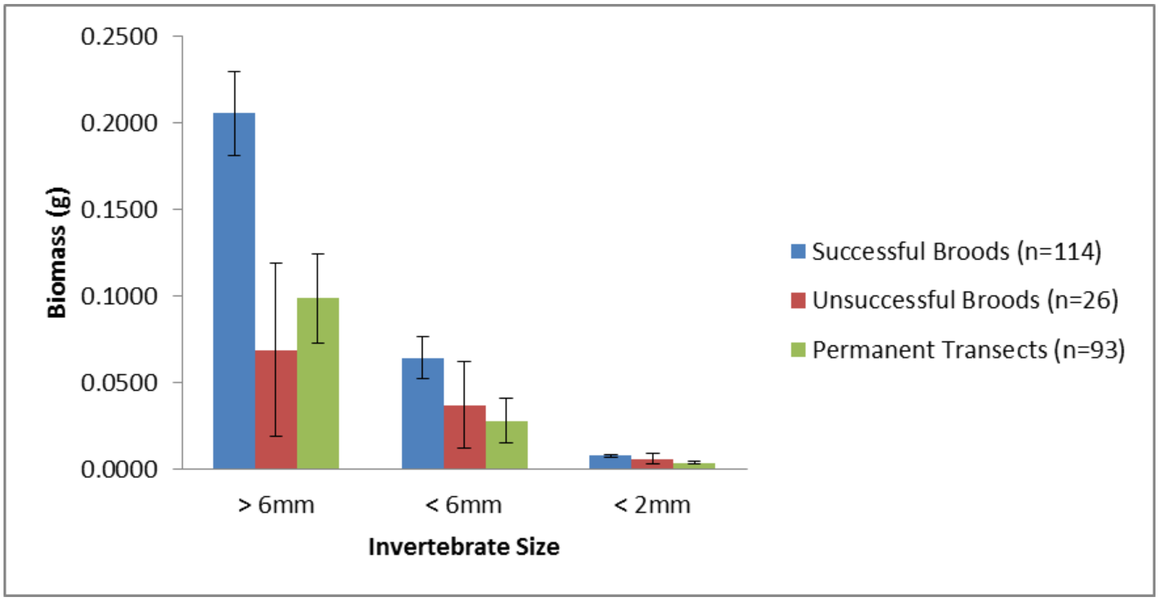
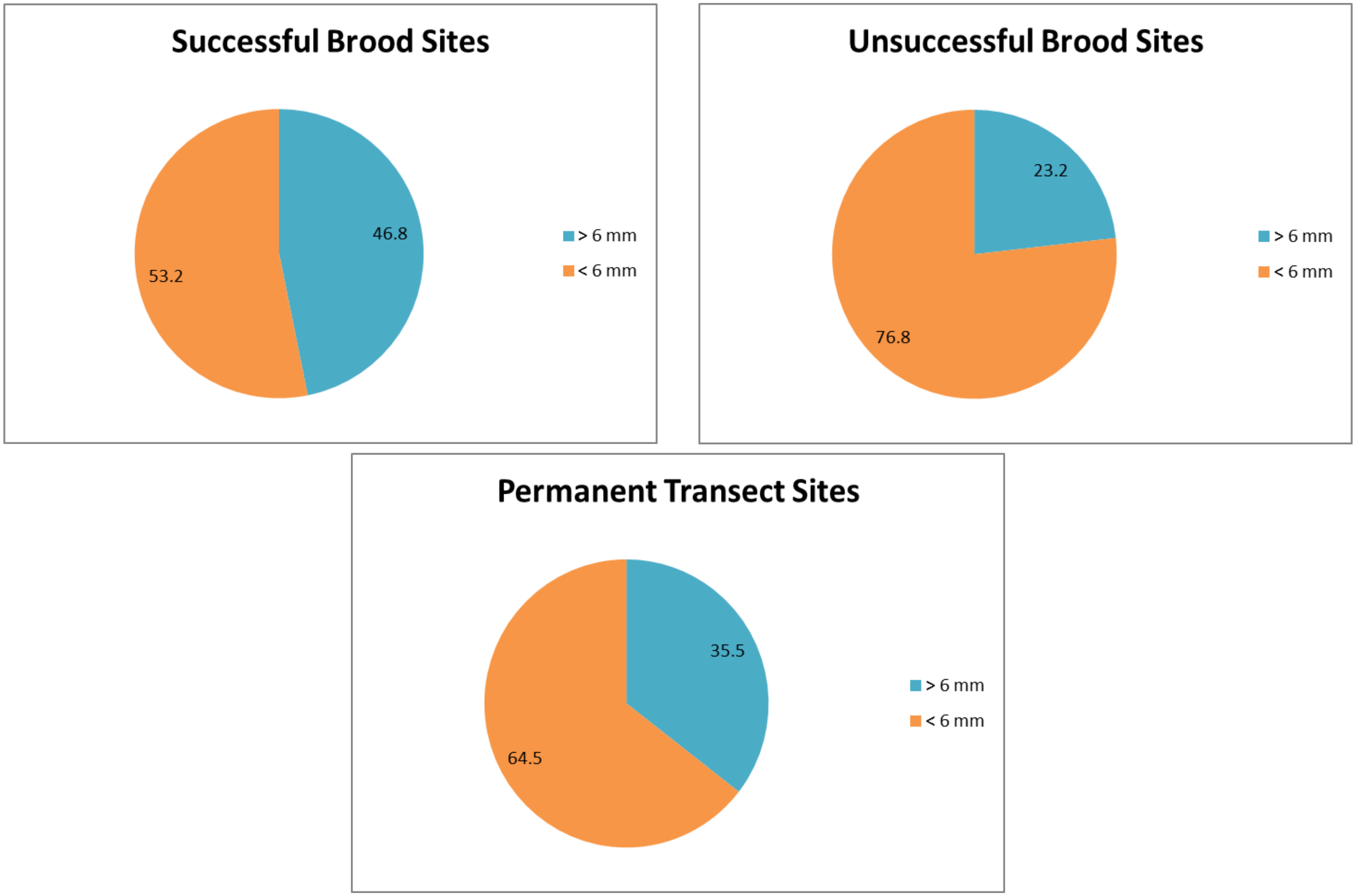


Figure 9. Mean invertebrate biomass (dry mass in grams) by size at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

The size of invertebrates found at successful and unsuccessful brood sites were substantially different (Table 5). Successful GPC broods occupied areas hosting relatively equal amounts of large (> 6 mm) and small (< 6 mm) invertebrates, while small invertebrates dominated at unsuccessful broods and permanent transects (Figure 10).

Table 5. Number and per cent (%) of invertebrates by size at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Sample	Size					
	n	> 6 mm		< 6 mm		Total no. of invertebrates
		No.	%	No.	%	
Successful Broods	114	5147	46.8	5844	53.2	10991
Unsuccessful Broods	26	357	23.2	1182	76.8	1539
Permanent Transects	93	1942	35.5	3529	64.5	5471



Successful Brood Sites

Unsuccessful Brood Sites

Permanent Transect Sites

Figure 10. Proportion of invertebrates by size at successful GPC brood sites (*n* = 114), unsuccessful brood sites (*n* = 26), and permanent transect sites (*n* = 93), northwest Minnesota June 14 – August 18, 2009.

Invertebrates of the Order Homoptera yielded a substantially higher biomass than any other Order weighed (Figure 11). One-way ANOVA detected marginal significance between samples within Diptera ($p = 0.092$). Tukey's HSD showed mean biomass of Diptera was higher for successful broods than permanent transects ($p = 0.090$). No significant difference was found between successful and unsuccessful broods ($p = 1.000$). Likewise, no significant difference was found between unsuccessful brood and permanent transects ($p = 0.393$). One-way ANOVA detected significance between samples within Homoptera ($p = 0.016$). Tukey's HSD showed mean biomass of Homoptera was significantly higher for successful broods than permanent transects ($p = 0.030$). Marginal significant difference was shown between successful and unsuccessful broods ($p = 0.099$). No significant difference was found between unsuccessful brood and permanent transects ($p = 0.911$). No significant differences were detected between samples within Coleoptera ($p = 0.602$), Hemiptera ($p = 0.312$), or Orthoptera ($p = 0.250$). Marginal significance was shown within the Other Order category ($p = 0.067$), but no significance was detected subsequent to Tukey's HSD analysis.

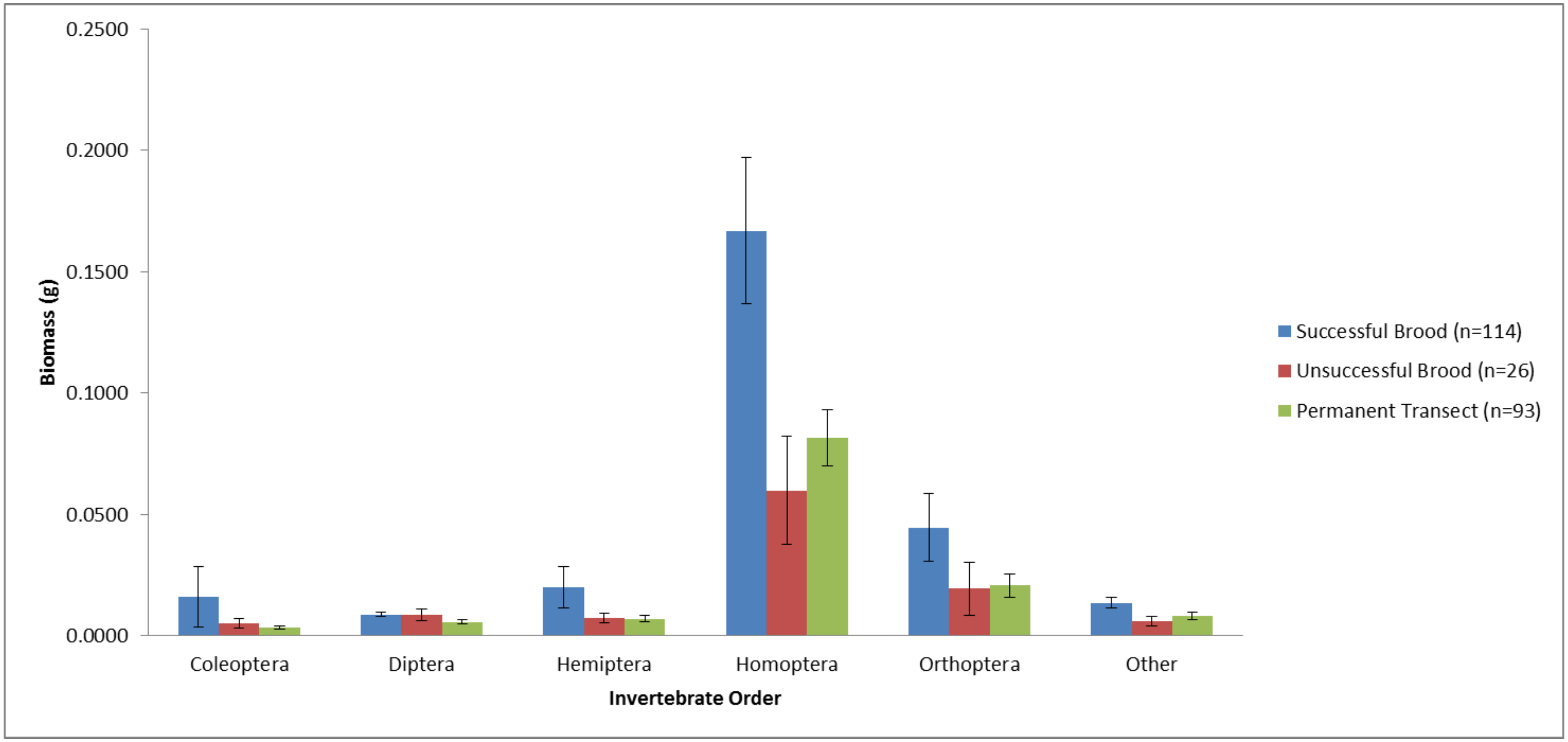


Figure 11. Mean invertebrate biomass (dry mass in grams) by Order at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Invertebrate composition (indexed as Order by proportion) was noticeably different between successful broods and unsuccessful broods, and successful broods and permanent transects, but less so between unsuccessful broods and permanent transects (Table 6). Homoptera dominated across all samples, but were highest for successful broods at 65% (Figure 12). Diptera and Hemiptera invertebrates were found in higher numbers at unsuccessful broods and permanent transects than successful broods.

Table 6. Number and per cent (%) of invertebrates by Order at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Sample	Order														
	n	Coleoptera		Diptera		Hemiptera		Homoptera		Orthoptera		Other		Total no. of invertebrates
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Successful Brood	114	296	2.7	1116	10.2	1073	9.8	7135	64.9	543	4.9	828	7.5	10991
Unsuccessful Brood	26	43	2.8	329	21.4	212	13.8	786	51.1	56	3.6	113	7.3	1539
Permanent Transect	93	104	1.9	733	13.4	888	16.2	2971	54.3	267	4.9	508	9.3	5471

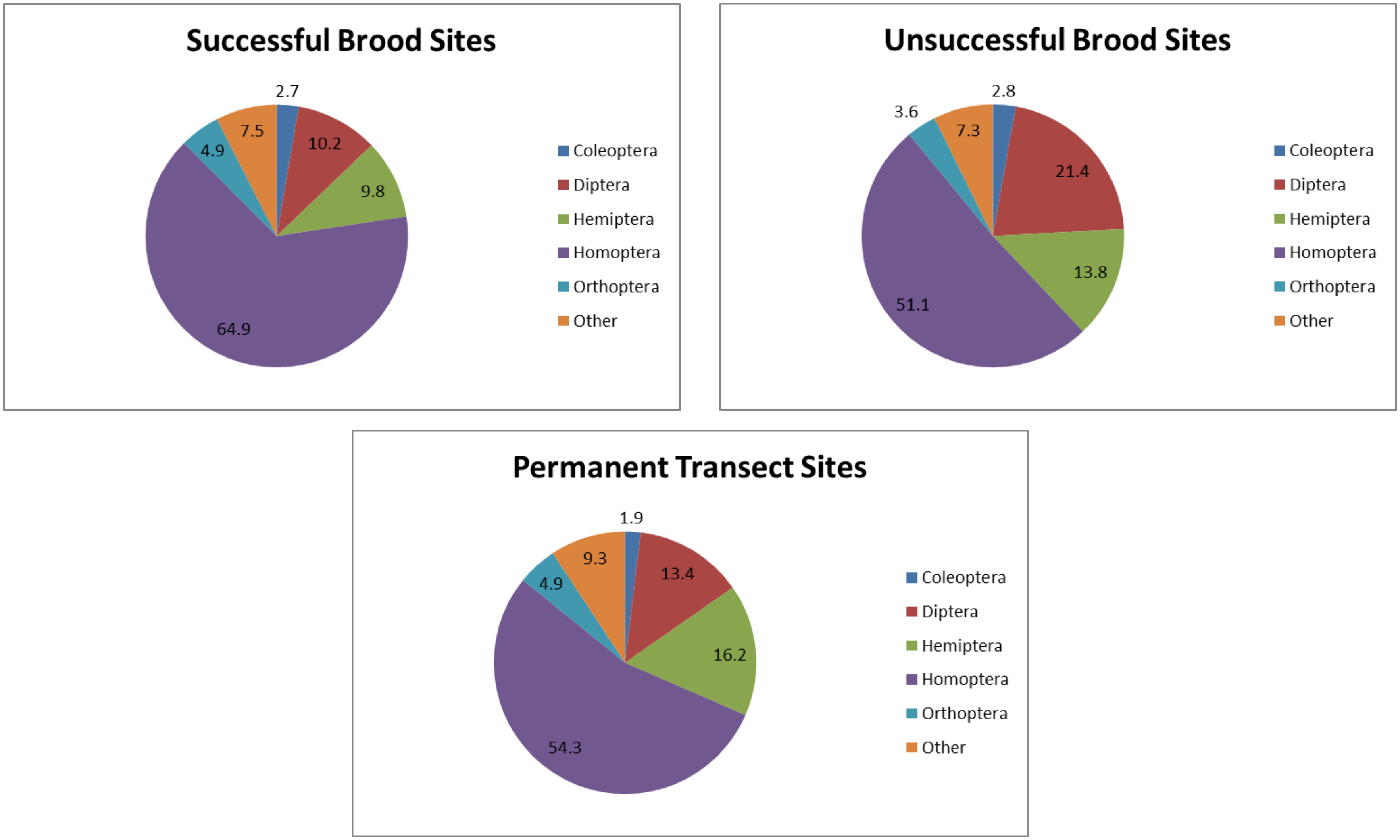


Figure 12. Proportion of invertebrates by Order at successful GPC brood sites (*n* = 114), unsuccessful brood sites (*n* = 26), and permanent transect sites (*n* = 93), northwest Minnesota June 14 – August 18, 2009.

Mean invertebrate biomass was higher for successful broods than unsuccessful broods throughout the entire study period (Figure 13). Two by four ANOVA detected a marginally significant main effect of brood type ($p = 0.065$), where mean biomass of successful broods (0.2769 grams) was greater than the mean biomass of unsuccessful broods (0.1118 grams). However, there was no significant main effect of age category ($p = 0.465$), and no significant interaction between brood type and age category ($p = 0.900$). Subsequent pairwise comparison tests revealed mean invertebrate biomass was significantly higher for successful broods than unsuccessful broods at 3-4 weeks of age ($p = 0.052$).

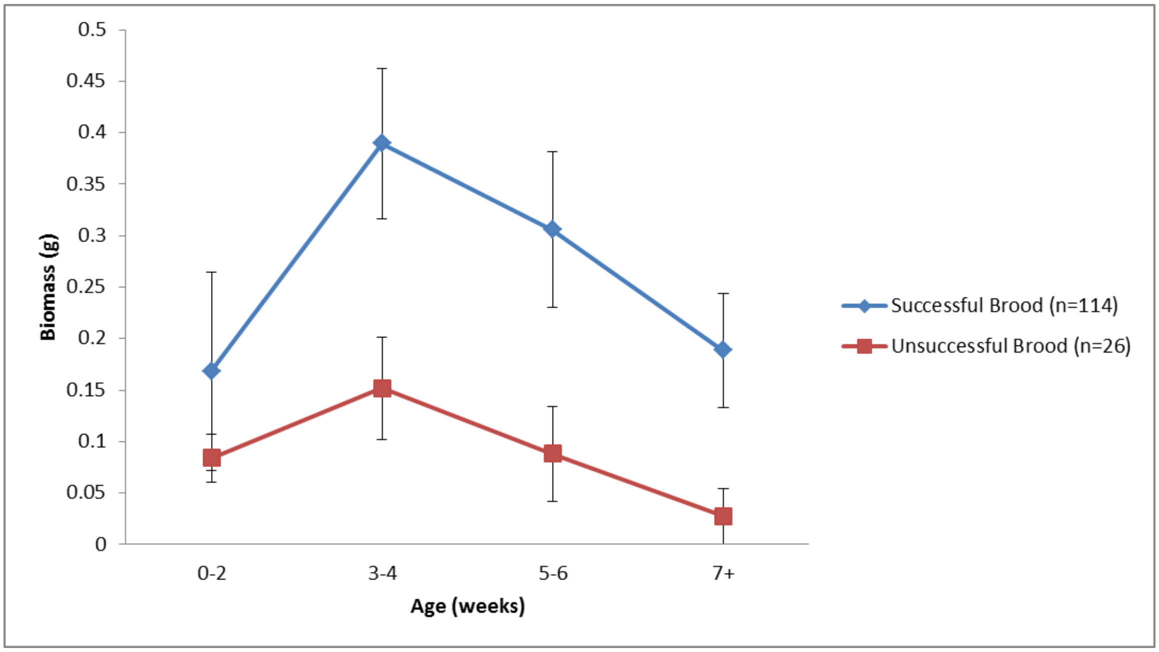


Figure 13. Mean invertebrate biomass (dry mass in grams) by brood age (weeks) at successful and unsuccessful GPC brood sites, northwest Minnesota June 14 – August 18, 2009.

The mean number of invertebrates was initially lower for successful broods than unsuccessful broods, but increased as the broods got older (Figure 14). Two by four ANOVA detected no significant main effect of brood type ($p = 0.104$), age category ($p =$

0.420) or interaction between brood type and age category (*p* = 0.624). Subsequent pairwise comparison tests revealed the mean number of invertebrates was significantly higher for successful broods than unsuccessful broods at 3-4 weeks of age (*p* = 0.034).

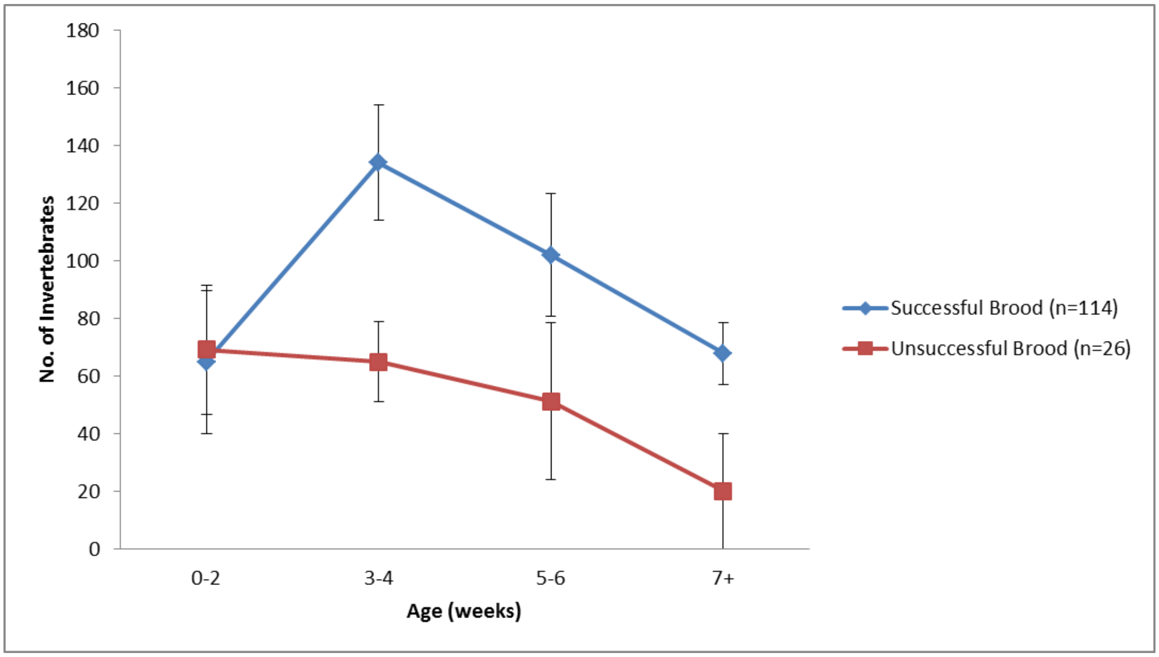


Figure 14. Mean number of invertebrates by brood age (weeks) at successful and unsuccessful GPC brood sites, northwest Minnesota June 14 – August 18, 2009.

When divided across five time intervals over the study period, mean invertebrate biomass was consistently higher for successful broods than unsuccessful broods or permanent transects (Figure 15). The beginning of July presented the largest difference when the mean biomass of invertebrates collected at successful brood sites was 3.4 and 2.7 times greater than the biomass at unsuccessful brood and permanent transect sites, respectively. Mean invertebrate biomass at successful brood sites decreased through the remainder of the field season. Mean invertebrate biomass at unsuccessful brood sites was relatively constant through the summer before decreasing substantially by the middle of

August. Mean invertebrate biomass at permanent transects decreased after the initial early July peak, but increased again at the end of the season.

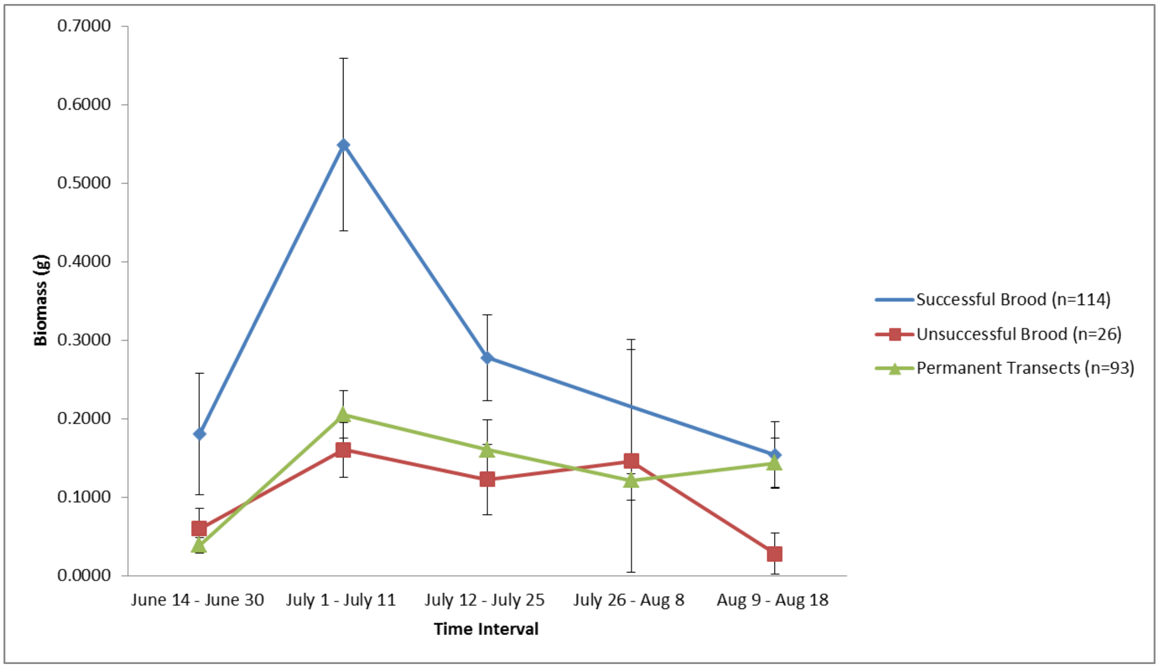


Figure 15. Mean invertebrate biomass (dry mass in grams) by time interval at successful GPC brood sites, unsuccessful brood sites, and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Measures of invertebrate abundance varied substantially between individual brood samples. Mean invertebrate biomass at successful brood sites (*n* = 20) ranged between 0.0302 and 0.9820 grams. Mean invertebrate biomass at unsuccessful brood sites (*n* = 7) ranged between 0.0327 and 0.1840 grams (Figure 16). The mean number of invertebrates at successful brood sites (*n* = 20) ranged between 19.2 and 222.3 insects, and the mean number of invertebrates at unsuccessful brood sites (*n* = 7) ranged between 20.8 and 101.0 insects (Figure 17).

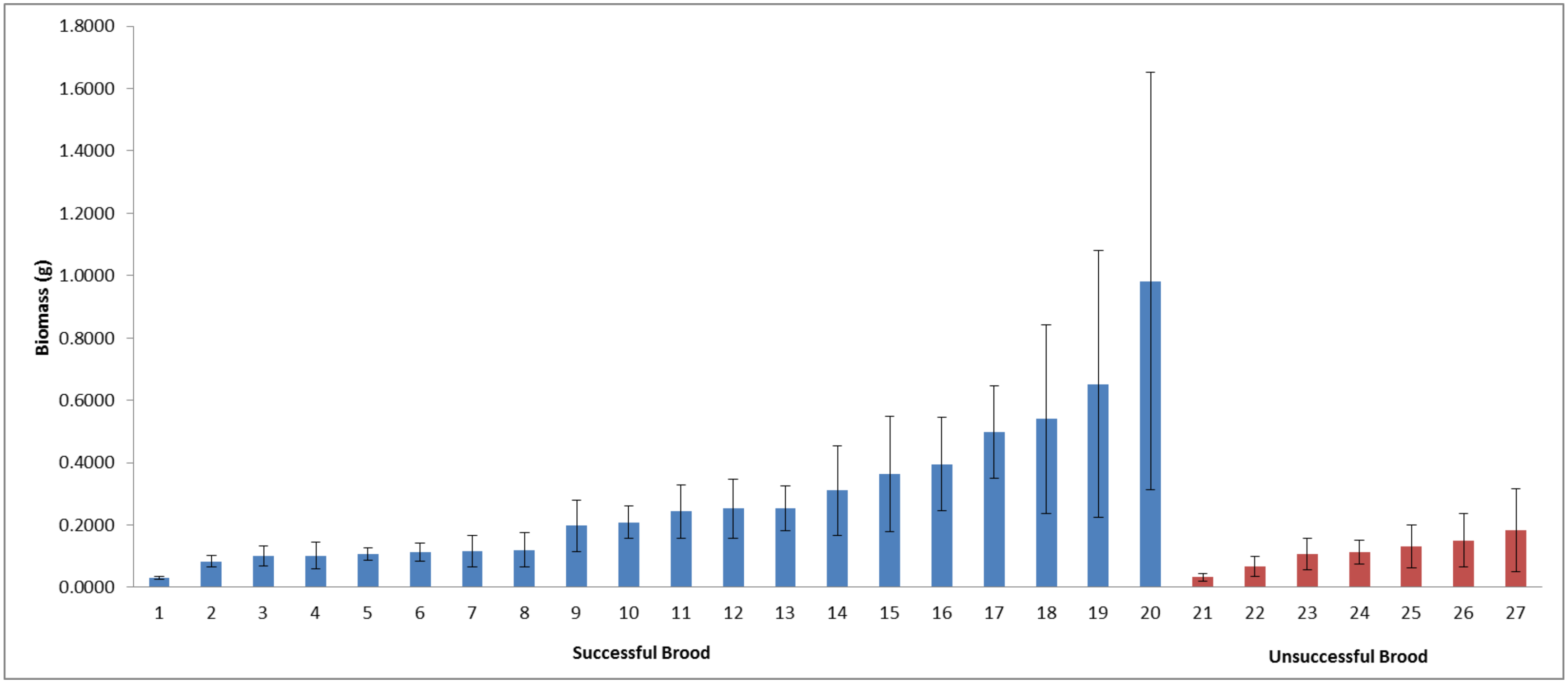


Figure 16. Mean invertebrate biomass (dry mass in grams) per brood at successful GPC brood sites (*n* = 20) and unsuccessful brood sites (*n* = 7), northwest Minnesota June 14 – August 18, 2009.

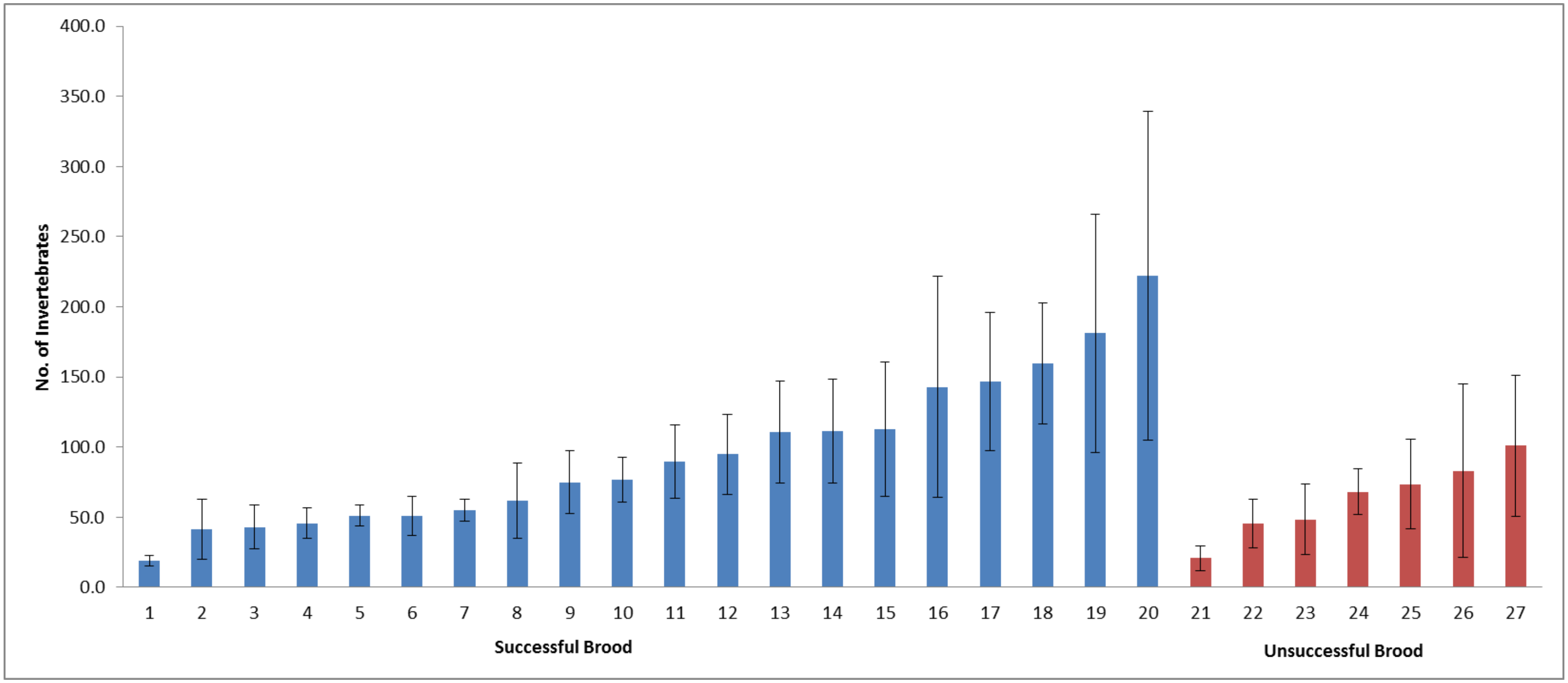


Figure 17. Mean number of invertebrates per brood at successful GPC brood sites (*n* = 20) and unsuccessful brood sites (*n* = 7), northwest Minnesota June 14 – August 18, 2009.

Brood Type in Relation to Habitat Characteristics

Successful and unsuccessful broods used grassland landscapes the majority of the time (both at 67.0%), followed by agriculture, edge between habitat types, and pastureland (Figure 18). Most edge occupancy occurred between grassland and agricultural fields, followed by grassland and roadways.

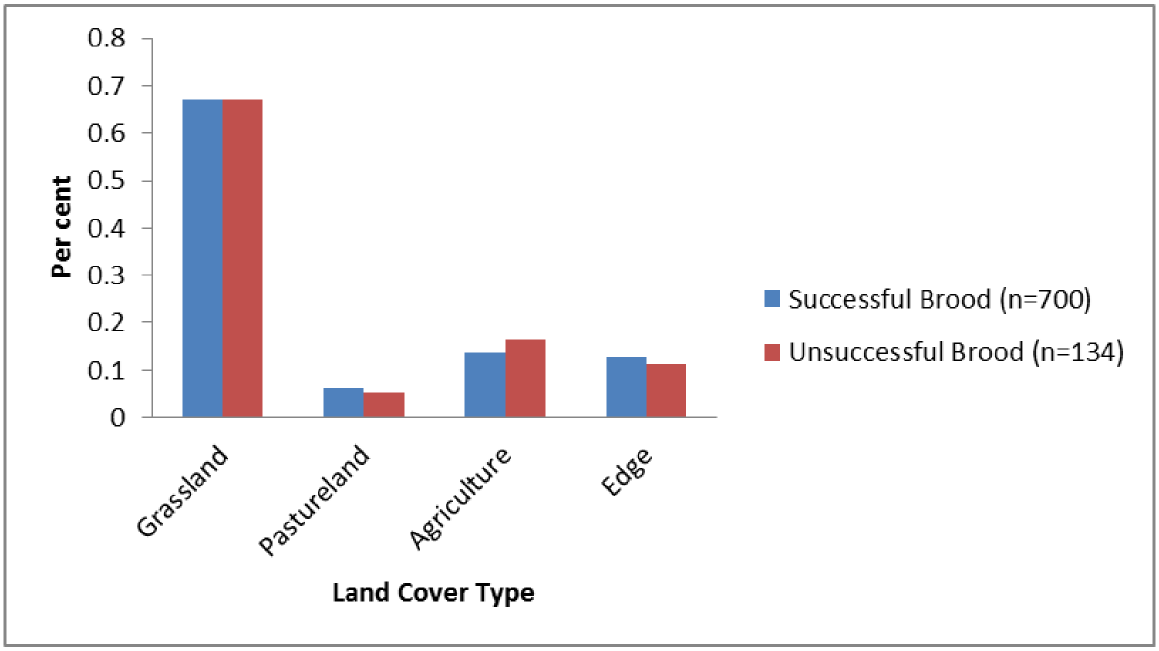


Figure 18. Per cent (%) of successful GPC brood locations and unsuccessful brood locations in macro-scale land cover types, northwest Minnesota June 3 – September 8, 2009.

Successful broods were located in Conservation Reserve Program (CRP) fields approximately half of the time (51.0%), while unsuccessful broods appeared to use them a little more frequently (56.0%) (Table 7).

Table 7. Number and per cent (%) of successful and unsuccessful GPC brood locations in Conservation Reserve Program (CRP) grasslands, northwest Minnesota June 3 – September 8, 2009.

Conservation Program Type	Sample			
	Successful Broods *n* = 700		Unsuccessful Broods *n* = 134	
	No.	% Use	No.	% Use
CRP	357	51.0	75	56.0
Non-CRP	343	49.0	59	44.0

Successful and unsuccessful broods spent most of their time on private land (Table 8) which makes up 97.4% of the study area. Both brood types were also located on county, state, and federal lands. Only one successful brood was located once on Nature Conservancy property, moving away from the nest shortly after hatch.

Table 8. Number and per cent (%) of successful and unsuccessful GPC brood locations in land ownership types, northwest Minnesota June 3 – September 8, 2009.

Ownership	Sample			
	Successful Brood *n* = 700		Unsuccessful Brood *n* = 134	
	No.	% Use	No.	% Use
Private	537	76.7	115	85.8
County	46	6.6	2	1.5
State	92	13.1	11	8.2
Federal	24	3.4	6	4.5
The Nature Conservancy	1	0.1	0	0.0

Analysis at the macro-scale showed successful broods spent significantly less time in grass-dominated habitats ($p < 0.001$) and more time in mixed grass/forb habitat ($p < 0.001$) than unsuccessful broods (Figure 19). Comparatively similar amounts of time were spent in agricultural ($p = 0.522$), other ($p = 0.907$), and edge ($p = 0.975$) habitats.

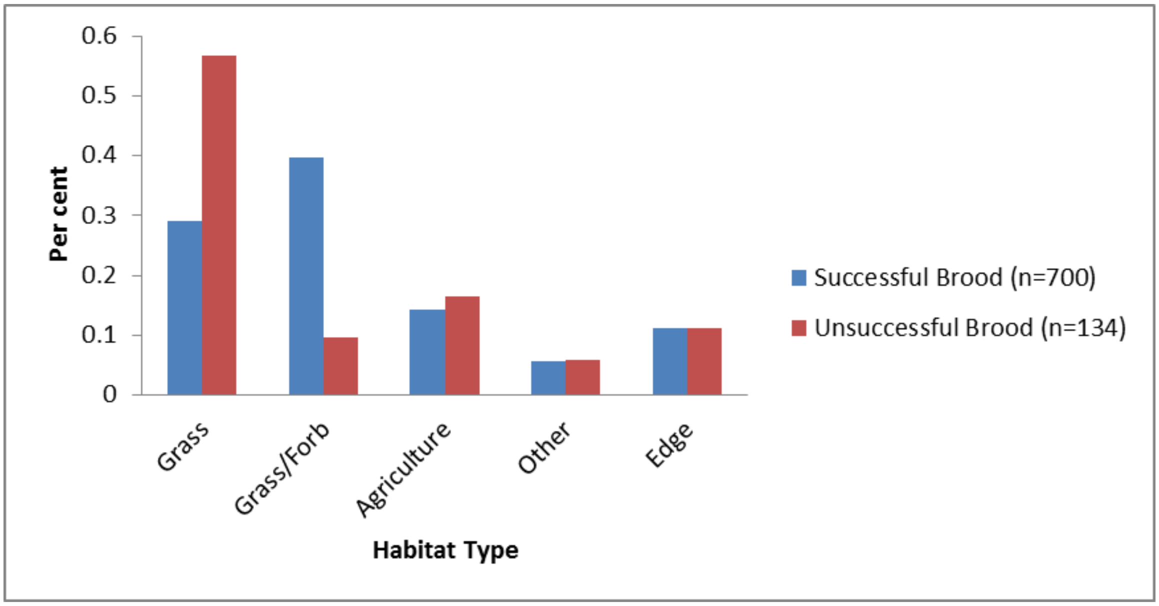


Figure 19. Per cent (%) of successful GPC brood locations and unsuccessful brood locations in macro-scale habitat types, northwest Minnesota June 3 – September 8, 2009.

Micro-scale vegetative analysis supported macro-scale brood use findings where successful broods showed preference for grass/forb mixtures (Figure 20). Unsuccessful broods were located more frequently in grass-dominated areas, but not significantly so (*p* = 0.192), while successful broods spent significantly more time in grass/forb communities (*p* = 0.017). A significantly higher percentage of unsuccessful broods was found in soybean vegetation than successful broods (*p* = 0.007). Unsuccessful broods were never located in alfalfa, wheat or fallow agricultural fields, therefore their significance could not be calculated.

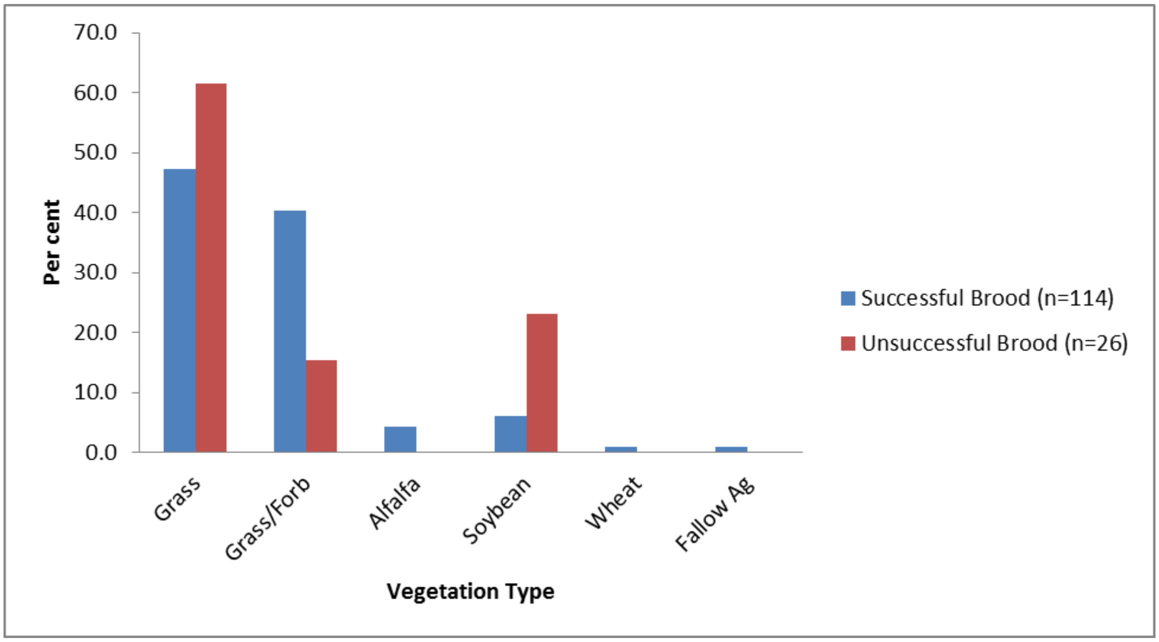


Figure 20. Per cent (%) of successful GPC brood locations and unsuccessful brood locations in micro-scale vegetation types, northwest Minnesota June 14 – August 18, 2009.

Higher invertebrate biomass was collected at successful brood locations than at unsuccessful brood locations in all vegetation types except soybeans (Figure 21). Two-way ANOVA detected no significant main effect of brood type (*p* = 0.333), vegetation category (*p* = 0.120) or interaction between brood type and vegetation category (*p* = 0.607). Subsequent pairwise comparison tests revealed mean invertebrate biomass was marginally significantly higher for successful broods than unsuccessful broods in grass-dominated habitats (*p* = 0.055).

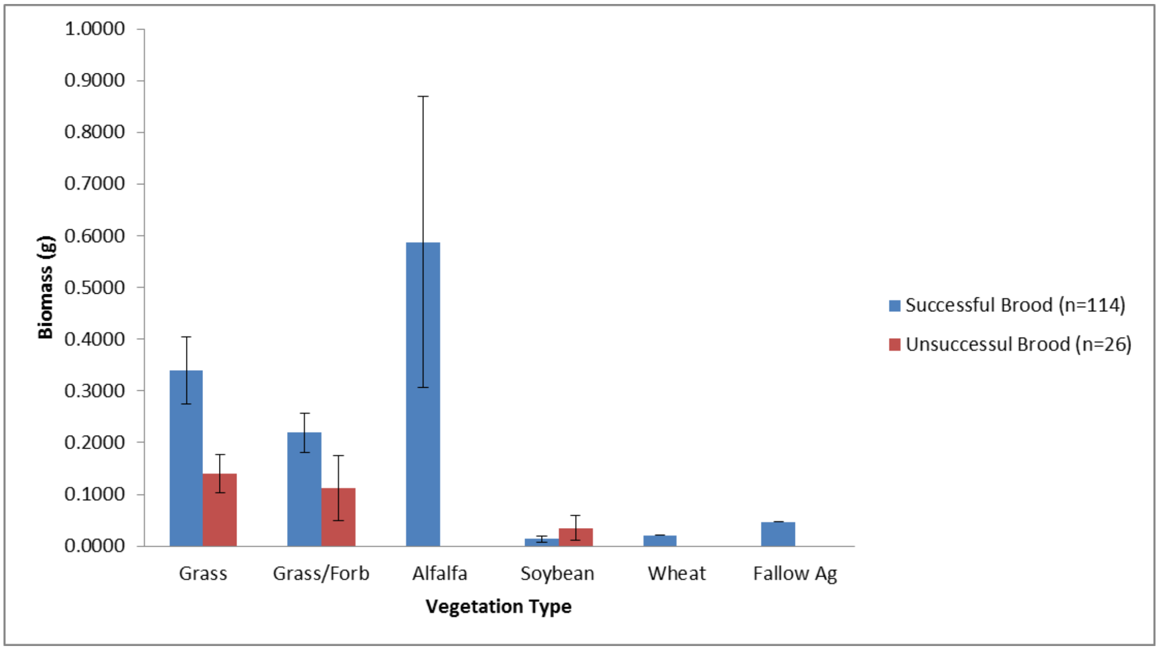


Figure 21. Mean invertebrate biomass (dry mass in grams) in micro-scale vegetation types where successful and unsuccessful GPC broods were located, northwest Minnesota June 14 – August 18, 2009.

When brood types were combined, invertebrate biomass was not significantly higher in habitats with mixed grass/forb vegetation versus those dominated by grass (*p* = 0.223) (Figure 22).

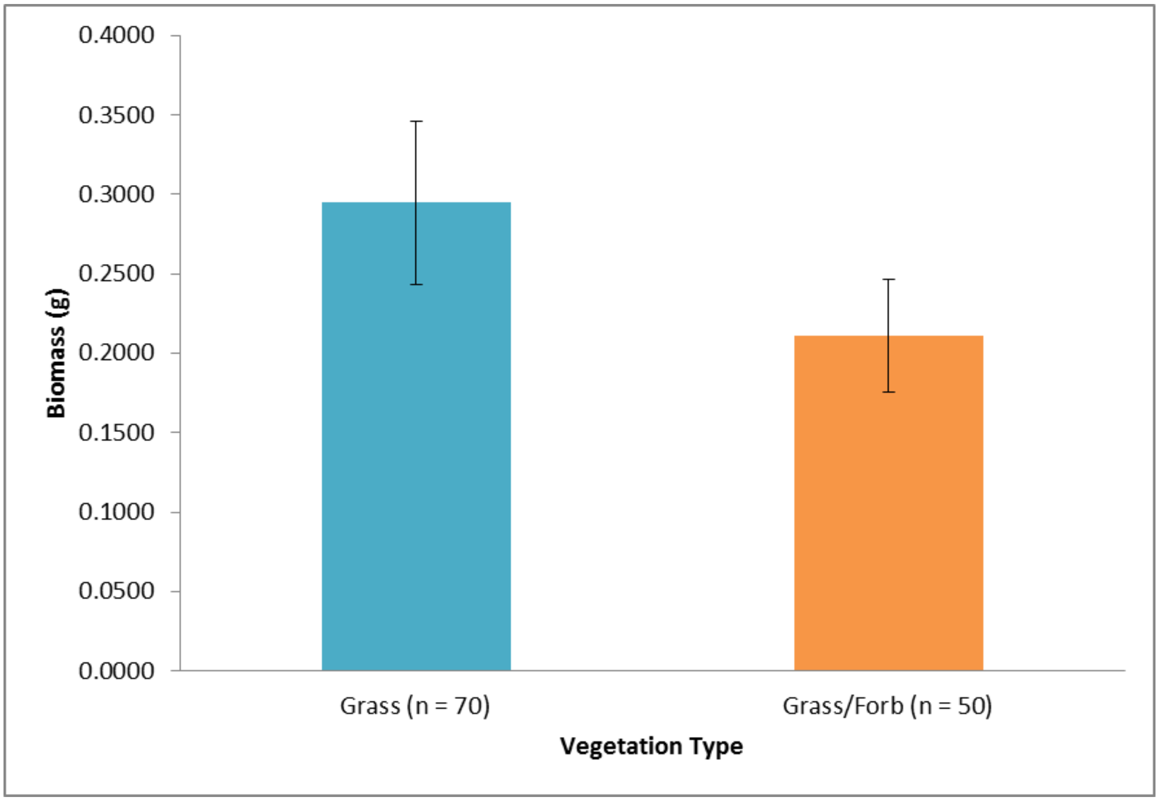


Figure 22. Mean invertebrate biomass (dry mass in grams) in grass and grass/forb vegetation types where combined successful and unsuccessful GPC broods were located, northwest Minnesota June 14 – August 18, 2009.

Overall, invertebrate biomass decreased with increased uncultivated forb presence, but there was no significant trend between forb abundance and invertebrate biomass in habitats where GPC broods were located (*n* = 108, *p* = 0.219) (Figure 23).

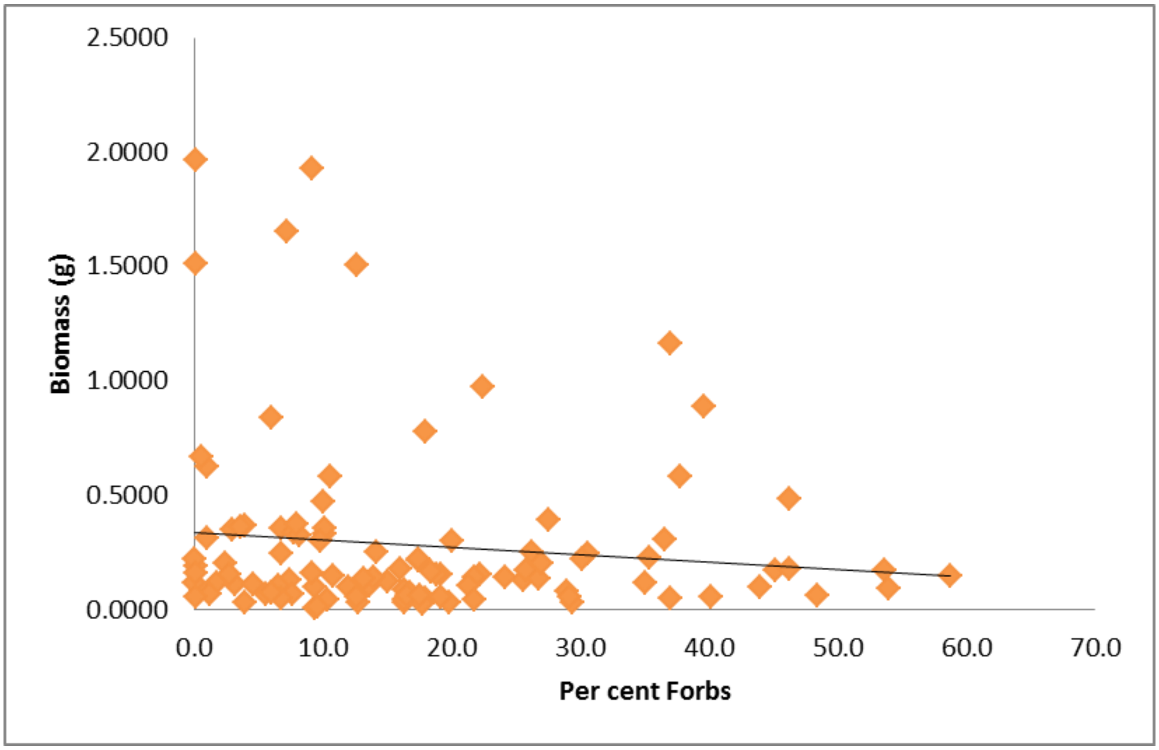


Figure 23. Linear regression illustrating mean invertebrate biomass relative to the per cent of uncultivated forbs in habitats where combined successful and unsuccessful GPC broods were located (*n* = 108), northwest Minnesota June 14 – August 18, 2009.

Invertebrate composition was different among various fob type habitats (Figure 24). Cultivated alfalfa fields and, to a lesser extent, soybean crops, showed substantial diversity within and between their respective habitat types. 31.3% of invertebrates within alfalfa were within the order Other, followed by Homoptera, Diptera and Hemiptera. At 6.9%, alfalfa had the largest proportion of Orthoptera of any forb type habitat. Almost half of the invertebrates found in soybeans were Homoptera, followed by 32.4% in Diptera. The largest percentage of Coleoptera was found in soybean fields at 7.7%. The occurrence of uncultivated forbs within grassland habitats appeared to have no substantial impact on the invertebrate Orders present. Homoptera dominated in both habitats, with < 17% and > 17% forb components. Beyond this, diversity was proportionally higher in habitats with < 17% forbs, while habitats with > 17% forbs had more invertebrates within the Orders Diptera, Hemiptera and Other.

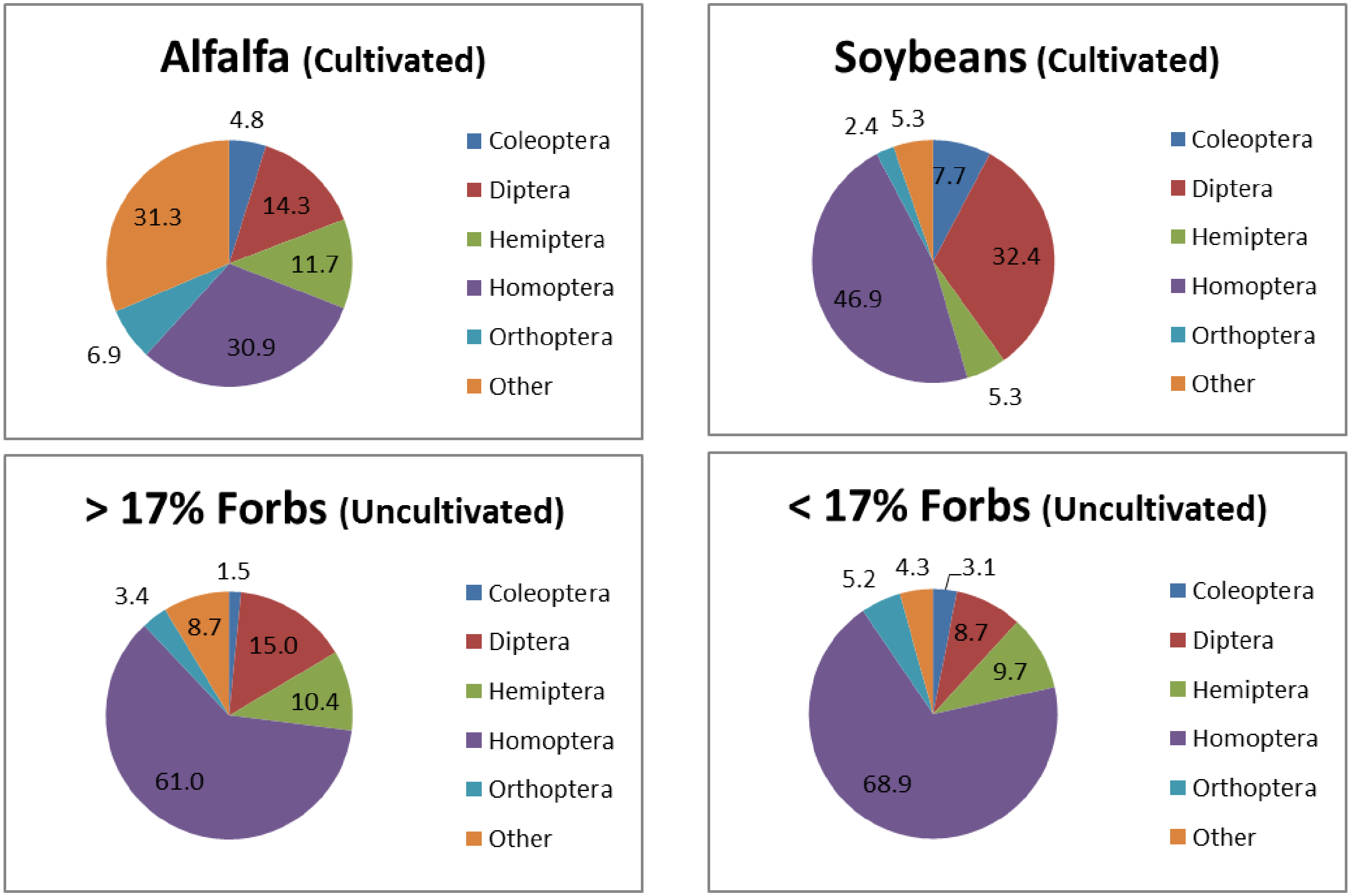


Figure 24. Proportion of invertebrates in forb type habitats where successful GPC broods were located; cultivated alfalfa (*n* = 5), cultivated soybeans (*n* = 13), < 17% uncultivated forbs (*n* = 63), > 17% uncultivated forbs (*n* = 45), northwest Minnesota June 14 – August 18, 2009.

Photo-plot analysis of vegetation causing visual obstruction supported the vegetation type data, since 42.7% of successful brood locations were in grass-dominated habitats and the vast majority of their remaining time was spent in various forb-type habitats. Further substantiating vegetation type data, obstruction category results for unsuccessful broods showed 12.3% of their time was spent in soybean fields (Table 9).

Table 9. Number and per cent (%) of vegetation types causing visual obstruction at successful and unsuccessful GPC brood sites, northwest Minnesota June 14 – August 18, 2009.

Obstruction Category	Successful Broods		Unsuccessful Broods	
	n = 90		*n* = 16	
	No.	%	No.	%
Grass	782	42.7	193	59.4
Grass/Forb	327	17.9	49	15.1
Forb/Grass	173	9.4	20	6.2
Grass/Legume	121	6.6	18	5.5
Soybeans	109	6	40	12.3
Legume/Grass	89	4.9	0	0
Legume	64	3.5	0	0
Forb	59	3.2	0	0
Grass/Other	34	1.9	5	1.5
No Vegetation	18	1	0	0
Other	18	1	0	0
Other/Grass	16	0.9	0	0
Other/Forb	12	0.7	0	0
Forb/Other	5	0.3	0	0
Wheat	4	0.2	0	0

Certain plant species provided the dominant cover during vegetation obstruction readings. Grasses included smooth brome (*Bromus inermis*), redtop (*Agrostis stolonifera*), timothy (*Phleum pretense*), prairie chord (*Spartina pectinata*), quack (*Agropyron repens*), big blue stem (*Andropogon gerardi*), and foxtail barely (*Hordeum* *jubatum*). The most ubiquitous non-leguminous forb was goldenrod (*Solidago mollis*). Bedstraw (*Galium boreale*), sunflower (*Helianthus petiolaris*), Canada thistle (*Cirsium arvense*) and milkweed (*Asclepias speciosa*) were also recorded. Legume forbs included alfalfa (*Medicago sativa*), birdsfoot trefoil (*Lotus corniculatus*), sweet clover (*Melilotus alba*) and clover (*Trifolium pretense*).

Just over half of site visits to both successful and unsuccessful broods were in undisturbed habitats (53.5% and 57.7%, respectively) (Figure 25). All other locations occurred in habitats disturbed by mowing, grazing, burning or cultivation, with unsuccessful broods spending 23.1% of their time in plowed fields, while successful broods occurred more often in mowed and moderately grazed habitats.

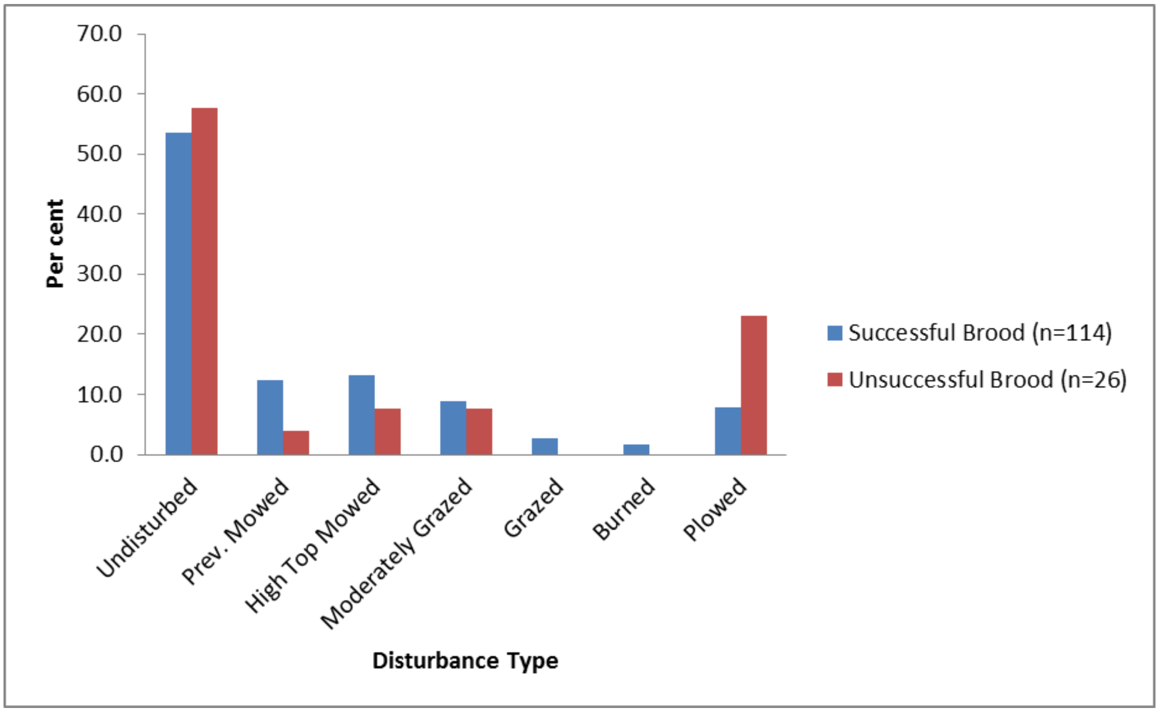


Figure 25. Per cent (%) of successful GPC brood locations and unsuccessful brood locations in disturbance types, northwest Minnesota June 14 – August 18, 2009.

As occurred in vegetation types, higher invertebrate biomass was collected at successful brood locations than at unsuccessful brood locations in all disturbance types except plowed fields (Figure 26). At successful brood sites, mean invertebrate biomass was highest in previously mowed vegetation, followed by moderately grazed pastures and high top mowed CRP. At unsuccessful brood locations, mean invertebrate biomass was also highest in previously mowed vegetation, followed closely by undisturbed vegetation.

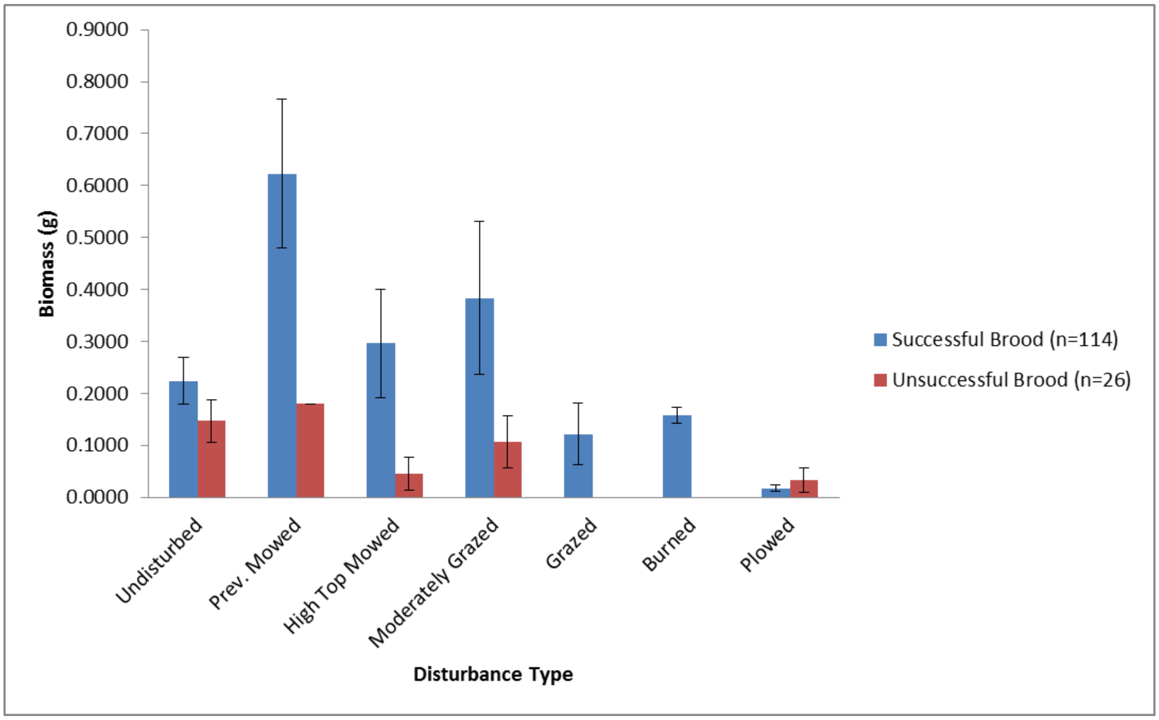


Figure 26. Mean invertebrate biomass (dry mass in grams) in disturbance types where successful and unsuccessful GPC broods were located, northwest Minnesota June 14 – August 18, 2009.

Brood use of undisturbed habitats was supported by the high number of broods located in habitats disturbed at least twelve months prior to use (Figure 27). In fact, of all successful and unsuccessful brood site visits in undisturbed habitat, all but two (one to each brood type) were disturbed at least 60 months (5 years) prior to use. Successful broods split their remaining time between habitats disturbed 0-6 months prior to use (21.9%) and 7-12 months prior to use (27.2%). Unsuccessful broods more frequently used habitats disturbed recently, spending 30.8% of their time in habitats disturbed 0-6 months prior to use and 15.4% of their time in habitats disturbed 7-12 months prior to use.

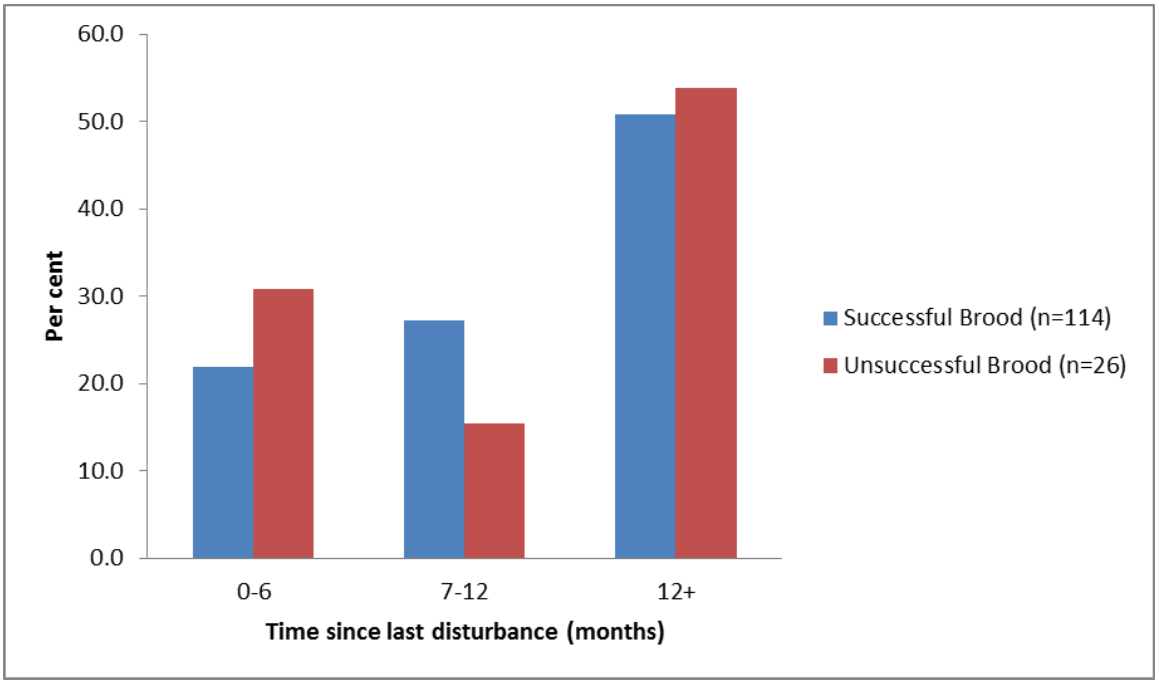


Figure 27. Per cent (%) of successful GPC brood locations and unsuccessful brood locations according to time since last disturbance, northwest Minnesota June 14 – August 18, 2009.

Across temporal disturbance periods, higher invertebrate biomass was collected at successful brood locations than at unsuccessful brood locations regardless of time since last disturbance (Figure 28). For both successful and unsuccessful broods, mean invertebrate biomass was highest in habitats disturbed 7-12 months prior to use.

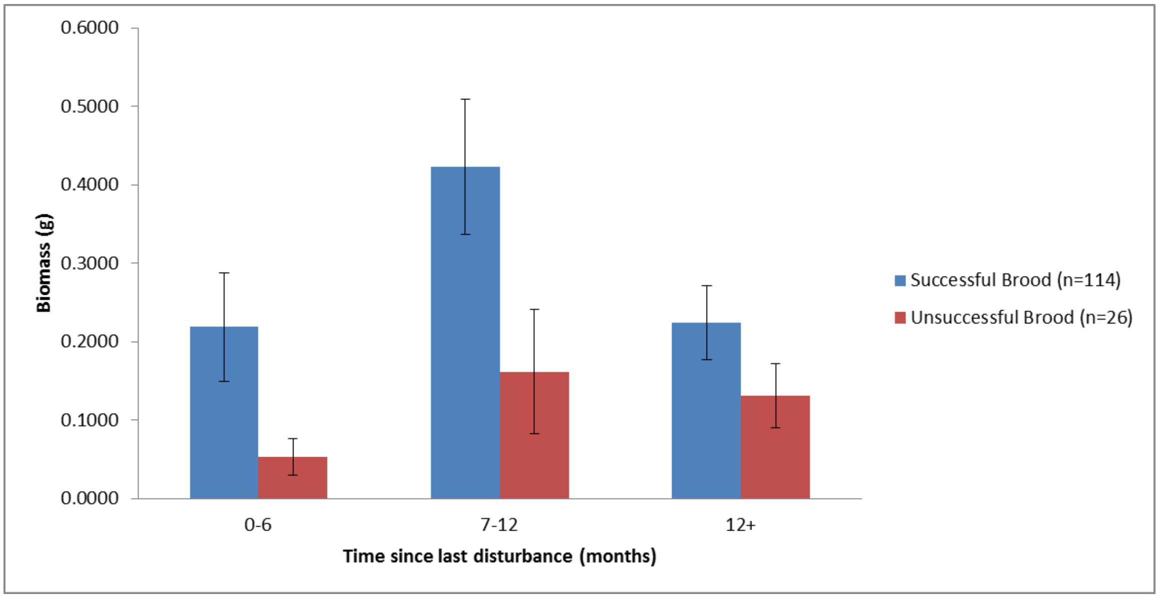


Figure 28. Mean invertebrate biomass (dry mass in grams) at successful GPC brood locations and unsuccessful brood locations according to time since last disturbance, northwest Minnesota June 14 – August 18, 2009.

Mean vegetation height was similar across all samples, and lowest at successful broods (Table 10).

Table 10. Mean vegetation height (cm) at successful GPC brood sites, unsuccessful brood sites and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Sample	*n*	cm	
Successful Broods	90	59	SD .17
Unsuccessful Broods	16	62	SD .16
Permanent Transects	73	61	SD .30

Mean vegetation effective height was also similar across all samples, but lowest at permanent transects (Table 11).

Table 11. Mean vegetation effective height (cm) at successful GPC brood sites, unsuccessful brood sites and permanent transect sites, northwest Minnesota June 14 – August 18, 2009.

Sample	*n*	cm	
Successful Broods	90	31	SD .12
Unsuccessful Broods	16	33	SD .09
Permanent Transects	73	29	SD .16

Successful broods occupied vegetation with lower effective height at earlier ages than unsuccessful broods (Figure 29). At 0-2 weeks of age, successful broods were located in vegetation where average screening height was 27.4 cm, versus 34.8 cm for unsuccessful broods. At 3-4 weeks, mean vegetation effective height increased for successful broods and decreased for unsuccessful broods, and this pattern continued at 5-6 weeks of age. At 7+ weeks, successful broods were located in vegetation with a mean effective height of 32.9 cm, and unsuccessful broods were located in vegetation with a mean effective height of 34.2 cm, which was almost the same in which they began.

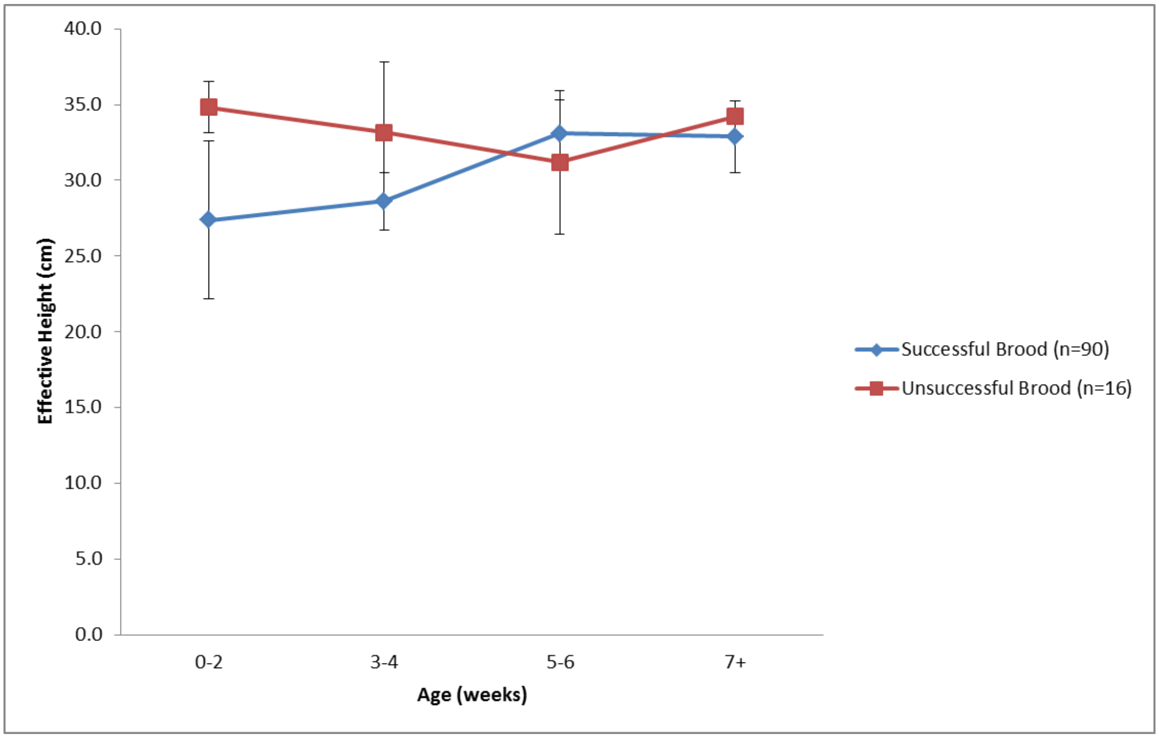


Figure 29. Mean vegetation effective height (cm) by age at successful GPC brood sites and unsuccessful brood sites, northwest Minnesota June 14 – August 18, 2009.

Time spent in each effective height class was similar between successful and unsuccessful broods, although successful broods were located a bit more often in shorter vegetation (Figure 30). Successful and unsuccessful broods occurred in vegetation with a screening height of 26 - 50 cm 64.4% and 75.0% of the time, respectively.

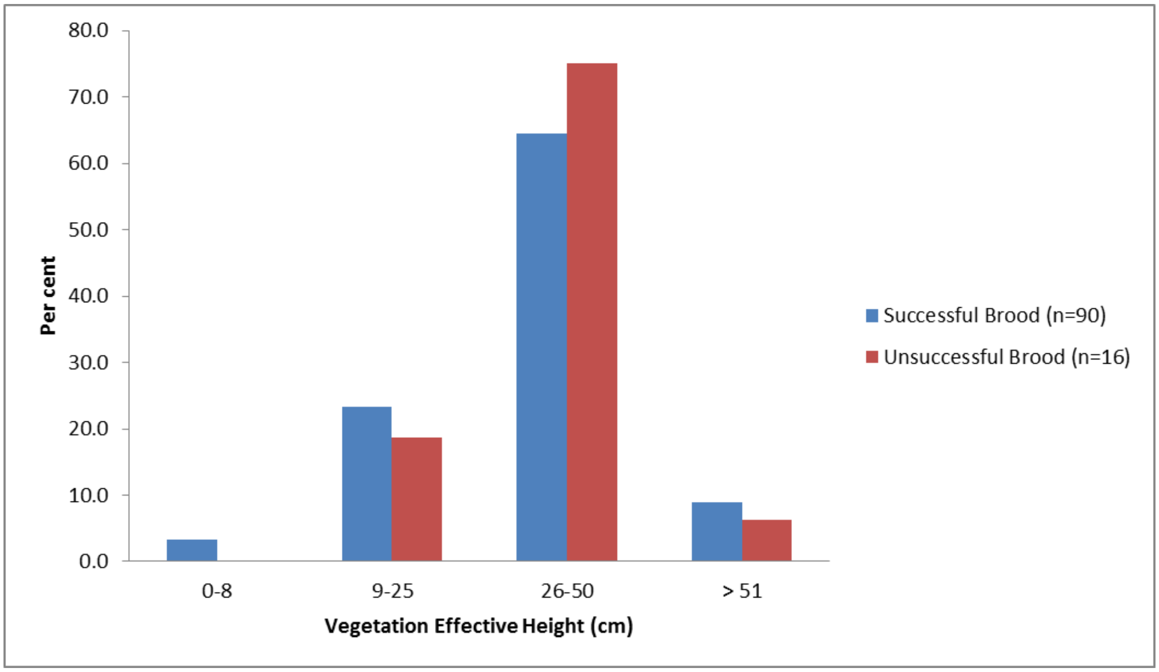


Figure 30. Per cent (%) of successful GPC brood locations and unsuccessful brood locations in vegetation effective height classes, northwest Minnesota June 14 – August 18, 2009.

Mean invertebrate biomass was consistently higher at successful brood locations than at unsuccessful brood locations in all effective height classes (Figure 31). Mean invertebrate biomass was simultaneously highest for successful broods and lowest for unsuccessful broods in vegetation with a screening height between 9 and 25 cm.

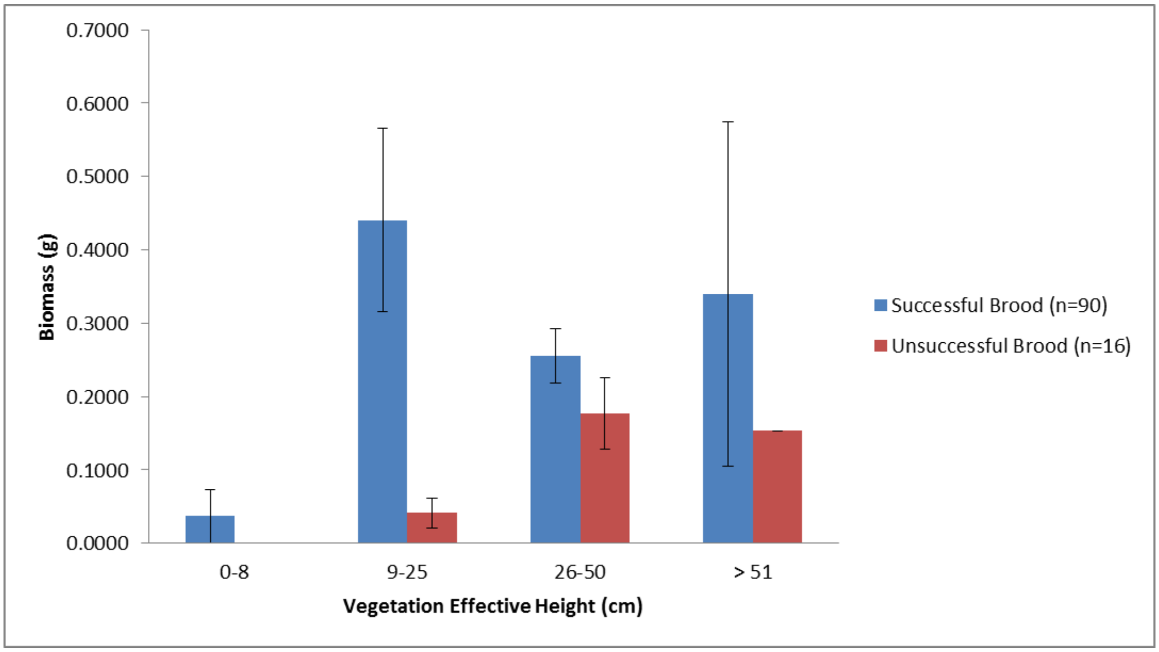


Figure 31. Mean invertebrate biomass (dry mass in grams) in vegetation effective height classes where successful and unsuccessful GPC broods were located, northwest Minnesota June 14 – August 18, 2009.

The proportion of vegetation effective height categories where successful broods were located varied according to disturbance type (Figure 32). The structural heterogeneity of the habitat (measured by the representative proportion of each effective height category) was greatest in plowed fields and lowest in grazed pastures, in which all measurements were 9 to 25 cm. Undisturbed habitats showed relatively low structural diversity, while the movement and grazing of cattle on moderately grazed pastures appropriately increased the number of different effective height categories.

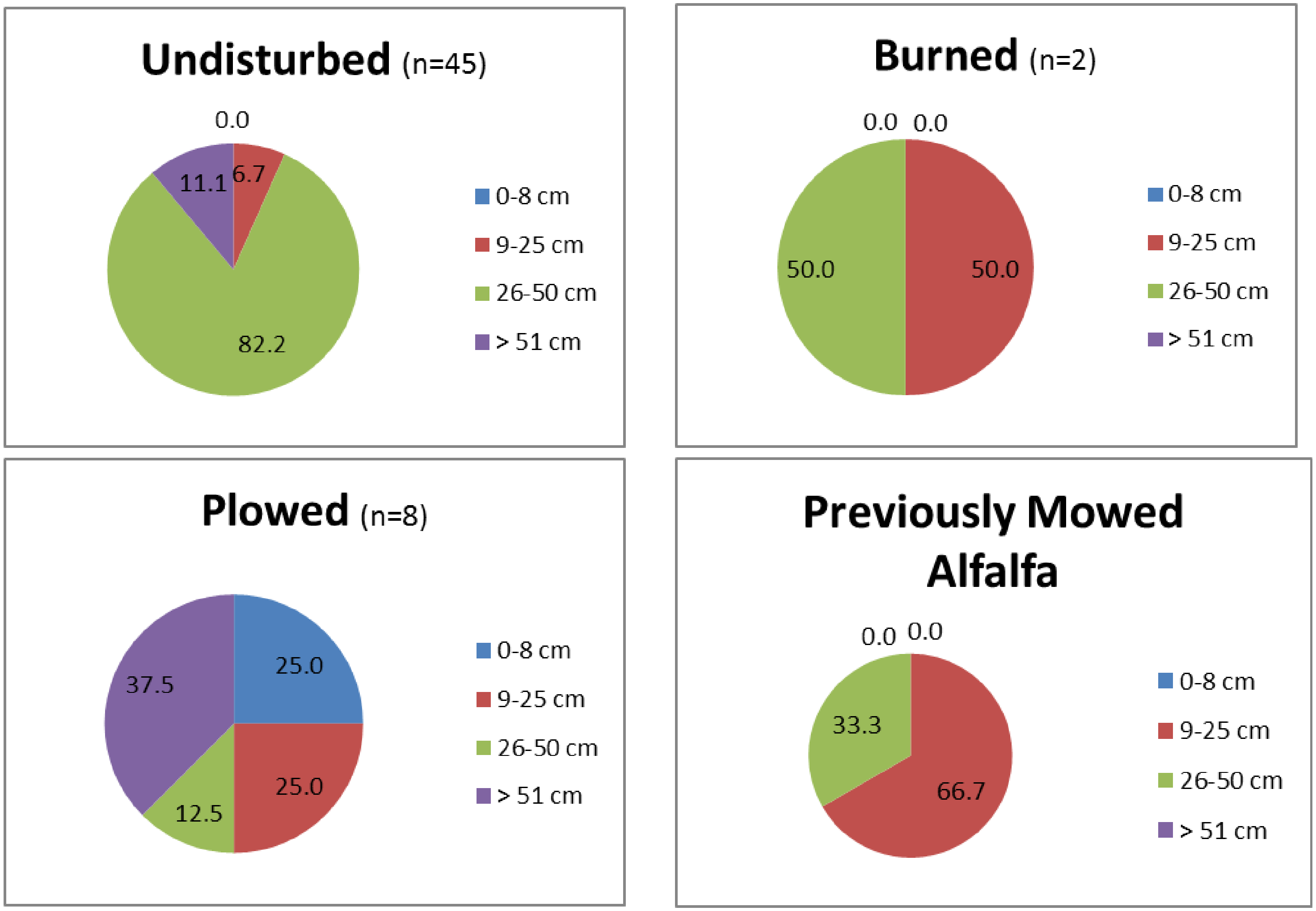


Figure 32. Proportion of vegetation effective height categories by disturbance type at successful GPC brood locations, northwest Minnesota June 14 – August 18, 2009.

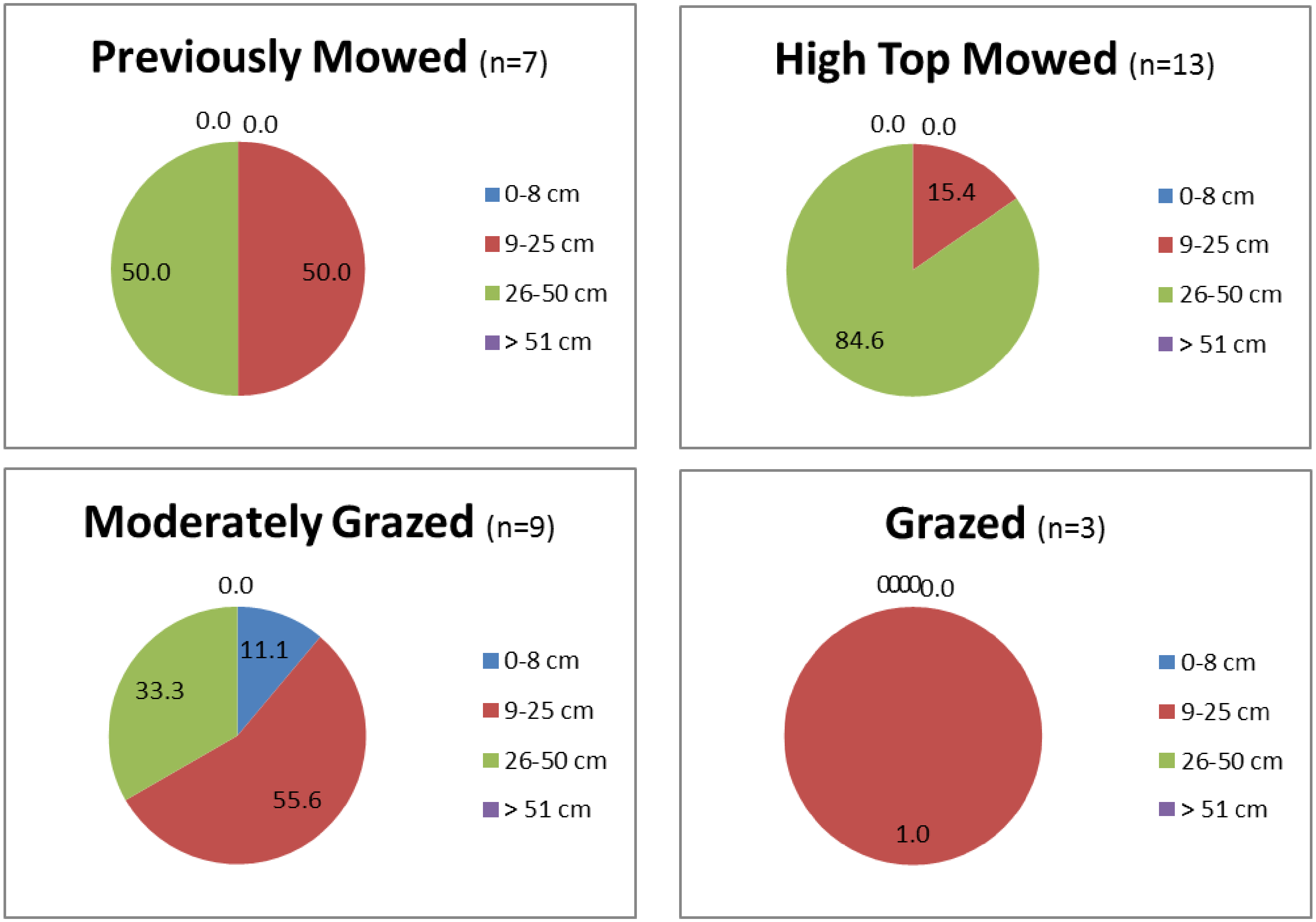


Figure 32. Proportion of vegetation effective height categories by disturbance type at successful GPC brood locations, northwest Minnesota June 14 – August 18, 2009 (Continued).

Permanent Transect Type in Relation to Invertebrate Characteristics

Among permanent transect habitat types, mean invertebrate abundance (indexed as biomass and number of insects) was highest in alfalfa hayfields and lowest in row crops. Mean invertebrate biomass was significantly different across samples (one-way ANOVA, $p = 0.001$) (Figure 33). Tukey's HSD showed mean invertebrate biomass was significantly higher for undisturbed CRP than row crops ($p = 0.003$) and also significantly higher for undisturbed CRP over native prairie ($p = 0.004$). There was marginal significance for undisturbed CRP over burned native prairie ($p = 0.094$). Mean invertebrate biomass across all other permanent transect types showed no significance.

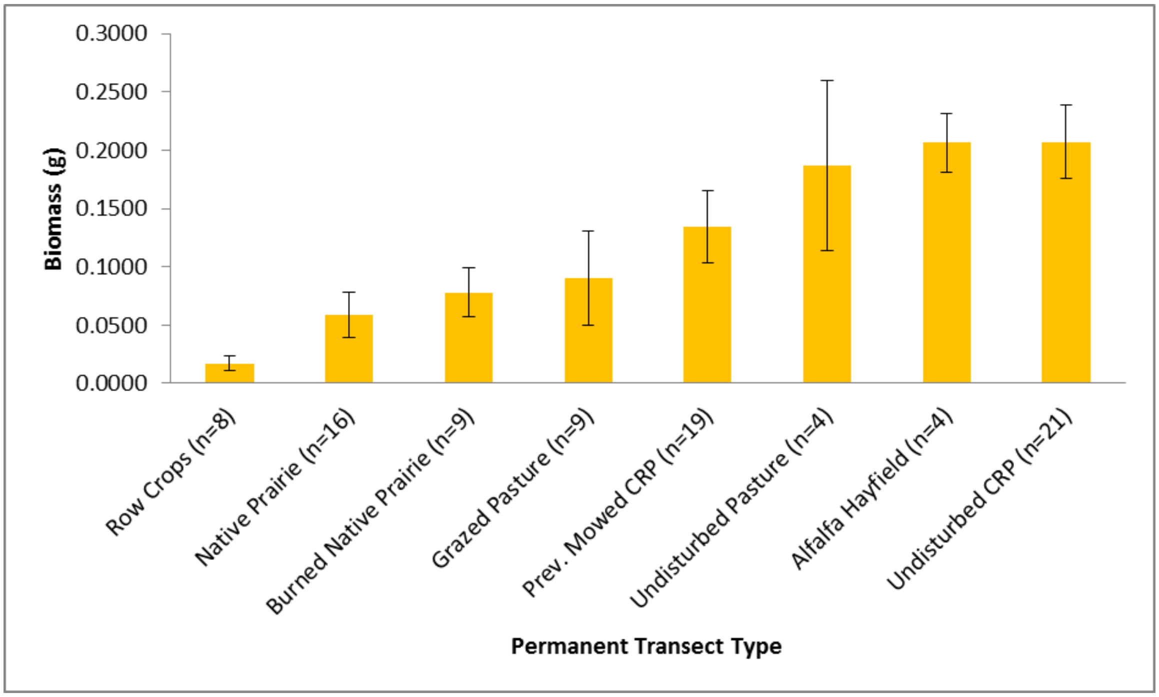


Figure 33. Mean invertebrate biomass (dry mass in grams) at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

There was no significant difference between the number of invertebrates across permanent transect types (one-way ANOVA, *p* = 0.216) (Figure 34). Overall, alfalfa fields and pasturelands held the highest number of invertebrates while row crops held very few.

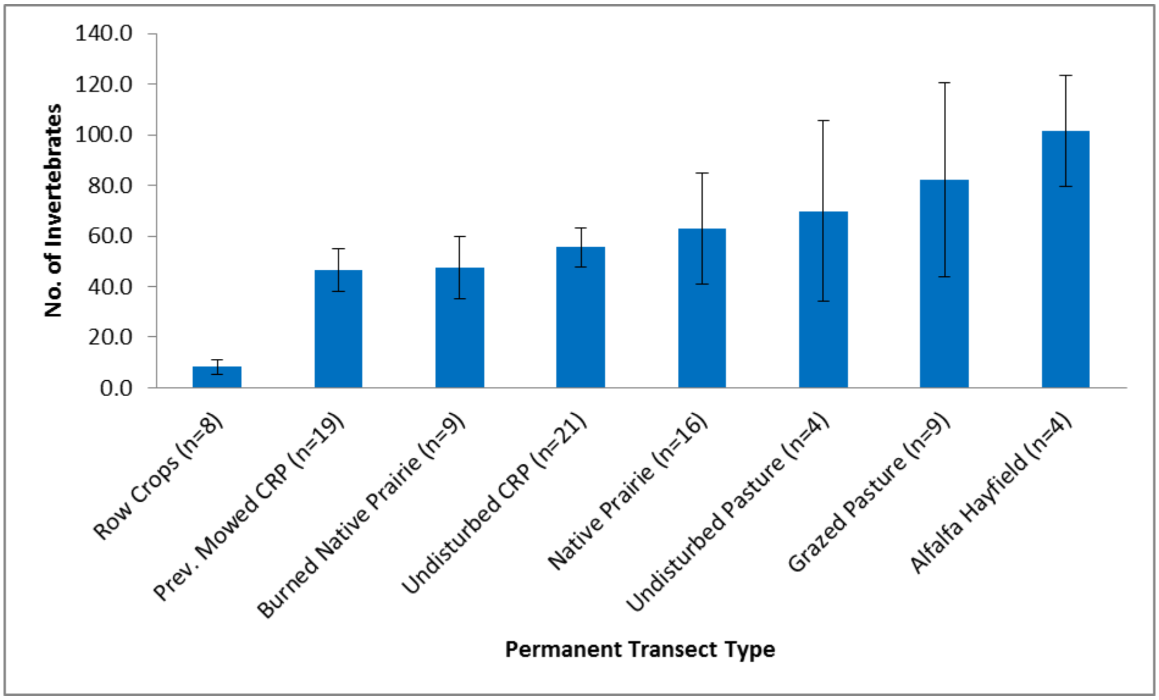


Figure 34. Mean number of invertebrates at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

Homoptera yielded a substantially higher biomass than any other Order weighed across permanent transect types, followed by Orthoptera (Figure 35). Mean biomass of Homoptera was highest in undisturbed CRP (0.1667 grams) and previously mowed CRP (0.0911 grams), followed by alfalfa hayfield (0.0774 grams), undisturbed pasture (0.0503 grams), grazed pasture (0.0422 grams), burned native prairie (0.0301 grams), native prairie (0.0215 grams), and row crops (0.0004 grams). Mean biomass of Orthoptera was highest in alfalfa hayfield (0.1032 grams) and undisturbed pasture (0.0893 grams), followed by undisturbed CRP (0.0256 grams), grazed pasture (0.0144 grams), previously mowed CRP (0.0132 grams), row crops (0.0075 grams), native prairie (0.0043 grams), and burned native prairie (0.0011 grams). Mean biomass of Hemiptera and Diptera was highest in undisturbed pasture (0.0205 and 0.0172 grams, respectively) and lowest in undisturbed CRP (0.0035 and 0.0011 grams, respectively). Mean biomass of Coleoptera was low overall, but highest in burned native prairie (0.0140 grams) and virtually absent from grazed pasture permanent transects (0.0002 grams). Mean biomass of invertebrates classed as Other was relatively consistent across permanent transect type; highest in previously mowed CRP (0.0109 grams) and absent in row crops (0.0000 grams).

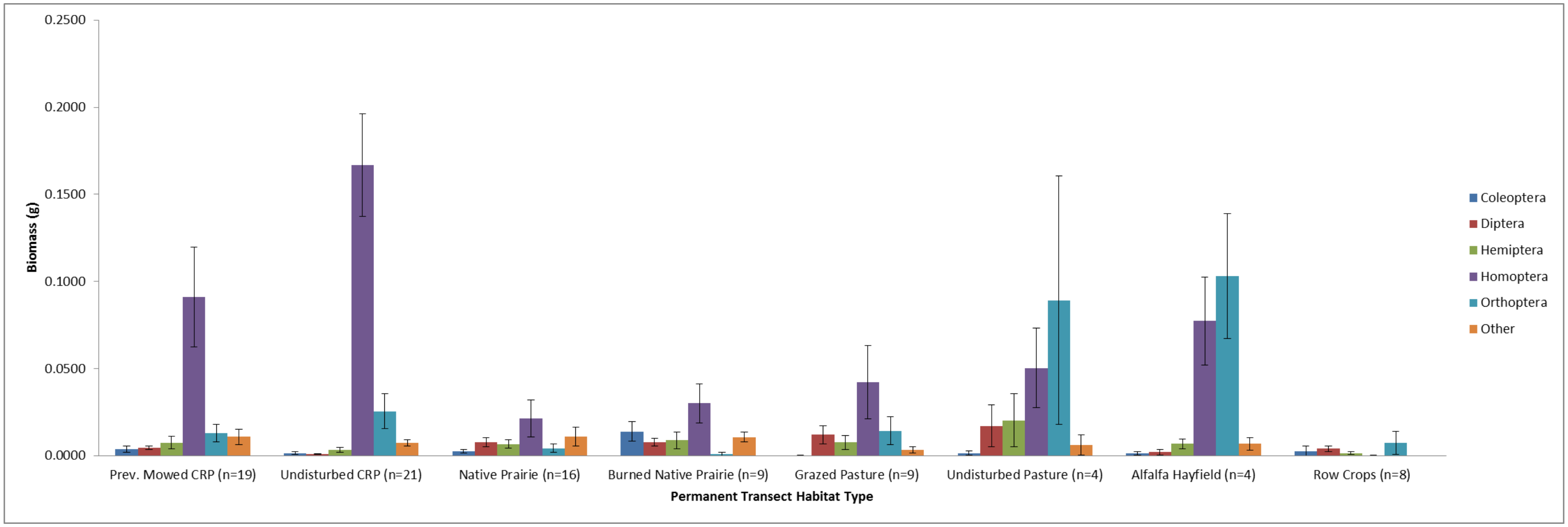


Figure 35. Mean invertebrate biomass (dry mass in grams) by Order at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

Total invertebrates were highest in undisturbed CRP and native prairie, followed by previously mowed CRP and grazed pasture (Table 12). Invertebrate composition (indexed as Order) was substantially different across permanent transect habitat types (Figure 36). Homoptera dominated in undisturbed CRP (81.2%), previously mowed CRP (61.3%), undisturbed pasture (60.6%), grazed pasture (54.9%), and alfalfa hayfield (54.2%) habitats. Orthoptera numbers were highest in alfalfa hayfield (22.9%), grazed pasture (9.2%), and undisturbed pasture (8.2%). Native prairie fostered the highest number of Hemiptera (52.0%), and row crops produced the highest numbers of Diptera (66.7%). Overall invertebrate diversity was greatest in burned native prairie and native prairie, followed by alfalfa hayfield and grazed pasture permanent transect habitat types.

Table 12. Number and per cent (%) of invertebrates by Order at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

Permanent Transect Type	*n*	Coleoptera		Diptera		Hemiptera		Homoptera		Orthoptera		Other		Total no. of invertebrates
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	
Prev. Mowed CRP	19	29	3.3	103	11.6	76	8.6	544	61.3	25	2.8	110	12.4	887
Undisturbed CRP	21	14	1.2	30	2.6	25	2.1	948	81.2	16	1.4	134	11.5	1167
Native Prairie	16	17	1.7	190	18.9	523	52.0	179	17.8	14	1.4	82	8.2	1005
Burned Native Prairie	9	32	7.5	100	23.4	100	23.4	123	28.8	3	0.7	69	16.2	427
Grazed Pasture	9	1	0.1	175	23.7	42	5.7	406	54.9	68	9.2	47	6.4	739
Undisturbed Pasture	4	3	1.1	57	20.4	16	5.7	169	60.6	23	8.2	11	3.9	279
Alfalfa Hayfield	4	6	1.5	23	5.7	42	10.3	220	54.2	93	22.9	22	5.4	406
Row Crops	8	1	1.5	44	66.7	10	15.2	8	12.1	3	4.5	0	0.0	66

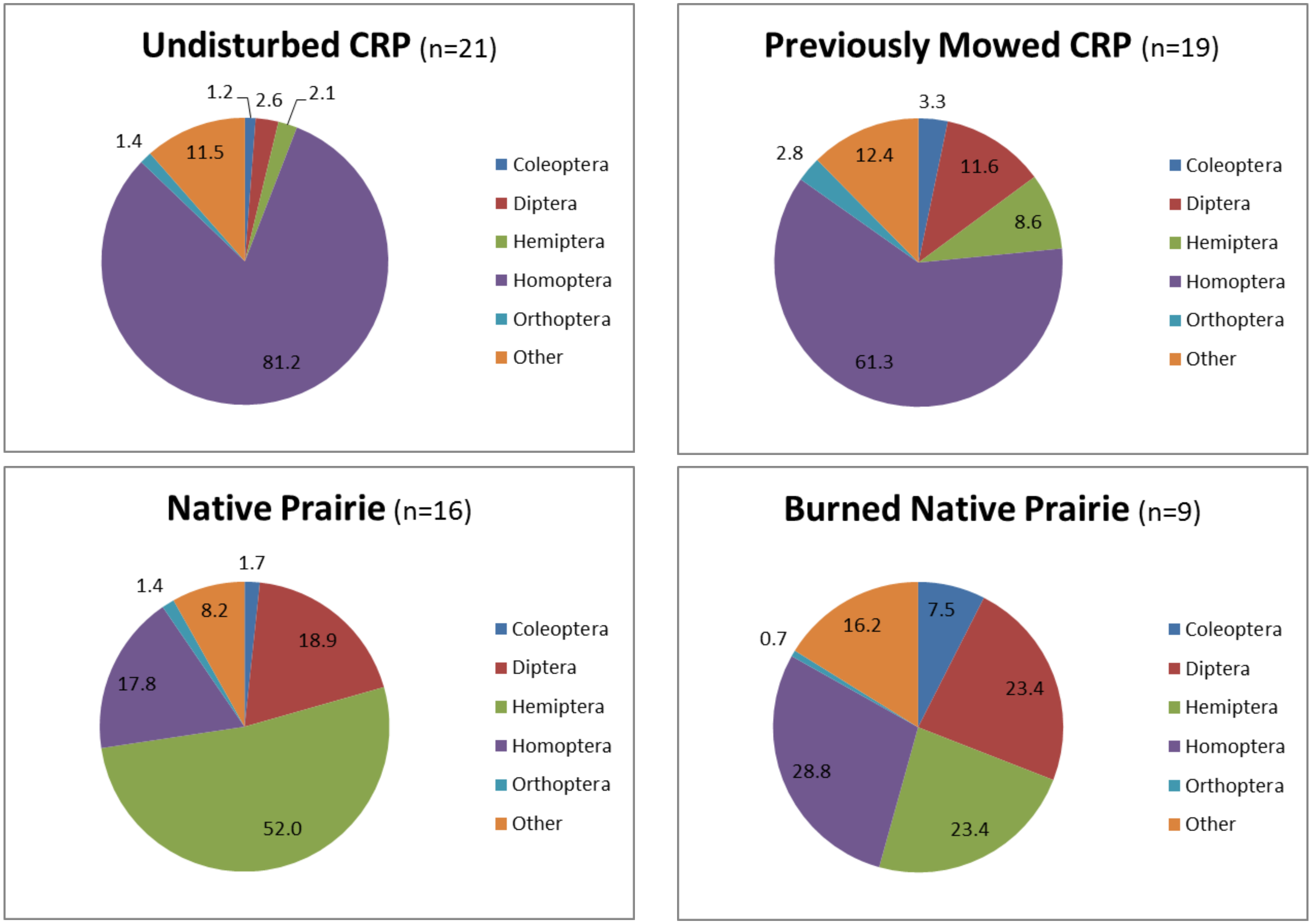


Figure 36. Proportion of invertebrates by Order at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

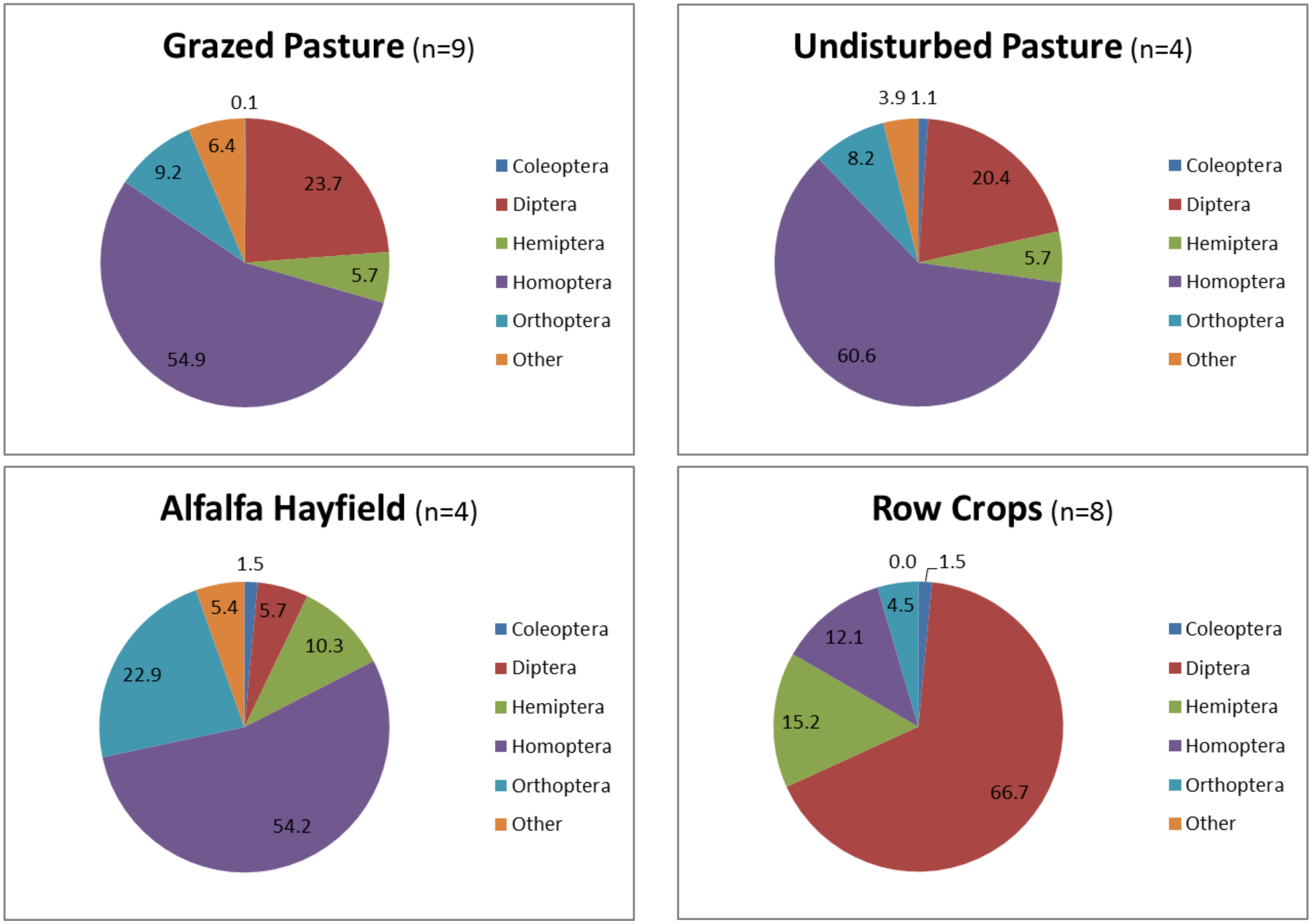


Figure 36. Proportion of invertebrates by Order at permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009 (Continued).

When all permanent transect types were combined and divided across five time intervals over the study period, mean biomass was consistently higher for Homoptera (Figure 37). Mean biomass of all invertebrate Orders increased between the end of June and the beginning of July. Mean biomass was highest between July 1 and July 11 for Homoptera, Hemiptera, Diptera, and Coleoptera. It was highest for Orthoptera between July 12 and July 25, and for invertebrates pooled as Other between August 9 and August 16. Mean biomass of Homoptera peaked in early July (0.1348 grams) and then decreased through to the middle of August (0.0722 grams), followed by a slight increase (0.0785 grams). Mean biomass of Orthoptera increased dramatically between the end of June (0.0003 grams) and the middle of July (0.0352 grams), where it remained for the rest of the field season. Mean biomass of Hemiptera first peaked in early July (0.0161 grams), decreased through the middle of July (0.0036 grams), before increasing throughout the remainder of the field season. Mean biomass of Coleoptera and Other followed similar patterns over time, both showing an initial peak in early July (0.0064 and 0.0124 grams, respectively) and again by the middle of August (0.0057 and 0.0124 grams, respectively). Diptera was the only Order where mean biomass peaked in early July (0.0145 grams) and decreased through the rest of the field season.

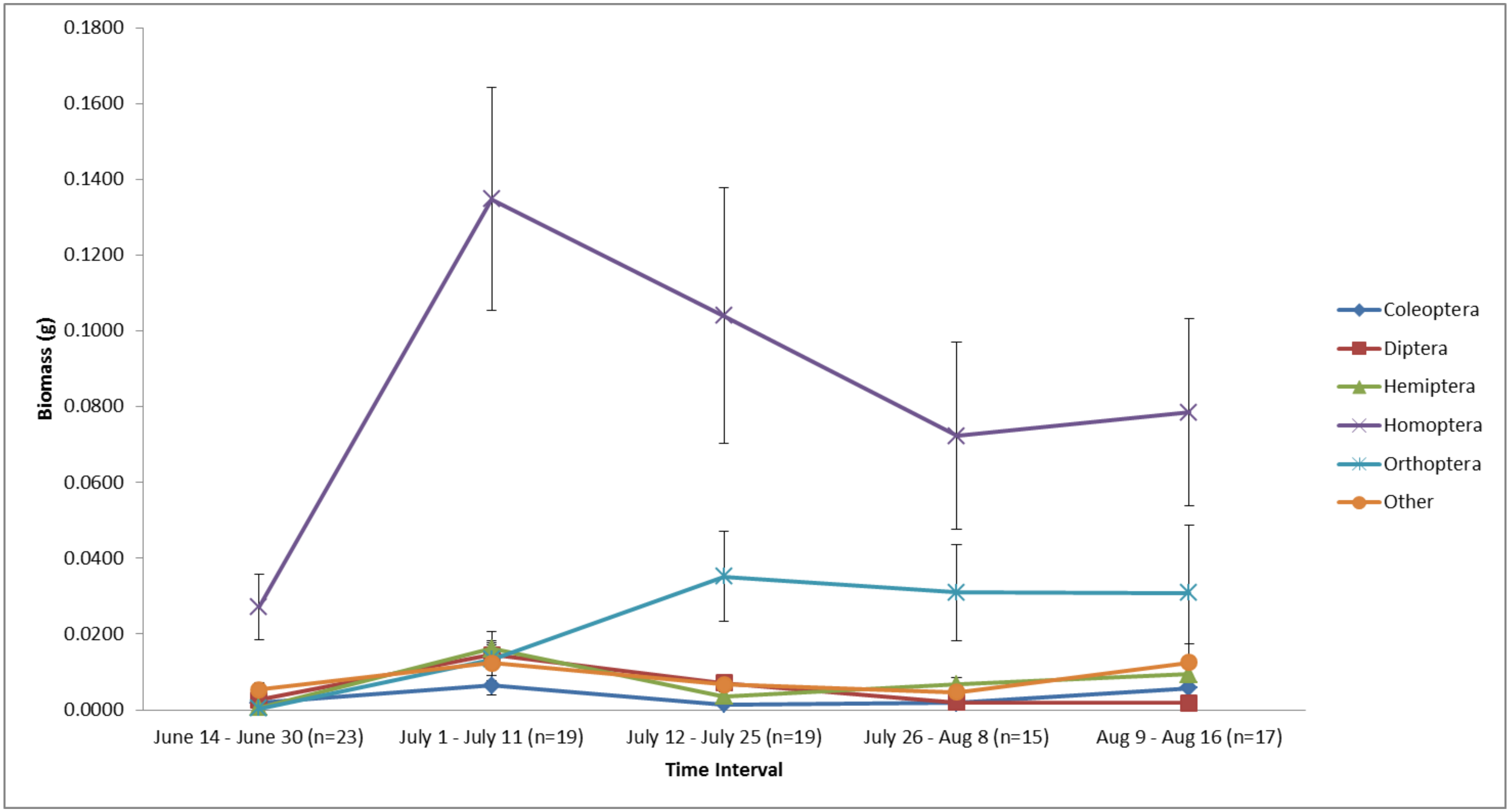


Figure 37. Mean invertebrate biomass by Order during five time intervals in combined permanent transect habitat types, northwest Minnesota June 14 – August 18, 2009.

DISCUSSION

In this chapter I discuss the results of the data analysis, beginning with a summary of study limitations. The second section reveals relationships among GPC broods, prairie invertebrates and grassland habitats. The thesis concludes with management recommendations for greater prairie chicken broods in northwest Minnesota prairie grasslands.

Study Limitations

This study occurred toward the end of a long term project in northern GPC habitat where data on GPC movement and behaviour have been gathered for over two decades. The spring/summer of 2009 was the first field season in which detailed information on invertebrates and brood habitat was collected. In subsequent years, invertebrate data collection has begun earlier in the field season enabling improved trend patterning. In this study, substantially more successful than unsuccessful broods were observed, and some unsuccessful brood variables lacked enough data for comparison and/or impeded possible statistical significance.

Only one method of collecting invertebrates was used in this study. All invertebrate sampling techniques are bias toward specific insects (Cooper and Whitmore 1990, Doxon et al. 2011). Sweep nets sample poorly in very tall and very short vegetation and their catch does not accurately represent all invertebrates available to foraging predators (Cooper and Whitmore 1990). Further to this, not all invertebrates in the habitat may be considered “available” to the predator since it is likely not all insects occurring in the habitat will be selected for consumption (Jones 1963, Whitmore et al.

1986, Cooper and Whitmore 1990). These study limitations can be accounted for by choosing sampling method(s) that collect across all invertebrate taxa proportionally (i.e. a combination of sweep netting and portable vacuum sampling) (Cooper and Whitmore 1990, Doxon et al. 2011). Choice of sampling technique(s) may be further influenced by first gathering dietary data on GPC broods, commonly done through faecal analysis, to determine the types and sizes of invertebrate prey eaten by GPC chicks (Cooper and Whitmore 1990, Doxon et al. 2011). Where these invertebrates reside in the vegetation may best determine which sampling method(s) to use. Moreover, answers to certain questions may be incomplete without the knowledge of preferred invertebrate resources. If possible, sorting to family or species would more accurately identify selected food items and further target habitat management regimes. It may also be that density estimates (measures of absolute abundance) would better measure interspecific invertebrate and/or habitat comparisons, in which case, sweep netting becomes an inappropriate sampling technique and different method(s) must be used (i.e. collecting vegetation, stationary suction traps, portable vacuum sampling, or direct observation) (Cooper and Whitmore 1990).

Previous studies have already established the long-term dominance of invertebrate fauna in *Tympanuchus* brood diets (*see* Savory 1989), including GPC broods and their apparent preference for Coleoptera and Orthoptera (Yeatter 1943, Jones 1963). Data on GPC brood diet were not collected during this study. Rather, the focus was placed on relative invertebrate abundance and composition in the habitats where GPC broods occur, and are thereby feeding. Therefore, in this study, invertebrate availability is defined simply as the prey types collected where GPC broods were located.

I did not use models to establish cause-and-effect relationships. Information resulting from these analyses illustrate observed associations between factors and should be interpreted as such.

Brood, Invertebrate and Habitat Relationships

This study was conducted to assess which northern prairie habitats produce invertebrate abundance and composition conducive to GPC brood success. Analyzed relationships illustrate northwest Minnesota GPC brood habitat by means of the invertebrate resources available and the vegetation characteristics used.

Brood Range Size & Movement

Mean brood range of successful broods (199.6 ha) was average among previous findings that ranged from 82.6 ha (Svedarsky 1979) to 379 ha (Ryan et al. 1998). Svedarsky (1979) and Newell (1987) found successful broods had smaller home range size than broodless hens, presumably due to mobility limitations. Conversely, Golner (1997) reported the seasonal home range of brooding hens to be much larger (173 ha) than the home range of non-brooding hens (19 ha). Likewise, in this study, successful brood range size (199.6 ha) was larger than unsuccessful brood range size (129.2 ha). Most likely, this was due in part to the longer duration of data collection on successful broods.

Although successful GPC broods averaged larger home range size overall, their movement away from the nest was more gradual than that of unsuccessful broods, likely because brood loss freed hens to move greater distances sooner. At two weeks of age, the average distance to nest for successful and unsuccessful broods was similar (658.2 m and

673.3 m, respectively) but less than that recorded previously in Minnesota (983.2 m) (Svedarsky 1979) and Kansas (871 m) (McNew 2010), further emphasizing the need for close proximity of nesting and brood rearing habitat (McNew et al. 2011*b*). In this study, all successful and unsuccessful radio-tagged GPC hens nested within 1.6 km of a known booming ground, though not necessarily the one where they were copulated. Upon hatch, hens and their broods moved, on average, less than 1 km from the nest into brood rearing habitat. Therefore, nesting habitat should be located within 1.6 km of known booming grounds, and brood rearing habitat should be maintained within 1 km of nesting habitat. Previous studies have also noted the GPC booming ground "sphere of influence" (Schwartz 1945) and central role of the booming ground in GPC ecology (Toepfer 1988, 2003).

The similar early movements of successful and unsuccessful broods may also indicate that hens continue to lose their broods at a significant rate at three and possibly four weeks of age, extending the critical survival period beyond the first two weeks of life. It is likely brood data should be collected through at least the first four weeks after hatch.

As other studies have also recorded (Svedarsky 1979, Silvy 1968 *in* Svedarsky 1979, Viers 1967 *in* Svedarsky 1979), I observed a number of successful broods make remarkable movements within the first week of life. One brood moved 1.48 km between 5 and 7 days post-hatch, and was 1.54 km from the nest at one week of age. Another brood was located 802 m from the nest only 3 days after hatch. One other brood was located 427 m from the nest the same day as was presumed to have hatched. Notably, this brood was re-located only 16 m from the nest site at 10 days post-hatch. Three other successful broods also made a return visit to the nest site (within 24, 27, and 33 m respectively) within the first two weeks post-hatch, and one brood was located 54 m from its nest at 9 weeks of age.

Although the relationship between brood range size and invertebrate biomass was not significant, there was a general trend toward increased brood movement when invertebrate biomass was low, and, conversely, decreased brood movement when invertebrate biomass was high. As other studies have shown (Southwood and Cross 1969, Erikstad 1985, Hill 1985, Rands 1986, Bergerud and Gratson 1988, Drut et al. 1994, Park et al. 2001), it is likely that invertebrate availability stimulates brood movement across the landscape, but that numerous other factors (e.g. landscape connectivity (Ryan et al. 1998), chick mobility, vegetation height, weather and predator occurrence), are also involved in the decision to re-locate.

Invertebrate Characteristics

Measured against unsuccessful brood locations and permanent transect sites, invertebrate abundance (biomass and number of invertebrates) was significantly greater in habitats occupied by GPC hens that successfully fledged chick(s). As other galliforme studies have suggested (Bergerud 1988, Ford et al. 1938, Loughrey and Stinson 1955, Jones 1963, Kobriger 1965, Southwood and Cross 1969, Peterson 1970, Hurst 1972, Potts 1970, Kastdalen and Wegge 1984, Green 1984, Erikstad 1985, Hill 1985, Rands 1985, Savory 1989, Burger et al. 1993, Drut et al. 1994, Madison et al. 1995, Baines et al. 1996, Panek 1997, Griffin et al. 1997, Park 2001, Jamison et al. 2002, Pratt et al. 2003, Hagen et al. 2005, Doxon and Carroll 2007, Morrow et al. 2010, Gregg and Crawford

2009), these findings indicate that GPC chicks are more likely to survive in habitats where invertebrate abundance is high, and that GPC broods seek habitats with increased invertebrate resources for consumption (Hill 1985, Hagen et al. 2005).

The significantly higher biomass and number of invertebrates greater than 6 mm found at successful brood locations is curious, since other studies have presumed there is a limit to the size of prey grouse chicks will consume (Hurst 1972, Davis et al. 1980). A number of factors likely influenced the results in my study. It may be that large invertebrates move less quickly than smaller invertebrates and are more easily captured by GPC chicks. Preference for larger invertebrates by GPC chicks could indicate optimal foraging practices whereby they consume high calorie invertebrates that take less time and energy to capture. Whitmore et al. (1986) observed pheasant chicks dissecting larger insects prior to ingesting them, while avoiding non-nutritive invertebrates < 3 mm. Also, it is likely that as they age, chicks consume larger invertebrates, and this would in turn correspond to the growth of invertebrates themselves over time. Of note, the number of Orthoptera not only peaked later in the season (mid-July), but were in greater numbers at their larger size across all samples. Finally, methodologically, sweep nets have been shown to collect higher numbers of large invertebrates (> 5 mm) (Doxon et al. 2011), which would not be unexpected in habitats with already high numbers of insects.

Increased invertebrate diversity has been shown to improve grouse chick survival (Krebs and Avery 1984, Borg and Toft 2000), which corresponds with the overall opportunistic nature of grouse as predators (Ford et al. 1938, Southwood and Cross 1969, Moreby 2004). Illinois (Yeatter 1943) and Oklahoma (Jones 1963) GPC chicks showed preference for Coleoptera and Orthoptera, but others have remarked invertebrates in these

Orders are already among the dominant populations in prairie grassland habitats (Smith 1940, *see* Tester and Marshall 1962, Hull et al. 1996, McIntyre and Thompson 2003). Moreover, invertebrate diversity is decreased at northern latitudes, and distribution is comparatively less across northern prairie states (Arenz and Joern 1996). In northern GPC range, Homoptera composed the greatest biomass and proportion (> 50%) of invertebrates across all samples, with significantly higher biomass found at successful brood locations. Conversely, Coleoptera and Orthoptera were observed in the fewest numbers (< 5%) in all samples. Overall, invertebrate diversity was greatest at unsuccessful brood locations, suggesting that higher invertebrate diversity is not more important than, nor does it compensate for, decreased invertebrate abundance. Successful GPC broods in northwest Minnesota appear most concerned about invertebrate availability as it relates to quantity, not species or composition, and likely subsist on those invertebrates most abundant and easiest to catch (Ford et al. 1938, Southwood and Cross 1969) in the habitats available to them.

Invertebrate abundance was highest for both successful and unsuccessful broods during the first two weeks of July. Unlike black grouse and capercaillie in Scotland (Baines et al. 1996), this does not appear to complement peak nest hatch in northwest Minnesota which occurred during the second week of June in 2009. It is likely this delayed invertebrate peak is influenced by the northern prairie climate. The adaptation of peak hatch to early July would prevent re-nesting by many hens that lose their initial nests, and would therefore decrease overall recruitment (Newell 1987). Nonetheless, it does appear that invertebrate abundance increased quickly between peak GPC hatch (mid-June) and the beginning of July, keeping pace with the increased pressure for resources.

Although the critical first two week period had passed for the majority of broods, invertebrate biomass was significantly higher for successful broods than unsuccessful broods during the first two weeks of July. The long term benefits of increased animal protein and the role it plays in fledgling success (Johnson and Boyce 1990) is reflected by higher invertebrate abundance at successful brood locations at three and four weeks of age, and throughout the entire field season. *Tympanuchus* spp. have been shown to consume primarily animal material for extended lengths of time (Kobriger 1965, Renhowe 1968, Davis et al. 1980, Rumble et al. 1988, Savory 1989), and one would expect to see higher invertebrate abundance in the habitats they use. These findings support those of other studies in which invertebrate availability is very important beyond the first two weeks of life (Potts 1980, *see* Burger et al. 1993, Savory 1989), suggesting, as did brood movement, that brood and invertebrate data should likely be measured through the first 4 weeks post-hatch, at least (Kobriger 1965, Renhowe 1968, Davis et al. 1980, Rumble et al. 1988, Toepfer 2003).

Invertebrate abundance varied greatly within successful and unsuccessful brood samples, though the most “successful” unsuccessful brood, from which was collected the greatest invertebrate biomass and number of insects, did not equal half of that which was collected from the locations of the most “successful” successful brood. Even at the individual level, invertebrate abundance was higher for the majority of successful broods in 2009. The substantial variation among broods, and, in particular, among successful broods, only confirmed that "…there is no such thing as an average prairie chicken" (Toepfer 2003).

Habitat Characteristics

As an obligate grassland species, northwest Minnesota GPC broods' strong preference for grassland landscapes over [grazed] pasture or agriculture was to be expected. In Missouri, Ryan et al. (1998) observed increased use of grassland habitats (native prairie and pastures) when the landscape was less fragmented by agriculture. However, in Kansas, McNew (2010) observed poor productivity in intensive-use contiguous grasslands. These findings, as they relate to northern prairie landscapes, would indicate that Minnesota GPC live in large blocks of low-use contiguous grassland habitat, conveniently scattered among various agricultural fields. Extensive use of CRP grasslands (> 50%) by Minnesota GPC broods further supports this suggestion.

Predictably, both macro-habitat type and micro-vegetation type analysis indicated successful broods were located in habitats with a measurable uncultivated forb component significantly more often than unsuccessful broods, and yet, invertebrate biomass in this mixed grass/forb vegetation was not significantly higher at successful brood locations. However, invertebrate biomass was notably higher at successful brood locations in grass dominated habitats (≥ 80% grass). These results suggest that although GPC broods would prefer mixed grass/forb habitats, forb-deficient grasslands that dominate the Minnesota landscape produce sufficient invertebrate resources to fledge GPC chicks.

Several prairie chicken studies have reported brood preference toward mixed grass/forb or forb dominated habitats (Jones 1963, Rumble et al. 1988, Golner 1997, Keenlance 1998, Jamison et al. 2002, Hagen et al. 2005, McNew et al. 2011*b*, Matthews et al. 2011), and a few have related invertebrate abundance with increased forb occurrence (Jones 1963, Jamison et al. 2002, Hagen et al. 2005), implying that prairie chicken broods select mixed forb habitats primarily for nutrition purposes. In this study, combined brood locations in mixed grass/forb habitats did not have significantly higher invertebrate biomass than did brood locations in grass dominated habitats. In fact, although not significant, there was a general trend toward decreasing invertebrate biomass as the presence of uncultivated forbs increased in Minnesota GPC brood habitat. This finding further explains successful brood use of, and significant invertebrate biomass in grass-dominated Minnesota prairie habitats. The incongruence of this inverse correlation to most other forb-invertebrate findings is likely the result of a confluence of factors, and says more about Minnesota prairie habitat and the grasslands available to GPC broods than it does anything else. Over the last twenty years, forb components have seceded out of many northern Minnesota grasslands and have been replaced by cool season monocultures of which many have been left undisturbed for long periods of time. Presumably, as the habitat evolves, so do the invertebrate species living in it, and the generalist predators feeding on them. Ultimately, GPC broods depend on two things: grass and the invertebrate prey within it. Variations within these two components exist all across GPC range, to which populations have adapted.

The circumstances under which forb-invertebrate data have been collected in other studies should be considered (Appendix 6). A few studies have focused on specific invertebrate species (Jamison et al. 2002, Hagen et al. 2005); the sample sizes of previous studies are generally smaller; none collected invertebrate data for the length of time seen in this study; and the most northern North American prairie study (Burger et al. 1993) was carried out in north central Missouri.

The most recent study by Hagen et al. (2005) in southwestern Kansas on LPC determined invertebrate biomass and vegetation structure played a larger role in brood site selection than did vegetation type, including the presence of forbs. Vegetation effective height and structure was also found to be more important than vegetation type. To this end, it is worth considering the vegetation structure of cool season smooth brome (*Bromus inermis*) which dominates Minnesota CRP grasslands, and in which high invertebrate biomass was found. The surface area of smooth brome leaves (12 mm wide and 15-40 cm long) is much larger than that of many other common species (e.g.. Kentucky blue grass, 5 mm wide and 5-40 cm long), and perhaps comparable to that of a forb. These relatively undisturbed fields of smooth brome enable prolonged invertebrate development and are among the first to green up in the spring when broods are beginning to hatch. If sustenance was to be considered the first priority of GPC chicks, they must become micro-habitat generalists as well, showing “preference” for whatever available vegetation provides the most invertebrate resources, which, in northwest Minnesota, does not appear to be uncultivated forb-dominant vegetation.

Hull et al. (1996) did not find a significant correlation between forb cover and invertebrate biomass or avian abundance in Kansas CRP and acknowledged that the occurrence of uncultivated forbs in the study area (0 – 23%) may have been below the threshold necessary to influence these variables. I suggest the same argument could be applied in this study area where the uncultivated forb component averaged only 17.0% (range 0 – 58.8%) at combined brood sites and 10.3% (range 0 – 46.8%) at combined permanent transects. It might also be noted that broods of other grouse species, particularly LPC and sage grouse, have been shown to consume more forb/plant material than GPC chicks (Jones 1963, Savory 1989), which could further explain an increase in forb components at their respective brood sites.

The influence of vegetative species on invertebrate composition should also be considered. Evans (1988) found the presence of invertebrates (Orthoptera) was species-specific according to the plant composition in the habitat, where forb-feeding grasshopper indices were positively correlated to the abundance of forbs. I did not identify invertebrates to species, therefore I could not determine the presence or absence of insects with a preference for forbs. However, the varied composition of invertebrates in various forb type habitats at combined Minnesota GPC brood sites lends some support to Evans' (1988) findings. Cultivated forbs (i.e. alfalfa and soybeans) hosted a substantially greater diversity of invertebrates than did uncultivated forbs. Invertebrate composition was less varied between uncultivated habitats themselves, separated according to the average quantity of forbs found at Minnesota GPC brood locations; < 17% and > 17% forb component. Invertebrate composition between these uncultivated forb types was different enough to consider that the vegetation preferences of specific invertebrate species could impact their occurrence, but similar enough to confirm that vegetation type alone does not determine the invertebrate species found therein. Hagen et al. (2005) showed that sand sagebrush density (not forbs) was the best indicator of, and negatively correlated with, Orthoptera biomass. And yet, a greater number of broods were located at the study site in which sand sagebrush was the preferred cover, even though it had fewer invertebrate resources overall. In North Dakota, Kobriger (1965) also located sharp-tailed grouse broods in wetland habitats with fewer preferred invertebrates for longer periods of time than they were in dry sand range sites that hosted significantly more selected invertebrates.

Some studies have indicated Orthoptera and Coleoptera are preferred by GPC broods (Yeatter 1943, Jones 1963), both of which were more abundant in Minnesota habitats with < 17% uncultivated forbs, and most abundant in cultivated alfalfa fields. However, the overall abundance of invertebrates in these two Orders in Minnesota GPC range appears less than that recorded elsewhere. Furthermore, a lack of faecal samples in my study makes it difficult to determine the impact of invertebrate species composition on brood success. Overall, although generally consistent, the forb-invertebrate relationship does not appear conclusive. Several factors including landscape scale habitat availability, soils and the climate of the location being studied likely play an important role in the influence of forbs on grouse broods and their invertebrate prey. In summary, neither invertebrate biomass nor brood habitat use can be predicted by forb presence alone.

Minnesota GPC broods were located in cultivated habitats less frequently than they were found in grass or grass/forb habitats. Only one successful brood used an alfalfa hayfield for an extended period of time (almost exclusively between 3 and 8 weeks of age) and no unsuccessful brood was ever located in alfalfa. This is despite the fact that invertebrate abundance was proportionally higher in alfalfa vegetation than any other habitat type. This finding further supports the importance of landscape scale habitat availability, while also emphasizing the role of forb *type* in invertebrate abundance indices. Unsuccessful brood hens tended to move into readily available, invertebrate-poor soybean fields shortly after the loss of their brood and fed there the remainder of the field season. Successful broods initially avoided soybeans but moved into them as they aged, where, by August, cover was excellent and insect fauna were no longer a concern for survival. Of note, there have been observations where GPC hens fledged chicks using soybean fields exclusively (J. Toepfer per. comm.).

Broods were located in disturbed vegetation less frequently than that reported in previous studies (Jones 1963, Svedarsky 1979, Newell 1987, McNew et al. 2011*b*). The disturbance periods of habitats in this study area generally fall into two categories: disturbed within the past year (typically pasturelands and agricultural fields), or relatively undisturbed for five, ten, and sometimes twenty years (usually CRP fields). Invertebrate biomass at successful brood sites in these undisturbed habitats was similar to that found in recently disturbed vegetation (0 – 6 months since last disturbance) which successful broods used the least frequently (21.9% of locations). Habitats disturbed 7 – 12 months prior to use housed the highest invertebrate biomass for both successful and unsuccessful broods and were therefore used less than might be expected. However, other studies have also observed brood avoidance of habitats disturbed the same year as data collection, where preference was for habitats disturbed 1 – 6 years prior to use (Toepfer 1988, Golner 1997, Keenlance 1998). In Nebraska, Matthews et al. (2011) also reported GPC brood selection of undisturbed cool season CRP grasslands in a study area where intense cattle grazing had decreased the availability of quality GPC brood habitat.

Minnesota GPC brood use of undisturbed vegetation was also unusual since invertebrate biomass was generally higher in other types of disturbed habitats. Invertebrate biomass was highest at successful brood sites in previously mowed CRP and moderately grazed pastures, and yet the proportion of time spent in these habitats was only 12.3 and 8.8 percent, respectively. This was likely due, in part, to the fact that previously mowed disturbance type included alfalfa hayfields which, as noted earlier, are high in invertebrate biomass, but infrequently used by the broods in this study, likely because of their relative dearth on the landscape. Both GPC brood use and invertebrate biomass were low in intensively grazed pastures and recently burned native prairie. As it relates to brood productivity, McNew (2010) reported decreased GPC brood survival in Kansas habitats with similar destructive disturbance regimes (i.e. intense grazing and annual spring burns). Because invertebrate response to habitat type and disturbance method tends to be species specific (Swengel 2001, Southwood and van Emden 1967, Jonas et al. 2002, Arenz and Joern 1996), knowledge of brood diet selection (via faecal samples) could augment these interpretations of GPC brood habitat selection.

Minnesota GPC brood use of temporal disturbance regimes also indicate limited habitat choice within the study area where invertebrate biomass appeared higher within less-used vegetative heights. Perhaps landscape scale disturbance types across Minnesota GPC range exist in too-large concentrated blocks, or they do not vary enough to influence brood habitat selection significantly.

The reported importance of vegetation structure to brood site selection and invertebrate abundance has already been discussed. Mean vegetation height and effective height were similar for successful broods, unsuccessful broods, and permanent transects, and were therefore not likely a primary factor in GPC brood survival. However, successful broods did appear to use habitats with a lower effective screening height (27.4 cm) at a younger age than unsuccessful broods, suggesting the influence of vegetation structure on young chick mobility may impact chick survival.

Similar to the findings of other studies (Newell 1987, Toepfer 1988, Norton et al. 2010, Matthews et al. 2011), successful and unsuccessful broods were located in vegetation with a mean effective height between 26 and 50 cm a majority of the time. However, although brood use of vegetation effective height was similar between successful and unsuccessful broods, invertebrate biomass at their locations within these effective height categories was not. Invertebrate biomass at successful brood sites was highest in the 9 – 25 cm effective height category versus 26 – 50 cm for unsuccessful broods. Differences in sample size may account for these results. Nonetheless, the results indicate successful brood selection of taller vegetation effective height categories was influenced by factors other than simply invertebrate resources, such as cover and protection from predators.

A closer look at the vegetation effective height categories and disturbance types at sites where successful broods were located revealed results inconsistent with the general assertion that structurally heterogeneous habitats produce more invertebrate resources and therefore increase brood success (Southwood and Cross 1969, Evans 1988, Siemann 1988, Murkin et al. 1994, Baines et al. 1996, Panek 1997, Knops et al. 1999, Koricheva et al. 2000, Vickery et al. 2001, Hagen et al. 2005, Rodgers 2005). The structure of the vegetation (measured as effective height) at various brood habitats was fairly consistent with the disturbance type recorded, meaning the level of disturbance met the expectations for height variability. However the invertebrate biomass collected at these sites was not. For example, based on vegetation structure alone, one would have expected to find similar invertebrate biomass in burned brood habitat as was found in previously mowed brood habitat, each with effective height categories split 50/50 between 9 – 25 cm and 26 – 50 cm. And yet the catastrophic nature of fire and the reduction of litter likely reduced invertebrate abundance at these burned locations during the time of measurement. Likewise, one might have expected decreased invertebrate biomass in homogenous (minimal structural diversity) undisturbed habitats, and increased invertebrate biomass in plowed fields (mostly soybeans) which had the greatest variation in habitat structure over time, yet the opposite was found true, indicating vegetation type (specifically forb type) and the way it is managed (conventional soybeans are treated with insecticides) further influence invertebrate abundance. Only pasturelands showed presumed heterogeneous results where moderate cattle grazing produced more structurally diverse vegetation and increased invertebrate biomass, while the homogeneous character of intensively grazed pastures left behind minimal invertebrate biomass. In summary, both brood use and invertebrate biomass are influenced, but not necessarily determined by, the overall structure of habitat vegetation.

The findings of this study are less decisive than those of Jones (1963) who observed clear relationships between GPC brood habitat, invertebrate abundance within that habitat, and the insects selected for consumption. Studying both LPC and GPC, Jones (1963) asserted that "…each species of prairie chicken is adapted to the vegetal character of its region." I suggest this argument could be taken one step further, whereby each population of prairie chicken (in this case GPC) is adapted to the character of its region.

The results of this study illustrate that GPC do not live in a laboratory, but rather a natural, dynamic environment of which not one habitat characteristic can explain the use and/or invertebrate abundance of successful brood selected sites.

The importance of invertebrate abundance, particularly within the first four weeks of life, is illustrated by the survival of successful GPC broods and the comparative dearth of invertebrate fauna found at unsuccessful brood sites. And yet, successful broods were not always located in vegetation characteristics that measured the highest invertebrate biomass. In Minnesota, the majority of successful GPC broods were found in relatively undisturbed grass and mixed grass habitats with an effective screening height between 26 and 50 cm. Consequently, the abundance of invertebrates within these combined habitat characteristics was at least above the threshold for survival and produced a sufficient amount of nutrition while still providing instinctively sought after cover and protection from predators. In the sandhills of Nebraska, Anderson (2012) found GPC broods selected habitats based on their availability. Brood use of Minnesota grasslands would likewise suggest their selection was based in large part on their availability across the landscape.

Habitat Management

The permanent transect types selected in this study represent different habitat types and disturbance regimes found across Minnesota GPC brood range, though not proportionally. They were selected randomly and were not necessarily located near dense GPC brood populations, making their overall availability unknown. However, all chosen transects had been used by GPC broods at some point in the last several years. The invertebrate resources measured within these habitat types help to identify current land use practices where GPC brood rearing may be successful based on invertebrate abundance, which is demonstrably a critical variable in brood survival, and influence to habitat selection.

Each sampled Minnesota prairie habitat measured different invertebrate abundance indices. Not surprisingly, invertebrate biomass was significantly higher in undisturbed CRP grasslands versus cultivated row crops (soybeans and wheat), but perhaps unexpectedly significantly higher compared to native prairie and burned native prairie sites. Native plant species are commonly considered the superior seed choice, mostly for historical and heterogeneous reasons (McIntyre and Thompson 2003, Rodgers and Hoffman 2005, Rodgers 2005). And generally vegetative monocultures are of little benefit to most wildlife species (Rodgers and Hoffman 2005). But if non-native plants can mimic the structurally heterogeneous characteristics of native prairie while providing added benefits like early season green up, superior cover, resistance to pest species, and easy maintenance, perhaps non-native grassland habitats deserve a second look. In Texas, while native prairie may be better overall, exotic CRP stands remain green all year and have proven a sufficient provider of grassland bird invertebrate prey (McIntyre and Thompson 2003). Positive GPC responses to non-native plantings, including brome (*Bromus inermis*) near-monocultures, have been acknowledged in southeastern Nebraska (Taylor 2000) and northwest Minnesota (Toepfer 2003), and the results of this study further corroborate that GPC hens can, in fact, fledge chicks in brome dominated grasslands. The smooth brome grasslands of many idle Minnesota CRP fields may not be disturbed using traditional methods (i.e. fire, grazing, mowing), but perhaps the impacts of less invasive, biological disturbances have been underestimated. Conceivably, inconspicuous disturbance devices (i.e. wind, water, drought, and animal movement, consumption and defecation) help to create patchy vegetation structures complex enough to meet the level of support required by invertebrate and GPC brood populations.

At the time of this study, it would appear that thresholds for invertebrate abundance and GPC brood success are being met, even in relatively undisturbed Minnesota CRP fields. Yet, based on the work and recommendations of other prairie studies (Southwood and Cross 1969, Baines et al. 1996, Evans 1988, Arenz and Joern 1996, Panek 1997, Siemann 1998, Knops et al. 1999, Morris 2000, Koricheva et al. 2000, Vickery et al. 2001, Giulio et al. 2001, Fuhlendorf and Engle 2004, Atkinson et al. 2005, Hagen et al. 2005, Buckingham et al. 2006, Fuhlendorf et al. 2006, Engle et al. 2008, Boyd et al. 2011), it is possible that Minnesota invertebrate and GPC brood success could improve beyond the results of this study (32.8%) even with a marginal increase in habitat heterogeneity achieved through seed variety and increased anthropogenic disturbance. Not only would these changes fill multiple GPC life cycle requirements where different seral stages of vegetative growth are required for breeding, nesting, brooding, feeding and roosting, they would also be of benefit to other wildlife species (Samson et al. 2003, Farrand et al. 2007).

Although differences were not significant, the number of invertebrates observed in alfalfa fields and pastures (in particular, moderately grazed pastures) was much greater than that seen in soybean and wheat fields and recently burned native prairie. The dearth of invertebrate abundance in burned native prairie sites was likely due to the early timing (spring) and occurrence just prior to data collection. The destructive nature of fire and the emigration routine of escaping invertebrates make almost all insect species scarce immediately following a burn (Swengel 2001). As has been observed in other studies (Tester and Marshall 1961, Warren et al. 1987, Evans 1988, Swengel 2001, Branson 2005), the possibility that invertebrate abundance at these sites increased in the two to three years following this project is supported by the small size and somewhat patchy nature of these burns. Meanwhile, high invertebrate numbers in pasturelands and alfalfa fields were likely tied to the structural integrity of these sites. The multi-faceted impacts of cattle (i.e. uneven grass consumption, trodding, dung) attract many insects which can believed just by observing the creative ways in which cows rid themselves of the endless summer pests. And although alfalfa fields are monoculture crops, the colourful flowers, the fruit, and the density of leaves all attract high numbers of invertebrates with significant biomass.

The abundance indices (biomass and number of invertebrates) of invertebrates in row crops, burned native prairie, undisturbed pasture, and alfalfa hayfields were all similar. That is to say, their respective biomass and invertebrate numbers were corresponding to their habitat type. Conversely, native prairie, grazed pastures (combined moderately and intensely grazed), and previously mowed CRP (combined high top and previously mowed) all showed opposing trends in biomass and numbers. Invertebrate biomass was low at native prairie sites (second only to row crops), and the number of insects found in the habitat was therefore greater than would have been expected. Grazed pastures showed a similar pattern with average biomass relative to the high number of invertebrates counted. The reverse was seen at previously mowed sites, where few invertebrates were collected relative to the high biomass weighed. These patterns indicate that native prairie and grazed pastures host higher numbers of small invertebrates, while previously mowed CRP sites produce lower numbers of large insects. Partly due to their minimal availability in the study area, as well as GPC avoidance of cattle in pastures, Minnesota GPC broods were infrequently located in native prairie or pastureland habitats, and occurred more often in previously mowed CRP grasslands. Nonetheless, these results further substantiate the hypothesis that GPC chicks practice optimal foraging techniques in pursuit of maximum sustenance. For this same reason, invertebrate biomass is likely more valuable than overall invertebrate numbers.

Invertebrate composition (indexed as Order) comparisons between native prairie and burned native prairie were not unlike those of Van Amburg et al. (1981) in northwest Minnesota which saw Homoptera, Coleoptera and Diptera abundance (biomass and numbers) increase post-burn while Orthoptera abundance decreased. However, Van Amburg et al. (1981) also reported no change in Hemiptera populations following fire. Rather, the results of this study were like that of Morris (2000), where the biomass of Hemiptera remained constant while their numbers decreased substantially, indicating the survival and/or immigration of large Hemiptera post-burn. Invertebrate composition was similar between undisturbed and grazed pastures (moderately and intensely grazed); however, the biomass of all species was higher in undisturbed pastures; most significantly, the biomass of Orthoptera was six times greater in undisturbed pastures than in grazed pastures, illustrating their uninhibited growth where disturbance frequency is low. These results support those of other studies (Morris 2000, O’Neill et al. 2003, Buckingham et al. 2006, Dennis et al. 2008, Onsager 2000) where invertebrate abundance, and specifically Orthoptera abundance, decreased alongside increased grazing pressure. Invertebrate composition was greater in CRP previously disturbed by mowing, however, the biomass of Homoptera and Orthoptera was higher in undisturbed CRP. Previous studies have also reported decreased invertebrate biomass and fewer large invertebrates (such as grasshoppers) in mowed habitats (Southwood and van Emden 1967, Jonas et al. 2002, Zalik and Strong 2008, Giulio et al. 2001, Schekkerman and Beintema 2007), although Tester and Marshall (1961) documented higher Orthoptera populations in mowed grasslands with increased litter. Overall, the anthropogenic disturbance techniques sampled in this study tended to increase invertebrate diversity, while simultaneously decreasing the biomass of most species. In burned native prairie, although only Orthoptera biomass decreased, invertebrate biomass remained low overall. Therefore, among disturbance types, fire had the least effect on overall invertebrate abundance.

Assuming that all appropriate habitat disturbance techniques increase vegetation heterogeneity to a greater extent than does non-disturbance, it would seem there is a threshold under which point too little disturbance affects minimal impact, and after which point, intense or repeated disturbance threatens to overwhelm and homogenize the habitat, destroying vegetation integrity and decreasing invertebrate biomass. The results of this study suggest that many Minnesota grasslands are disturbed too infrequently or are disturbed using inferior methods at inappropriate times, thereby diminishing the potential results of their efforts.

Homoptera biomass was higher than that of all other Orders across all permanent transect habitat types except undisturbed pasture, alfalfa hayfield and row crops where Orthoptera biomass was highest. However, these results do not necessarily correspond to the number of invertebrates (measured proportionally) found in these Orders and habitat types. Due to the large size of individual grasshoppers, Orthoptera biomass was disproportionally higher than their actual presence in all permanent transect types. Therefore, Homoptera were found in the greatest numbers in all habitat types except native prairie which was dominated by Hemiptera (52%) and row crops with 66.7% Diptera. Burned native prairie was the only habitat type where no one invertebrate Order made up more than 50% of those collected. Overall, relative to biomass and percentage of insects, invertebrate composition was highest in burned native prairie and lowest in undisturbed CRP. However, the indices of invertebrate abundance with all insect Orders combined were precisely the opposite of this finding where biomass was highest in undisturbed CRP and among the lowest in burned native prairie. And since, overall, GPC broods seem to consider the presence and substance (size) of food more important than its assortment, it would appear undisturbed CRP is better GPC brood habitat than recently burned native prairie.

Jonas et al. (2002) in Kansas found that, overall, old fields of relatively undisturbed native and non-native vegetation with increased plant biomass and accumulated litter were the most structurally diverse grasslands and produced higher invertebrate abundance than infrequently cut brome and/or annually mowed native prairie. They also found that Coleoptera responded more to vegetation composition with increased diversity and species richness in native prairie habitats, while Orthoptera were influenced by disturbance type with increased diversity and species richness in infrequently mowed *Bromus inermis*. These findings, along with those of this study, further emphasize the Order-specific response of prairie invertebrates to grassland types and disturbance regimes. They also illustrate region-specific responses of insects and, in this study, GPC, whereby populations seem to have adapted to their local habitat. This fact, as well as local population demographics, must be taken into consideration where ecosystem-based management is the goal.

Temporally, invertebrate biomass of combined permanent transect types peaked for all invertebrate Orders during the first week of July, except Orthoptera which peaked mid-July (July 12 – July 25) and then remained fairly consistent while invertebrates of the other Orders decreased substantially. The eruption of insects between mid-June and the beginning of July indicates that invertebrates were starting to appear in large numbers not long after the majority GPC chicks were also hatching (June 10, 2009), keeping pace with the increasing demand for brood food. The delay of Orthoptera resources may be anatomically beneficial to GPC chicks whose ease of large grasshopper consumption and/or dismemberment would no doubt increase with age.

Conclusion and Recommendations

The results of this study emphasize the isolation of Minnesota GPC populations, and the unique northern habitats to which they have adapted. The sustainability of Minnesota GPC is foremost dependent upon the amount of grass on the landscape. The dispersal of GPC across their Minnesota range dictates the need for at least 1,424 km^2 of habitat containing at least 467 km^2 (or 33% of total) of relatively undisturbed grassland in order to prevent a genetic bottleneck (Vodehnal and Haufler 2008, Toepfer 2003, Hamerstrom et al. 1957). Even at its peak enrollment, CRP in Norman and Clay Counties totaled below this recommended core area at 430 km^2, and has continually declined.

Other federal and state programs help supplement these hectares, but it was CRP that cultivated GPC population increases and its volatile loss will no doubt cause the population to decline. Increased landowner enrollment in permanent conservation easements could simultaneously help to secure and connect these critical grasslands and their GPC inhabitants (Vodehnal and Haufler 2008).

The explosion of GPC populations alongside the establishment of CRP in Minnesota throughout the 1990s demonstrates their robustness as a species. The results of this study further illustrate their ability to maximize their usage of the grasslands available to them; GPC hens can successfully fledge chicks in smooth brome (*Bromus inermis*) dominated northwest Minnesota habitats. But the continued loss of available grasslands demands that remaining habitat be of superior quality for maximum productivity. With improved availability and quality of revisited grassland sites, it is likely Minnesota brood success would surpass the 32.8% found in this study area.

All GPC brood studies list similar management recommendations that are, at the same time, unique and specific to their location and range. Targeted, ecologically based techniques that are defined by northwest Minnesota prairie habitats will likely be more effective toward producing healthy invertebrate and GPC populations than would generalized assumptive systems (Bidwell and Engel 2005, Farrand et al. 2007). Future studies should begin by identifying the preferred invertebrate diet of Minnesota GPC broods, after which the specific management techniques that increase these groups of insects can be determined (Moreby 2004).

Like all gallinaceous birds, survival of young chicks is a critical factor in sustaining healthy GPC populations. The following recommendations are made based on the results of this study which identified the invertebrate and vegetation characteristics necessary to successfully fledge GPC chicks in present day northwest Minnesota prairie habitats, as well as those characteristics that may improve current and future brood success, giving input to the fate of this prairie flagship species and its subspecies.

1. Maintain and supplement established federal and state grassland conservation easements and increase permanent conservation easements.

Managers should avoid the loss of CRP and other conservation tracts with improved incentives and technical assistance in grassland maintenance. The Minnesota Department of Natural Resources should continue to recruit land owner easements through the Minnesota DNR Farm Bill Assistance Partnership program. Large blocks, smaller parcels and buffer zones should all be considered and negotiated.

2. Consider the placement and availability of grassland refuges to wildlife.

The basic tenants of wildlife habitat management call for the provision of food, water, shelter and space *in the correct arrangement on the landscape*. Macro-scale habitat availability should be further evaluated, especially in light of the continued loss of CRP.

3. Maintain large, contiguous blocks of occasionally disturbed grass located < 1 km from undisturbed nesting habitat.

Minnesota GPC hens can successfully fledge chicks in relatively undisturbed grasslands that provide abundant invertebrates and excellent cover and protection from predators. Improving current fledging success will require adaptive management strategies discussed below. Quality brood habitat should be located adjacent to popular nesting areas to decrease early GPC brood movement and increase brood survival. In this study, all successful and unsuccessful radio-tagged GPC hens nested within 1.6 km of an active booming ground. Booming ground locations are central to all other GPC life cycle activity (Toepfer 2003). Therefore, appropriate nesting habitat should be within 1.6 km of a booming ground, and, in turn, suitable brood habitat should be located < 1 km from nesting grasslands.

4. Establish and maintain vegetation of successional effective heights between 9 and 50 cm.

Successful GPC broods were located in habitats with a mean effective height between 25 and 35 cm 64.4% of the time, and vegetative heights increased as they aged. They also frequently used habitats with an effective height between 9 and 24 cm (23.3% of locations); the substantially higher invertebrate biomass held in these shorter habitats warrant their inclusion on the landscape.

5. Plant and augment current habitats by seeding native and non-native multi-species vegetation.

Make habitat available to more invertebrate species by planting native and non-native mixed vegetation. Uncultivated forb components should be included but not dominant in the habitat. Studies should further investigate Minnesota invertebrate and GPC response to various uncultivated forb species. Cultivated alfalfa appears to be the superior habitat type for GPC broods due to its invertebrate abundance, ease of mobility and thick cover. In 2009, the first alfalfa hayfields were mowed at the end of June, while some waited until mid-July before beginning harvest, allowing re-nests to hatch and ensuring the escape of more mobile broods. However, alfalfa maturation and harvest is weather dependant and unrelated to specific dates. Land owners cannot be expected to delay harvest in years when alfalfa matures earlier in the season. In this sense, mixed, grass-dominated vegetation is the most suitable habitat for Minnesota GPC broods.

6. Improve disturbance treatments and practice adaptive management following their evaluation.

In northwest Minnesota, land designated as CRP twenty years ago is beginning to be removed from the stabilization program and is being converted to agriculture and livestock regimes at an ever increasing rate. If dedicated grassland habitats are not managed to compensate for present day land losses, this increase in agricultural activity could upset the grass-agriculture ratio needed to sustain northern GPC populations.

Historical GPC habitat consisted of tall grass prairie with natural sporadic disturbances. Current grassland management techniques should be irregular and patchy across the landscape to reflect the impact of the original devices, creating more heterogeneous habitats for all GPC life cycles, including brood rearing. Controlled burns were seen to increase invertebrate abundance and composition, even immediately after their event. Infrequent burns (> 3 years) should be practiced by more managers and landowners to attract diversified invertebrate quantities and enhance long term habitat integrity. Livestock grazing is an inextricable part of the prairie ecosystem and should continue. However, infrequent, light to moderate rotational regimes should prevail. Delayed stocking and/or early removal of livestock would prevent invertebrate extirpation from pasturelands and would allow GPC broods to use these valuable grasslands for longer periods of time. Previously mowed habitats were the second most often used grassland habitat by successful GPC broods after undisturbed CRP, likely due to increased chick mobility in the growing vegetative understory and the high invertebrate biomass found therein. Its destructive nature precludes it from annual treatments, but it is likely many undisturbed CRP parcels would see longer-term benefits from infrequent mid-late summer mowing regimes (≥ 3 years), especially where invertebrate and GPC refuge-strips are incorporated into the pattern. Because so many Minnesota grasslands have been left undisturbed for several years, sometimes decades, these suggestions relative to disturbance techniques should be re-evaluated subsequent to implementation and methods and/or frequency adapted accordingly.

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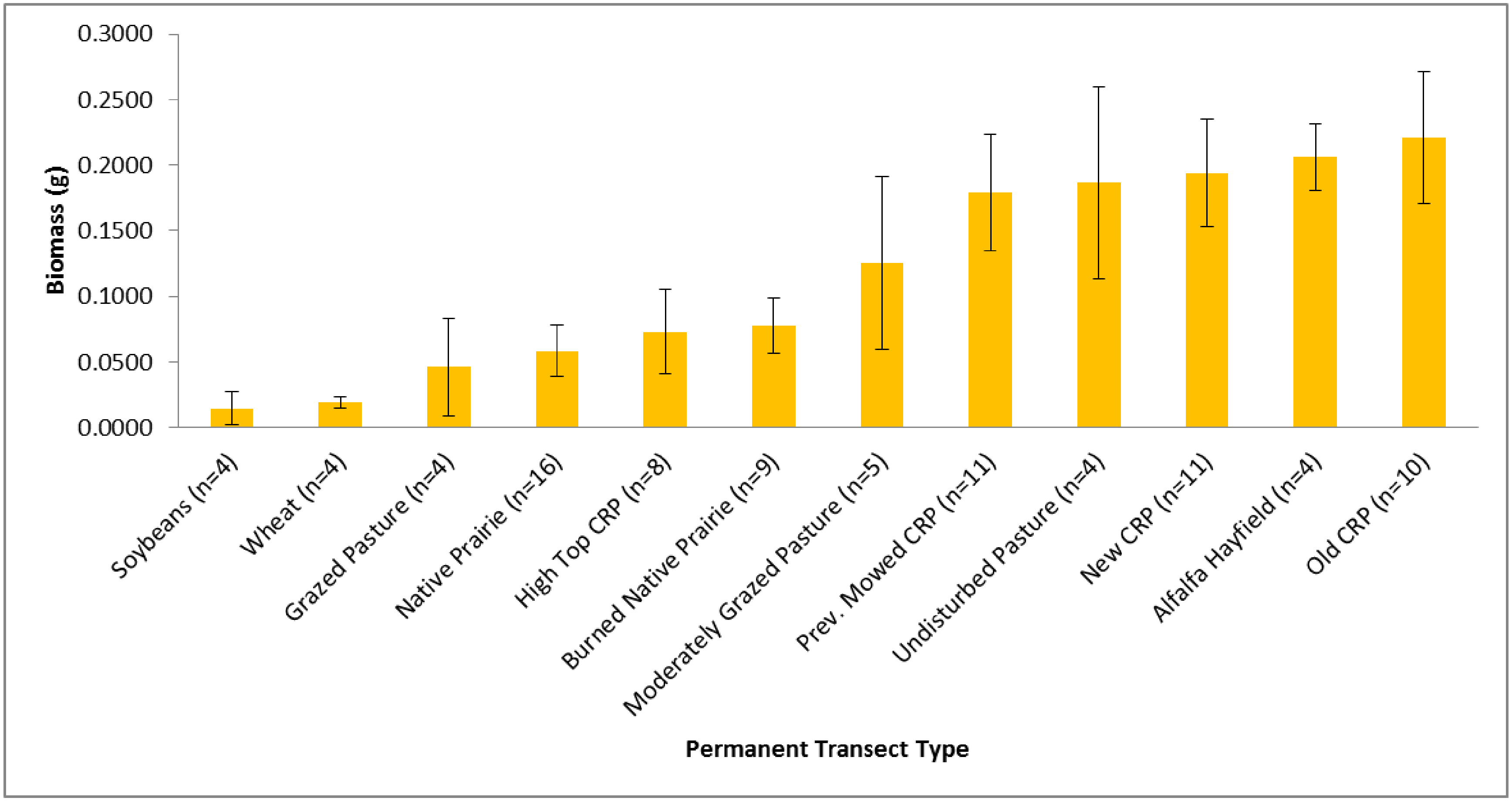
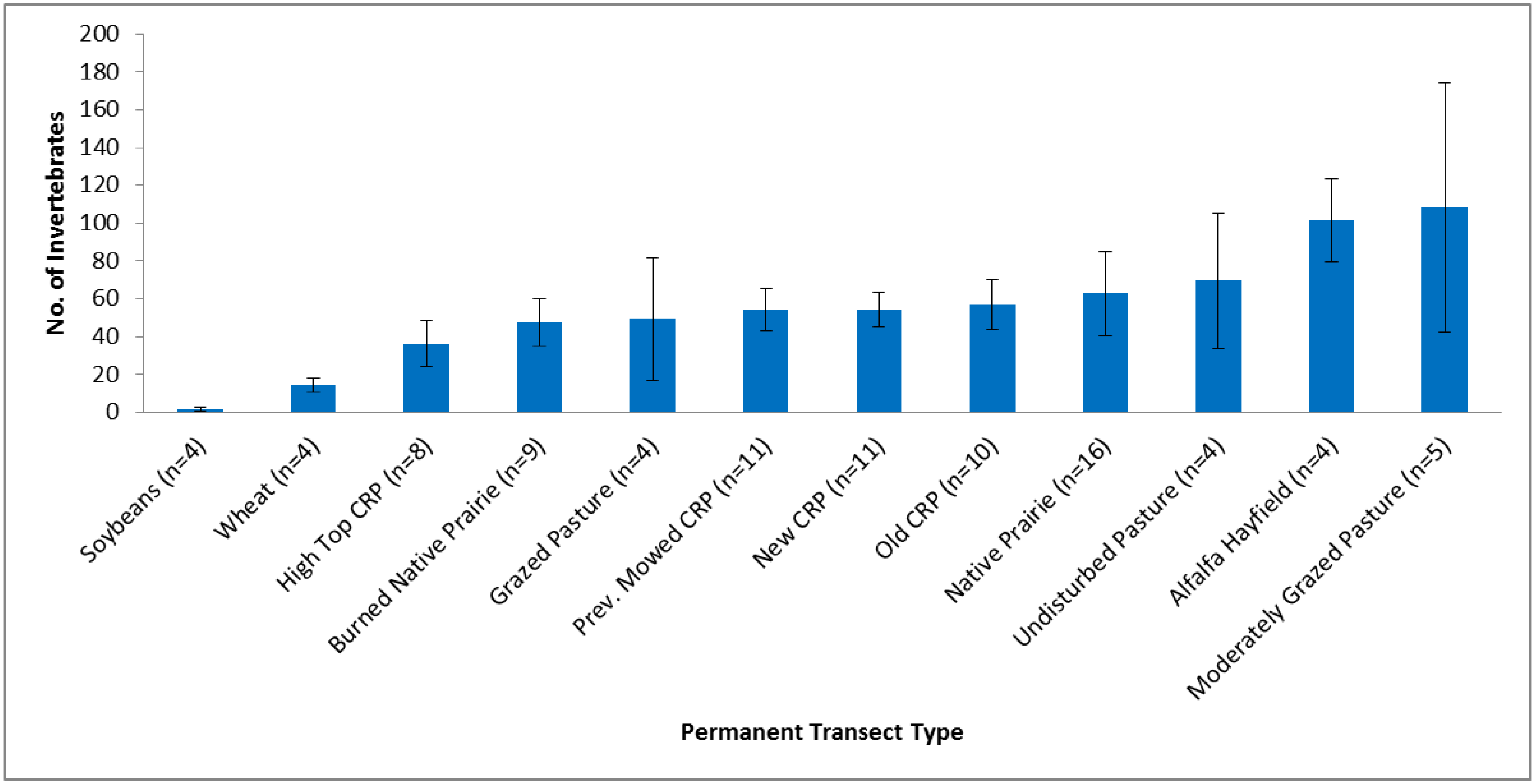
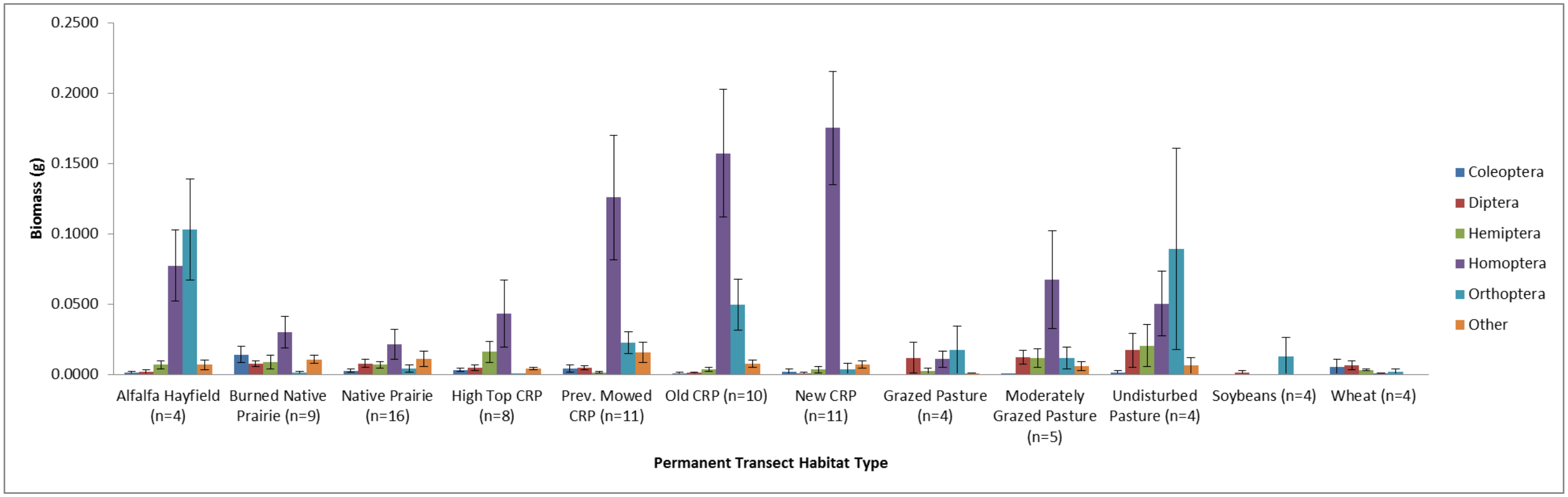
APPENDICES



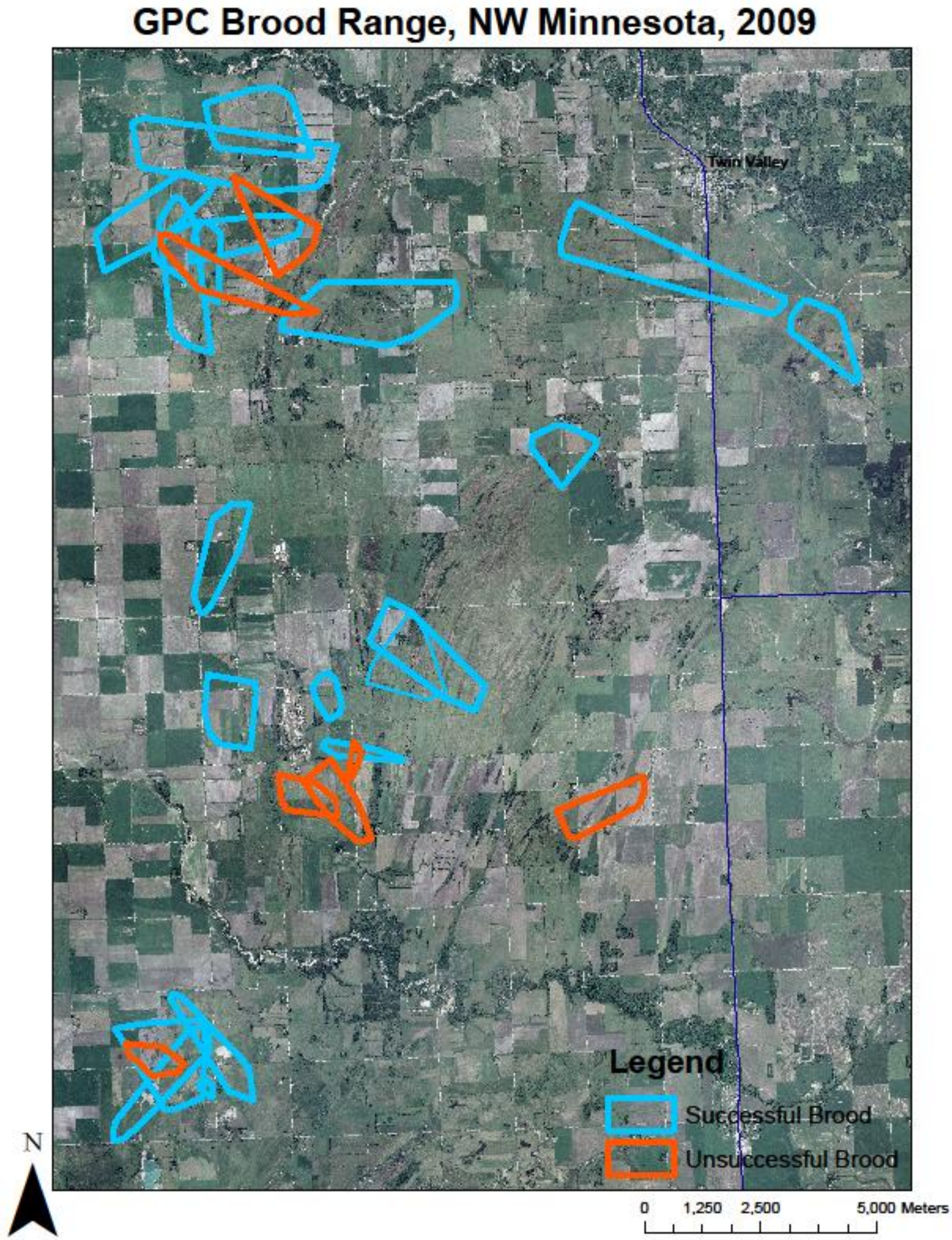
Appendix 1. Mean invertebrate biomass (dry mass in grams) at detailed permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.



Appendix 2. Mean number of invertebrates at detailed permanent transect sites by habitat type, northwest Minnesota June 14 – August 18, 2009.

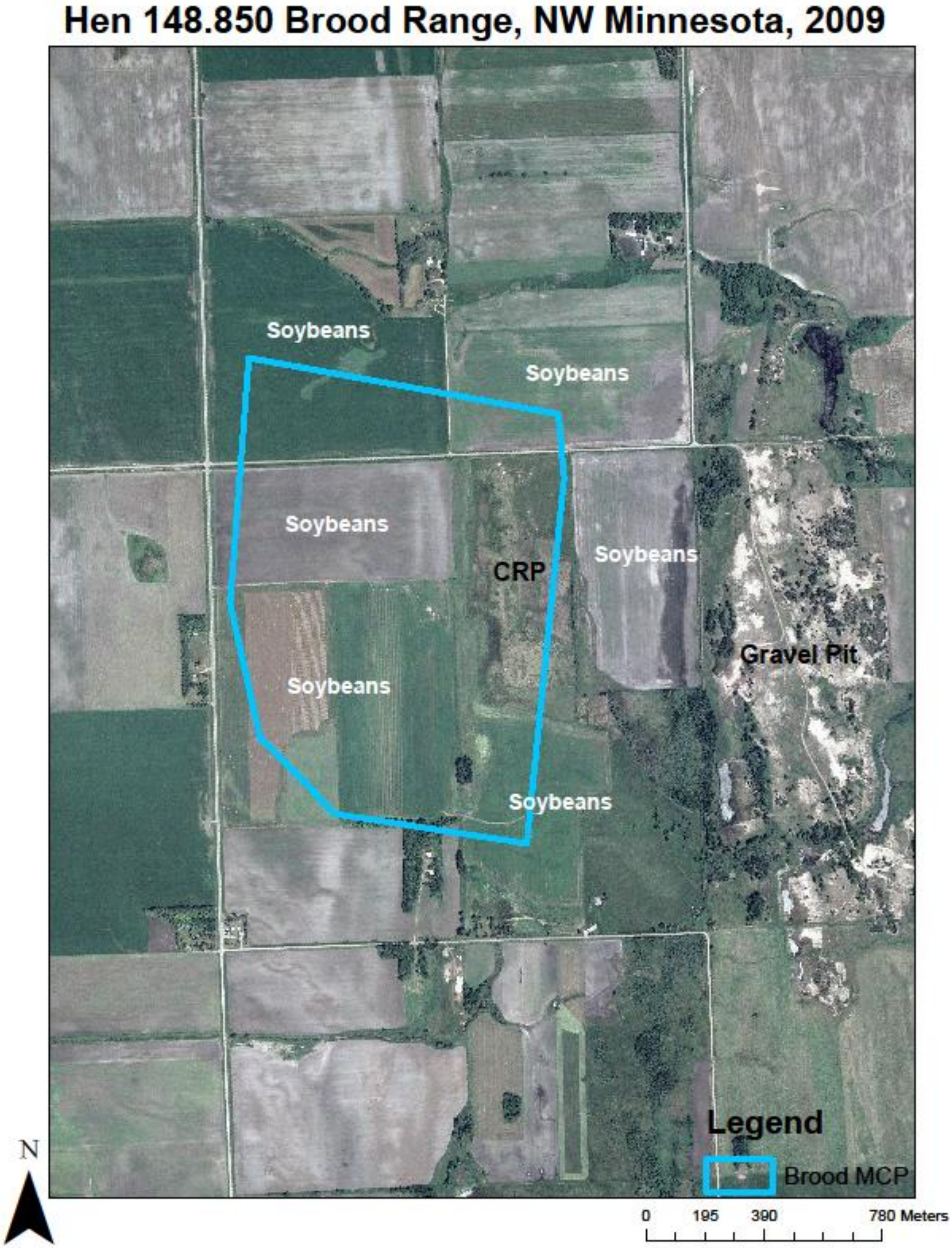


Appendix 3. Mean invertebrate biomass (dry mass in grams) by Order at detailed permanent transect habitat types, northwest Minnesota June 14 – August 18, 2009.



Appendix 4. Brood range of GPC successful broods (n = 20) and unsuccessful broods (n = 7), northwest Minnesota June 3 – September 8, 2009.

Appendix 5. Brood range of radioed GPC hen 148.850, northwest Minnesota June 3 – September 8, 2009.



Appendix 5. Brood range of radioed GPC hen 148.850, northwest Minnesota June 3 – September 8, 2009.

Appendix 6. Relationship between invertebrate biomass and forb habitats as recorded in various galliforme studies.

Study	**Species**	**No. of Broods or Samples**	**Isolated Invertebrate**	**Method of Collection**	**Time Interval**	**Result**
Jones (1963)	LPC and GPC	?	?	?	?	Invertebrate density increased with forb component in habitat.
Southwood and Cross (1969)	Partridge	?	n/a	Suction apparatus and sweep net	June and July	More invertebrates found in weedy habitats.
Hill (1985)	Pheasant	7 broods	n/a	Dietrick vacuum and sweep net	First two weeks after hatch	Invertebrate biomass highest in weedy habitats.
Burger et al. (1993)	Bobwhite quail	48 samples	n/a	Vacuum	July 1 - August 15	Invertebrate biomass significantly higher in habitats dominated by red clover.
Drut et al. (1994)	Sage grouse	64 samples	n/a	Pitfall traps	June and July	Invertebrate availability was higher at the study site with higher forb and grass availability.
Jamison et al. (2002)	LPC	5 broods	Acrididae (Orthoptera)	Sweep net at brood use areas (14 samples) and pitfall traps in veg sampling areas (135 samples)	June and July (sweep net) and 5 days in June (pitfall traps)	Invertebrate biomass associated with forbs, although no habitat was dominated by forbs.
Hagen et al. (2005)	LPC	16 broods	Acrididae (Orthoptera)	Sweep net (71samples)	Up to 60 days post hatch	Forb presence showed small but positive effect on Orthoptera biomass.
Syrowitz (2013)	GPC	20 broods	n/a	Sweep net at successful brood sites (114 samples) and veg sampling (permanent transect) sites (93 samples)	June 14 - August 18	Invertebrate biomass decreased as forb presence increased (non-significant).