DISSERTATION

PRAIRIE DOGS, PLANTS, AND POLLINATORS:
TRI-TROPHIC INTERACTIONS AFFECT PLANT-INSECT FLORAL VISITOR WEBS IN SHORTGRASS STEPPE

Submitted by

Kelly Hardwicke

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado State University

Fall 2006

ProQuest Information and Learning Company
300 North Zeeb Road
P.O. Box 1346
Ann Arbor, MI 48106-1346

COLORADO STATE UNIVERSITY

July 20, 2006

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY KELLY HARDWICKE ENTITILED PRAIRIE DOGS, PLANTS, AND POLLINATORS: TRI-TROPHIC INTERACTIONS AFFECT PLANT-INSECT FLORAL VISITOR WEBS IN SHORTGRASS STEPPE BE ACCEPTED AS FUFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Boris C. Kondratieff

Thomas J Stohlg

Adviser

Department Chair

ABSTRACT OF DISSERTATION

TRI-TROPHIC INTERACTIONS AFFECT PLANT-INSECT FLORAL VISITOR WEBS OF THE SHORTGRASS STEPPE: PRAIRIE DOGS, PLANTS, AND POLLINATORS

I investigated how black-tailed prairie dogs (*Cynomys ludovicianus*) altered pollinator habitat, specifically in terms of bare ground cover and floral resources, on northeastern Colorado's Pawnee National Grassland, in 2003 through 2005. I also measured changes in habitat utilization by insect floral visitors on and off prairie dog colonies, and assessed differences in community composition of both entomophilous plants and anthophilous insects. Lastly, I constructed plant-insect visitor webs describing the relative frequency of different interactions on- and off-colonies in 2004 and 2005. Over the entire study, I sampled the plant and insect communities of seven paired colony and off-colony sites on the Shortgrass Steppe Long-term Ecological Research site.

On colonies, there was greater cover of forbs and bare ground, more inflorescences/m^2 in all three years, more open flowers/m^2 in 2004 and 2005, and greater floral biomass presented by the most frequently visited plant species in 2005 (the only year floral biomass was measured). Floral visitation by the insect community and several individual generalist and specialist groups occurred at greater rates on colonies. There is evidence that insect visitation increases with floral biomass patch density, and even mound density, but there were not higher than expected rates of insect visitation given the greater average floral resource densities on prairie dog colonies. On-colony populations of several plant species in 2004 and 2005 experienced greater visitation, but one important floral resource, *Opuntia humifusa*, was visited more off-colonies.

Diversity (H') was greater on colonies for both entomophilous plant species and insect groups in 2004 and 2005, and there was greater plant species and insect functional group richness on colonies in all three years. Mutualistic webs were more complex on colonies, and less dominated by a core of interactions between halictid bee groups and *Opuntia*. Plant species on colonies were generalized, receiving the highest median number (5.5) of insect visitor groups, but colony insect communities were specialized, visiting the lowest median number (3) of plant species.

These results suggest a significant tri-trophic interaction, driven by prairie dogs, which benefits insect floral visitors, including native pollinators. By altering vegetation, prairie dogs influence plant-pollinator networks in shortgrass steppe.

Kelly Hardwicke
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Fall 2006

ACKNOWLEDGEMENTS

I could not have completed this dissertation without the help and encouragement I received from so many people throughout the last five years. First and foremost, I thank Jim Detling, my mentor throughout this entire process, and the reason I was even able to attend CSU in the first place. I first realized how much I enjoyed pollination research in my second year, while taking my committee member Shanna Carney Henk's excellent plant reproduction course. After many intense conversations, and excellent advice from my more-advanced peer, and best friend in the CSU biology department, David Logue, I knew that I could do this thing. More thanks still to Boris Kondratieff, who taught me how to ID insects, and provided so much entomological information and expertise that I actually felt good about planning and excecuting a dissertation based so heavily on identification of a taxon that I have much interest in, but until three years ago, little experience with. Tom Stohlgren gave me my first job in the field after working in the Salk Institute's Core Cytometry and Molecular Imaging Facility for the three years previous. Working for his project in the Grand Staircase Escalante National Monument reaffirmed my ardor for assessing ecosystems, and working outside to learn about the US west I love so much. It had to be pretty cool to make me feel it was worth leaving behind my lasers.

This research was supported, in part, by the National Science Foundation Grant DEB 0217631 for the Shortgrass Steppe Long-Term Ecological Research Project. Thanks to everyone that has helped me and given me knowledge and suggestions there.

Many thanks to Dr. Paul Opler for his identification of lepidopteran specimens, Dr. Terry Griswold of the University if Utah for his identification of important hymenopteran groups, and Dr. Phillip Chapman for statistical consultation.

Laurel Hartley started her Ph.D in the Detling Lab at the same time as myself, and has been helpful and kind to me more times than I can count, but most directly helped with this project by hiring me in 2002 to take data on many of the same research sites for *her* dissertation. It was then I first noticed the particular differences on prairie dog towns that allowed me to formulate my first hypotheses about pollinators on the high plains of northeastern Colorado. Thanks also Chrissy Alba Lynn for editing assistance, and all my other academic siblings who gave me encouragement and support throughout my time at CSU: J.P. Farrar, M. Nikki Grant, Kim McGraw, and Heather Blackburn.

This section would not be complete without acknowledgement of the huge role my parents, W.M. and Judy Hardwicke, have played in allowing me to complete this dissertation. They have ever been a source of inspiration and emotional and financial support without which I could never have accomplished this degree. They provided me vehicles to do field work in, and let me keep dead bugs in their freezer.

Finally, this dissertation is dedicated to Eric Olson, my love, my husband, who braved 110° F July steppe weather, and took care of me, and read drafts, and clipped flowers, and listened to me talk and talk and talk about bees.

TABLE OF CONTENTS

I. INTRODUCTION AND OVERVIEW TO DISSERTATION

Northeastern Colorado, where the Pawnee National Grasslands (PNG) is located, is a windswept, sunbeaten place. Nevertheless, there are flowers to be found there, at times in great densities (> 300 inflorescences per m^2, or eight dry grams highly attractive floral biomass per m^2 when in full flower). While doing fieldwork for another project in the summer of 2002 on prairie dog colonies on the PNG, I noticed that these dense patches of flowers seemed to be more frequent on the colonies. Black-tailed prairie dogs (*Cynomys ludovicianus*) were already known to concentrate grazing pressure on palatable graminoids in Great Plains grasslands, increasing forb cover on their colonies (Bonham and Lerwick 1976, Coppock et al. 1983a, Archer et al. 1987, Whicker and Detling 1988, Hoogland 1995, Winter et al. 2002, Detling 2006). It seemed logical that this increase in forbs should translate into an increase in floral resources, and that insects might respond favorably to this. However, floral resources had never been specifically measured, either on or off black-tailed prairie dog colonies of mixed grass or shortgrass steppe grasslands.

Data on pollinator communities of the shortgrass steppe were also needed. The shortgrass steppe provides a fascinating pollinator fauna, members of a larger insect floral visitor community including those that are not effective pollinators for some or all of the plants they visit. It is a community dominated by solitary and loosely communal bee species, mainly ground dwelling because the steppe is almost treeless. Ground-dwelling bees build their nests in patches of bare ground (Petanidou and Ellis 1993, Michener 1999), so they might also be attracted to prairie dog colonized habitat because it typically has greater cover of bare ground (Whicker and Detling 1988, Winter et al. 2002). As predicted by optimal foraging and patch theories (Bronstein 1995), greater floral resource densities attract a larger community of insect visitors to an area (Thompson 1981, Sowig 1989, Kunin 1997), although this does not always mean higher per-flower or per-plant visitation rates (Bosch and Waser 2001, Schiller et al. 2001). These two habitat alterations enacted by prairie dogs -- an increase in bare ground and a possible increase of floral resources stemming from the known increase in forb cover -- are the two major points of rationale for this study. Here, I provide evidence showing that prairie dogs do indeed increase floral resources and attract a larger, more species-rich insect community to colonized sites. This represents a significant tri-trophic interaction affecting vegetation and insect communities in shortgrass steppe.

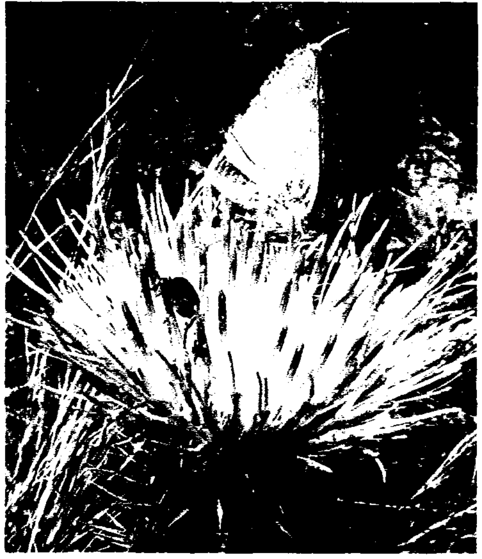


Plate 1 - Insect community visitation. *Hesperia uncas* (Hesperiidae) and *Epicauta ferruginea* (Say) (Meloidae) simultaneously visiting the native thistle *Cirsium ochrocentrum*. PHOTO: K. HARDWICKE, JULY 2005.

I was also interested in whole communities and a full mutualistic interaction network. Using a graphical technique introduced by Memmott (1999), the structure of whole networks can be studied. This allows for identification of particularly important plant and insect taxa within the system, for example cornucopian plant species that provide resources to a large proportion and wide range of insect taxa. These webs also illuminate which plant and insect groups might be specialist or generalist in their foraging tendencies, and identify interactions creating redundancy of ecological function that impart increased resilience to the network (Memmott et al. 2004). A suite of more technical network measures, including compartmentalization, nestedness, and web connectivity, can also be calculated using this approach (Memmott 1999, Dicks et al. 2002, Bascomponte et al. 2003, Jordano et al. 2003). I wished to record the frequency, and not just the presence or absence of, specific diurnal interactions likely resulting in pollination.

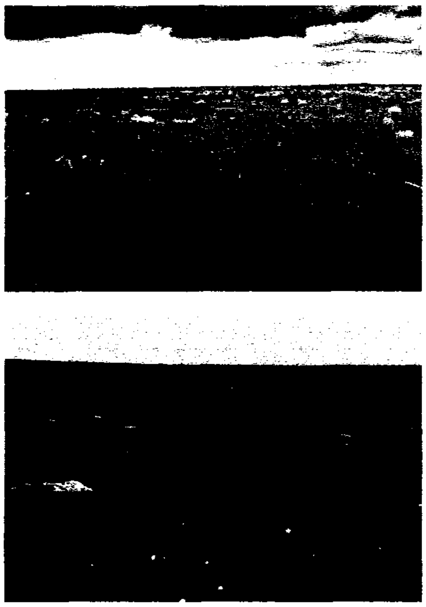


Plate 2 – Typical off-colony habitat (above) compared to a colony site (below) at a similar time of year. Note the visibility and density of floral patches on the colony.
PHOTOS BY K. HARDWICKE, 6/2005

Olesen and Jordano (2002) conducted a meta-analysis to discern patterns governing differences in networks at geological scales, comparing networks from differing latitudes, elevations, and temperate vs. tropical ecosystems. I wanted to compare local networks in the presence of this tri-trophic interaction: could networks adjacent to each other, and therefore with the same potential species pool, be significantly different in structure? Prairie dogs seemed a likely candidate for changing many processes and community characteristics governing a plant-insect floral visitor network, thus providing an opportunity to present the first well-documented, multiple site example of *local* community processes, enacted by ecosystem engineers (Miller et al. 1994, Ceballos et al. 1998, Kotliar 2000, but see Stapp 1998) which have important effects on the structure of pollination networks.

The three chapters to follow are presented in near-publication format, and so some amount of explanation that applies to design decisions over the entire three-year study is warranted. Insect visitation sampling proceeded very similarly in all three years: I patrolled paired on- and off-colony areas of about 530 m^2 for 40 minutes each in a series of concentric transects, capturing all pollinators (or apparent pollinators) and noting what plant species each had been foraging on. This basic methodology did not change from 2003 to 2005, but I did sample different colony sets in each year, as colonies were extirpated by plague, expanded into available off-colony comparison areas, or I increased the number of sampled colonies. I also increased sampling power on each colony yearly, from four sampling pairs per colony in 2003 (N=16 total), to five sampling pairs per colony in 2004 (N=25 total), to six sampling pairs per colony in 2005 (N=24 total).

Vegetation sampling changed more markedly over the three years, in an attempt to increase statistical power and more comprehensively sample the amount and layout of floral resources and percent bare ground. To capture more rare species and accurately assess differences in diversity and species-area relationships of entomophilous plants, I based my original 2003 sampling designs on the Modified-Whitaker multi-scale sampling plot (Stohlgren et al. 1995). I then doubled the area sampled in each plot, and increased the number of subplots per 200-m^2 large plot, in 2004. However, this approach ultimately lacked an ability to accurately measure the patterns of spatial heterogeneity of floral resources in the two habitat types. Therefore, in 2005 I sampled using many small (1 m^2) plots randomly distributed over large, contiguous portions of each colony and paired off-colony site. This way, I could also feasibly sample for floral biomass, as removing flowers from plots as large as the insect sampling areas would certainly affect the system under study. Maps were extrapolated from the many (56 per site) small plots that were, in turn, used to estimate average values of bare ground, mound density, and floral resource density in the large visitation sample areas. Because of the differences in colony sites, sampling intensity, and vegetation plot layouts in the three years, each year is considered to be a separate experiment, and data were generally not collapsed over years. I also conservatively analyzed differences in on- and off-colony site types, essentially considering colonies, not individual plots or sampling periods, as replicates. Given low power constrained by not collapsing over years and using conservative analysis techniques, I feel the following results are impressive in the consistent picture they give of insect utilization of floral resources on the shortgrass steppe.

In Chapter 1, I analyze data from 2003 and 2004, and find evidence of greater bare ground and entomophilous forb cover, greater inflorescence densities for both the whole community and several individual species, and greater insect visitation rates on colonies in both years. I also show that community composition of both plants and insects can change markedly from year to year. Whether or not there was higher diversity of plant species and insect groups in a given year on colonized patches, there was consistently higher insect group richness found on colonies. In Chapter 2, I again found similar changes in landscape characteristics and pollinator community composition and abundance on colonies. Additionally mound density was sampled, as was floral biomass presented by the 16 most frequently visited forb species in that year. Though again there were higher rates of insect visitation to the whole floral community on vs. off colonies, and to colony populations of several individual plant species, I found no higher rates of visitation of the plant community per unit (g/m^2) of floral biomass on- compared to off-colonies, therefore giving no evidence of higher per-flower or per-plant pollination service to on-colony populations. In fact, as also seen in Chapter 1, insects visited populations of *Opuntia humifusa* more frequently in uncolonized grassland. Multiple regression of several possible predictors of insect visitation showed that floral biomass and mound density correlate positively with habitat utilization by insects.

Chapter 3 describes the effects of prairie dogs on plant-pollinator network structure. I show that on-colony webs have lower connectivity, more plant species, insect groups and types of foraging interactions, and are much more complex in structure. Halictid bee group visitation of *Opuntia* cactus largely dominated off-colony webs, while colony webs were based on a higher proportion of interactions hosted by *Sphaeralcea coccinea* and other plant species. Further, insect groups found in both habitat types relied proportionally less on *Opuntia* when visiting colony sites. Although plants are more generalized on colonies, receiving visits from a higher median number of insect groups, insects are more specialized and visit fewer plant species per group on colonies. Two larger groups -- all Lepidoptera and parasitic/predatory Hymenoptera -- visited colonies more, utilized more plant species, and had higher species diversity on colonies.

This dissertation and the work described within ultimately represent an effort to describe patterns of anthophilous insect community composition and habitat usage in a mosaic of prairie dog colonies and uncolonized shortgrass steppe. Colonies are visually and fundamentally different from the surrounding grassland in terms of the resources available to, and conditions encountered by, all insect floral visitors. This in turn affects shortgrass steppe insect populations in varied and, in some cases, surprising ways.

LITERATURE CITED

Archer, S., M.G Garrett, and J.K. Detling. 1987. Rates of vegetation change with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie.

Vegetatio **72:**159-166.

Bascompte, J., P. Jordano, C.J. Melian, and J.M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences **100:**9383-9387.

Bonham, C.D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management **29**:221-225.

Bosch, M., and N.M. Waser. 2001. Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. Oecologia **126:**76-83.

Bronstein, J.L. 1995. The plant-pollinator landscape. *In* Mosaic Landscapes and Ecological Processes (eds L. Hansson, L. Fahrig, and G. Merriam). Chapman and Hall, London, pp. 256-288.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41:**161-172.

Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983. Plant-herbivore interactions in a North American mixed grass prairie. I. Effects of black-tailed prairie dogs on interseasonal above-ground plant biomass an nutrient dynamics and plant species diversity. Oecologia **56**:1-9.

Detling, J.K. 2006. Do prairie dogs compete with livestock? *In* Conservation of the black-tailed prairie dog (ed J.L. Hoogland). Island Press, Washington, D.C.

Dicks, L.V., S.A. Corbet, and R.F. Pywell. 2002. Compartmentalization in plant-insect flower visitor webs. Journal of Animal Ecology **71:**32-43.

Hoogland, J.L. 1995. The black-tailed prairie dog – social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

Jordano, P., J. Bascompte, and J.M. Olesen. 2003. Invariant properties in coevolutionary networks of plant animal interactions. Ecology Letters **6**:69-81.

Kotliar, N.B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology **14**:1715-1721.

Kunin, W.E. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology **85**:225-234.

Memmott, J. 1999. The structure of a plant-pollinator food web. Ecology Letters **2**:276-280.

Memmott, J., N.M. Waser, and M.V. Price. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London B **271**:2605-2611.

Michener, C.D. 1999. The bees of the world. John Hopkins University Press, Baltimore, Maryland.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology **8**:677-681.

Olesen, J.M., and P. Jordano. 2002. Geographic patterns in plant-pollinator mutualistic networks. Ecology **83**:2416-2424.

Petanidou, T., and W. N. Ellis. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. Biodiversity Letters **1**:9-22.

Schiller, J.R., P.H. Zedler, and C.H. Black. 2000. The effect of density-dependent insect visits, flowering phenology, and plant size on seed set of the endangered vernal pool plant *Pogogyne abramsii* (Lamiaceae) in natural compared to created vernal pools. Wetlands **20**:386-396.

Sowig, P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia **78**:550-558.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. Conservation Biology **12**:1253-1259.

Stohlgren T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.

Thomson, J.D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. Journal of Animal Ecology **50**:49-59.

Whicker, A.D., and Detling, J.K. 1988. Ecological consequences of prairie dog disturbances. Bioscience **38**:778-785.

Winter, S.L., J.F. Cully Jr., and J.S. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management **55**:502-508.

CHAPTER 1

TRI-TROPHIC INTERACTIONS in SHORTGRASS STEPPE: PRAIRIE DOGS, FORBS, and INSECT POLLINATORS

Abstract. Black-tailed prairie dogs (*Cynomys ludovicianus*) are colonial rodents whose intensive herbivory, vegetation clipping, and extensive burrowing greatly modify colonized patches. Certain aspects of this modification, such as an increase in bare ground and forbs, could affect pollinating insects favorably, although few data on this guild exist for the North American shortgrass steppe. I sampled a total of six prairie dog colonies and six similar uncolonized sites for bare ground and forb cover, inflorescence and open flower density, and insect floral visitation in 2003 and 2004. Bare ground, forb cover, and total number of inflorescences and open flowers on prairie dog colonies were approximately double that on uncolonized sites in both years, although floral resources were not significantly so ($\alpha < 0.05$) in 2003. Diurnal insect floral visitors, primarily pollinators, visited flowers at twice the rate on colonies as off in both years, indicating preferential utilization of prairie dog colonies as foraging habitat. Of the 25 most-visited plant species, most had denser inflorescences, and experienced higher populational visitation rates on colonies, although in many cases this was not significant by statistical convention. In a given year, insect diversity (H', by functional-taxonomic groups) displayed similar patterns to floral resource diversity. Insect group richness was higher on colonies in both years, while plant species area curves showed that species richness remained similar on colonies over both years, yet there were significantly fewer species found off-colonies only in 2004. Our results constitute evidence for a terrestrial tri-trophic interaction with potential consequences for management and conservation of shortgrass steppe flora and insects.

Keywords: black-tailed prairie dogs; Cynomys ludovicianus; *entomophilous plants; insect floral visitors; floral resources; habitat utilization; trophic interactions; pollinators; keystone species*

INTRODUCTION

Black-tailed prairie dogs (*Cynomys ludovicianus*) alter vegetation structure and composition in both the mixed-grass prairie (Coppock et al. 1983a, Whicker and Detling 1988) and the shortgrass steppe (Bonham and Lerwick 1976, Winter et al. 2002). In both ecosystems, perennial grasses dominate the ground cover in uncolonized areas, but in colonized habitat, where prairie dogs' strong grazing pressure is directed primarily towards palatable graminoids, grass cover declines and forbs increase in abundance (Detling 2006). Prairie dog foraging also reduces total plant biomass, litter, and canopy height, and their extensive burrowing creates mounds of bare soil where seeds can germinate (Bonham and Lerwick 1976, Coppock et al. 1983*a*, Archer et al. 1987, Hoogland 1995, Winter et al. 2002, Guenther and Detling 2003).

Certain plant (e.g. cutleaf nightshade, *Solanum triflorum*) and animal species such as Mountain Plover (*Charadrius montanus*), Burrowing Owl (*Athene cunicularia*), and black-footed ferret (*Mustela nigripes*) are found primarily on colony sites (Miller et al. 1990, Hoogland 1995, Kotliar et al. 1999, VerCauteren et al. 2001). Studies conducted on the mixed-grass prairie have shown preferential utilization of colonized area by large ungulate herbivores such as bison (*Bison bison*) and pronghorn (*Antilocapra americana*) (Coppock et al. 1983*b*, Krueger 1986). Colonies are patches of altered landscape where vegetation, and thus herbivore utilization, both differ from that in less disturbed grassland. On a smaller scale, two invertebrate herbivores, root-feeding nematodes (Ingham and Detling 1986) and grasshoppers (Russell and Detling 2003), were more abundant on colonies. Because black-tailed prairie dogs' influence on plant and animal communities is unique, substantial, and disproportionately large compared to their relative abundance in the community, some consider them keystone species of North American grassland ecosystems (Miller et al. 1994, Kotliar et al. 1999, Kotliar 2000, but see Stapp 1998), or classic examples of ecosystem engineers (Ceballos et al. 1999). Relatively little attention has been directed towards potential influence of prairie dogs on insect communities.

Entomophilous (insect-pollinated) forbs are often more abundant and diverse, both in terms of total species richness (Bonham and Lerwick 1976) and Shannon-Wiener diversity indices (Farrar 2002), on colony sites than off in shortgrass steppe. It follows that the abundance and diversity of floral resources used by pollinators should differ similarly between these two landscape types as well, unless prairie dogs are so successful at removing and cropping all ground cover that relatively few flowers remain. Although several studies have assessed relative species mix and cover between prairie dog colonies and the surrounding uncolonized shortgrass steppe (Bonham and Lerwick 1976, Winter et al. 2002, Farrar 2002), no studies have quantified floral resources on a community-wide basis.

Pollinators, and all insect floral visitors, could find colony patches more attractive if they are more resource-rich than the surrounding uncolonized steppe, but there are other reasons that could contribute to increased utilization of colonies by insects. Winter et al. (2002) found reduced visual obstruction on colonies in the shortgrass steppe, so any floral resources present on colonies may be more visible and attractive to pollinators, regardless of whether floral density is significantly increased. Because above ground biomass and litter are lower on colonies in the shortgrass steppe (Farrar 2002), and mound entrances are often bare or sparsely vegetated, prevalence of bare ground may be greater on older or densely populated colonies. Many pollinators thermoregulate in the warm microclimates created by bare, high-reflective surfaces (Willmer 1983). Also, burrows and other bare soil on colonies might contribute to a greater abundance of ground-dwelling bees, which require exposed soil to construct their nests (Petanidou and Ellis 1993, Michener 1999). Moreover, bombyliid flies (beeflies) and meloids (blister beetles), other pollinating taxa common on the shortgrass steppe, are intimately tied to the locations of bee hives, as their larvae are incubated inside of these nests (Michener 1999).

The foregoing suggests that prairie dog colonies potentially affect pollinator communities in grasslands. In this study, I investigated how black-tailed prairie dogs affect the floral resource density and diversity on the shortgrass steppe, and how visitation rate and diversity of diurnal insect floral visitors compare between colonized patches and the surrounding, uncolonized, shortgrass matrix.

METHODS

Study Sites

All prairie dog colonies used in this study were on the Pawnee National Grassland (PNG) in northeastern Colorado, and were selected for their large size and accessibility. Nearby uncolonized sites specifically paired to each colony had similar soil types, land use history, aspect, and topography. Cattle have seasonally grazed all study sites since land purchase by the US Forest Service (late 1930s – early 1940s). Four colonies (PNG USFS colony numbers 5, 8, 62, and 66) were sampled in 2003 and five colonies (PNG USFS colonies 5, 8, 35, 66, and 83) were sampled in 2004. Colonies 5, 8, and 35 are located on the far eastern PNG, and are all relatively large (mean area in 2003 was 113 ha). Colonies 62, 66, and 83 are located in the western portion of the PNG, and are smaller (mean area in 2003 was 36 ha). Colony 62 was driven extinct by plague (*Yersinia pestis*) in May 2004, and was thus not used in 2004. All other study colonies expanded in area throughout both growing seasons.

Vegetation Sampling

I assessed floral resources by estimating cover of entomophilous species, and counting total inflorescences and number of open flowers of any flowering entomophilous plant within six randomly placed large plots (described below) on each colonized and uncolonized area. Plant nomenclature follows *Flora of the Great Plains* (McGregor 1986). Inflorescences are a less time-sensitive measure of available floral resources than open flowers, because they can be counted from before buds open to after fruit set. Counts of open flowers provide an estimate of floral resources available to insects on the day of sampling, but species with many small flowers will be overrepresented, while those with fewer large flowers will be underrepresented with respect to their contribution to total resource availability.

Sampling did not proceed identically in 2003 and 2004 because 1) sampling was increased in 2004 to better describe spatially heterogeneous floral resources, and 2) different weather patterns altered community flowering phenology between years. The first issue was addressed in 2004 by studying one more colony, doubling the area of large plots, and sampling more subplots per large plot. Because of a cool wet spring, sampling commenced in late May, 2003 and continued until the weather changed abruptly to a very dry, hot phase in early July, at which point very few plants flowered for the remainder of the growing season. In 2004, sampling again began in late May, but a warm, dry spring followed by a wetter summer allowed late-summer/early fall-flowering plants to flower at much greater intensities than in 2003, so sampling continued through early September.

Large vegetation plots were based on the Modified-Whittaker multi-scale sampling plan, in which large plots are surveyed for species presence or absence, and variously sized subplots are used to gather more detailed vegetation measurements, in this case floral resource measurements such as inflorescence and flower density (Stohlgren et al. 1995). In 2003 the large plots were 100 m^2 (20 x 5 m), and each contained one 1-m^2 (0.5 x 2 m) and two 10-m^2 (2 x 5 m) subplots (total subplots per site = 18). In 2004, because I expanded sampling, each large plot was 200 m^2 (25 x 8 m), and contained two 1-m^2, two 10-m^2, and one 20-m^2 (2 x 10 m) subplots (total subplots per site = 30). In both years, cover was estimated to the nearest 1% for each forb species and bare ground in the 1-m^2 subplots (Stohlgren et al. 1995).

Diurnal Insect Floral Visitor Sampling

In each year, a subset of the large vegetation plots was randomly assigned to colonized-uncolonized pairs, and revisited for sampling of insect visitors. I sampled an approximately 530 m^2 circular area around each plot by walking in a series of concentric transects for 40 minutes, and used a sweepnet to capture all insects observed engaging in pollinator-type foraging behavior on any open flower. This gave a total of $N = 16$ pairs (four per colony) or 21.3 total observation hours in 14 non-consecutive days in 2003, and $N = 25$ pairs (five per colony) or 33.3 total observation hours in 19 non-consecutive days in 2004. Plot pairs were sampled for insect visitation during times of heavy flowering in the overall area. I used consecutive pairwise sampling to ensure that time of day (to the nearest two-hour block) and weather was controlled within pairs, and the same researcher carried out all insect sampling in both years. All insect sampling occurred between 0900 and 1600 hrs on days when the weather was sunny, warm (from 27 - 42 °C), and not excessively windy (not more than 10 m/s gusts). As each insect was captured, I recorded the plant species it had been foraging on, then killed it by freezing for later pinning and identification. I did not collect obviously incompetent vectors (e.g., those making no contact with sexual parts of flowers) or florally destructive taxa whose foraging behavior did not suggest significant pollen movement or stigmatic deposition, like small beetles (nitidulids, weevils), homopterans, and thrips, or relatively immobile or territorial predators like spiders and asilid flies.

Insects were identified to family and then placed into one of 45 morphospecific groups (Appendix A1) based on their size, coloration, family/subfamily, pile density and length, presence of and scopa type, and larval host plant (for Lepidoptera). For example, the bee family Apidae was broken up into four categories: 1) very large (21 - 28 mm), primitively eusocial, corbiculate bumblebees (*Bombus* spp.) with long tongues; 2) large- to medium-sized (12 - 22 mm), solitary, anthophorid bees with long tongues and "loose pollen" scopa (primarily *Melissoides* and *Anthophora* spp.); 3) medium- to small-sized (8 - 10 mm), solitary, anthophorid bees (primarily *Melissoides* spp.) with relatively shorter tongues and smaller scopa; and 4) small (7 - 8 mm), pileless, parasitic bees with short tongues and no scopa (*Nomada* spp.) (groups H3-6 respectively, see Appendix A1). All lepidopterans were identified to species because each relies upon differing host plant species for their larval success and possibly presence in an area (Ehlrich 1989). Measures of Shannon-Weiner diversity (H') based on groups delineated not only taxonomically, but also using biologically relevant information such as size (Woodward et al. 2005) and pile length, allow quantification of higher-level taxonomic diversity while also providing insight into the functional diversity of the community.

Statistical Analyses

In analyses of community-wide and species-specific floral resources and insect visitation rates, as well as bare ground and forb cover, data were not collapsed over years because differing variance in all measurements between years, as well as the significant differences in methodology. I used Proc Mixed in SAS to perform a two-way ANOVA, with site type as a fixed effect and colony pair as a random effect. The *P*-values shown are for the site type (on or off-colony) by colony pair interaction, which had 3 d.f in all 2003, and 4 d.f. in all 2004 analyses. While the colonies used in the study were not technically random (as they were selected for large size), the rationale for this mode of analysis is that in considering the colonies themselves to be the replicates, not individual plot, subplot, or sampling period measurements, this analysis is conservative enough to provide inferences about large prairie dog colonies on the northeastern Colorado shortgrass steppe in general. All floral and insect count data were √-transformed for analysis, but have been presented untransformed, except for species-specific inflorescence density, which is shown in units of difference in mean $\sqrt{(\text{inflorescences})}/m^2$ for reasons of scale. Because data could not be combined across years for analysis, and sampling power was greatest in 2004, only 2004 data were used in all species-specific analyses of inflorescence density and landscape visitation rates. No multiple comparison tests were used, so caution should be used in interpreting the 50 species-specific on-off colony comparisons. However, significance is indicated to the $\alpha < 0.10$ level, as in some instances power was low and plant species were not found on all sites, or because there was a large between-site variation in density. For comparisons of Shannon-Weiner diversity (H') of both entomophilous plant species and insect functional groups, one H' value was calculated for the each site, which was a measure of whole-site, whole season diversity for the area, and these values were then analyzed by pairwise t-test (d.f. = 3 in 2003, and d.f. = 4 in 2004) Analyses were run using SAS version 8.02 for Windows; Microsoft Excel v. X and Aabel v.1.3.8 for Mac OS.

RESULTS

Landscape Change and Floral Resources

There was a two-to-three-fold higher percentage of bare ground on than off prairie dog colonies in both years ($P < 0.01$ in 2003; $P < 0.04$ in 2004; Fig. 1.1A), as well as twice as much cover of entomophilous species on colonies ($P < 0.02$ in 2003; $P < 0.04$ in 2004; Fig 1.1B). Total open flower density was not significantly different on and off colonies in 2003 ($P = 0.31$), but flowers were nearly three times more abundant on colonies in 2004 ($P < 0.008$; Fig. 1.1C). Combined inflorescence density of all entomophilous species was greater on colonies in both years ($P = 0.054$ in 2003; $P < 0.02$ in 2004; Fig. 1.1D).

Pooling all floral resources for comparison (Fig. 1.1C and D) makes it difficult to control for relative size of flowers, per-flower resource contribution, or their importance and attractiveness to the diurnal insect floral visitor community. Therefore, I investigated important entomophilous plants' individual responses to prairie dog colonization by comparing density of inflorescences on and off colonies for the 25 most visited plant species across both years (Fig. 1.2A). Inflorescences of three of these 25 species (*C. minima* - little cryptantha, *S. coccinea* - scarlet globemallow, *and V. bracteata* - bigbract verbena) were significantly more dense on colonies ($\alpha \leq 0.02$), while four more species were weakly significantly more dense on colonies (*Astragalus* spp., $P < 0.08$; *C. incanum*, $P < 0.06$, *C. undulatum* – wavyleaf thistle, $P < 0.09$; and *H. spinulosus*, $P < 0.1$; Fig. 1.2A).

Insect Floral Visitation

I recorded 349 and 735 diurnal insect floral visitors in 2003 and 2004, respectively. The proportional makeup of the flower-visiting insect community changed markedly from 2003 to 2004 at the order level. In 2003, hymenopterans (bees and wasps) and lepidopterans (butterflies and moths) together made up more than 90% of the captures in approximately equal proportions. In 2004, hymenopterans dominated the recorded visits (72% of all 2004 captures), dipterans (flies) were abundant in the late summer (16%), and lepidopterans were relatively rare (8%). Coleopterans (blister and longhorn beetles) were comparatively minor components of the anthophilous steppe community in both years, with only 4% of the captures in both 2003 and 2004. In both years, insects visited the entomophilous community on colonies at about twice the rate (captures/sample period) observed on uncolonized areas ($P < 0.008$ in 2003; $P < 0.006$ in 2004; Fig. 1.1E). Overall, I recorded a total of 350 insect floral visitors in 31 functional groups on uncolonized sites in the two years, and 734 individuals in 43 functional groups on colonized sites (Appendix A1).

The two most-visited entomophilous species in 2003 were the small-headed yellow aster *Picradeniopsis oppositifolia* (17% of all visits) and *S. coccinea* (16%). In 2004, the two most-visited genera were prickly pear cacti (*Opuntia polyacantha* and *O. humifusa* together comprised 52% of all captures), and another yellow aster, *Chrysopsis* *villosa* (8%). Two of the 25 most visited species were visited at higher rates ($\alpha \leq 0.05$) at the landscape level on colony sites *(E. asperum and S. coccinea)*; while four others showed a weakly significantly higher visitation rate on colonies (*C. serrulata* - Rocky Mountain beeplant, $P < 0.1$; *M. tanacetifolia* – purple tansy aster, $P < 0.075$; *S. tridenticulatus* – threetooth senecio, $P < 0.09$; and *V. bracteata*, $P < 0.06$; Fig. 1.2B). One plant species, *O. humifusa* – plains prickly pear, was weakly significantly visited more off-colonies ($P < 0.09$, Fig. 1.2B).

Community Diversity

Floral resource diversity (H'), based on inflorescence counts, was not significantly different on and off colonies in 2003 ($P = 0.34$) but was nearly twice as great on colonies in 2004 ($P < 0.03$, Fig. 1.3A). The insect community showed a similar pattern, since in 2003 diversity (H') was not different between site types ($P = 0.97$; Fig. 1.3B), but in 2004 insects were 40% more diverse on colonies ($P < 0.05$; Fig. 1.3B). However, anthophilous insect group richness was significantly greater on colonies in both years ($P < 0.04$ in 2003; $P < 0.05$ in 2004, Fig. 1.3C).

Species-area curves indicated no difference in plant species richness at any spatial scale between on- and off-colony sites in 2003 (Fig. 1.4A). However, while 2004 values for species richness remained similar on colonies to that observed in 2003, off-colony richness was markedly lower at every spatial scale measured in that year (Fig. 1.4B).

DISCUSSION

Colonies: Resource-rich habitat for anthophilous insects

Relative abundance, community composition, and local density of floral resources all contribute to the attractiveness of an area to pollinators (Thomson 1981, Rathke 1988, but see Bosch and Waser 2001). I found evidence of differences in all of these measures of floral resources between prairie dog colonies and paired off-colony sites in the shortgrass steppe. Large, active prairie dog colonies on the shortgrass steppe contained a greater density of floral resources than comparable uncolonized areas, and these colonized areas also had a more abundant and group-rich anthophilous insect community (Fig. 1.1 and 1.3). This differential arthropod abundance and richness was observed in both years, despite considerable variation in annual weather patterns and the important and prevalent biota.

An increase in floral density is almost certainly not the only alteration of habitat that affects the local distribution, community composition, and abundance of anthophilous insects in this system. In a given year, the diversity (H') of the functional groups of floral insect visitors is likely affected by the observed species diversity of the floral resources themselves (Fig. 1.3), and my data suggest that at least in some years and on some prairie dog colonies, diversity of both groups is greater on colonies. Likewise, while there was a high similarity in species richness of forbs on and off colonies at all spatial scales in 2003, but in 2004 species richness decreased off colonies at all spatial scales while on colony richness remained similar to 2003 values (Fig. 1.4). However, insect group richness was consistently greater on colonies compared to off (Fig 3), perhaps indicating that even when uncolonized steppe presents a similar number of forb species as on colonies, some of these forb species may not be dense or common enough off colonies to support the quantity of insect groups found on colonies.

Prairie dogs also induce considerable change on a microhabitat scale that may benefit floral insect visitors. As suggested for grasshoppers (Russell and Detling 2003), the increase in bare ground (Fig. 1.1A) enlarges the area suitable for building entrances to underground burrows and hives for bees and predatory wasps, which also benefits those taxa that parasitize hymenoptera. Overall, bare ground is an important habitat consideration for nest-building insects in a treeless steppe environment, and for other insects it provides space for basking and puddling behavior (Willmer 1983, Boggs and Dau 2004). Similarly, the decrease in canopy height and litter on colonies (Whicker and Detling 1988, Winter et al. 2002) will also affect microhabitats experienced by insects. Visibility of floral patches will be higher on colonies, as will the proportion of flowers in full sun versus those partially or completely shaded by taller vegetation. Many insects prefer full-sun foraging because it allows them to more passively maintain flight temperature (Willmer 1983). The structural complexity of the microhabitats must also differ at the scale perceived by insects, due to changes in plant species composition, an increase in bare ground, and a decrease in canopy height and litter.

Implications for management and conservation

The foregoing suggests that prairie dog colonies provide high-quality habitat and resources for many anthophilous steppe insects, and are capable of supporting a larger and more diverse insect community than typical of similar grassland without prairie dogs. Insect floral visitors depend on resources presented by entomophilous flowers for energy in the form of nectar, and in some taxa additionally for protein for themselves or their offspring. If insect populations preferentially utilize the increased density of certain forbs on colonies, then these populations would be at least weakly facultative in their reliance on colonized habitat, like Kotliar et al.'s (1999) examples of Ferruginous Hawks (*Buteo regalis*) and Golden Eagles (*Aquila chrysaetos*). As in these species, prairie dog density is a likely predictor for high local abundance or even presence of certain pollinating insects in the steppe.

In North American tallgrass prairie, Panzer and Schwartz (1998) found plant community composition to be a good indicator of an area's ability to retain rare insect species, and recommended a vegetation-based approach to insect conservation. Here we find that colony flora is altered in such a way that total floral resources, as well as resources presented by several specific forb species (Fig. 1.2), are more dense, and in some cases, more diverse than in the surrounding grassland. Higher trophic levels, for example insectivorous birds, may also benefit from increased anthophilous insect populations on colonies, and more research into the possible cascade of community effects driven by prairie dog colonization is warranted. In any case, our results provide further evidence that prairie dogs do impact the steppe community sufficiently to be considered ecosystem engineers (Ceballos *et al.* 1999, Kotliar *et al.* 1999).

The vegetational effects of prairie dog colonization increase with colony age (Archer et al. 1987, Whicker and Detling 1988), and tend to quickly revert following colony extinction (Hartley 2006). Unlike those on the eastern prairies, shortgrass steppe colonies are subject to periodic extinction events stemming from sylvatic plague (Stapp et al. 2004), which truncate periods of continuous colonization on any one site in this system. Thus, it is unlikely that a radically different flora and insect visitor fauna could be found on all colonies. Indeed, periodic extirpation-recolonization events, combined with the strong abiotic pressures on vegetation in the shortgrass steppe, probably cause temporal and spatial fluctuations in many of the changes in vegetation and insect habitat use described here. Because sylvatic plague is introduced in North America (Antolin *et* *al.* 2000), frequent colony extirpations likely represent a new stress on anthophilous steppe insect populations facultatively dependant on colony habitat.

Effects on entomophilous plant populations

To what extent the entomophilous plants in this system depend on specific insect floral visitors for pollination services is essentially unknown, because an insect species that visits a plant to forage could range from the most competent (i.e., able to successfully move conspecific pollen to the stigma of another individual), evolutionarily important pollen vector for that plant species to a completely incompetent vector that is essentially nectar thieving. Floral larceny could have a range of complicated and indirect effects on forb species in this community, from apparent competition to facilitation between plants, and these effects may even include fitness benefits in the form of increased outcrossing rates for some plants (Irwin et al. 2001). Although the scope of this study could not include a determination of precisely which insect taxa were competent vectors for which plant species, we excluded the most obvious floral larcenists. As for the floral visitors we did observe, it is logical that some subset of this group represents the competent pollination vectors for diurnally insect-pollinated plants of the shortgrass steppe.

It is therefore possible that pollination and outcrossing rates differ between the two habitat types for at least some of the entomophilous plants in this system. Not only were visitation rates higher on a per-area basis on colonies (Fig. 1.1E), indicating high utilization of the colonies as foraging habitat, and suggesting higher local abundance of anthophilous insects, eight of 25 entomophilous plant species had higher populational visitation rates on colonies, while only one was visited at a higher frequency in uncolonized areas (Fig. 1.2B). Some of the plant species showing significant differences in visitation rate produced more inflorescences in the habitat type where they exhibited the highest visitation rate, suggesting some effect of local inflorescence density in determining community visitation rates in this system. Colony populations of many forb species may not actually experience greater per-individual or per-flower visitation frequencies, because these rates do not always correlate positively with higher population-level visitation (Schiller et al. 2000).

Higher visitation rates on colonies for most plant species, whether on a population- or per-capita scale, could imply increased seed set for colony populations of those entomophilous plants, assuming the total visitation rate correlates with the rate of effective pollination. Fahnestock et al. (2003) studied seed bank composition and abundance on prairie dog colonies in the mixed-grass prairie and found that the seed banks were significantly altered on colony sites. Seed banks from colonies tended to have a higher species richness and evenness, were forb- rather than graminoid dominated, had more annual seeds, and had a much higher density of germinating seeds per sample. To date most prairie dog effects on vegetation appear to be of lesser magnitude in the arid shortgrass steppe than in the mixed-grass prairie, but it seems likely from the results presented here that seed banks on steppe colony sites would differ similarly.

Conclusions

I believe this study provides substantial evidence for an important tri-trophic interaction between black-tailed prairie dogs, shortgrass steppe vegetation, and the anthophilous insect community. Here there is further indication that prairie dogs act as ecosystem engineers, by creating and enhancing habitat for many entomophilous forb species. This then benefits populations of pollinators and other insect floral visitors that depend on and, in some cases, have important mutualistic interactions with these plants. In this trophic interaction, where the presence and habitat use of one guild increases the abundance of two others, appropriate management for native steppe forbs and their pollinators might focus on maintenance of prairie dog populations as a driving or stabilizing guild in the community. Conservation of a thriving native pollinator community, as well as many coevolved pollination partnerships on the shortgrass steppe, requires recognition of the role of large, older, and densely populated black-tailed prairie dog colonies as favorable habitat for these trophic guilds.

LITERATURE CITED

Antolin, M.F., P. Gober, B. Luce, D.E. Biggins, W.E. Van Pelt, D.B. Seery, M. Lockhart, and M. Ball. 2000. The influence of sylvatic plague on North American wildlife at the landscape level, with special emphasis on black-footed ferret and prairie dog conservation. *Transactions of the 67th North American Wildlife and Natural Resources Conference*, Dallas, Texas, April 3-7.

Archer, S., M.G Garrett, and J.K. Detling. 1987. Rates of vegetation change with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio **72:**159-166.

Boggs, C.L., and B. Dau. 2004. Resource specialization in puddling Lepidoptera. Environmental Entomology **33:**1020-1024.

Bonham, C.D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. Journal of Range Management **29:**221-225.

Bosch, M., and N.M. Waser. 2001. Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs.

Oecologia **126**:76-83.

Ceballos, G. J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41**:161-172.

Coppock, D.L., J.K. Detling, J.E. Ellis, and M.I. Dyer. 1983*a*. Plant-herbivore interactions in a North American mixed grass prairie. I. Effects of black-tailed prairie dogs on interseasonal above-ground plant biomass an nutrient dynamics and plant species diversity. Oecologia **56**:1-9.

Coppock, D.L., J.E. Ellis, J.K. Detling, and M.I. Dyer. 1983*b*. Plant-herbivore interactions in a North American mixed grass prairie. II. Responses of bison to modification of vegetation by prairie dogs. Oecologia **56**:10-15.

Detling, J.K. 2006. Do prairie dogs compete with livestock? *in* J.L. Hoogland, editor. Conservation of the black-tailed prairie dog. Island Press, Washington, D.C.

Ehlrich, P.R. 1989. The structure and dynamics of butterfly populations. *In* The Biology of Butterflies. Ed. by R.I. Vane-Wright and P.R. Ackery. Princeton University Press, Princeton, New Jersey, pp. 25-40.

Fahnestock, J.T., D.L. Larson, G.E. Plumb, and J.K. Detling. 2003. Effects of ungulates and prairie dogs on seed banks and vegetation in a North American mixed-grass prairie. Plant Ecology **167**:255-268.

Farrar, J.P. 2002. Effects of prairie dog mound-building and grazing activities on vegetation in the central grasslands. M.S. Thesis, Colorado State University, Fort Collins, Colorado.

Gigawiz Software. 2001 – 2005. Abel Version 1.5.8. Gigawiz Software, Ltd. Tulsa, Oklahoma.

Guenther, D.A., and J.K Detling. 2003. Observations of cattle use of prairie dog towns. Journal of Range Management **56**:410-417.

Hartley, L. 2006. Plague and the black-tailed prairie dog: An introduced disease mediates the effects of an herbivore on ecosystem structure and function. Ph.D. thesis, Colorado State University, Fort Collins.

Hoogland, J.L. 1995. The black-tailed prairie dog – social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

Irwin, R.E., A.K. Brody, and N.M. Waser. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia **129**:161-168.

Ingham, R.E., and J.K. Detling. 1986. Nematode population-dynamics from different aged prairie dog colonies. Journal of Nematology **18**:638-638.

Kotliar, N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management **24**:177-192.

Kotliar, N.B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology **14**:1715-1721.

Krueger, K. 1986. Feeding relationships among bison, pronghorn, and prairie dogs – an experimental analysis. Ecology **67**:760-770.

Microsoft Software. 1985 – 2001. Microsoft Excel Version X for Mac®. Microsoft Corporation. Redmond, Washington.

McGregor, R.L. 1986. The flora of the Great Plains. T.M. Barkley, R.E. Brooks, and E.K. Schofield, editors. University Press of Kansas, Lawrence, Kansas.

Michener, C.D. 1999. The bees of the world. John Hopkins University Press, Baltimore, Maryland.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management **14**:763-769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology **8**:677-681.

Panzer, R., and M.W. Schwartz. 1998. The effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693-702.

Petanidou, T., and W.N. Ellis. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. Biodiversity Letters **1**:9-22.

Rathcke, B. 1988. Interactions for pollination among coflowering shrubs. Ecology **69**:446-457.

Russell, R.E., and J.K. Detling. 2003. Grasshoppers (Orthoptera: Acrididae) and black-tailed prairie dogs (Sciuridae: *Cynomys ludovicianus* (Ord)): Associations between two rangeland herbivores. Journal of the Kansas Entomological Society **76**:578-587.

SAS Institute. 1999. SAS version 8.02. SAS Institute, Inc. Cary, North Carolina, USA.

Schiller, J.R., P.H. Zedler, and C.H. Black. 2000. The effect of density-dependent insect visits, flowering phenology, and plant size on seed set of the endangered vernal pool plant *Pogogyne abramsii* (Lamiaceae) in natural compared to created vernal pools. Wetlands **20**:386-396.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands.

Conservation Biology **12:**1253-1259.

Stapp, P., M.F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog populations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment **2:**235-240.

Stohlgren, T.J., M.B. Falkner, and L.D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117:**113-121.

Thomson, J.D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. Journal of Animal Ecology **50:**49-59.

VerCauteren, T.L., S.W. Gillihan, and S.W. Hutchings. 2001. Distribution of Burrowing Owls on public and private lands in Colorado. Journal of Raptor Research **35:**357-361.

Whicker, A.D., and J.K Detling. 1988. Ecological consequences of prairie dog disturbances. Bioscience **38:**778-785.

Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology **8:**455-469.

Winter, S.L., J.F. Cully Jr., and J.S. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management **55:**502-508.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology and Evolution **20:**402-409.

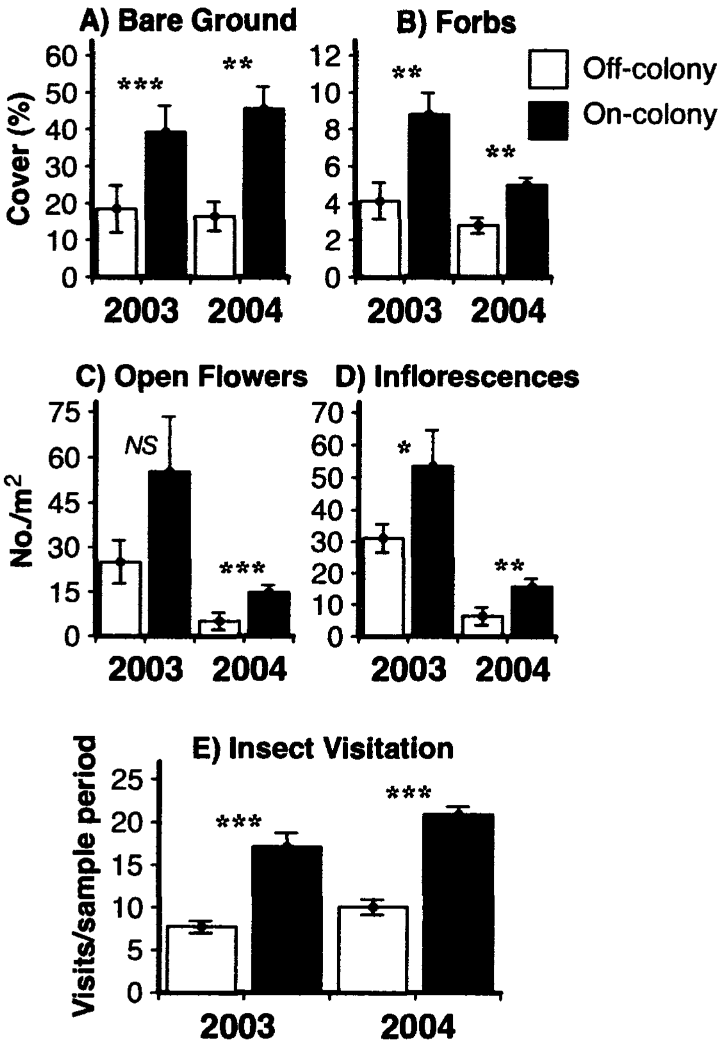


FIGURE 1.1– Prairie dog colonies in shortgrass steppe affect vegetational cover characteristics (A, B), overall floral resource density (C, D), and habitat utilization by diurnal anthophilous insects (measured by visits per 40 minute sampling period, E). For all comparisons, $N = 4$ sites in 2003, $N = 5$ sites in 2004, means ± SE shown. Cover of A) bare ground and B) all entomophilous forb species; density of C) open flowers and D) inflorescences; and E) community-wide insect floral visitation rates were all greater on colonies than off in both years, though floral resources were not significantly so in 2003. P values indicated as: * $P < 0.1$, ** $P < 0.05$, *** $P < 0.01$. NS = not significant.

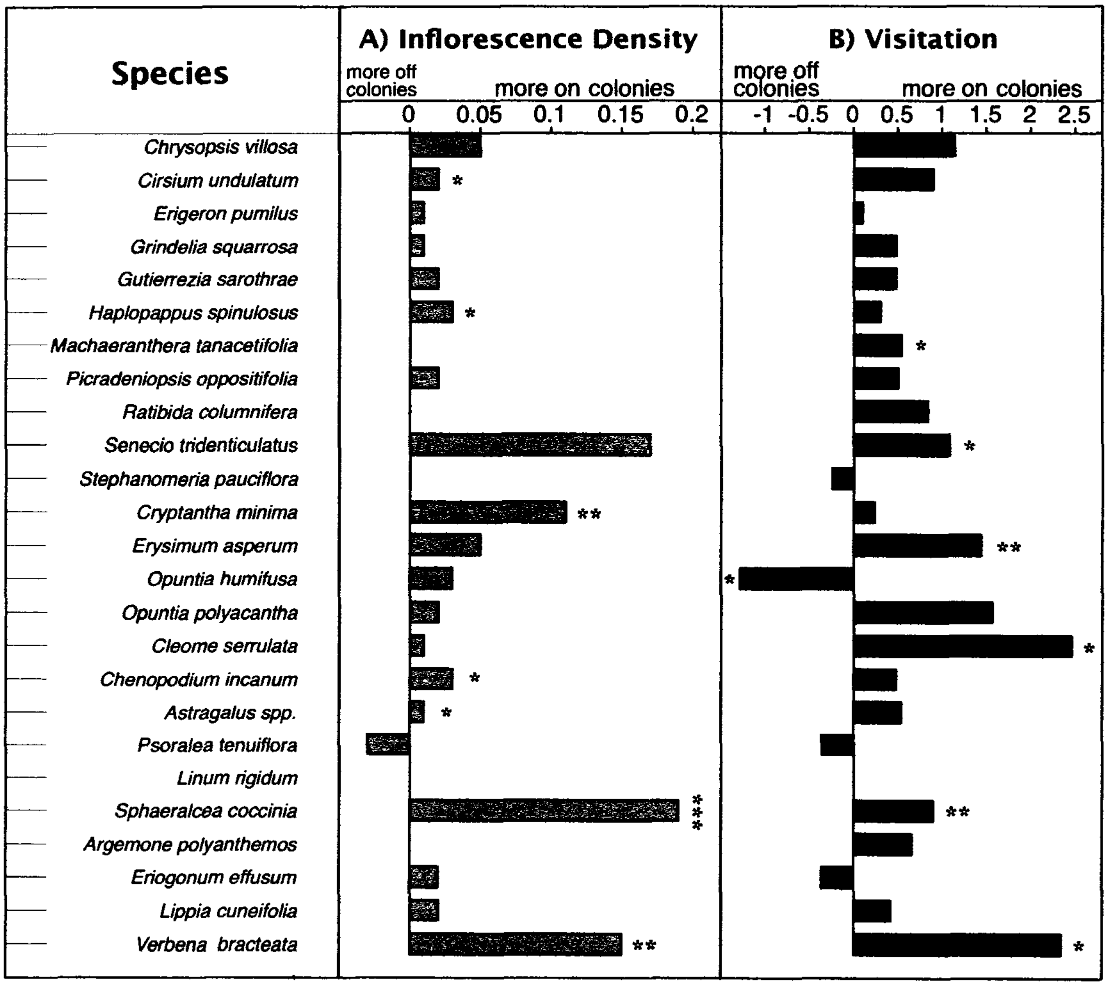


FIGURE 1.2 – Differences in species-specific inflorescence densities and visitation rates on and off colonies in 2004. These are the 25 most-visited plant species for both years, representing more than 94% of all recorded visits in 2004. A positive value indicates a greater density or rate on colonies, and a value of zero indicates no difference in colony vs. off-colony populations of that plant. A) Difference in mean colony and mean off-colony inflorescence density, shown in √(inflorescences)/m^2 for each of 25 species. B) Difference in mean on- and off-colony specific visitation rates (visits/species/hour) for the same 25 plant species. P-values indicated as: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

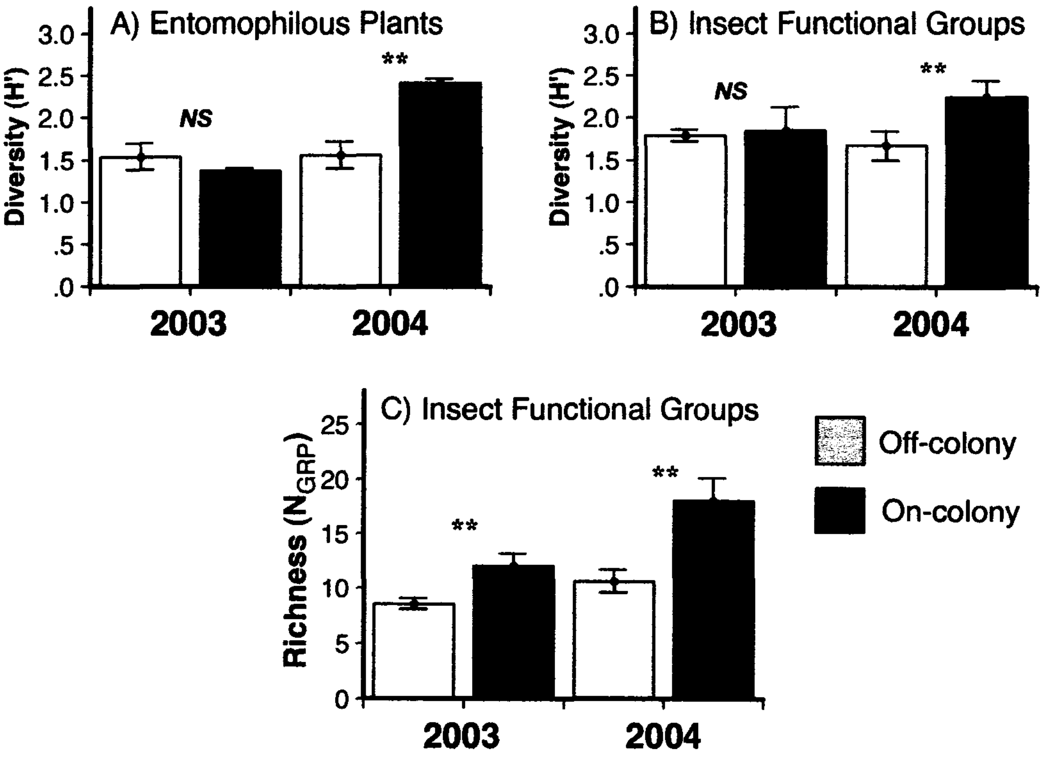


FIGURE 1.3 – Shannon–Weiner (H') diversity indices (site means ± SE) for A) entomophilous plants, determined from whole-season inflorescence counts, and B) diurnal insect floral visitor groups. C) Insect functional group richness (site means ± SE), from whole-season counts. For all analyses, $N = 4$ for 2003, and $N = 5$ for 2004. P values indicated as ** $P < 0.05$. NS = not significant.

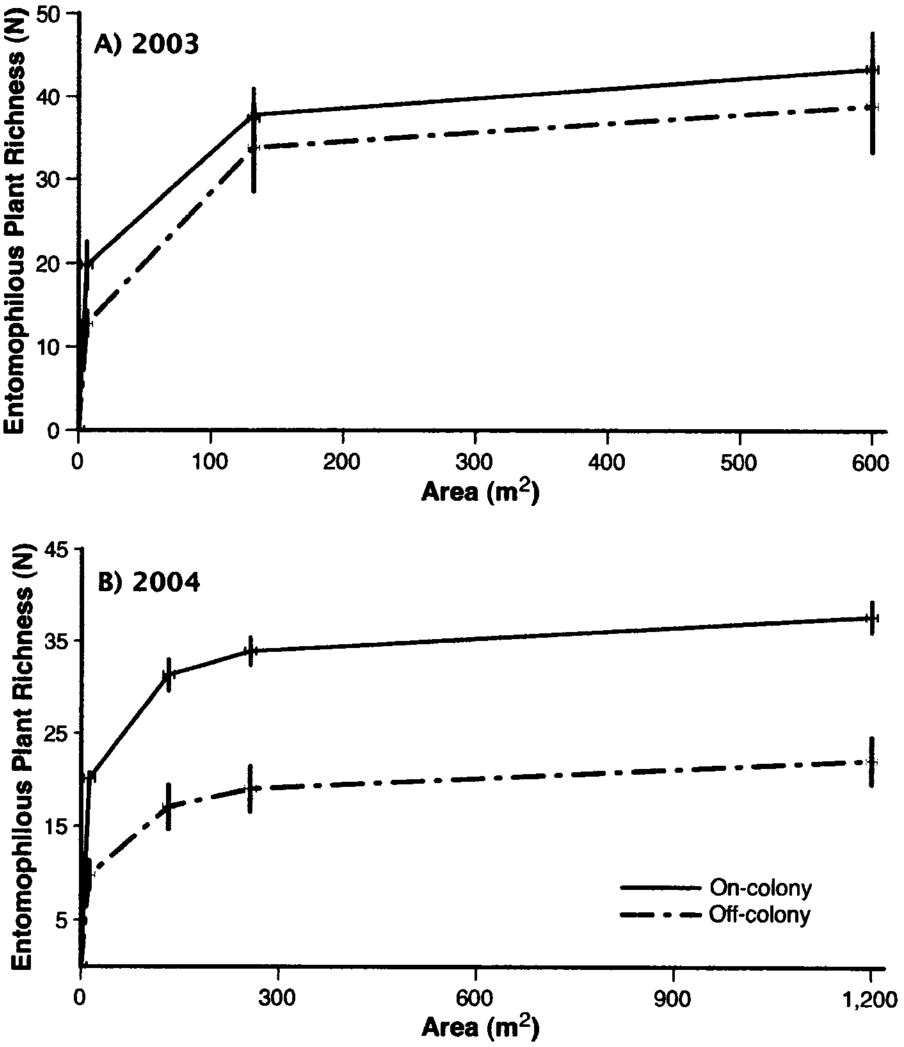


FIGURE 1.4 -- Plant species-area curves for all on- and off-colony sites for A) 2003, and B) 2004. Mean species richnesses at all sampling scales (± SE) shown for both colony and off colony sites. Species richness is only for entomophilous plants, and area refers to total area sampled per site. For all area classes, $N = 4$ for 2003 and $N = 5$ for 2004.

CHAPTER 2

SPATIAL ASSESSMENT of PRAIRIE DOG COLONIES: EFFECTS on SHORTGRASS STEPPE POLLINATOR COMMUNITIES

Abstract. --- Black-tailed prairie dogs increase bare ground, floral resources, and inflorescence diversity, and some or all of these effects likely contribute to higher landscape-level insect visitation rates and greater richness of the insect floral visitor community. To better discern the mechanisms involved in this tri-trophic interaction, in 2005 I used spatially explicit, small-plot sampling techniques to assess cover of bare ground, all entomophilous species, and number of open flowers and inflorescences on each of four prairie dog colonies and four similarly sized, paired off-colony sites on the Pawnee National Grasslands. I also estimated floral biomass of the16 most-visited entomophilous plants, and recorded burrow mound density. Delaunay triangulation was used to create spatial maps for each colony and paired off-colony site for bare ground, entomophilous forb cover, floral biomass, and mound density. I captured and identified insect floral visitors on six randomly located, on- and off-colony large plot pairs at each site to assess floral visitation rates. I used multiple regression and stepwise model selection to isolate the spatial variables best predicting trends in landscape insect visitation rates and functional group richness. Cover of bare ground and floral resources, total open flower and inflorescence densities, and floral biomass were all greater on colonies. Species-specific landscape visitation rates for six of the 16 most-visited plant species were also significantly greater on colonies, while *Opuntia humifusa* was visited more off-colonies. Floral biomass explained much of the variance in off-colony insect visitation rates, but mound density explained more variance in on-colony insect visitation rates. There is no evidence for greater pollinator habitat utilization on colonies than expected given the denser floral biomass found on these colonies, suggesting that colony populations of plants do not typically receive more per-flower or per-plant visits.

Keywords: *patch heterogeneity, landscape visitation rates, floral biomass, pollinators,* Cynomys ludovicianus, *mound density, spatial mapping, entomophilous plants, ecosystem engineers*

INTRODUCTION

There is a compelling connection between prairie dog (*Cynomys ludovicianus*) related changes in bare ground and floral resources and increased landscape floral visitation rates, which were seen both for the entire entomophilous floral community as well as several entomophilous shortgrass steppe forb species individually (Chapter 1). While no previous study has specifically measured floral resources on and off prairie dog colonies on either the mixed-grass prairie or the shortgrass steppe, many prior studies have measured increases in bare ground and forb cover, and decreases in graminoid cover and visual obstruction following colonization (Whicker and Detling 1988, Hoogland 1995, Winter et al 2002). As discussed previously, the effects of prairie dog colonization on these community properties increase with age (Coppock et al. 1983, Archer et al. 1987, Whicker and Detling 1988), and this observation, as well as careful pairing of abiotic characteristics at on-and-off-colony comparison sites, illustrate clearly that the activities of prairie dogs over time are responsible for these changes in grassland vegetational characteristics. Therefore, the finding that insect floral visitation rates increase on colonies should not be interpreted as pollinators and prairie dogs being separately and independently attracted to the same favorable steppe habitat patches, but that some aspect or combination of effects of colonization are responsible for altering steppe habitat in such a way that it becomes more attractive to the pollinating insect community. Yet simple average values of these community changes do not describe spatial heterogeneity of the habitat or provide mechanistic clues to precisely which aspect(s) of prairie dog colonial behavior drive changes in habitat utilization by the steppe anthophilous insect community.

The prairie dog-induced habitat alterations that affect the steppe pollinator community are likely of long-term coevolutionary importance for at least some entomophilous plant species and insect visitor groups, because of the historical prevalence of large colonies once common in North American mid-continental grasslands (Lewis and Clark 1804, Koford 1958). Some of the vegetational and abiotic changes induced by *Cynomys* colonization may also be caused by other disturbances and landscape features on the shortgrass steppe. For example, enhanced nitrogen availability, large patches of bare ground, or changes in forb density or species composition might be found along unpaved roadsides, riparian corridors, on certain soil type patches, or areas of recent nutrient application like fallow fields, but these areas are likely to be invaded by exotic species (Kotanen et al. 1998). Other organisms on the steppe may also create disturbances with roughly similar effect, such as the removal of biomass by large ungulates like bison and domestic cattle, or more meticulous microhabitat shaping by smaller, colonial members of the community like western harvester ants (*Pogonomyrex occidentalis*) (Coffin and Laurenroth 1990, Alba-Lynn 2006). Many of the specific activities of prairie dogs apparently do drive the important floral and pollinator community changes that define this tri-trophic response, but similar effects on both the forb and insect trophic levels might be caused by other disturbances elsewhere on the steppe.

However, some individual habitat changes are specific to prairie dog colonies (Kotliar 2000). Perhaps the most obvious alteration that prairie dogs are directly responsible for is the construction and maintenance of mounds that surround their burrow entrances. Mounds on *C. ludovicianus* colonies on the shortgrass steppe have an average basal area in of 2.3 m^2, and these denuded areas reach a density of over 350 m^2/ha of mound disturbance (Farrar 2002). There are three distinct mound forms with corresponding specific functions for colony members (Hoogland 1995). Because of differences in their thermoregulatory functions for the underlying burrow system (Hoogland 1995), the three mound types also are likely to have distinct thermographic profiles within the microclimate experienced by pollinating insects compared to other types of bare ground. Prairie dog mounds also typically have a relatively hard-packed surface, a large burrow opening, and are also often only partially denuded of even common dietary components such as *Sphaeralcea* species (Fagerstone et al. 1981, Farrar 2002, Mellado et. al 2005); therefore their particular effects are not identical to those of other large mounds found on the steppe, such as harvester ant mounds (Coffin and Laurenroth 1990, Alba-Lynn 2006). In this way, differential attractiveness of colony habitat to pollinators as might relate directly to the presence of the mounds themselves. Because these are specific to prairie dog colonies, the precise changes in pollinator habitat utilization and community composition found on colonies would not be expected to occur elsewhere, due to other steppe community members like harvester ants, or human disturbance.

Potential mechanisms related to prairie dog colonization driving the previously observed (Chapter 1) increase in landscape-level diurnal floral visitation and alteration of insect floral visitor community composition were selected after consideration of two years of study of vegetation and abiotic characteristics. Three general environmental changes possibly affecting pollinator populations occur on prairie dog colonies. First, an increase in bare ground could provide more area for ground-dwelling bee nest entrances, thermoregulatory basking behavior, and lepidopteran puddling activities (Willmer 1983, Petanidou and Ellis 1993, Michener 1999, Boggs and Dau 2004). Bare ground cover also reduces visual obstruction (Winter et al. 2002), possibly enhancing attraction to floral patches. Second, an increase in the density of floral resources known to be important to the anthophilous insect community should attract a greater number of insect visitors (Thompson 1981, Bronstein 1995, Kunin 1997). Lastly, an increase in mound density may affect insect visitation because denuded mound entrances will increase bare ground in a way specific to colonies, and floral resources may be spatially correlated with mounds (Farrar 2002).

Insect group diversity (H') appears to be affected, at least in a given year, by entomophilous plant diversity (Chapter 1). Further, insect group richness was consistently higher on colonies (Chapter 1). Plausible spatial covariates for insect group richness include: 1) overall floral resource density, as a more dense population of floral resources may attract a wider variety of insects; 2) the number and community make-up of important entomophilous plant species in open flower in the area at the time of sampling; 3) an increase in mound density, and 4) cover of bare ground, which may provide more area for, and a greater breadth of, potential nest sites for ground dwelling bees.

I investigated which of these spatial features, and possible temporal covariates such as date and time of day of insect sampling, best predicted the observed landscape-level insect visitation rates and group richnesses. This represented an attempt to understand what about prairie dog colonies may be attractive to the pollinator community, as well as how much this may be specific to colonies versus other steppe patch types. In addition, I show that previous trophic patterns in community structure and insect habitat utilization (Chapter 1) were repeated in 2005. Finally, landscape visitation rates do not necessarily correlate with per-plant or per-flower visitation rates (Schiller et al. 2000, Bosch and Waser 2001), or rates of visitation by effective pollinators, an important consideration when making statements regarding potential benefits to plant reproduction (Mayfield et al. 2001, Kay and Schemske 2004). I thus examined indirect evidence for higher community, or per area, visitation rates than would be expected given the higher inflorescence density found on prairie dog colonies.

METHODS

Study Sites

The four prairie dog colonies used in this study were located on the Shortgrass Steppe Long-term Ecological Research (SGS LTER) site, on the Pawnee National Grasslands (PNG) in northern Colorado. Colonies were selected for their large size, accessibility, and availability of a similar (in terms of soil type, land use history, and aspect) off-colony comparison site within 0.5 km. Furthermore, due to the spatially explicit sampling scheme used in 2005, the off-colony comparison sites had to encompass a contiguous area similar in size to the area sampled on its colonized pair site. For these reasons, colonies 35 (used in 2004, Chapters 1 and 3), and 66 (used in both 2003 and 2004, Chapters 1 and 3) no longer met site selection criteria, and were excluded from the 2005 study. The colonies I used for this study were PNG colonies 5 and 8 (also used in 2003 and 2004), colony 30, and colony 83 (also used in 2004). Colonies 5, 8, and 30 were located on the eastern PNG, while colony 83 was located on the western section.

Vegetation Sampling

On each colony and paired off-colony site, 56 randomly placed 1-m^2 plots were sampled for floral resources, bare ground, and the mound density of the surrounding area. On each plot, floral resources were measured by visually estimating cover to the nearest 1% of all entomophilous forb species. Open flowers or open asteraceous heads were also counted for each species, as one measure of floral resources available to the insect community. Inflorescences of entomophilous forbs, a less time-sensitive measure of floral resources, were also counted. Cover of bare ground was estimated to the nearest 1%, and all prairie dog mounds within a 5 m radius of the center of each 1-m^2 plot (a 78.5 m^2 circle) were counted to estimate mound density in the surrounding area.

For each of 16 most frequently visited plant species ($\geq$ 20 visits per species) in 2005, I estimated floral biomass during full flowering by clipping fully open flowers, or open heads of asteraceous plants, from plots where they were encountered, during each species' peak flowering period. At least 20 samples for each species, more depending on availability of fully open flowers or capitae, were harvested. These samples were then dried at 50° C to a constant mass (about 2-7 days). Because many species were in open flower for only 2-3 weeks, I estimated floral biomass from less contingent and time-sensitive inflorescence data for spatial mapping. Regressions of dry floral biomass against inflorescence number (both ln-transformed) were used to develop a predictive equation for each species. These equations were then used to convert inflorescence densities to biomass (g/m^2) of open flowers for each species when in full flower. The floral mass estimates for all 16 species were summed for each plot. Differences in mean visitation rates between all on- and off-colony sites were also calculated for these species. Plant nomenclature follows McGregor (1986).

Insect Visitation Sampling

As in previous years (Chapter 1), all insect visitor sampling was conducted on randomly distributed, paired on- and off-colony plots which were consecutively observed by a single investigator. Sampling plots were again circular areas approximately 530 m^2 in area that were patrolled in a series of concentric transects. However, sampling of each site was increased in 2005 to six 40-minute periods per colony and off-colony site, resulting in a total of 24 plot-pairs or 32 observation hours in 23 non-consecutive days. All insect sampling occurred between 9:00 A.M. and 3:00 P.M. when the weather was warm (from 27 - 42 °C), clear, and not excessively windy (< 10 m/s gusts). All insects observed in pollinator-type foraging behavior were captured by sweepnet for the 40 minutes. I sampled consecutively, starting the second member of the on-off plot pair within 20 minutes of concluding the first, to control for weather and time of day. The plant species each insect had been visiting at time of capture was recorded. Insects were killed by freezing and as in Chapter 1, identified to one of 48 functional-taxanomic groups based on their size, family, life history, pile density and length, presence of and scopa type, and larval host plant (for Lepidoptera) (Appendix A2). I did not collect obviously incompetent vectors (e.g., those never contacting sexual parts of flowers) or florally destructive taxa whose foraging behavior did not suggest significant pollen movement or stigmatic deposition, like small beetles (nitidulids, weevils), homopterans, and thrips, or relatively immobile or territorial predators like spiders and asilid flies.

Statistical Methods

I used Proc Mixed in SAS to perform a two-way ANOVA, with site type (on- vs. off-colony) as a fixed effect and colony pair as a random effect, for on-off colony comparisons of bare ground and entomophilous forb cover, open flower and inflorescence density, floral biomass, insect visitation rates, and visits per unit (g/m^2) of floral biomass. The *P*-values shown are for the site type (on or off-colony) by colony pair interaction, which had 3 d.f. While the colonies used in the study were not technically random (as they were selected for large size and other criteria), the rationale for this mode of analysis is that in considering the colonies themselves to be the replicates, not individual plots or sampling period measurements, this analysis is conservative enough to provide inferences about large prairie dog colonies on the northeastern Colorado shortgrass steppe in general. Because *Opuntia* was not visited in >50% of sampling periods and therefore individual period *Opuntia* visitation rates will not always spatially correlate to its density, a single site average for *Opuntia* inflorescence density was calculated, and a single value in visits/hour for *Opuntia* visits at each site. This was compared using a paired t-test with 3 d.f. All floral and insect count data were √-transformed for analysis, but are presented untransformed. For comparisons of Shannon-Weiner diversity (H') and plant species and insect group richness, a single whole-season diversity and richness value was calculated for the plant and insect communities at each site. These were then compared using a paired t-test in Abel version 1.5.8 for Mac. Due to the conservative nature and low statistical power of these analyses, no multiple comparison adjustments were used.

Construction of spatial maps. --- Spatial maps were created for each on- and off-colony site for 1) bare ground, 2) entomophilous forb cover, 3) floral biomass of the 16 most visited plant species, and for on-colony sites only, 4) prairie dog mound density. These maps were constructed using the measures from the 56 1-m^2 plots randomly distributed over each site. I contour-mapped the data with Abel 1.5.8 for Mac using Delaunay triangulation, and then used the contour values to extrapolate means for each variable listed above for all 530-m^2 sampling areas. All maps, including tables of mean values at each insect visitation plot location, are presented in Appendix B.

Multiple regression, correlation, and model selection. --- Insect counts and group richness for each 40 minute sampling period were regressed, using Proc Reg in SAS, on a suite of continuous variables that included the spatially mapped and estimated values listed above, as well as number of plant species visited in that sampling period, number of non-*Opuntia* plant species visited in that sampling period, time of day, and date. The categorical (dummy) variables colony (1-4) and site type (1 or 2) were also included in the regressions. I used stepwise selection, with the limit for inclusion and exclusion of a significant variable set at α=0.1, to obtain values and *P*-values for the individual βs. However, to arrive at the "best-fit" model, I used selection based on Mallow's C_p, and considered residual plots and R^2-statistics for each model. Variables were ln-transformed in some cases if this improved model fit. I also used Proc Corr to examine correlation of the spatial variables associated with each insect sampling period. To test for small-scale spatial correlation of mound density and floral resources, I looked for correlation between all on-colony vegetation 1-m^2 plot values of both 1) inflorescence density and 2) floral biomass of the 16 most-visited plant species and number of mounds within a 5-m radius.

Finally, to graphically assess predictive quality of significant model variables, I used the Y on X linear curve-fit function in Abel, which uses an algorithm designed to minimize the χ^2 value of the dependant variable in the linear regression, for on- and off- colony values for insect visitation vs. floral biomass (both ln-transformed) and on-colony insect visitation vs. mound density (again, both ln transformed so χ^2 values would be directly comparable).

RESULTS

Landscape Change and Floral Resources

There was more than twice as much area covered by bare ground on colonies as on uncolonized sites in 2005 ($P < 0.04$, Fig. 2.1E), and nearly six times as much cover of entomophilous forb species on colonies ($P < 0.003$, Fig 2.1A). Inflorescence and open flower density showed similar trends, with more than six times the number of each found on colonies as off ($P < 0.007$ and $P < 0.03$, respectively, Fig 2.1B and C). Finally, estimated floral biomass of the 16 most visited species was almost five times greater on colonies ($P < 0.001$, Fig 2.1D).

Insect Visitation

Overall, about 2.5 times as many insects were captured in colonies than in off-colony sites in 2005 (952 captures on and 384 captures off). Similarly, landscape diurnal floral visitation rates (number captures per 40-minute sample period) were more than twice as great on colonies compared to off colonies ($P < 0.002$, Fig 2.2A). However, when total insect visits (#/sample period) were corrected for the estimated values for floral biomass (g/m^2 of the 16 most-visited plant species) for each sampled area, visits did not differ between colony and off-colony site types ($P = 0.49$, Fig 2.2B). *Opuntia* *polyacantha* and *O. humifusa*, on the other hand, did receive more visits off-colonies than would be expected based on average *Opuntia* inflorescence densities at each site ($P <$ 0.09, Fig. 2.2C). Insect community make-up differed in one obvious way between the two site types. Proportionally, off-colony sites had a much lower richness of Lepidoptera than on-colony sites (Fig 2.2D). For other orders, off-colony sites had lower total group richness of anthophilous beetles (Coleoptera), flies (Diptera), and bees and wasps (Hymenoptera), but these were not proportionally different from the richnesses for these same insect orders in colonized sites (Fig 2.2D). In both site types, Hymenoptera, especially bees, had the most groups and captures (598 total hymenopteran captures in 21 functional groups on colonies, and 292 captures in 11 groups off colonies).

Plant species-specific visitation rates. --- Populations of six of the 16 most visited plant species had significantly higher whole season mean visitation rates (visits/hour) on colonies than off in 2005 ($\alpha \leq 0.10$, Fig. 2.3). These were mostly early-season flowering forbs including *Senecio tridenticulatus* (Asteraceae, $P < 0.04$), *Penstemon albidus* (Scrophulariaceae, $P < 0.03$), *Sphaeralcea coccinea* (Malvaceae, $P = 0.01$), *Cryptantha minima* (Boraginaceae, $P < 0.04$), and *Erysimum asperum* (Brassicaceae, $P = 0.05$). Colony populations of one mid-late season flowering species, *Verbena bracteata* (Verbenaceae), were also visited more frequently ($P < 0.07$). Populations of only one plant species, *Opuntia humifusa* (Cactaceae), were visited significantly more frequently off-colonies ($P < 0.07$, Fig. 2.3). Overall, the trend was for higher species-specific insect visitation rates on-colonies (Fig. 2.3), a result that agrees with the overall community visitation rate (Fig 2.2A).

Community Diversity and Richness

Shannon-Weiner insect functional group diversity (H') was slightly but consistently higher on colonies (about 30% greater on colonies, $P < 0.004$, Fig. 2.4A). Species-level diversity (H') of entomophilous inflorescences was more than twice as great on-colonies compared to off-, and was more variable ($P < 0.08$, Fig. 2.4A). Entomophilous plant species richness and insect functional group richness showed much more consistent trends between the two communities, as both were approximately twice as rich on-colonies ($P < 0.005$ for both plants and insects, Fig. 2.4B).

Predicting Insect Visitation Rates and Group Richness

Spatial maps generated for bare ground, entomophilous forb cover, and floral biomass of the 16 most visited species in 2005 illustrate spatial heterogeneity in foraging habitat on both the colonies and paired off colony sites used for this study (Appendix B). There is also spatial variation in local mound density on all four colonies (Appendix B).

Regression of insect visits on potential spatial, temporal, and ecological correlates generated a model that indicated floral biomass, mound density, and time of day as the best predictors for number of anthophilous insects captured in a given place and time (Mallow's $C_p = 1.407$, next lowest model C_p score > 2). Stepwise selection also indicated these same three predictors, floral biomass ($P < 0.04$), mound density ($P < 0.001$), and time of day ($P < 0.10$) to be individually significant. Following a ln-transform of both insect counts and floral biomass to improve R^2 values and residuals, the final, best fit model ($R^2 = 0.66$, $F = 29.03$, $P < 0.001$) indicates that insect visits increase as both floral biomass and mound density increases, and decrease later in the day.

Regression of insect visits on floral biomass showed that insect visits off-colonies are more correlated with floral biomass than on colonies (Fig 2.5A). Off-colony insect visits show a positive relationship with increasing biomass and a significantly ($\alpha \leq 0.05$, 95% C.I. of regression does not include slopes ≤ 0, Fig 2.5A) positive slope, estimated by the equation:

$$\ln(\text{off-colony visits}) = 1.5*\ln(\text{g floral biomass/m}^2) + 1.9 \ (r = 0.68, \chi^2 = 6.78, 23 \text{ d.f.})$$

Alternatively, on-colony insect visits show a positive, but much weaker correlation with floral biomass, and the slope is not significant ($\alpha > 0.05$, 95% C.I. of regression does include slopes ≤ 0, Fig 2.5A). The on-colony relationship between insect captures and biomass is estimated by the equation:

$$\ln(\text{on-colony visits}) = 0.3*\ln(\text{g floral biomass/m}^2) + 3.3 \ (r = 0.32, \chi^2 = 7.19, 23 \text{ d.f.})$$

I also regressed colony insect visits on mound density, and found there to be a much stronger relationship of colony insect visitation to mound density than floral biomass. Colony insect visits show a positive relationship with increasing mound density and a significantly ($\alpha \leq 0.05$, 95% C.I. of regression does not include slopes ≤ 0, Fig 2.5B) positive slope, estimated by the equation:

$$\ln(\text{on-colony visits}) = 0.43*\ln(\text{mounds/78.5m}^2) + 3.4 \ (r = 0.53, \chi^2 = 5.80, 23 \text{ d.f.})$$

There was no evidence of a significant correlation at the small scale of individual plots for prairie dog mound density and floral biomass ($r = 0.102$, $P = 0.46$, $N = 224$ plots), or between mound density and inflorescence density ($r = 0.064$, $P = 0.88$, $N = 224$ plots).

Finally, a similar approach was used to predict values of insect group richness. I regressed insect groups per sample period on the potential spatial, temporal, and ecological correlates. The model for insect group richness with the lowest observed

Mallow's C_p indicated site type, number of insect visits, time of day, number of plants visited, number of non-*Opuntia* plants visited, and cover of bare ground as the best predictors (Mallow's $C_p = 5.76$, next lowest model C_p score > 6.5). Stepwise selection also indicated these same six predictors to be individually significant. The final, best-fit model ($R^2=0.77$, $F=6.18$, $P < 0.02$) indicates that insect groups increase on colonies, with insect visits, with the number of non-*Opuntia* plant species visited, with increasing cover of bare ground, and later in the day, and decrease on plots where *Opuntia* was visited. Unlike the data for total insect captures, there was no evidence of differences in predictive value of any of these variables between the on and off-colony sites.

DISCUSSION

Prairie dog colonies on the shortgrass steppe provide hotspots of resource density and diversity to the insect floral visitor community. In 2005, there was significantly greater floral resource density on prairie dog colonies compared to similar uncolonized habitat. Not only were there more inflorescences and open flowers observed, but the floral biomass presented by 16 forbs important to the anthophilous insect community was also significantly greater in colony habitats. Floral resources were also more diverse and species-rich on colonies. This, coupled with the increase in cover of bare ground on colonies, illustrates similar habitat alterations observed between on- and off-colony sites in 2003 and 2004 (Chapter 1). Beyond providing more evidence for the tri-trophic interaction, this study explicitly measures the spatially heterogeneous nature of floral resources, bare ground, and even mound density of colonies on these sites (Appendix B). There were patches on each colony with an equivalent floral biomass density to patches on its off-colony comparison site, but colonies always had a higher maximum patch density and more high-density patches (Appendix B). The difference in floral resources appears to be a key factor in attracting a more diverse and numerous anthophilous insect community.

Are colony populations of plants really receiving greater pollination service? Effective pollination is directly related to rates of per flower visitation by competent and effective visitors that deliver conspecific pollen, and not necessarily populational visitation rates as measured here. In fact, the ratio of visits per g/m^2 floral biomass is not different between on and off colony sites, providing no evidence that pollinators visit individual plants or flowers more often on-colonies (Fig 2.2). Fahnestock et al. (2003) found increased seed densities, higher seed germination rates, and a more forb-rich flora in colony seed banks of the mixed-grass prairie, so it is still possible that colony populations of at least some plants experience higher fecundity than in off-colony populations. Prairie dogs carry out many of the same landscape alterations in shortgrass steppe as they have been shown to do in mixed grass prairie, but typically to a lesser degree (Bonham and Lerwick 1976, Archer et al. 1987, Whicker and Detling 1988, Winter et al. 2002, Hartley 2006). Perhaps the same is true of increases in fecundity; greater seed set for many plant species due to denser populations that produce more flowers may occur on colonies in the mixed grass prairie. In any case, the more abundant, forb-rich seed bank found on mixed grass prairie dog colonies may not be a direct result of enhanced pollination service, but rather some other aspect of the different habitat type: lessened competition for light, water, or more available N (Archer and Detling 1986, Whicker and Detling 1988).

Colonized habitat provides for a more abundant, functional group-rich insect community. Patch heterogeneity, especially where there are qualitative as well as quantitative differences in resources as seen here, theoretically increases the number of species that can coexist in a given landscape (Hanski 1995). Some pollinator species employ differing habitat selection tactics and foraging strategies, presumably based on their ability to win competitive interactions, or on trade-offs between energy spent searching for food in low density habitats vs. energy spent on more competitive interactions per day in high-density habitats (Bronstein 1995). Usually, the individuals or species found in high quality patches must deal with increased interference competition. Those that are competitively excluded from this high-resource environment, even those utilizing differing populations of the same flower, can take a different strategy and visit lower density patches in smaller groups (Sowig 1989). This has been seen in congeneric *Trigona* bee species, which specialize on the same plant species but segregate to different populations with higher or lower density (Johnson and Hubbell 1975). Irwin et al. (2001) suggest that avoidance of competition among insect floral foragers is not trivial, as even inefficient or larcenist visitors may have effects on plant reproduction by affecting the behavior of pollinators when they and the larcenists compete for the same resource.

Colony habitat, with different community composition and greater floral resource densities than found off-colonies, does not appear to attract more insect visitors than would be expected based solely on differential resource bases (Fig. 2.2B). However, the positive correlation of insect visitation with mound density (Fig. 2.5B), which was not closely spatially correlated with floral biomass, suggests that it may not be just the greater floral resources that are responsible for the attractiveness of colony habitat to pollinators. High heterogeneity in habitat patch quality, as shown here with prairie dog colonies, could contribute directly to localized persistence of some anthophilous insect species. Colonies may host source insect populations with higher reproductive success than populations found on uncolonized grassland, either because floral density is at some threshold level, or because of some other aspect of the habitat such as more bare soil surface available for nest building. These colony populations may then inflate visitation rates observed in nearby uncolonized habitat sinks (Pulliam and Danielson 1991). Unlike the landscape visitation rates measured on colony sites, which were not different than off-colony visitation rates when differential floral resource bases were taken into account (Fig. 2.2B), increased rates of visitation to *O. humifusa* (Fig. 2.3) off colonies seem to indicate a real preference, regardless of where they choose to nest, by *Opuntia*-visitors for off colony foraging habitat. This is because there is evidence that *Opuntia* is visited even more frequently than would be expected, given the relative amounts of floral resources presented by this cactus on each site type (fig 2.2C). One explanation for this is decreased interference competition from other anthophilous insects, which are more numerous and more diverse on colonies. Also, uncolonized habitat may be preferred by *Opuntia*-foragers if they experience decreased rates of predation (Dukas 2005). Predatory and parasitic hymenopterans were more numerous and species rich on prairie dog colonies in this system in 2004 and 2005 (Chapter 3, Fig. 3.7B and D).

Colonies may also contribute to providing essential habitat required for presence or persistence of several Lepidopteran species in shortgrass steppe. Lepidopteran functional groups were delineated by species, because each moth or butterfly found in this study tends to have a different set of suitable larval food species (Appendix A2).

Habitat selection in nectar-foraging butterflies is related to oviposition behavior because females tend to visit flowers close to patches of plants suitable for hosting their larva (Ehrlich 1989). Except for *Hesperia uncas* (Hesperiidae), whose larval food species (blue grama, *Bouteloua gracilis*) is known to be more common off prairie dog colonies (Bonham and Lerwick 1976, Winter et al. 2002, Farrar 2002, and Hartley 2006), most of the butterflies caught in this study prefer a variety of entomophilous forb species more common, or at least more diverse, on colonies (Appendix A2). This agrees with the greater richness of Lepidoptera observed on colonies (Fig. 2.2D).

As might be expected, floral biomass is a good predictor of insect visitation rate, as it was a significant factor in the final model for insect visitation, and insects did not visit one habitat type over the other given the relative floral resource densities found on and off prairie dog colonies. It is worth noting that there seems to be a decoupling of floral biomass and insect visitation within colony habitats, as floral biomass only has a strong, significant, positive correlation with insect visitation rate off colonies when the site types are analyzed separately (Fig. 2.5A). Insect visitation on colonies increases more strongly with mound density, another significant predictive correlate in the best-fit model. It seems likely that mounds provide good nesting habitat, as they are highly visible and typically bare (Michener 1999). Bees (Apiodeae), the dominant group in 2005, must return to their nests repeatedly; therefore, a greater nest density should inflate population densities in the immediate area. Other pollinators use highly reflective bare ground to thermoregulate (Willmer 1982, Michener 1999), and soil temperatures on prairie dog colonies are about 2-3° warmer than similar uncolonized grassland (Archer and Detling 1986). Mounds, as thermoregulatory platforms, might be especially attractive when surrounded by higher density floral patches than what is typically found in uncolonized grassland (Fig. 2.1, Appendix B). Insect group richness appears to be a more complex variable to predict, based on the numerous significant predictors in the best-fit model and the low overall model F – value. Richness often increases in higher quality, qualitatively different landscape patches (Hanski 1995).

This tri-trophic interaction inflates anthophilous insect abundance because prairie dogs, much like Paine's (1966) original keystone species example of *Pisaster* starfish, graze the otherwise dominant graminoid community members enough to release the population growth of other plants, changing community composition and increasing richness and diversity. In tallgrass prairie, plant species richness and other vegetation characteristics were good predictors of retention of rare insect species and overall insect community diversity (Panzer and Schwartz 1998). While further evidence may be warranted to classify black-tailed prairie dogs as keystone species on the shortgrass steppe (Stapp et al. 1998), their role as ecosystem engineers that affect the abundance of many community members appears to be both wide-reaching and important (Miller et al. 1994, Kotliar et al. 1999, Ceballos et al. 1999, Kotliar 2000). Shortgrass steppe insect floral visitor communities, including pollinators, differ in predictable and consistent ways under prairie dog disturbance.

LITERATURE CITED

Alba-Lynn, C. 2006. Prairie dogs and harvester ants as disturbance agents on the shortgrass steppe: Implications for habitat heterogeneity. M.S. Thesis, Colorado State University, Fort Collins, Colorado.

Archer, S., and J.K. Detling. 1986. Evaluation of potential herbivore mediation of plant water status in the North American mixed-grass prairie. Oikos **47**:287-291.

Archer, S., M.G Garrett, and J.K. Detling. 1987. Rates of vegetation change with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio **72**:159-166.

Boggs, C.L., and B. Dau. 2004. Resource specialization in puddling Lepidoptera. Environmental Entomology **33**:1020-1024.

Bonham, C.D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on short grass range. Journal of Range Management **29**:221-225.

Bosch, M., and N.M. Waser. 2001. Experimental manipulation of plant density and its effect on pollination and reproduction of two confamilial montane herbs. Oecologia **126**:76-83.

Bronstein, J.L. 1995. The plant-pollinator landscape. *In* Mosaic Landscapes and Ecological Processes. Ed. by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London, pp. 256-288.

Coffin, D.P. and W. Laurenroth. 1990. Vegetation associated with nest sites of western harvester ants (*Pogonomyrex occidentalis*) in a semiarid grassland. American Midland Naturalist **123**:226-235.

Ceballos, G. J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41**:161-172.

Dukas, R. 2005. Bumble bee predators reduce pollinator density and plant fitness. Ecology **86**:1401-1406.

Ehlrich, P.R. 1989. The structure and dynamics of butterfly populations. *In* The

Biology of Butterflies. Ed. by R.I. Vane-Wright and P.R. Ackery. Princeton University Press, Princeton, New Jersey, pp. 25-40.

Fahnestock, J. T., D. L. Larson, G. E. Plumb, and J. K. Detling. 2003. Effects of ungulates and prairie dogs on seed banks and vegetation in a North American mixed-grass prairie. Plant Ecology **167**:255-268.

Fagerstone, K.A., H.P. Tietjen, and O. Williams. 1981. Seasonal variation in the diet of black-tailed prairie dogs. Journal of Mammalogy **62**: 820 – 824.

Gigawiz software. 2001 – 2005. Abel version 1.5.8 for Mac. Gigawiz Software, Ltd. Tulsa, Oklahoma.

Farrar, J. P. 2002. Effects of prairie dog mound-building and grazing activities on vegetation in the central grasslands. M.S. Thesis, Colorado State University, Fort Collins, Colorado.

Hanski, I. 1995. Effects of landscape pattern on competitive interactions. *In* Mosaic Landscapes and Ecological Processes. Ed. by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London, pp. 203-224.

Hartley, L. 2006. PhD Dissertation, Colorado State University, Fort Collins.

Hoogland, J.L. 1995. The black-tailed prairie dog – social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

Irwin, R.E., A. K. Brody, and N. M. Waser. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia **129**:161-168.

Johnson, L.K., and S.P. Hubbell. 1975. Contrasting foraging and coexistence of two bee species on a single resource. Ecology **56**:1398-1406.

Kay, K.M., and Schemske, D.W. 2004. Geographic patterns in plant-pollinator mutualistic networks: comment. Ecology **85**:875-878.

Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs **3**:5-78.

Kotanen, P.M., J. Bergelson, and D. L. Hazlett. 1998. Habitats of native and exotic plants in Colorado shortgrass steppe: a comparative approach. Canadian Journal of Botany **76**:664-672.

Kotliar, N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management **24**:177-192.

Kotliar, N.B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology **14**:1715-1721.

Kunin, W.E. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology **85**:225-234.

Lewis, M. and W. Clark. 1804. From the Vermillion to the Teton (Bad) River. *In* The Journals of Lewis and Clark. Ed. by B. Devoto, Houghton Mifflin Co., Boston, Massachusetts pp. 23-33.

Mayfield, M.M, N.M. Waser, and M.V. Price. 2001. Exploring the 'most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. Annals of Botany **88**:591-596.

McGregor, R.L. 1986. The flora of the Great Plains. T.M. Barkley, R.E. Brooks, and E.K. Schofield, editors. University Press of Kansas, Lawrence, Kansas.

Mellado, M., A. Olvera, A. Quero, and G. Mendoza. 2005. Diets of prairie dogs, goats, and sheep on a desert rangeland. Rangeland Ecology and Management **58**: 373 – 379.

Michener, C.D. 1999. The bees of the world. John Hopkins University Press, Baltimore, Maryland.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology **8**:677-681.

Paine, R.T. 1966. Food web complexity and species diversity. American Naturalist **100**:65-75.

Panzer, R., and M.W. Schwartz. 1998. The effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693-702.

Petanidou, T., and W. N. Ellis. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. Biodiversity Letters **1**:9-22.

Pulliam, H.R. and B.J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist **137**:50-66.

SAS Institute. 1999. SAS version 8.02. SAS Institute, Inc. Cary, North Carolina, USA.

Schiller, J.R., P.H. Zedler, and C.H. Black. 2000. The effect of density-dependent insect visits, flowering phenology, and plant size on seed set of the endangered vernal pool plant *Pogogyne abramsii* (Lamiaceae) in natural compared to created vernal pools. Wetlands **20**:386-396.

Sowig, P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). Oecologia **78**:550-558.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands.

Conservation Biology **12:**1253-1259.

Whicker, A.D., and Detling, J.K. 1988. Ecological consequences of prairie dog disturbances. Bioscience **38**:778-785.

Willmer, P. G. 1983. Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology **8**:455-469.

Winter, S.L., J.F. Cully Jr., and J.S. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management **55**:502-508.

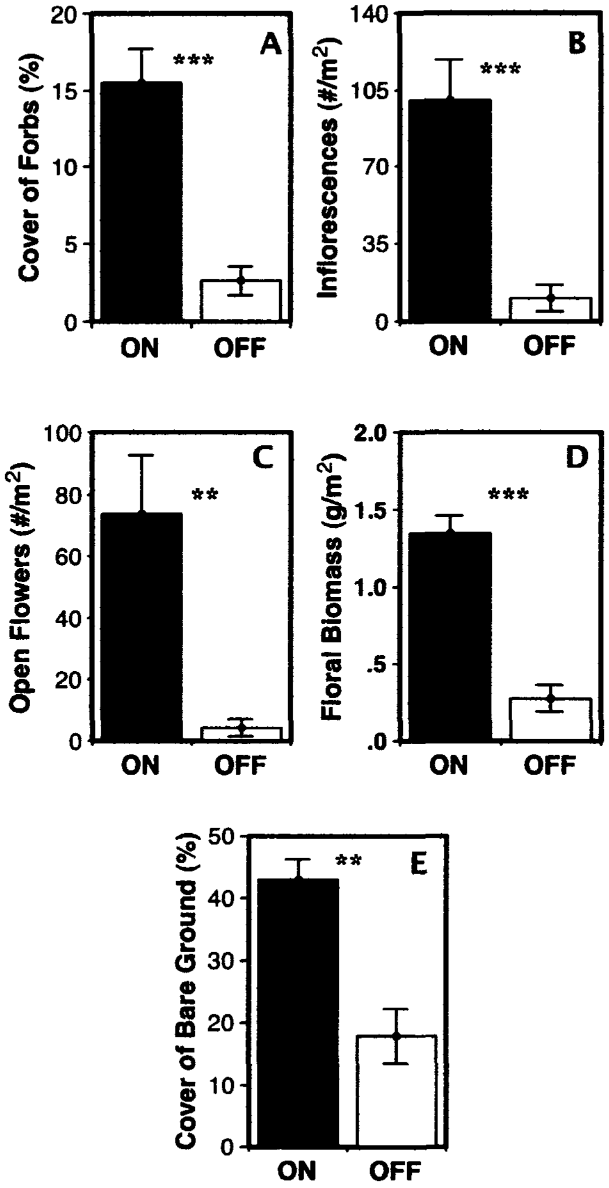


FIGURE 2.1 – Floral resources and bare ground on and off four prairie dog colonies in 2005. Untransformed colony means ($N = 4$) and standard error bars shown. A) Percent cover of all entomophilous forbs. B) Total inflorescence density (number of all inflorescences/m^2). C) Total open flower density (number of all open flowers or open capitae/m^2). D) Estimated floral biomass of 16 most visited entomophilous species in 2005 (dry mass in g/m^2). E) Percent cover of bare ground. P – values indicated as ** $P < 0.05$, *** $P < 0.01$.

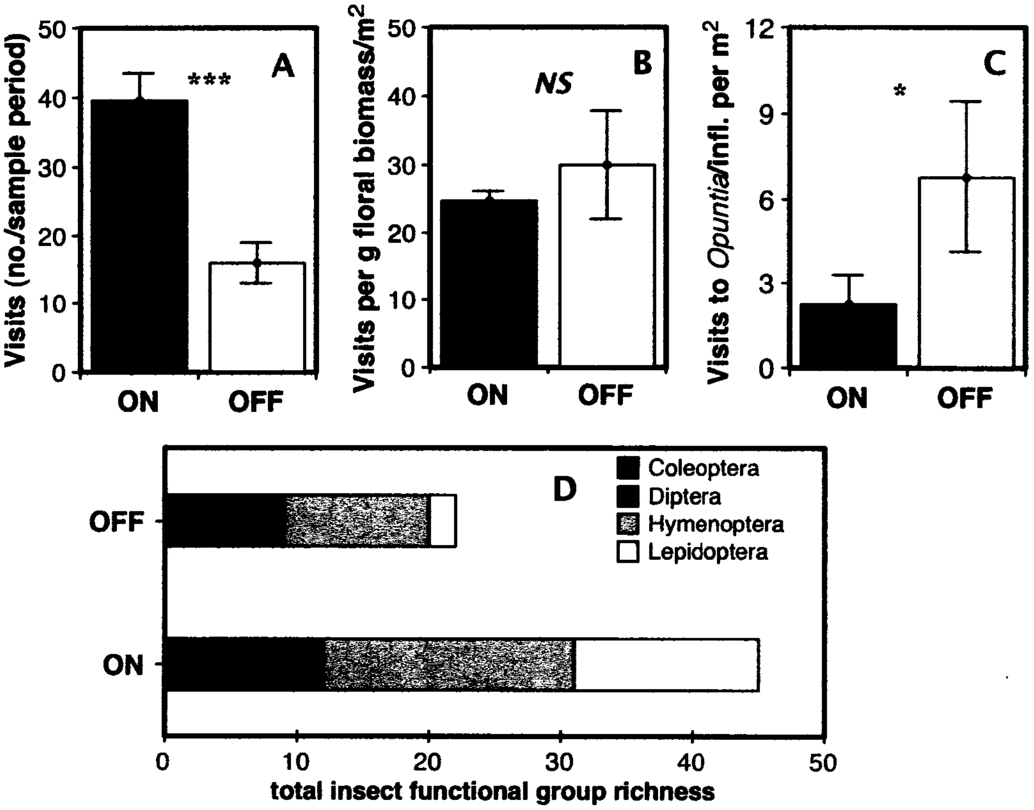


FIGURE 2.2 -- Landscape insect visitation on and off colonies in 2005. Untransformed means shown, ± S.E. A) Anthophilous insect visitation rate, in number of observed visits per sample period. B) All insect visits per sample period divided by floral biomass (in g/m^2) in the sampling area, showing evidence that while colony plant communities receive more visits in a given time and area, by-individual or per flower visitation rates may be equivalent on colonized and uncolonized areas. C) Visits/hour (whole-site sums) to both *Opuntia* species, divided by mean site inflorescence densities (*Opuntia* visits/hour per *Opuntia* infl./m^2). D) Total insect functional group richness (N_{GRP}) over the entire 2005 growing season and in all sites, by insect order. *P* -- values indicated as * - $P <$ 0.01, *** - $P <$ 0.01, NS = not significant.

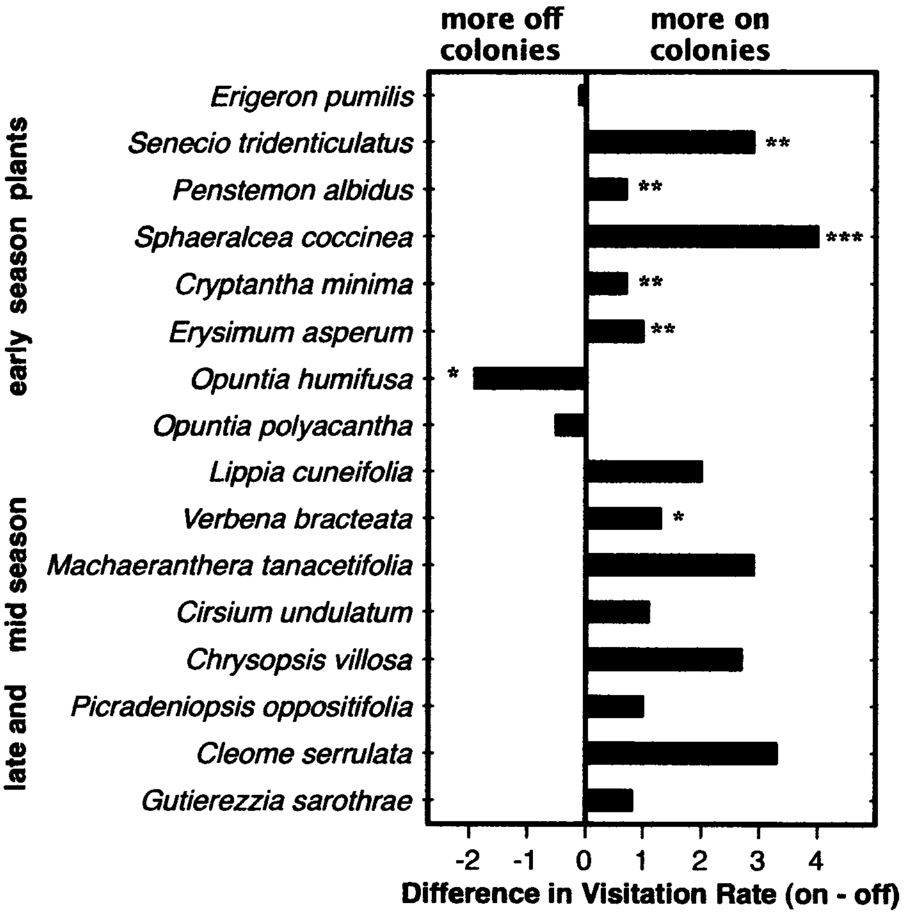


FIGURE 2.3 -- Species-specific differences in landscape visitation rate of 16 frequently visited plants on and off colonies in 2005. Difference in on- and off-colony whole-season means (visits/hour) shown. Plants listed in order of seasonal phenology, beginning with early-season flowering species. *P*-values indicated as * - $P < 0.10$, ** - $P \leq 0.05$, *** - $P \leq 0.01$.

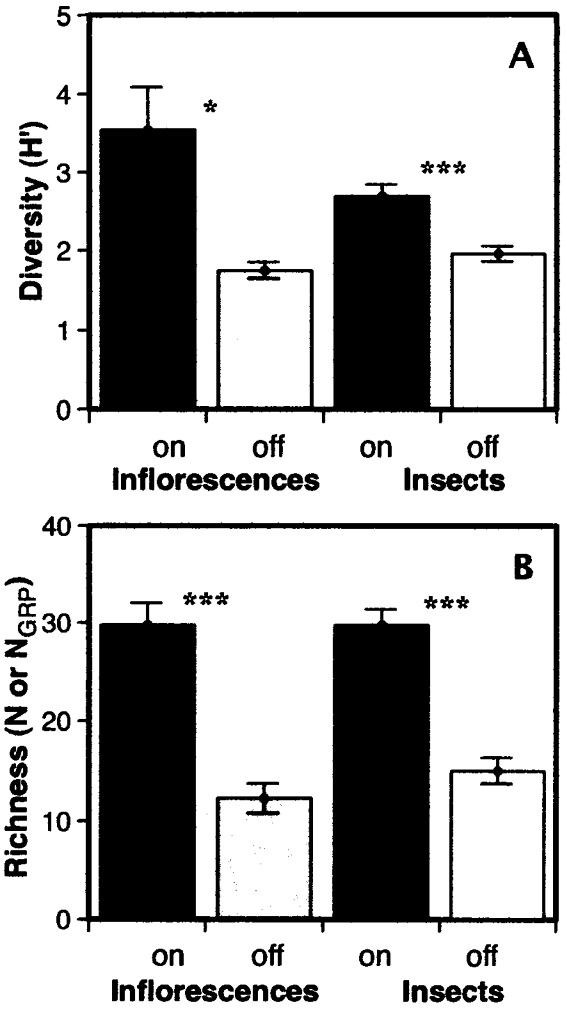


FIGURE 2.4 -- Comparison of diversity (H') and richness of the plant and anthophilous insect communities on and off colonies in 2005. A) Whole site/season Shannon-Weiner diversity (H') for plant species by inflorescence count, and for insect visitor functional group. B) Mean whole site and season plant species richness (N) and insect functional group richness (N_{GRP}). Colony means shown, ± S.E ($N = 4$). P-values indicated as * - $P < 0.10$, *** - $P < 0.01$.

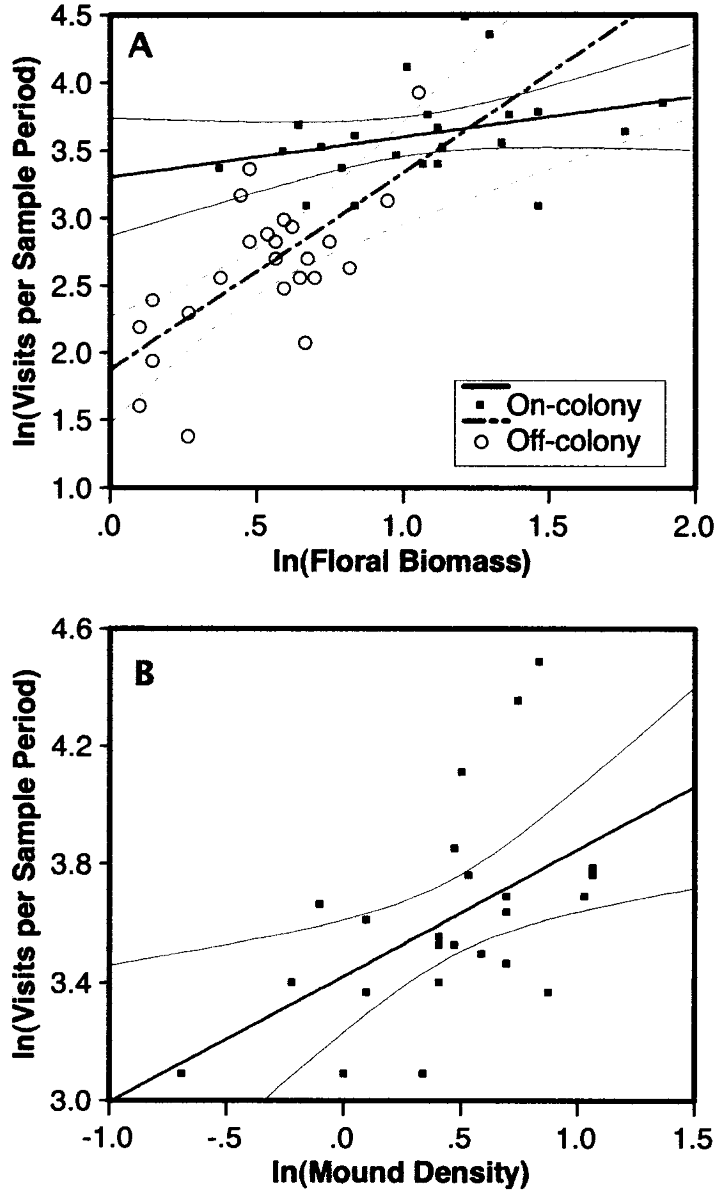


FIGURE 5 -- Linear regression of insect visits on A) floral biomass, for both on- and off-colony insect sample periods, and B) prairie dog mound density for on-colony sample periods only. Y on X linear regression lines shown with 95 % confidence interval on the slope (finer boundary lines).

CHAPTER 3

POLLINATION NETWORKS on SHORTGRASS STEPPE: PRAIRIE DOGS INFLUENCE WEB STRUCTURE and GENERALIZATION

Abstract ----. Plant-insect floral visitor mutualistic networks, and the rules that govern their assembly and emergent properties, are a relatively new area of study. Here I describe plant-insect floral visitor networks on the shortgrass steppe of North America, comprised almost completely of the native Nearctic faunal and floristic species pool. Specifically, I investigate changes in web structure, community composition, and relative degree of specialization among both insect visitors and plant hosts, all occurring in the presence of a strong grassland community disturbance agent, black-tailed prairie dogs (*Cynomys ludovicianus*), in 2004 and 2005. Compared to prairie dog colonies, networks on uncolonized sites had a lower species pool of both plants and insects, and had an greater reliance on the core interaction involving prickly pear cactus (*Opuntia* spp.) and colonial *Agapostemon* bees (Halictidae). Colony plants were visited by a higher median number of insect visitor groups than off-colony plants, but colony insects exhibited more specialized foraging tendencies, as colony insect groups had a lower median number of host plants. Insect floral visitor community composition of different sites was studied with combination analysis, and communities of all colonized sites in both years showed similar differences in all factors when compared to uncolonized site communities. Polylectic insect groups appear to benefit from an enriched floral resource pool on colonies, as many of these groups utilize colony habitat at greater rates, and all visit more plant species, showing decreased dependence on *Opuntia.* This is true of both narrowly defined polylectic functional groups as well as larger categories such as all Lepidoptera and all predatory and parasitic hymenoptera. Some oligolectic insects also utilize colonized habitat at greater rates. Logically, regional patterns in plant-insect visitor networks must be understood to decipher broader geographical, elevational, and landscape-level patterns. These results illustrate the breadth and strength of effects a strong community driver, by creating locally distinct habitat patch types, can have on pollination network structure and composition.

Keywords: Cynomys ludovicianus*; pollinators; plant-animal mutualistic networks; trophic interactions; habitat utilization; polylectic; oligolectic;* Sphaeralcea coccinea

INTRODUCTION

The field of pollination ecology is venerable and well established, dating back to Darwin and before, yet we know little about whole guilds of pollinators and how they, and the plants on which they forage, function as communities (Olesen and Jordano 2002). Much of our knowledge of pollination systems has been based on studies involving one plant species and the pollination service that it receives, or on a specific pollinator species and its behavior, flower choice and constancy, and pollination efficacy. Even uncommon and relatively ineffective pollinators can have effects on plant strategies and fitness, either through direct plant-insect interactions or alteration of the behavior of other pollinators in the system (Irwin et al. 2001, Mayfield et al. 2001). This, and the recent awareness that pollination systems are more generalized than previously believed (Jordano 1987, Waser et al. 1996, Olesen and Jordano 2002), has led to an interest in the study of whole-community plant-pollinator networks (Memmott 1999, Olesen and Jordano 2002, Kay and Schemske 2004). Within a given area, only network studies can show which plants are important forage for multiple insect species, which are visited very little compared to their relative abundance, and which plants host specialist (i.e., mono- or oligolectic) species. Studies of plant-insect visitor mutualistic networks also allow exploration of issues concerning geographical and ecological patterns in emergent network properties, such as nestedness and connectivity, prevalence of generalist versus specialist interactions, compartmentalization of plant and insect interactions especially important to the community, and system stability and resilience (Memmott 1999. Dicks et al. 2002, Olesen et al. 2002, Bascomponte et al. 2003, Jordano et al. 2003, Memmott et al. 2004). One factor that has received much attention is the effect of overall network species richness on network properties.

This being said, past network studies have had several problems. Some researchers question the usefulness of network studies where little attempt is made to distinguish effective pollinators from floral larcenists (Kay and Schemske 2004). While this does mask information concerning plant reproductive success, another perspective is that the information gained regarding forager community structure, and identification of those plants, insects, and common interactions that form the stable core for a given network, could be useful conservation and management tools. Additionally, few studies have scored the relative frequency of interactions (Dicks et al. 2002), or measured networks at more than one or two sites in a landscape, which is the scale at which most management and conservation decisions would be made. There is even confusion over the true meaning of commonly used network measures such as connectivity (Kay and Schemske 2004). Overall, there appears to be a lack of data on what might drive emergent properties and network qualities such as degree of specialization, either in different ecosystems or within a given system, where the same possible species pool exists for all local networks.

Black-tailed prairie dogs' (*Cynomys ludovicianus*) effects on grasslands differ from those of other herbivores because their colonial nature concentrates their effects on vegetation they consume, they affect the soil through intensive burrowing, and they clip tall vegetation to shape the habitat, and reduce visual obstruction (Whicker and Detling 1988, Hoogland 1995, Winter et al 2002). The intensity and unique quality of their effects, coupled with evidence of obligate dependence or facultative increases in abundance of several other prairie species, has led to consideration of prairie dogs as important drivers of community structure, ecosystem engineers, or even keystone species (Miller et al. 1994, Ceballos et al. 1999 Kotliar et al. 1999, Kotliar 2000, but see Stapp 1998). The landscape disturbances they create increase bare ground, entomophilous forbs, and floral resource abundance on the shortgrass steppe that, in turn, increase habitat utilization by the insect floral visitor community (Chapters 1 and 2). Prairie dog colonization on the shortgrass steppe thus creates an interesting opportunity to study how changes in floral resources alter the plant-insect visitor trophic networks of local patches in a larger grassland matrix.

Comparison of on- and off-colony networks will also permit a unique investigation of a strong community driver, the historically common prairie dog (Lewis and Clark 1804, Koford 1958), on a plant-insect visitor mutualistic network. Furthermore, patterns of specialization or general structure of networks at a latitudinal or elevational scale cannot be fully interpreted without investigation of the extent of differences in networks in the same geographic area (thus involving the same potential species pool). Thus, comparison of near- to adjacent networks will provide insight into within-community network differences. Finally, prairie dog colonies and nearby uncolonized areas on shortgrass steppe are noteworthy in that they do not support naturalized populations of the European honeybee (*Apis mellifera*), which may reduce community importance of native and nonsocial bees in most other North American ecosystems (Schaffer et al. 1983, Paton 1993, Kearns 1998).

In this study, I address four questions concerning diurnal plant-insect visitor networks on the shortgrass steppe. 1) How do overall web structure and basic network measures like connectivity vary in the presence of prairie dogs, and compare to other systems? 2) Which insect groups, plants, and interactions are especially important and common, and how might prairie dogs affect species richness, relative frequency and importance of insects, plants, and visitation interactions? 3) Does the degree of specialization differ between plant and insect communities, and does this change in the presence of prairie dogs? 4) Do prairie dogs affect specialization tendencies of specific groups?

METHODS

Study Sites

All prairie dog colonies used in this study were on the Pawnee National Grassland (PNG) in northeastern Colorado, and were selected for their large size (> than 100 ha in 2004) and accessibility. Nearby, uncolonized, paired comparison areas for each colony had similar soil type, land use history, aspect, and topography. Cattle have seasonally grazed all study sites since land purchase by the US Forest Service (late 1930s – early 1940s). Five colonies (PNG colony numbers 5, 8, 35, 66, and 83) were sampled in 2004 and four colonies (PNG colonies 5, 8, 30, and 83) were sampled in 2005. Colonies 5, 8, 30, and 35 are located on the far southeastern PNG, and colonies 66 and 83 are located approximately 100 km to the west, in the northeastern portion of the PNG. Colony 35 was not used again in 2005 because by that spring it had expanded into all available uncolonized comparison sites. Colony 66 was not used in 2005, because it did not fit selection criteria for spatially explicit vegetation sampling used that year (Chapter 2). Colony 66 is located on a relatively uncommon soil type (Platner loam), so its uncolonized comparison area was located much farther away (>3.2 km) than all other pairs of on- and off-colony sites, all located < 1 km away from each other). Colonies 5 and 8 were extirpated by plague (*Yersina pestis*) at the end of sampling in late summer of 2005, but all other colonies increased in area throughout both growing seasons.

Vegetation Sampling

I assessed floral resourçes in 2004 by counting total inflorescences and scoring phenological state (early, full, late, or not in flower) for all entomophilous plants within five subplots (two 1-m^2, two 10-m^2, and one 20-m^2). These subplots were placed within six randomly placed large (200-m^2) plots on each on-and off-colony site ($N = 30$ total subplots in a total of 6 large plots per site), based on a modification of the multi-scale Modified-Whitaker sampling scheme (Stohlgren et al. 1995, Chapter 1). In contrast, in 2005, I again counted inflorescences and scored phenological information, but within 56 1-m^2 plots per site, randomly distributed over the colonies and similarly sized, nearby uncolonized sites (total $N= 448$ plots) (Chapter 2). The dissimilar vegetation sampling used to estimate plant inflorescence abundance for construction of webs in the two years reflects differing goals for vegetation analyses presented elsewhere: in 2004 larger areas allowed capture of more rare plant species and construction of species-area curves, and in 2005 more numerous small plots were used to construct spatial maps of community vegetation measures and mound density (see Chapters 1 and 2). Plant nomenclature follows McGregor (1986).

Vegetation sampling commenced in both years in late May and continued through the end of the summer flowering season in early September. Sampling in both years was focused on two periods, one in late spring – early summer (late May – early July) and one in late summer (early August – early September), which corresponded to two discernable peaks in floral density, and involved different plant species (Figure 1).

Diurnal Insect Visitation Sampling

In 2004, a subset of the large (200 m^2) vegetation plots (five of six per area) was randomly assigned to colonized-uncolonized pairs, which were sampled consecutively, within 20 minutes of each other, to control as much as possible for time of day and weather sources of variation in insect habitat utilization. A circular plot of approximately 530 m^2 that enclosed each 200-m^2 plot was sampled for insect visitors over a 40-minute period. I patrolled this area in a series of concentric transects and captured, with a sweepnet, each insect engaged in pollinator-type foraging behavior on any open flower.

In 2005, insect sampling proceeded nearly identically to sampling in 2004, except six, rather than five, randomly distributed areas within each colonized and uncolonized area were sampled in the same pairwise manner. Sampling each area within a pair for 40 minutes gave a total of $N = 25$ pairs or 33.3 total observation hours in 19 non-consecutive days in 2004, and $N = 24$ pairs or 32 total observation hours in 23 non-consecutive days in 2005. In both years, pairs were sampled for floral insect visitation during times of heavy flowering in the overall area, and all insect sampling occurred between 0900 and 1600 hrs on days when the weather was clear, warm (from 27 - 42 °C), and not excessively windy (not more than 10 m/s gusts). As each insect was captured, I recorded what plant species it had been foraging on, then killed it by freezing for later pinning and identification. I did not collect florally destructive taxa whose foraging behavior did not suggest significant pollen movement or stigmatic deposition, like small beetles (nitidulids, weevils), homopterans, and thrips, or relatively immobile or territorial predators like spiders and asilid flies. I also made qualitative observations of likelihood of effective pollination of common plants by different insect groups, based on morphology, contact with one or both sexual parts of flowers, and insect behavior.

Insects were identified to family and then placed into one of 53 functional-taxonomic groups (Appendix A3) based on their size, family, life history, pile density and length, presence of and scopa type, and larval host plant (for Lepidoptera), as per Chapters 1 and 2. Although it was not possible to resolve every specimen to species, the characteristics used to group the insect visitors into appropriate body shape, size and life history classes should provide much information on community structure and functionality (Woodward et al. 2005).

Important Insect Functional Groups

The common and prevalent polylectic (generalist) genera chosen for detailed examination were; 1) *Agapostemon angelicus* and *A. texanus,* 2) small or minute bees in the family Halictidae, 3) large solitary bees in the family Anthophoridae, 4) the skipper *Hesperia uncas,* and 5) large, short piled beeflies (functional groups H12, H15, H4, L1, and D3 respectively, see Appendix A3). Each of these polylectic functional groups was present in significant numbers in both 2004 and 2005, captured in 22 or more paired sampling periods, and captured on all six colony sites used in this study. The oligolectic (specialist) species considered in detail in this paper were *Panurginus beardsleyi* and *Andrena gardineri*, both bees in the family Andrenidae; and the longhorn beetle *Crassidus pulchellus* (functional groups H1, H2, and C2, see Appendix A3). These were nearly exclusively observed in 2005, when each of the three was very abundant on at least two colony sites. Finally, two higher-level groupings were examined. All

Lepidoptera (functional groups L1-16, Appendix A3) were analyzed as a group because this charismatic insect order is often of special management and conservation concern. Predatory and parasitic hymenoptera (functional groups H6-8, H11, H13, H17 and H21-25, Appendix A3) constitute a subguild of interest within these networks, since they are also foraging for appropriate insect prey in addition to nectar, and thus may affect the behavior, abundance, or distribution of other insect visitors in this system.

Graphical and Statistical Methods

Mutualistic plant-insect visitor webs were constructed as per Memmott (1999). Here I used untransformed inflorescence count data, averaged by site; insect visit data was also untransformed but summed by site, so that width of interaction connectors accurately reflects the proportion of observed visits to each plant species. Approximately 90% of all recorded interactions in each year are shown in the webs, but because more insects were captured in 2005, all interactions with ≥2 recorded visits are shown in 2004 webs, and all interactions with ≥3 recorded visits are shown in 2005.

For polylectic and larger group-specific visitation rates, I used the sum of square root-transformed per-period group-specific abundance data to calculate a single whole-season per-hour rate for each on- and off-colony site. I had an unbalanced factorial design because different colonies were measured in each year. A two-year average was thus taken for colonies 5, 8, and 83. A paired t-test of the final per-hour means for each on- and off-colony site (5, 8, 30, 35, 66, and 83) was performed on each of the 7 selected groups, giving 5 d.f. for each test. For oligolectic species, which were primarily captured in 2005 only (only two individuals from any of these species were captured in 2004), site means from 2005 were used for the paired t-tests, giving 3 d.f for these comparisons. As no multiple comparison tests were used, the 10 group-specific inferences should be interpreted accordingly. However, using colony means (*N*=6) instead of data from all individual sample periods (*N*=49) make each of these comparisons conservative analyses of potential differences in on- versus off-colony insect visitation rates. Shannon-Weiner diversity indices (based on functional groups) for Lepidoptera and parasitic and predatory hymenoptera were calculated for each on- and off-colony site, and a paired t-test was performed separately for each year. Combination factor analysis, which creates axes that combines variables to describe variation between groups, was performed for each year using presence and abundance data for each of 49 insect functional groups in each colony and paired off-colony site. The criterion for inclusion of a significant factor was explanation of 10% of variance in the insect communities. All statistical analyses were performed using Microsoft Excel version X for Mac and Abel version 1.5.8 for Mac.

RESULTS

Community Phenology

Weather differed in the two years. A very dry early spring in 2004 resulted in a poor spring floral resource base until the prickly pear cacti (*Opuntia humifusa* and *O. polyacantha*) flowered profusely, while a wetter spring in 2005 produced prolific flowering from several spring species such as threetooth ragwort (*Senecio tridenticulatus*), white plains penstemon (*Penstemon albidus*), and scarlet globemallow (*Sphaeralcea coccinea*). The late summer peak proceeded similarly in both years, with small-headed, yellow composites like snakeweed (*Gutierizzia sarothrae*) and *Chrysopsis villosa* providing much of the resource base for the late-season anthophilous insect community. Common insect genera and plant species' phenological differences are illustrated (Figure 3.1).

Network Structure and Properties

On prairie dog colonies, more plant species (P) and insect functional groups (I) formed plant-insect floral visitor webs than off colonies (Figure 3.2). In 2004 there were 19 plant species visited off and 31 species visited on all colonies; 22 insect functional groups were observed off and 37 groups on colonies. Similarly, in 2005, there were 18 plant species visited off and 33 species visited on colonies; and 22 insect groups captured off and 49 groups on colonies. There were also a greater number of link types (L, each unique L represents an insect functional group visiting a plant species) on than off colony webs in both years (L = 145 on, and 64 off colonies in 2004; L = 190 on, and 75 off colonies in 2005; Fig. 3.2). Connectivity {(L*100)/(P*I)}, a statistic thought to increase with the relative amount of generalization in a network (Olesen and Jordano 2002, but see Kay and Schemske. 2004) was lower on colonies than off in 2004 (12.6 on- and 15.3 off-, and 12.1 for all sites combined) and in 2005 (12.3 on and 18.9 off, and 12.4 for combined).

Measures of median levels of generalization for insects and plants are shown calculated over both years, to capture the widest possible range over different years and sites of visitors for each plant species, and plant species used by each insect group (Fig. 3.3). On-colony networks had a higher median number of insect visitor groups per plant species (5.5 insect groups per plant) than either off-colony (3.0) or combined (5.0) networks, and the highest number of insect groups (27) hosted by any plant species (*C. serrulata*, Fig. 3.3). Conversely, although on-colony networks also had a higher maximum number of plant species visited by any one insect group (*Agapostemon* species, Fig. 3.3), insect groups utilized fewer plant species on colonies (median 3.0 plants per insect group) than both off-colony (4.0) and combined (3.5) networks (Fig. 3.3).

Factor Analysis of Insect Communities

I used combination factor analysis to investigate differences in insect communities on and off prairie dog colonies in each year. Three significant combination factors were isolated, and these were essentially the same for both years. Factor 1 explained the highest proportion of variance in insect communities, and increased with overall insect abundance and site community group richness. Factors 2 and 3 explained about 20% and 12% of the variance, respectively, and describe insect species evenness, hymenopteran and lepidopteran richness, and presence or absence of rare species. In both years, on and off colony sites separated out very similarly: uncolonized sites had lower Factor 1 scores than colonized sites, and they had less variance in their measures for Factors 2 and 3 (Fig. 3.4).

Polylectic Insect Groups

Group-specific visitation rates. Common generalist insect groups were captured more frequently on colonies, and relied proportionately less on *Opuntia* cactus blooms (Fig. 3.5A-E). *Agapostemon* bees, the most common insect group in both years, forage primarily on *Opuntia,* especially off colonies (Fig. 3.5A). *Agapostemon* visited colonized sites at about a 25% greater rate, but this was not significant (P=0.174, Fig. 3.5A-inset). Small halictine bees showed a moderate specialization on *Opuntia* (Fig. 3.5B), and as a group utilize uncolonized habitat at the same rate as colonized (P=0.49, Fig. 3.5B-inset). Large anthophorid bees visited a wide variety of plant species on colonies, but were primarily observed visiting *Opuntia* off-colonies (Fig. 3.5C). Large anthophorids visited colony sites nearly four times as much as off-colony sites ($P < 0.005$, Fig. 3.5C-inset). *Hesperia uncas* skippers were most often observed visiting *Cirsium* thistles, and showed a similar pattern of utilizing more plant species on colonies (Fig. 3.5D); and also visited colonies at over three times the rate as uncolonized habitat ($P < 0.013$, Fig. 3.5D-inset). On colonies, large, short-piled beeflies (Bombyliidae, Fig. 3.5E) appeared to preferentially forage on two species of plants in the Verbenaceae that are not abundant -- and which were not visited -- off colonies (*L. cuneifolia* and *V. bracteata*, Fig. 3.5E). These beeflies utilized on-colony habitat at nearly five times the rate of uncolonized grassland ($P < 0.027$, Fig. 3.5E-inset).

Qualitative assessment of pollination efficacy for polylectic groups. Females of the cryptic species complex *Agapostemon angelicus* and *A. texanus* (Fig. 3.5A) appeared to be good potential pollinators for most of the plant species they visited, although they did not always make contact with *Opuntia* stigmas. However, the other common halictid functional group that commonly visited *Opuntia*, small bees in the genera *Halictus, Dialictus, and Lasioglossum* (Fig. 3.5B), only appeared to be good potential pollinators of small-flowered plants and composites, and never contacted stigmas on the large flowers of *Opuntia*. Large anthophorid bees (Fig. 3.5C) appeared to be good potential pollinators for all or most of the plant species they visited. The skipper *H. uncas* did not pick up much pollen or contact sexual parts of most of the flowers it visited with more than its proboscis and tarsi, with the major exceptions of *Cirsium* thistles and *Opuntia* cactus. Finally, large, short-piled beeflies are likely to be only moderate to poor pollinators at best for the majority of plants they visit, as they seemed to not pick up much pollen, or make significant contact with either stamens or stigmas.

Common Oligolectic Insect Species

Group-specific visitation rates. The three most abundant oligolectic species (each comprising one functional group) all showed a trend for visiting populations of their preferred host species at a greater rate in colonized areas, although due at least in part to low power arising from short seasonality and patchy distribution this was not always significant (Fig. 3.6). The andrenid bee *Panurginus beardsleyi* visited *S. coccinea* at nearly five times the rate on colonies as off ($P < 0.07$, Fig. 3.6A). *Andrena gardineri* was never observed at off-colony sites, and although a total of over 40 individuals were captured in multiple sampling periods on three colonies in 2005, this was not significant ($P = 0.23$, Fig. 3.6B). Approximately twice as many *Crossidus pulchellus* longhorned beetles were captured visiting *G. sarothrae* on colonies, but this also was not significant ($P = 0.36$, Fig. 3.6C).

Qualitative assessment of pollination efficacy for oligolectic groups. Panurginus beardsleyi (oligolectic on *S. coccinea*) and *A. gardeneri* (apparently monolectic in this system on *S. tridenticulatus)* both appeared to be excellent pollinators of their chosen host plants. The longhorn beetle *C. pulchellus* is an oligolectic visitor to the small, composite heads of *G. sarothrae.* Its foraging behavior and sternal pile suggest it is likely a moderate to good pollination vector for this plant; however, it probably ingests a large proportion of the pollen produced by the florets it visits.

Larger Insect Floral Visitor Groups

All Lepidoptera were more diverse ($P < 0.1$, 2004; $P < 0.05$, 2005; Fig. 3.7C) on colonies in both years, and also visited many more plant species (Fig. 3.7A). The lepidopteran community utilized colonized habitat at nearly six times the rate (measured by community visitation rates, $P < 0.004$, Fig. 3.7A inset) as they did uncolonized sites over both years. Lepidoptera in general may not always be effective pollinators due to infrequent or glancing contact with sexual parts of many flowers they visit (P. A. Opler, *pers. communication*), but in this system did at some times appear to make the necessary contact required for pollination of *Cirsium*, *Cleome, Erysimum,* and *Opuntia.*

Many of the same on- vs. off-colony differences were observed for predatory and parasitic Hymenoptera. Predatory and parasitic bees and wasps were more diverse by Shannon-Weiner indices ($P < 0.1$, 2004 and 2005; Fig. 3.7D) on colonies in both years, and also visited many more plant species (Fig. 7B inset). The predatory community utilized colonized habitat at over three times the rate ($P < 0.016$, Fig. 3.7B) as they did uncolonized grassland combined across both years. In this system, cuckoo parasites included *Nomada* (Apidae), *Augochlora* (Halictidae) and *Tiphia* (Tiphiidae) bees, and chrysidid wasps; predatory wasps included sphecid wasps such as bee-hunters (*Philanthus* spp.) and *Ammophila* spp. (AMO in Fig. 3.3), and members of the Vespidae, Braconidae, Pompilidae, and Ichneumonidae.

DISCUSSION

The degree of generalization vs. specialization inherent in pollination systems may be widely variable between different ecosystems and may correlate with latitude, elevation, or species richness, but there are not enough studies to fill in a pattern even using metanalysis (Olesen and Jordano 2002). This study constitutes the first measure for the North American shortgrass steppe, a middle-latitude, relatively high elevation (1475-1650 m), semi-arid grassland. It is notable that this system is relatively unaffected by either invasive plants, which hosted less than 0.1% of all recorded insect visitors, or by naturalized honeybees (*A. mellifera*). Shortgrass steppe values for connectivity (12.1 – 18.9) fall well within the range reported for other temperate networks (2.0 – 25.0, Olesen and Jordano 2002), and are surprisingly similar between years given the differences in presence or prevalence of important taxa that would seem to affect a measure of specialization (e.g., a large percentage of oligolectic insects observed in 2005, but not 2004). This underscores the importance of carefully interpreting connectivity measures (Kay and Schemske 2004). Understanding global patterns in plant-pollinator network structure and properties involves investigating differences in networks resolved at smaller spatial scales, and under differing abiotic and community conditions within the same landscape.

Black-tailed prairie dog colonies support altered plant and insect floral visitor communities in grassland patches adjacent to uncolonized sites that are similar in all other aspects except for the disturbances created by these rodents (Chapters 1 and 2). One result of the differences in both plant and insect community make-up between patch types is that plant-insect floral visitor networks differed greatly between colonized and uncolonized steppe (Figs. 3.2 and 3.3). Although paired on- and off-colony sites were always within 3.2 km of each other, and often were immediately adjacent, colony networks had greater functional group and species richness for both the insect and floristic trophic levels. Greater cover of entomophilous plants, as well as greater density and diversity (H') of inflorescences, attracted a more abundant and diverse (H') insect floral visitor community in both years (Chapters 1 and 2). This was not the only difference in the networks on prairie dog colonies. Colony populations of insects, especially important polylectic groups such as *Agapostemon* bees (AGA) and small halictids (HAL), relied less on *O. humifusa* and *O. polyacantha* (OPUh and OPUp) cactus flowers (Figs. 3.2 and 3.5). In fact, *O. humifusa* is one of very few individual plant species that actually experienced a higher landscape-level visitation rate off colonies (Chapters 1 and 2). Colony networks, on the other hand, were supported by a wider variety of flowering plant species, some of which, like *C. serrulata, S. tridenticulatus, P. albidus, L. cuneifolia,* and *V. bracteata,* were rarely, if ever, observed at off-colony sites. Thus, it is possible that colony networks have greater resilience to disturbance- or disease-based *Opuntia* loss, or a temporally fluctuating abiotic environment, as there are a larger number of functionally overlapping and common insect visitor species and groups that might visit any given plant species, as well as a wider variety of plant species that may flower profusely in a given year's conditions.

Specialization in plant-pollinator mutualistic interactions was at one time thought to be the rule, but consideration of whole networks has led to questions of whether discretely coevolved specialization or more opportunistic generalization is more common (Waser et al. 1996). The lower connectivity values for on-colony webs in both years indicates a higher degree of network-level specialization on prairie dog colonies. Because connectivity measurements are highly variable among different systems, obscure plant versus insect tendencies for specialization, and have other interpretive and quantitative problems (Kay and Schemske 2004), I used median number of visitor groups per plant and median number of plants utilized per insect group as estimates of relative specialization. The use of functional groups rather than species-level identification introduces two biases in determining specialization. First, grouping underestimates how many insect species are visiting plants in the system, but compared to strict species-level identification it overestimates how many plant species a morphospecies (which may be more than one cryptic species) of insects visits. Second, bias is introduced by rare versus common insect groups and commonly visited plants. If a plant species was only observed being visited once, by this method the data is recorded as *1 visitor*, which might be interpreted as a highly specialized plant. Yet it is more accurate to note that we have little information about the nature of specialization for such interactions because of their very rarity. The range for a group's recorded number of mutualistic partners is affected by the number of times I observed that group.

Given these biases, the median number method still illuminates the additive nature of combining two nearby webs, as in some cases, e.g. *C. villosa* (CHR, having 19 recorded visitor groups on, 14 groups off, and 22 groups over all sites; Fig. 3.3), differing groups are visiting a given plant species on and off-colonies. The same is true for certain insect groups visiting different plant species, e.g. *Agapostemon* bees, which visited 21 plant species on- and 11 plant species off-colonies, and 23 over both site types (Fig. 3.3). Median visitors and host species illustrates specialization tendencies on and off prairie dog colonies, and in the combined web. Colony networks are more generalized, having a higher median number of insect visitor groups recorded for each plant species than either the off-colony or combined networks (Fig. 3.3). However, they are more specialized when viewed the opposite way, because despite having a much greater maximum number of plants visited by some broadly polylectic insect groups (e.g. *Agapostemon* bees, Figs. 3.3 and 3.5A), they have a lower median number of plant species utilized by insect groups than either off-colony or combined networks. This agrees with the greater prevalence of specialist insect groups on colonies observed in 2005 (Fig. 3.6), and also makes sense when considering the greater and more diverse floral resource base on colonies. For any particular insect group, the richer rewards of the on-colony floral communities provide a greater number of plant species that have dense, large populations so as to feasibly support specialists, or alternatively, for a generalist to focus upon. Also, a greater number of rare insect species, which was also observed on colonies, will pull this median down, since they are necessarily observed visiting few plants. Further, more plant species means a more continuous resource base, as sequentially flowering plant species can support insect populations for longer, and over a greater variety of seasonal conditions (Waser and Real 1979). For the plants, however, the effect of the enhanced community floral resources is an increased, more species-rich anthophilous insect community, which translates to more visitor species per plant.

Combination factor analysis of the insect communities shows that off-colony insect visitor communities typically have more in common with other off-colony sites, even those located 100 km apart, than with their paired colony site which is 3 km or less away (Fig. 3.4). The analysis also points out that there is greater insect abundance and group richness (Factor 1) on colonies, and a greater variation in presence of rare species, and insect community make-up at the order level (Factors 2 and 3, Fig. 3.4).

Inspecting specific and important polylectic groups shows that even when a group exhibits similar rates of habitat utilization on and off-colonies (e.g. small halictids-HAL, Fig 3.5B), their foraging strategy, on a group level, significantly changes between the two habitat types. Generalist insects utilized more plant species, and in some cases, different species, in on vs. off-colony communities. All three bee groups, and even the skipper *H.*

uncas, exhibited proportionally lower reliance on *Opuntia* cactus flowers on colonies, even when populations of the same groups utilize *Opuntia* heavily on uncolonized sites (Fig. 3.5). In years when *Opuntia* does not flower as densely as in 2004 and 2005, or in cactus-poor areas, prairie dog colonies likely represent a significant resource base and refuge for these polylectic groups, ensuring their continued presence in an area. Even when *Opuntia* does flower profusely on the shortgrass steppe, colonies typically provide additional and more diverse floral resources, as well as suitable nesting habitat offered by mounds. This allows for increased local abundance of these generalist insect populations (Chapters 1 and 2). A larger number of densely flowering, co-occurring plant species may also provide a wider variety of floral morphology choices for behavioral specialization by individual foragers within generalist groups (Heinrich 1982). For social generalists such as bumblebees (*Bombus nevadensis* and *B. pennsylvanicus* in this system), this may mean that hives are more likely to be supported over the entire season on colonies as the potential pool of acceptable forage species is expanded. For the more prevalent solitary and communally nesting bees in this system, this may partly explain increased group numbers on colonies, as solitary bees seem to be subject to temporal fluctuations in abundance which is partially affected by availability of specific floral resources (Cane and Payne 1993, Petanidou and Ellis 1993, Kearns et al. 1998).

As a case in point, populations of specialist pollinators in this system, two of which are solitary bees, seem to be capricious. All three common oligolectic species (Fig. 3.6) were mostly or only recorded in 2005, even though they all appeared on the same sites they were absent from (5, 8, and 83) the previous year. Each of the three species was very abundant (often the most common species in a sampling period) in 2005 for short portions of the growing season, which closely corresponded to the phenological flowering peak of their chosen host plant (Fig. 3.1). This provides evidence of greater phenological compartmentalization in grassland webs where specialists are particularly important, since this may increase the proportion of interactions confined to a short period of time. Further, the relative abundance and importance of specialists may change drastically depending on the year or site type. In 2005, these three specialist groups comprised 15.6% (148 of 950 insects) of all captures on colonized sites, but only 7.6% (29 of 378 insects) of all off-colony captures. It is worth noting that for at least the two andrenid bees, colonies can provide the necessary habitat and dense populations of *S. coccinea* and *S. tridenticulatus* apparently required to support large populations of these early-season oligolects.

Lepidopterans are charismatic insects often of special management concern (Samways 1994). Predatory and parasitic Hymenoptera are of interest because, while also foraging for nectar, they comprise a top trophic level in the plant-pollinator network when preying on other insect groups. Although these two higher-order assemblages have little in common, both groupings illustrate the effects of black-tailed prairie dog colonization over more general categories of insects (Fig. 3.7). Both Lepidoptera and hymenopteran predators and parasites were more abundant, visited more host plants, and had a higher diversity on colonies in both years (Fig. 3.7), indicating that colonies are extremely important habitat patches for these groups on the shortgrass steppe. Lepidopterans may be attracted to a more diverse floral resource and larval host plant base, and predators may be attracted to abundant and diverse prey on colonies. The observation that many bees are more abundant in the same colonized areas where hymenopteran predators such as *Philanthus* are also more abundant conflicts with earlier reports of lowered bee abundance in the presence of increased predators (Dukas 2005). Alternately, preferential use of uncolonized grassland as *Opuntia*-foraging habitat by some insect groups off colonies may be partly due to decreased predation pressures (Chapter 2). Benefits of prairie dog colonization may alleviate drawbacks of a more abundant insect community for some insect groups facing greater predation risk or rates of brood parasitism.

Habitat types and plant communities responsible for supporting greater or more diverse populations of insects must be recognized to make appropriate conservation and management decisions that affect pollinators. In tallgrass prairie, preserving plant species richness is an important first step in preserving rare insect species (Panzer and Schwartz 1998). Pollinator populations are in decline worldwide (Samways 1994, Kearns et al. 1998). Native pollinator service is of increasing economic value to growers of crops that honeybees do not pollinate, such as alfalfa and sunflowers, which are both grown in cultivated areas within the shortgrass steppe. Therefore, the potential economic benefit of prairie dog colonies that support abundant populations of native North American grassland pollinators must not be overlooked. Colonized patches act in concert with uncolonized grassland to support endemic, local species such as *Hesperia uncas,* a skipper found more often on colonies but whose larval host plant, blue grama (*B. dactyloides),* is more abundant in uncolonized areas (Winter et. al 2002). The tri-trophic interaction involving prairie dogs, plants, and insect floral visitors affects landscape floral visitation rates, insect and plant communities, and network structure. Although part of the community evolutionary history of the shortgrass steppe, prairie dogs are now restricted to a small portion of the area they previously inhabited (Lewis and Clark 1804, Koford 1958, Miller et al 1994, Detling 2006). Black-tailed prairie dog management must be considered in conservation of native shortgrass steppe pollinator and insect floral visitor populations.

LITERATURE CITED

Bascompte, J., P. Jordano, C.J. Melian, and J.M. Olesen. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences **100**:9383-9387.

Cane, J.H., and J.A. Payne. 1993. Regional, annual, and seasonal variation in pollinator guilds: Intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). Annual Review of the Entomological Society of America **86**: 577-588.

Ceballos, G. J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41**:161-172

Detling, J.K. 2006. Do prairie dogs compete with livestock? *in* J.L. Hoogland, editor. *Conservation of the black-tailed prairie dog.* Island Press, Washington, D.C.

Dicks, L.V., S.A. Corbet, and R.F. Pywell. 2002. Compartmentalization in plant-insect flower visitor webs. Journal of Animal Ecology **71**:32-43.

Dukas, R. 2005. Bumble bee predators reduce pollinator density and plant fitness. Ecology **86**:1401-1406.

Gigawiz software. 2001 – 2005. Abel version 1.5.8 for Mac. Gigawiz Software, Ltd. Tulsa, Oklahoma.

Heinrich, H. 1976. The foraging specializations of individual bumblebees. Ecological Monographs **46:**105-128.

Hoogland, J.L. 1995. The black-tailed prairie dog – social life of a burrowing mammal. University of Chicago Press, Chicago, Illinois.

Irwin, R.E., A.K. Brody, and N.M. Waser. 2001. The impact of floral larceny on individuals, populations, and communities. Oecologia **129:**161-168.

Jordano, P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. The American Naturalist **129:**657-677.

Jordano, P., J. Bascompte, and J.M. Olesen. 2003. Invariant properties in coevolutionary networks of plant animal interactions. Ecology Letters **6:**69-81.

Kay, K.M., and Schemske, D.W. 2004. Geographic patterns in plant-pollinator mutualistic networks: comment. Ecology **85**:875-878.

Kearns, C.A., D.W. Inouye, and N.M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics **29**:83-112.

Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs **3**:5-78.

Kotliar, N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management **24:**177-192.

Kotliar, N.B. 2000. Application of the new keystone-species concept to prairie dogs: how well does it work? Conservation Biology **14:**1715-1721.

Lewis, M. and W. Clark. 1804. From the Vermillion to the Teton (Bad) River. *In* The Journals of Lewis and Clark. Ed. by B. Devoto, Houghton Mifflin Co., Boston, Massachusetts, pp. 23-33.

Mayfield, M.M., N.M. Waser, and M.V. Price. 2001. Exploring the 'most effective pollinator prinicple' with complex flowers: bumblebees and *Ipomopsis aggregata*. Annals of Botany **88**:591-596.

McGregor, R.L. 1986. The flora of the Great Plains. T.M. Barkley, R.E. Brooks, and E.K. Schofield, editors. University Press of Kansas, Lawrence, Kansas.

Memmott, J. 1999. The structure of a plant-pollinator food web. Ecology Letters **2**:276-280.

Memmott, J., N.M. Waser, and M.V. Price. 2004. Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society of London B **271**:2605-2611.

Michener, C.D. 1999. The bees of the world. John Hopkins University Press, Baltimore, Maryland.

Microsoft Excel version X for Mac®. 1985 – 2001 Microsoft Corporation. Richmond, Washington.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology **8**:677-681.

Olesen, J.M., L.I. Eskildsen, and S. Venkatasamy. 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Diversity and Distributions **8**:181-192.

Olesen, J.M., and P. Jordano. 2002. Geographic patterns in plant-pollinator mutualistic networks. Ecology **83:** 2416-2424.

Panzer, R., and M.W. Schwartz. 1998. The effectiveness of a vegetation-based approach to insect conservation. Conservation Biology **12**:693-702.

Paton, D.C. 1993. Honeybees in the Australian environment: does *Apis mellifera* disrupt or benefit the native biota? Bioscience **43**: 95-103.

Petanidou, T., and W. N. Ellis. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. Biodiversity Letters **1**:9-22.

Samways, M.J. 1994. *Insect Conservation Biology*. Chapman and Hall, New York, New York.

Schaffer, W.M., D.W. Zeh, S.L. Buchmann, S. Kleinhans, M.V. Schaffer, and J. Antrim. 1983. Competition for nectar between introduced honeybees and native North American bees and ants. Ecology **64**: 564-577.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. Conservation Biology **12:**1253-1259.

Stohlgren T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. Vegetatio **117**:113-121.

Waser, N.M., and L.A. Real. 1979. Effective mututalism between sequentially flowering plant species. Nature **281**:670-672.

Waser, N.M., L. Chittka, M.V. Price, N.M. Williams, and J. Ollerton. 1996. Generalization in pollination systems, and why it matters. Ecology **77**:1043-1060.

Whicker, A.D., and Detling, J.K. 1988. Ecological consequences of prairie dog disturbances. Bioscience **38**:778-785.

Winter, S.L., J.F. Cully Jr., and J.S. Pontius. 2002. Vegetation of prairie dog colonies and non-colonized short-grass prairie. Journal of Range Management **55**:502-508.

Woodward, G., B. Ebenman, M. Emmerson, J.M. Montoya, J.M. Olesen, A. Valido, and P.H. Warren. 2005. Body size in ecological networks. Trend in Ecology and Evolution **20**:402-409.

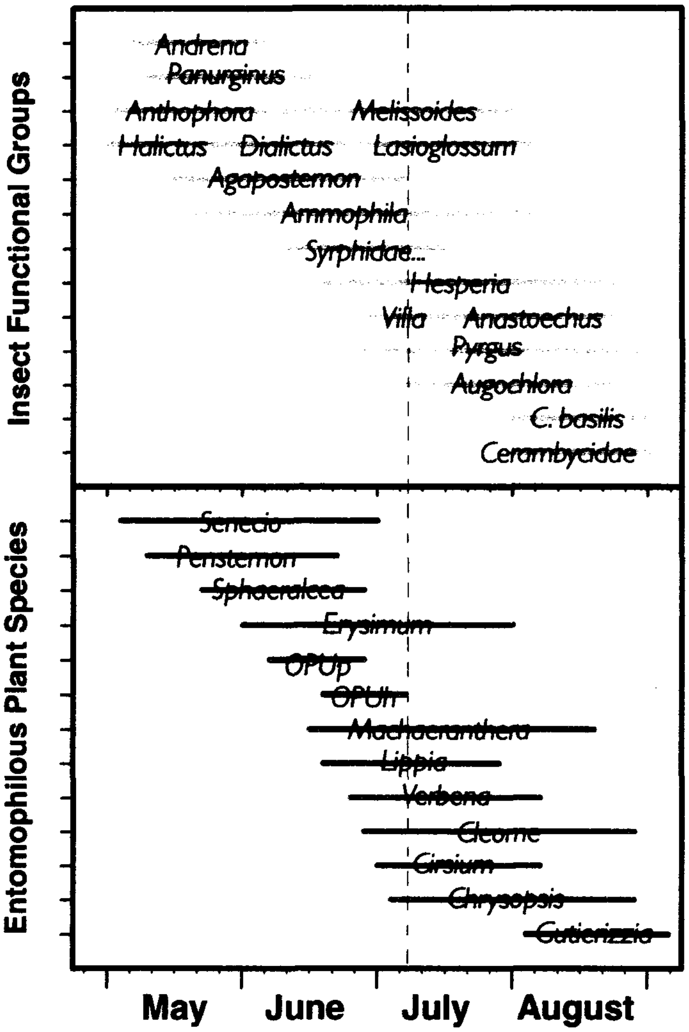


FIGURE 3.1: Phenological information for common and important A) anthophilous insect functional groups and B) entomophilous plant species. The dotted line represents the boundary between early and late season sampling. OPUp and OPUh refer to *Opuntia polyacantha* and *O. humifusa*, respectively. There appears to be some degree of phenological compartmentalization of the shortgrass steppe plant-insect visitor network, as early season insect groups are restricted to early season plants, and late season groups necessarily visit late season plants. However, mid-season insect groups and plants bridge these compartments, as do those with long periods of seasonal activity.

FIGURE 3.2: Plant-insect floral visitor trophic webs for off (A and C) and on (B and D) prairie dog colonies in 2004 and 2005. All network diagrams illustrate the whole season interaction record for that year and habitat type, only show taxa visited at that site type in that year, and only display links with ≥ 2 recorded visits (2004, A and B) or ≥ 3 recorded visits (2005, C and D) for clarity; however web statistics listed are for the complete webs. Color of the top row and of the interaction connectors corresponds to the insect order: oranges, reds, and yellows for hymenoptera, blues for Lepidoptera, greens for Diptera, and purples for Coleoptera. Plants are listed in order of seasonal phenology, beginning with early-season flowering species, but color of the bottom row does not correspond to any plant grouping. Link widths (triangle sizes) are directly proportional to the number of all visits recorded in a given site type and year. Note the greater prominence in off-colony networks of a core of interactions formed by halictid bee groups *Agapostemon* (AGA) and small to minute *Halictidae* (HAL) visiting *Opuntia* cactus (OPUp and OPUh) in both years, and the increased importance of non-*Opuntia* species like *S. coccinea* (SCO) in 2005. On-colony networks also contain a strong core of similar taxa and interactions, but also have a much greater diversity of common plants, insect groups, and linkages, including many important taxa completely absent from the off-colony webs like *S. tridenticulatus* (SEN).

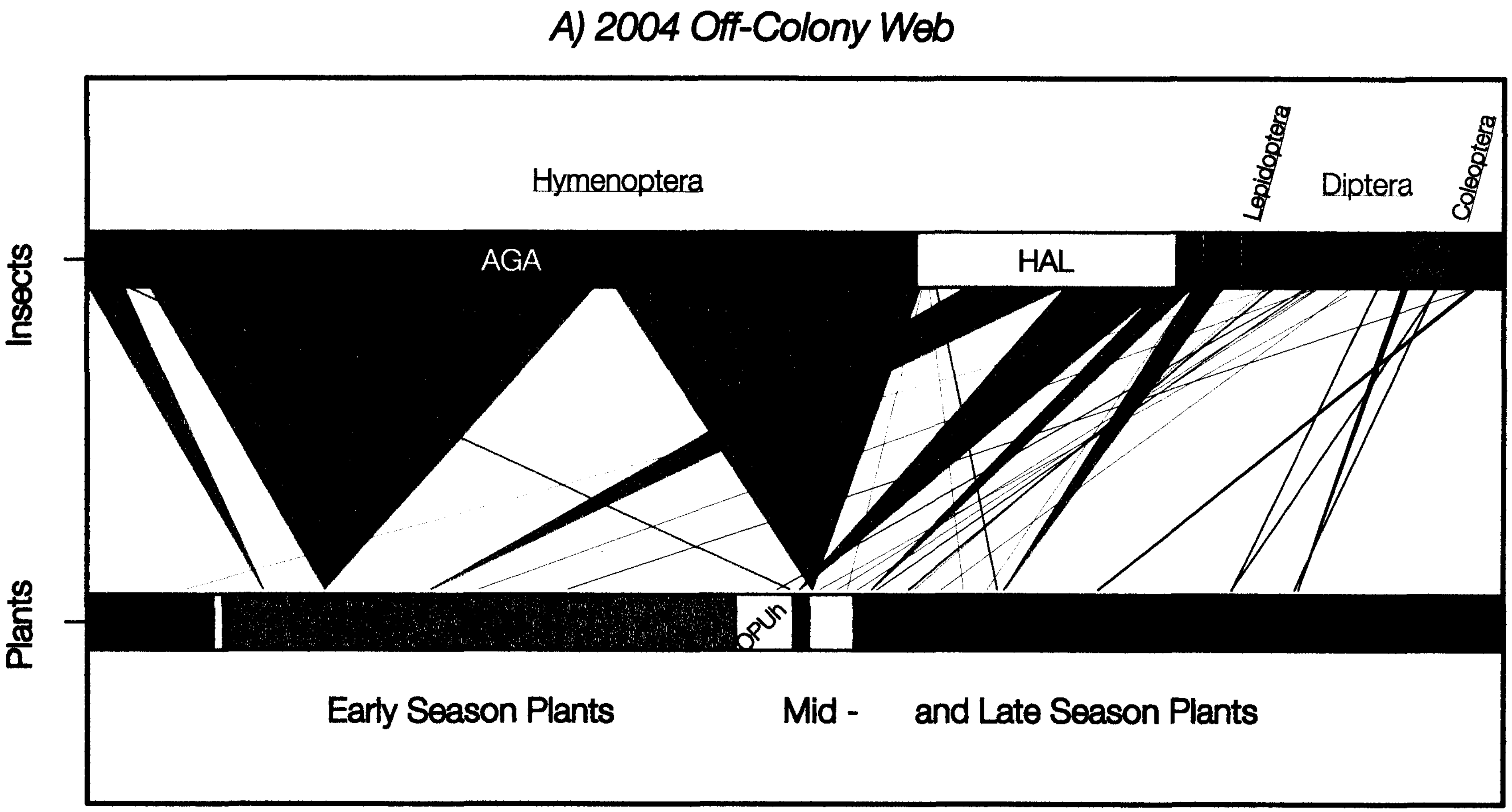
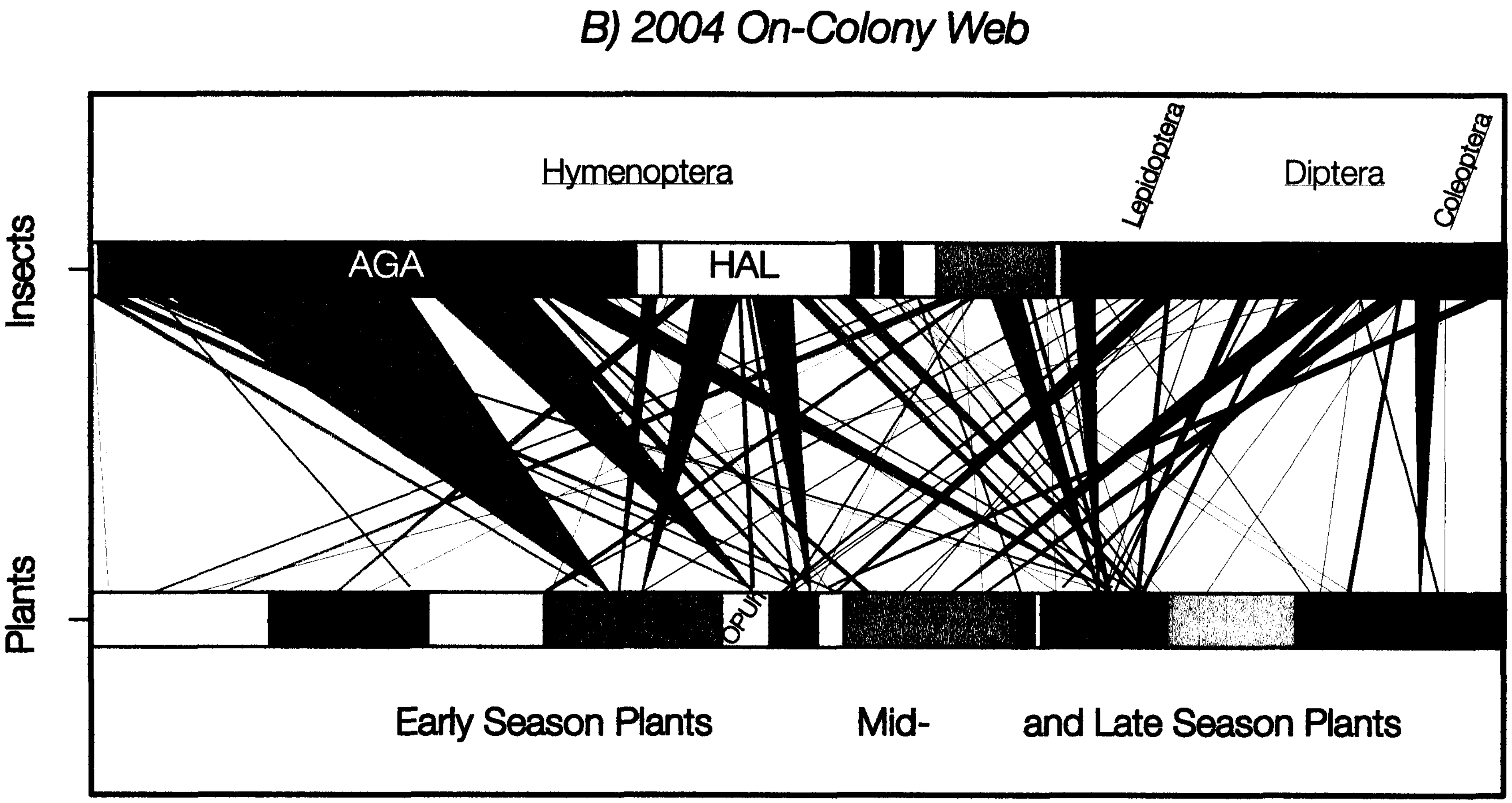


FIGURE 3.2A. 2004 off-colony web. 19 plant species (P) 22 insect functional groups (I) 64 links (L), and connectivity (C) 15.3.



B) 2004 On-Colony Web

FIGURE 3.2B. 2004 on-colony web. P = 31, I = 37, L = 145, and C = 12.6.

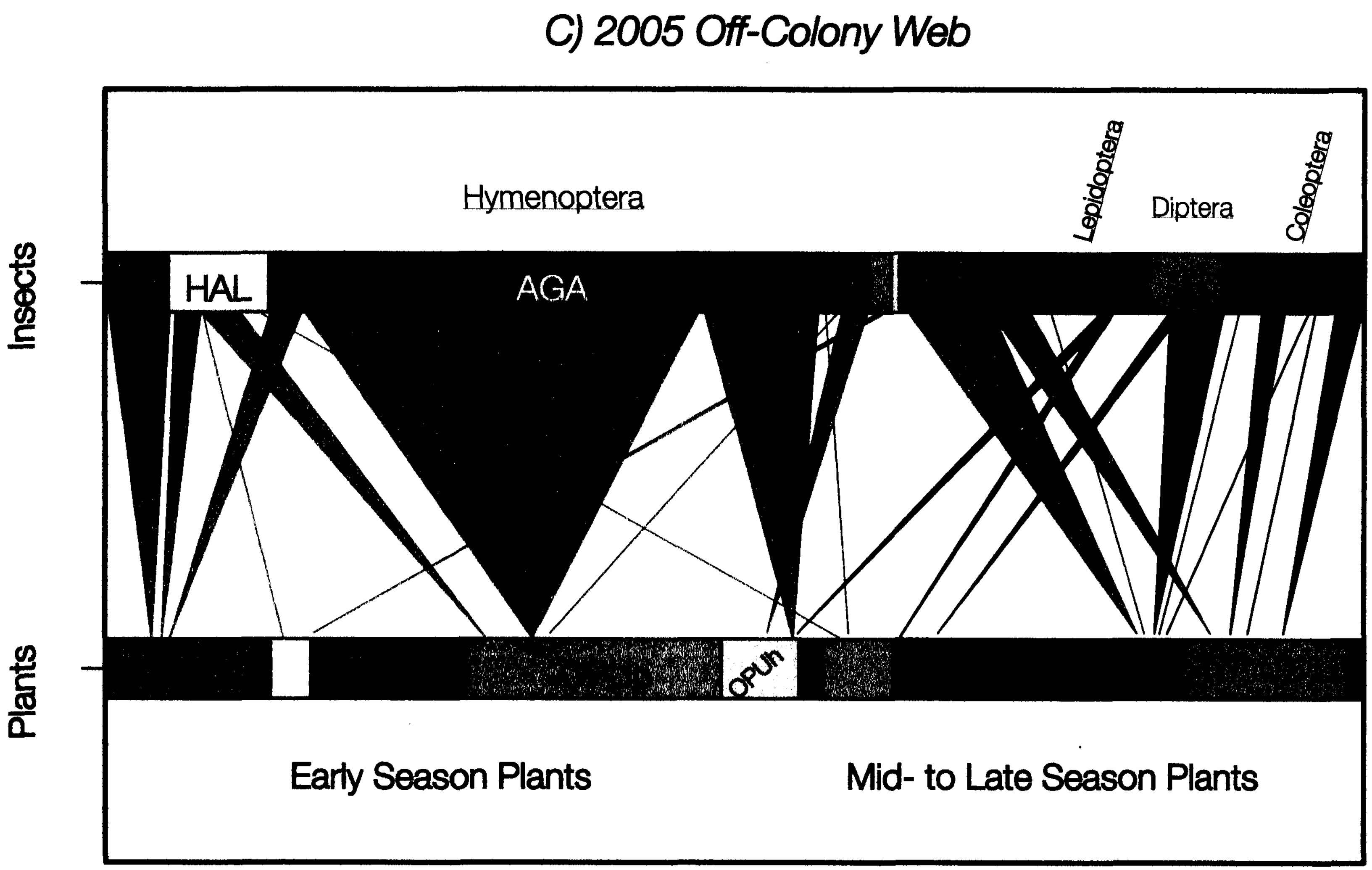
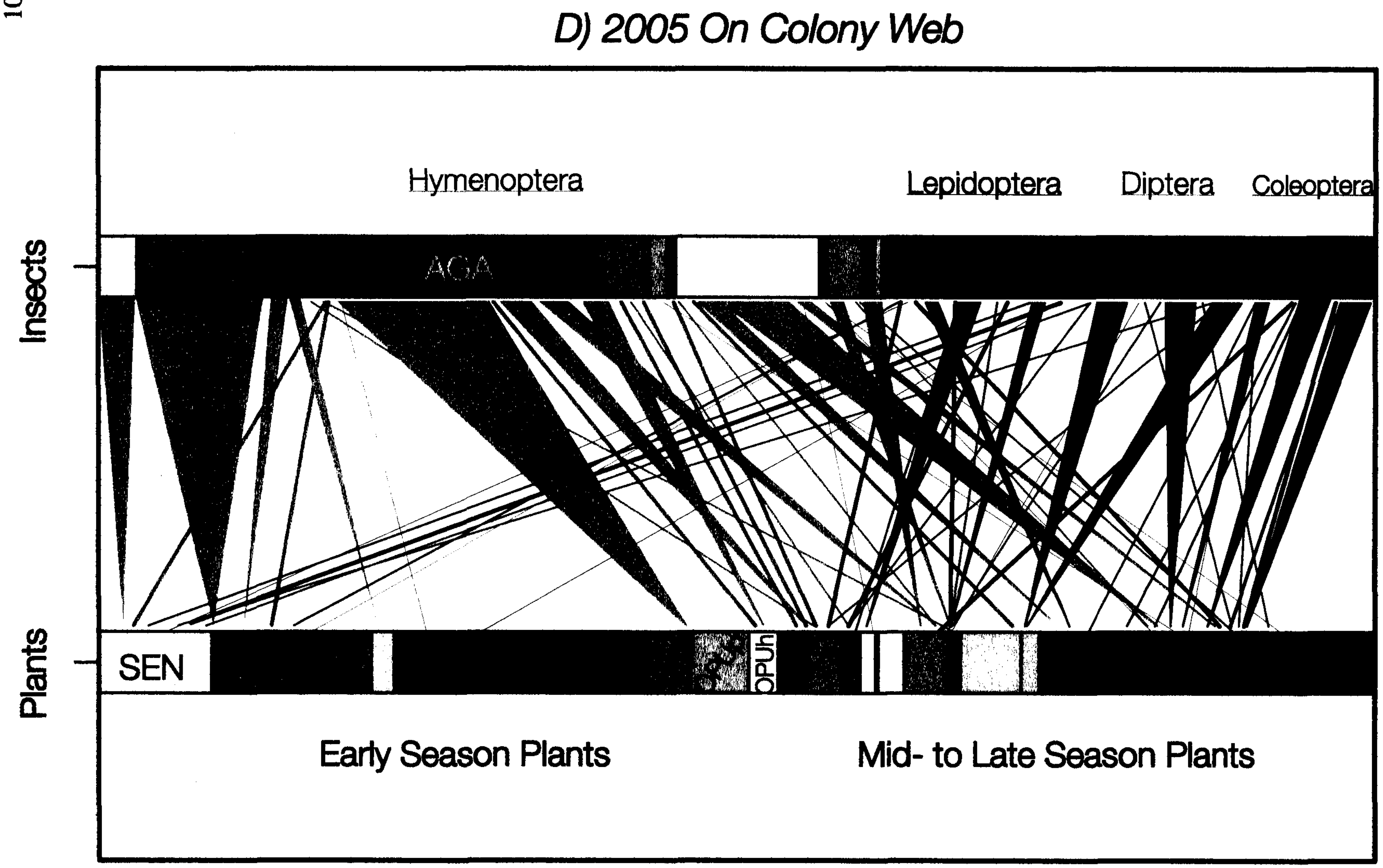


FIGURE 3.2C. 2005 off-colony web. P = 18, I = 22, L = 75, and C = 18.9).



D) 2005 On Colony Web

FIGURE 3.2D. 2005 on-colony web. P = 33, I = 49, L = 190, and C = 12.3.

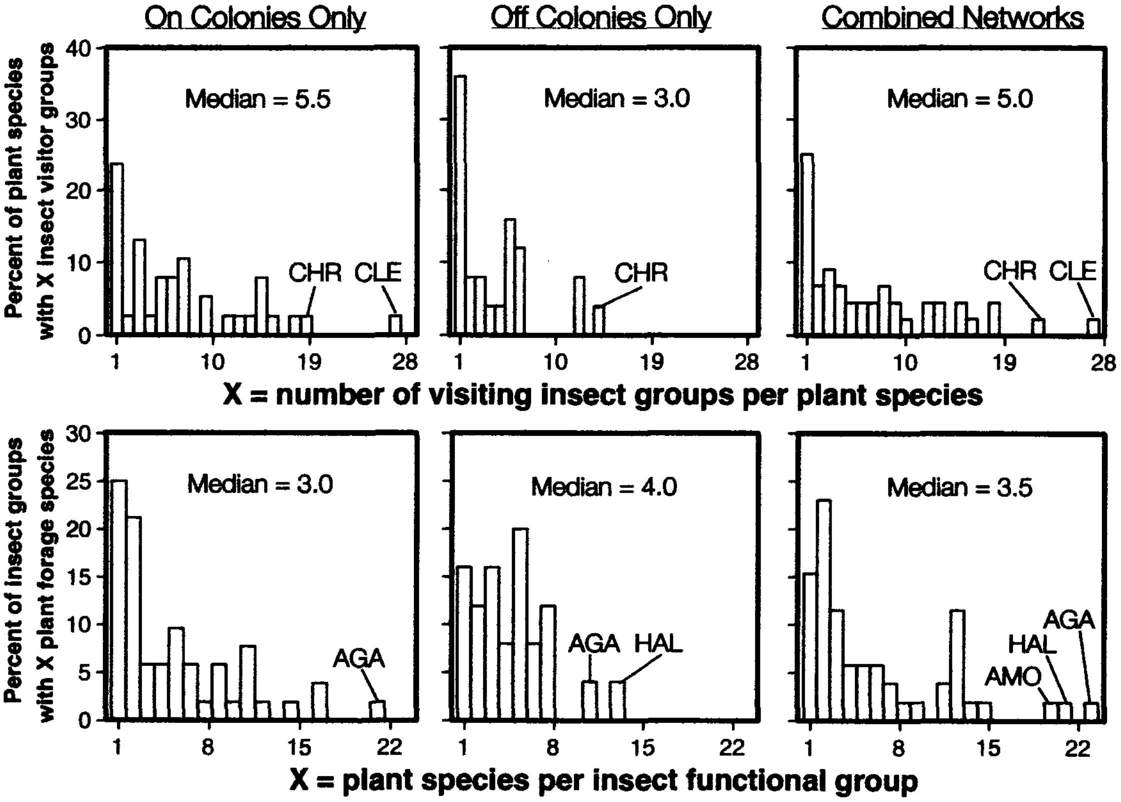


FIGURE 3.3: Distributions of (top row) number of visitor groups recorded at each plant species, and (bottom row) number of plant species visited by each insect functional group for both on and off- colonies, and for all sites combined, in 2004 and 2005. Plant abbreviations indicated as CHR – *Chrysopsis villosa*; CLE – *Cleome serrulata*. Insect group abbreviations indicated as AGA – *Agapostemon* spp.; HAL – small halictid bees, e.g. *Halictus, Dialictus*; AMO – *Ammophila* predatory wasps.

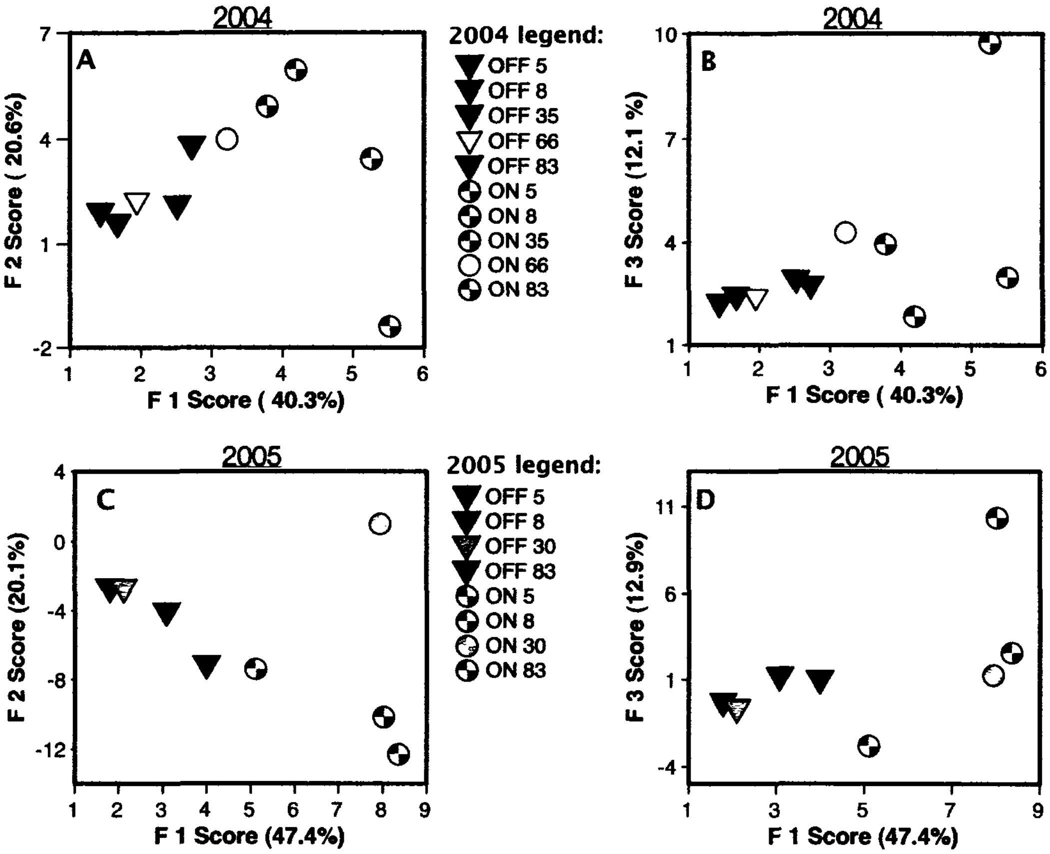


FIGURE 3.4: Factor analysis of the anthophilous insect communities found at each on- and off-colony site in 2004 (A and B) and 2005 (C and D). On-colony insect communities had higher factor 1 scores in both years, and they also had more variability in factor 2 (A,C) and factor 3 (B,D). Axes label percentages refer to the % variance explained by each combination factor for site insect communities in each year. Factor 1 describes insect abundance and group richness, while factors 2 and 3 relate information about relative mix and diversity of rare versus common groups, and community order-level make-up.

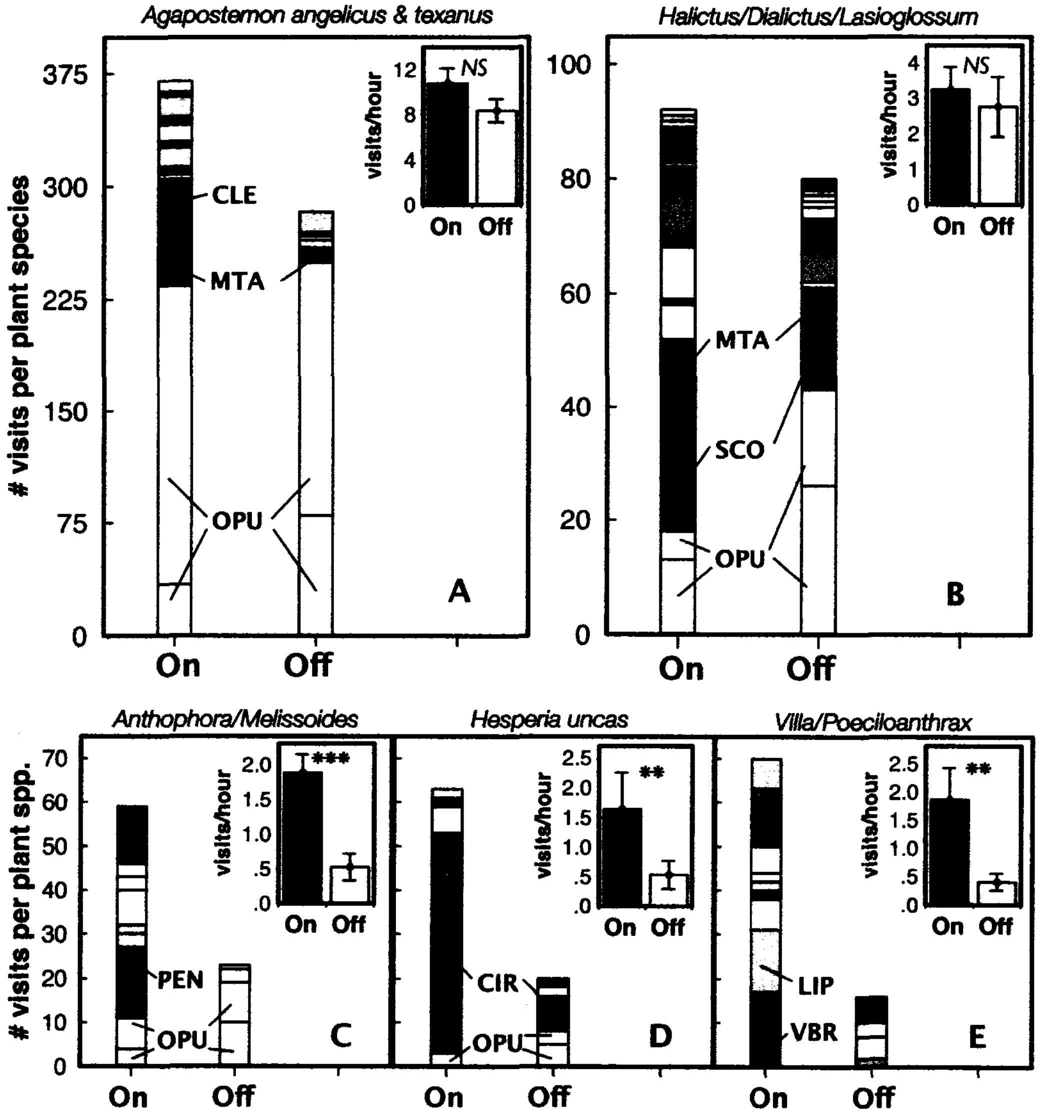


FIGURE 3.5: Visitation of different plant species (main charts) and by mean site visitation rates (insets) for five common polylectic insect functional groups. P-values indicated as $^{**}P < 0.05$, $^{***}P < 0.01$, NS = not significant. In all cases $N = 6$. Plant abbreviations as follows: OPU – *Opuntia humifesa* (lower, darker sections) and *O. polyacantha* (higher, lighter sections); CLE – *C. serrulata*; MTA – *Machaeranthera tanacetifolia*; SCO – *S. coccinea*; PEN – *Penstemon albidus*; CIR – *Cirsium* thistles; LIP – *Lippia cuneifolia*; VBR – *Verbena bracteata*.

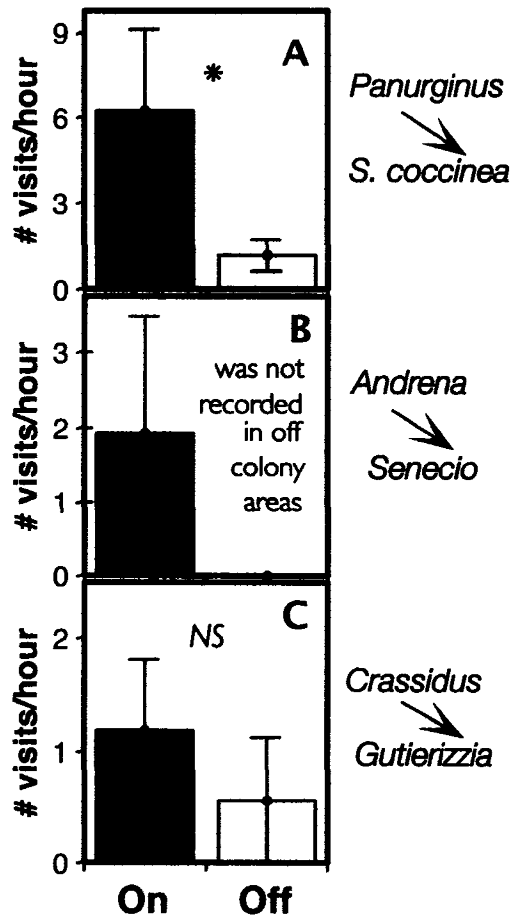


FIGURE 3.6: Habitat utilization of three short-season, oligolectic species that were common, and in some cases only present, in 2005. *Panurginus* and *Andrena* are both early season bees in the family Andrenidae, and *Crassidus* is a late season longhorn beetle (Cerambycidae). A) *P. beardsleyi* visitation of *S. coccinea*; B) *A. gardineri* visitation of *S. tridenticulatus*; and C) *C. pulchellus* visitation of *G. sarothrae*. *P*-values indicated as **P* = 0.07. NS = not significant.

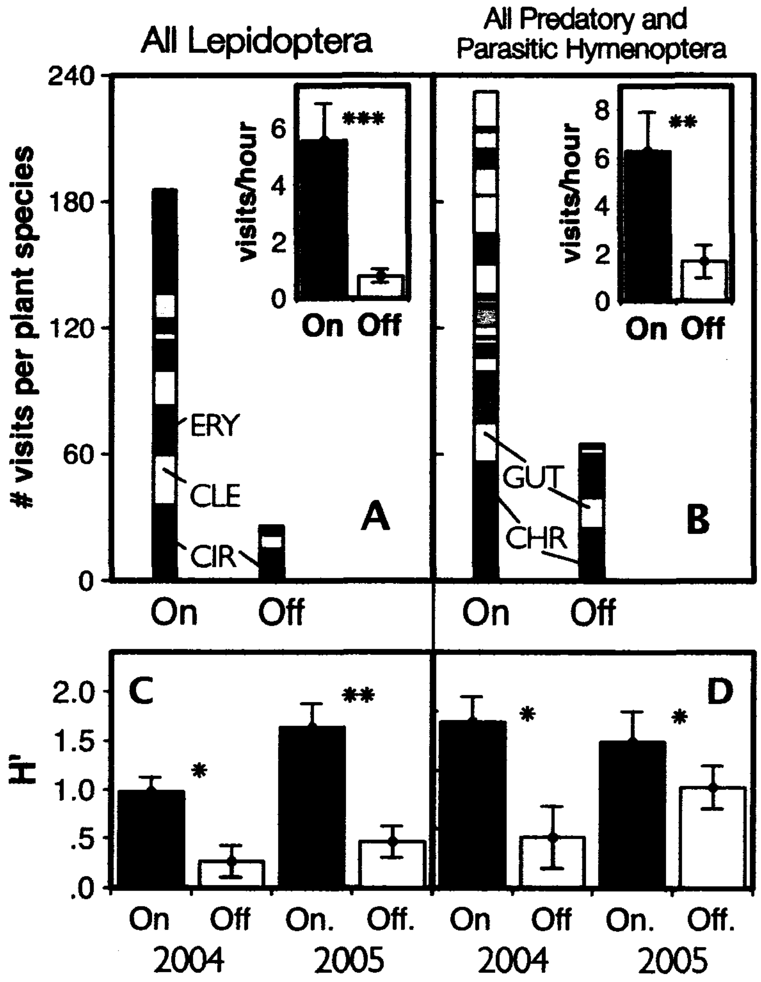


FIGURE 3.7: A) Visitation rates for all Lepidoptera. B) Visitation rates of all predatory and parasitic hymenoptera combined. For A and B, large chart shows all visits by plant species, and inset shows whole site whole season visitation rates, mean ± SE shown and $N = 6$. Plant abbreviations as follows: CIR – *Cirsium*; CLE – *C. serrulata*; ERY – *E. asperum* western wallflower; CHR – *C. villosa*; and GUT – *G. sarothrae*. C) Species-level diversity (H') of all Lepidoptera by colony sites for both years. D) Species-level diversity (H') of all predatory and parasitic hymenoptera by colony sites for both years. For C and D, mean ± SE shown and $N = 5$ for 2004 and $N = 4$ for 2005. P values indicated as $^{*}P < 0.1$, $^{**}P < 0.05$, $^{***}P < 0.01$.

V. CONCLUSION AND RECOMMENDATIONS

Several conclusions can be drawn from the research presented here. First of all, black-tailed prairie dogs influence vegetation structure in a fundamental way, so that floral resources and bare ground cover are greater on colonies than in similar uncolonized grassland. The altered vegetation is not spatially homogenous, but is patchy. The prairie dog colonies themselves are clearly a differing habitat patch type, composed of about 40% bare ground, some of this elevated and packed (mound surfaces), interspersed with dense aggregations of floral resources, and in many cases a more diverse and species-rich entomophilous plant community than can be found off-colony. On colonies, soil temperatures are warmer (Archer and Detling 1986), and due to the low canopy height and increase in bare ground, the floral resources are very visible. On the other hand, off-colony sites have only about 20% bare ground and scattered floral resources interspersed and sometimes hidden beneath a taller, graminoid canopy dominated by blue grama and buffalo grass. *Opuntia* cactus species are common in both habitat types, and with the possible exception of *Cirsium undulatum* and *C. ochrocentrum* capitae, present the single largest, most resource rich, and visible flowers in both colonized and uncolonized patch types.

It is not surprising that the anthophilous insect community reacts to these differences. In fact, it is likely native steppe insects have been utilizing the differential resource base on prairie dog colonies for long enough to develop important coevolved mutualisms. Lepidoptera may preferentially visit colonies for the increased chance of finding the appropriate larval host plant (Elrich 1989). Parasitic and predatory

Hymenoptera may be attracted to higher host and prey densities. Many insect groups are found in greater abundance on colonies, and it is still unknown how many, if any, are obligately dependant on prairie dogs. For a typical bee pollinator, this means that in a local area with prairie dog colonies, there are three main generalized nesting and foraging strategies. It could avoid colonized patches all together, nesting in a patch of bare soil likely surrounded by grasses and foraging in the typically sparser floral resource base off-colonies, possibly specializing on *Opuntia*, a cornucopian resource that is also common off colonies. Alternatively, a bee could take advantage of possibly superior, and certainly more densely bare, nesting ground on-colonies (Michener 1999), but then travel up to hundreds of meters away to forage in the relative calm of low-density off-colony sites. An insect with this strategy could be avoiding competition from a more diverse and abundant insect floral visiting community (Bronstein 1995), specializing on long flights and searches between plants but exerting little effort in avoiding or winning competitive interactions, and more likely avoiding predatory and parasitic Hymenoptera. Finally, a bee could live on and forage exclusively within colonized patches. In this case, the insect may be risking higher rates of predation or parasitism and encountering more individuals and different species of competitors for nectar and pollen. However, an insect with this strategy will spend less energy traveling to and between floral resources, have a large available area for nest building, and be able to choose from a larger subset of entomophilous forbs from which to forage. When these three life histories and foraging

Plate 3. An andrenid bee visits *Sphaeralcea coccinea.*
Photo: K. Hardwicke 6/2005

strategies are considered, it becomes evident how grassland patch heterogeneity caused by prairie dogs allows for more insect species in the local area based on differences in habitat selection.

When Capts. M. Lewis and W. Clark first crossed the North American Great Plains in 1804, they noted the remarkable size of prairie dog colonies, and how they seemed to provide a focusing of grassland resources utilized by a variety of other animals in the community:

> ...this plane extends with the same bredth from the creek below to the distance of near three miles above parrallel with the river, and it is intirely occupyed by the burrows of the *barking squiril* heretofore described; this anamal appears here in infinite numbers and the shortness and virdue of the grass gave the plain the appearance throughout it's whole extent of beatifull bowling green in fine order....a great number of wolves of the small kind, hawks, and some pole-cats were to be seen. I presume that those anamals feed on this squirril.
>
> -Meriwether Lewis, 1804, p.28

Though Lewis does not remark specifically on flowers or pollinators in his discussion of the "barking squiril," the rest of his description seems to be quite accurate in terms of community ecology and the difference in vegetation found on colonies (Miller et al. 1994, Kotliar 1999, Ceballos et al. 1999). Shortgrass steppe prairie dog colonies are becoming more ephemeral due to periodic and common extirpation by plague (*Yersina pestis*) (Stapp et al. 2004), and based on accounts earlier in the century (Koford 1958), as well as Lewis and Clark's (1804) own descriptions and the assessment of prairie dog and black-footed ferret conservation researchers (Miller et al. 1990), prairie dogs now occupy a small proportion of their original habitat due to eradication efforts.

Because the effects of colonization do increase with age (Archer et al. 1987), colonized habitat patches with dense floral resources today are probably scarce compared to historic levels. Pollinator populations are in decline worldwide, both in terms of species richness and population density, and North American insect communities pose no exception to this trend (Samways 1994, Kearns et al. 1998). Conservation of older and larger shortgrass steppe prairie dog colonies represents a major step towards management that will benefit native insect floral visitors, including rare species and possible obligate prairie dog colony dwellers. In addition, insects are known to be a major organismal pathway for making energy from lower trophic levels available for higher trophic levels. An increased anthophilous insect community means more resources for birds and mammals that include these insects in their diet.

Plate 4. An anthophorid bee visits prickly poppy (*Argemone polyanthemos*).
Photo: K. Hardwicke, July 2004

Clearly one can never learn all there is to know about a given system in three years, but in a community this fascinating, located on an LTER site, there are obvious directions where further study in warranted. To begin, pollination syndromes of many of the entomophilous flowers common on the shortgrass steppe, for example *Oenothera* spp., indicates that these white, fragrant, tubular flowers are nocturnally pollinated. There exists an entire half of the story told here that can only be measured after dark. Also, bee nest densities were inferred in this study but never directly measured. It remains to be experimentally discovered whether more anthophilous insects nest on colonies or not. Do greater rates of habitat utilization really mean higher local abundance on colonies? Thirdly, experimental studies may be of some use, especially in separating mechanisms and providing the ability to infer causation directly -- when is it the flowers, and when is it the bare ground that attracts more abundant insect communities? There are significant logistical issues involved in putting out experimental arrays of plants in this system, but perhaps these are not insolvable. 4) Per-plant or per-flower rates of visitation need to be calculated to fully answer the question of whether plants receive greater pollination service on colonies. Three groups would be logical to begin with, for reasons of community importance and being found in both patch types: *Opuntia* spp., *Cirsium* spp., and *Sphaeralcea coccinea.*

Though there is much work to be done to fully understand the mechanisms behind, and the full story of, pollination networks on the shortgrass steppe, it can be seen from the research presented here that black-tailed prairie dog colonization has real and profound effects on anthophilous insect communities. This tri-trophic interaction should be considered carefully in management decisions dealing with steppe pollinator conservation, and maintenance of a diverse set of interactions, plant species, and insect species. In a more theoretical sense, however, this research also illustrates the possible extent to which nearby, and even adjacent pollination networks drawing from the same potential species pool, can be altered in the presence of an environmental engineer.

LITERATURE CITED

Archer, S. and J.K. Detling. 1986. Evaluation of potential herbivore mediation of plant water status in the North American mixed grass prairie. Oikos 47:287-291.

Archer, S., M.G Garrett, and J.K. Detling. 1987. Rates of vegetation change with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. Vegetatio **72**:159-166.

Bronstein, J.L. 1995. The plant-pollinator landscape. *In* Mosaic Landscapes and Ecological Processes. Ed. by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London, pp. 256-288.

Ceballos, G. J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. Journal of Arid Environments **41**:161-172.

Ehlrich, P.R. 1989. The structure and dynamics of butterfly populations. *In* The Biology of Butterflies. Ed. by R.I. Vane-Wright and P.R. Ackery. Princeton University Press, Princeton New Jersey, pp. 25-40.

Hanski, I. 1995. Effects of landscape pattern on competitive interactions. *In* Mosaic Landscapes and Ecological Processes. Ed. by L. Hansson, L. Fahrig, and G. Merriam. Chapman and Hall, London, pp. 203-224.

Kearns, C.A., D.W. Inouye, and N.M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annual Review of Ecology and Systematics **29**:83-112.

Koford, C.B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs **3**:5-78.

Kotliar, N.B., B.W. Baker, A.D. Whicker, and G. Plumb. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management **24**:177-192.

Lewis, M. and W. Clark. 1804. From the Vermillion to the Teton (Bad) River. *In* The Journals of Lewis and Clark. Ed. by B. Devoto, Houghton Mifflin Co., Boston, Massachusetts, pp. 23-33.

Michener, C.D. 1999. The bees of the world. John Hopkins University Press, Baltimore, Maryland.

Miller, B., C. Wemmer, D. Biggins, and R. Reading. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management **14**:763-769.

Miller, B., G. Ceballos, and R. Reading. 1994. The prairie dog and biotic diversity. Conservation Biology **8**:677-681.

Samways, M.J. 1994. *Insect Conservation Biology*. Chapman and Hall, New York.

Stapp, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. Conservation Biology **12**:1253-1259.

Stapp, P., M.F. Antolin, and M. Ball. 2004. Patterns of extinction in prairie dog populations: plague outbreaks follow El Niño events. Frontiers in Ecology and the Environment **2**:235-240.

VI: DATA APPENDICES

APPENDIX A: INSECT FUNCTIONAL GROUPS

APPENDIX B: SPATIAL MAPS FOR 2005

APPENDIX C: LISTS OF ENTOMOPHILOUS PLANT SPECIES ON AND OFF PRAIRIE DOG COLONIES

Appendix A-1. A table listing the component groups and characteristics of the functional-taxonomic grouping scheme used in 2003 and 2004 studies, discussed in Chapter 1. Also noted are which groups were observed on- and off- black-tailed prairie dog colonies.

COLEOPTERAN GROUPS

GRP	Family	Genera/Species	Size (mm)[¥]	Pile[‡]	ON	OFF
C1	Cantharidae	*Chauliognathus basilis*	11 - 12	None		X
C2	Cerambycidae	*Crossidus pulchellus**, *Typocerus sinuatus*	11 - 12	SD, none	X	X
C3	Meloidae	*Epicauta stuarti*, *Nemognathus piazatus*, *N. bicolor*	10 - 12	SD	X	X
C4	Meloidae	*Epicauta ferruginea*	6 - 8	SD	X	X
C5	Melyridae	*Collops bipunctatus*	6 - 7	SS		X

DIPTERAN GROUPS

GRP	Family	Genera/Species	Size (mm)	Pile[‡]	ON	OFF
D1	Acalyptratae	Various acalyptrate families	3 - 5	SS, none	X	X
D2	Bombyliidae	*Anastoechus* spp.*, *Bombylius* spp.	8 - 10	LD	X	X
D3	Bombyliidae	*Chrysanthrax* spp., *Exoprosopa decora*, *Poecilanthrax alcyon*, *Villa villa**	9 - 13	SD, SS	X	X
D4	Bombyliidae	*Phthiria* spp.	4 - 6	none	X	X
D5	Tabanidae	*Chrysops* spp.	10	SS	X	
D6	Syrphidae	*Copestylum caudatum**, *Eristalis stipator*	7 - 10	SD, none	X	X

HYMENOPTERAN GROUPS

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa[§]	Social[†]	ON	OFF
H1	Andrenidae	*Andrena gardineri*	11 - 14	Met/Fe	Sol/Col	X	
H2	Andrenidae (Panurgini)	*Panurginus beardsleyi*	8 - 9	Met/Ta	Sol/Col	X	
H3	Apidae (Apinae)	*Bombus nevadensis*, *B. pennsylvanicus*	21 - 28	Cor	Eu	X	X

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa[§]	Social[†]	ON	OFF
H4	Apidae (Anthophorinae)	*Melissoides* spp.*, *Anthophora montana*	12 - 22	Ta/Met	Sol/Col	X	X
H5	Apidae (Anthophorinae)	*Melissoides* spp	8 - 10	Fe/Ta	Sol/Col	X	X
H6	Apidae (Anthophorinae)	*Nomada* spp.	7 - 8	None	Para(H)	X	X
H7	Braconidae	*Vipio* spp., *Chelarus* spp.	6 - 9	None	Pred(CL)	X	X
H8	Chrysididae	*Chrysis* spp.	6 - 7	None	Para(H)	X	X
H9	Colletidae (Colletinae)	*Colletes* spp.	6 - 8	Met/Fe	Sol/Col	X	
H10	Halictidae (Halictini)	*Agapostemon angelicus* and *texanus*	9 - 11	Fe/Ta	Col	X	X
H11	Halictidae (Augochlorini)	*Augochlora* spp.	6 - 7	None	Para(H)	X	
H12	Halictidae (Augochlorini)	*Augochlora* spp.	13 - 15	Fe/Ta	Sol	X	X
H13	Halictidae	*Dialictus* spp., *Halictus* spp, *Lasioglossum* spp., various DuPoureinae	5 - 8	Fe/Ta	Sol/Col	X	X
H14	Ichneumonidae	*Agrypon* spp.	9 - 10	None	Pred	X	X
H15	Megachilidae	*Megachile* spp.	16	Met	Sol	X	
H16	Megachilidae	*Osmia* spp., *Anthidium* spp.	7 - 12	Met	Sol	X	X
H17	Sphecidae (Sphecinae)	*Ammophila* spp.*, *Chalybion* spp., *Prionyx* spp.	13 - 18	None	Pred(HL)	X	X
H18	Sphecidae (non-petiolate)	*Stizus* spp., *Tachytes distinctus*, *Bicyrtes* spp.	12 - 15	None	Pred	X	
H19	Sphecidae (Philanthini)	*Philanthus* spp.	8 - 10	None	Pred(H)	X	X
H20	Vespidae	*Stenodynerus* spp. *Euodynerus* spp.	8 - 13	None	Pred(CL)	X	X

LEPIDOPTERAN GROUPS

GRP	Family	Species	Size (mm)	Larval Host Plant	ON	OFF
L1	Hesperiidae	*Hesperia uncas*	28 - 38	*Bouteloua gracilis* Blue grama	X	X
L2	Hesperiidae	*Pyrgus communis*	25 - 35	*Sphaeralcea coccinea*	X	X
L3	Nymphalidae	*Vanessa cardui*		*Cirsium* spp., other Asteraceae	X	
L4	Nymphalidae	*Euptoieta claudia*	40 - 50	*Viola nuttallii, Portulaca oleracea*	X	X
L5	Pieridae	*Pontia occidentalis**, P. protodice*	37 - 45	*Cleome serrulata,* Brassicaceae	X	X
L6	Pieridae	*Nathalis iole*	23 - 24	yellow Asteraceae	X	
L7	Lycaenidae	*Lycaena rubidus*	30	*Rumex venosus*	X	
L8	Lycaenidae	*Plebeius lupini*	22	*Eriogonum effusum*	X	
L9	Pyralidae	*Aphomia sociella*	27 - 29	Develops in bee nests	X	X
L10	Noctuidae	*Cucullia asteroides*	44	*Solidago* and other Asteraceae	X	
L11	Noctuidae	*Euoxa auxiliaris*	40 - 42	unknown	X	
L12	Noctuidae	*Schinia jaguarina*	28 - 30	unknown	X	X
L13	Noctuidae	*Schinia roseitincta*	16	unknown	X	
L14	Noctuidae	*Therasea augustipennis*	29 - 31	unknown	X	X

* These species make up the majority of a given functional group, where multiple species are listed.

¥ Size measured as body length, excluding proboscis, antennae and non-scopa bearing hind tarsi, except in Lepidoptera, where size refers to forewing span as measured from spread specimen collection.

‡ Pile characteristics (for Coleoptera and Diptera): **SS**-short and sparse, **LD**-long and dense, **SD**-short and dense, **none**-no pile that could reasonably be assumed to contribute to pollen carryover

§ Scopa presence and type (for Hymenoptera): In this key, all descriptions use the term "scopa" to indicate a specialized area of pile used to dry-pack pollen for transport back to the nest. **Cor**-corbiculate bees, which mix pollen and nectar to form a putty that is packed into hind tarsal indentations; **Fe**-femoral scopa, which are close in to the body, usually on the hind legs; **Ta**-tarsal scopa, which are distal to the body, usually on the hind legs; **Met**-metasomal scopa, which are on the underside of the abdomen; **none**-no scopa of any type are indicative of males and parasitic and predatory groups that do not collect pollen for a brood.

† Sociality/life history characteristics (for Hymenoptera): **Eu**-eusocial, where one queen lays eggs for an entire colony of female workers. In this case, the only taxon to even loosely fit this definition is *Bombus*, which is actually primitively eusocial since only the queen overwinters; **Col**-colonial, where females collectively aggregate their nests, either with one main entrance or several individual entrances, but all still mate and lay eggs. Benefits include sharing of nest guarding duties against brood parasites and nest predators; **Sol**-solitary bees, which do not aggregate nests or share brood-raising duties; **Para(CDHL)**-parasitic wasps and bees, which lay their eggs in another species nest to develop, with order they are known to parasitize indicated as C-Coleoptera, D-Diptera, H-Hymenoptera, L-Lepidoptera; **Pred(CDHL)**-predatory wasps, which typically have solitary burrows (although some Vespidae can be colonial or even social). These wasps kill or parasitize a prey item and lay their eggs so that the brood consumes the prey item. Order of prey item they are known to utilize indicated.

Appendix A2. A table listing the component groups and characteristics of the functional-taxonomic grouping scheme used in the 2005 study, discussed in Chapter 2. Also noted are which groups were observed on- and off- black-tailed prairie dog colonies.

Coleopteran Groups

GRP	Family	Genera/Species	Size (mm)¥	Pile‡	ON	OFF
C1	Cantharidae	*Chauliognathus basilis*	11 - 12	None	X	X
C2	Cerambycidae	*Crossidus pulchellus**, *Typocerus sinuatus*	11 - 12	SD, none	X	X
C3	Meloidae	*Epicauta stuarti,* *Nemognathus piazatus,* *N. bicolor*	10 - 12	SD	X	X
C4	Meloidae	*Epicauta ferruginea*	6 - 8	SD	X	X
C5	Melyridae	*Collops bipunctatus*	6 - 7	SS	X	
C6	Scarabaeidae	*Euphoria inda*	15	LD	X	

Dipteran Groups

GRP	Family	Genera/Species	Size (mm)	Pile‡	ON	OFF
D1	Acalyptratae	Various acalypterate families	3 - 5	SS, none	X	X
D2	Bombyliidae	*Anastoechus* spp.*, *Bombylius* spp.	8 - 10	LD	X	X
D3	Bombyliidae	*Chrysanthrax* spp., *Exoprosopa decora,* *Poecilanthrax alcyon,* *Villa villa**	9 - 13	SD, SS	X	X
D4	Bombyliidae	*Phthiria* spp.	4 - 6	none	X	X
D5	Tabanidae	*Chrysops* spp.	10	SS	X	
D6	Syrphidae	*Copestylum caudatum**, *Eristalis stipator*	7 - 10	SD, none	X	X

Hymenopteran Groups

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa§	Social†	ON	OFF
H1	Andrenidae	*Andrena gardineri*	11 - 14	Met/Fe	Sol/Col	X	
H2	Andrenidae (Panurgini)	*Panurginus beardsleyi*	8 - 9	Met/Ta	Sol/Col	X	X
H3	Apidae (Apinae)	*Bombus nevadensis, B. pennsylvanicus*	21 - 28	Cor	Eu	X	

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa[§]	Social[†]	ON	OFF
H4	Apidae (Anthophorinae)	*Melissoides* spp.*, *Anthophora montana*	12 - 22	Ta/Met	Sol/Col	X	X
H5	Apidae (Anthophorinae)	*Melissoides* spp	8 - 10	Fe/Ta	Sol/Col	X	X
H6	Apidae (Anthophorinae)	*Nomada* spp.	7 - 8	None	Para(H)	X	X
H7	Braconidae	*Vipio* spp., *Chelarus* spp.	6 - 9	None	Pred (CL)		X
H8	Chrysididae	*Chrysis* spp.	6 - 7	None	Para(H)		X
H9	Colletidae	*Colletes* spp.	9 - 11	Met/Fe	Sol	X	
H10	Colletidae	*Tiphia* spp.	12 - 14	Met	Para(H)	X	
H11	Halictidae (Halictini)	*Agapostemon angelicus* and *texanus*	9 - 11	Fe/Ta	Col	X	X
H12	Halictidae (Augochlorini)	*Augochlora* spp.	6 - 7	None	Para(H)	X	
H13	Halictidae	*Halictus* spp.	13 - 15	Fe/Ta	Sol	X	
H14	Halictidae	*Dialictus* spp., *Halictus* spp, *Lasioglossum* spp., various DuPoureinae	5 - 8	Fe/Ta	Sol/Col	X	X
H15	Halictidae	*Nomia* sp.	9 - 11	Fe	Sol/Col	X	
H16	Ichneumonidae	*Agrypon* spp.	9 - 10	None	Pred	X	X
H17	Megachilidae	*Megachile* spp.	16	Met	Sol	X	
H18	Megachilidae	*Megilla* spp.	14 - 17	Met	Sol	X	
H19	Pompilidae		15 - 20	None	Pred (spiders)	X	
H20	Sphecidae (Sphecinae)	*Ammophila* spp.*, *Chalybion* spp., *Prionyx* spp.	13 - 18	None	Pred(HL)	X	X
H21	Sphecidae (non-petiolate)	*Stizus* spp., *Tachytes distinctus, Bicyrtes* spp.	12 - 15	None	Pred	X	
H22	Sphecidae (Philanthini)	*Philanthus* spp.	8 - 10	None	Pred(H)	X	
H23	Vespidae	*Stenodynerus* spp. *Euodynerus* spp.	8 - 13	None	Pred(CL)	X	X

LEPIDOPTERAN GROUPS

GRP	Family	Species	Size (mm)	Larval Host Plant	ON	OFF
L1	Hesperiidae	*Hesperia uncas*	28 - 38	*Bouteloua gracilis* Blue grama	X	X
L2	Hesperiidae	*Pyrgus communis*	25 - 35	*Sphaeralcea coccinea*	X	X
L3	Nymphalidae	*Vanessa cardui*		*Cirsium* spp., other Asteraceae	X	
L4	Nymphalidae	*Euptoieta claudia*	40 - 50	*Viola nuttallii, Portulaca oleracea*	X	
L5	Nymphalidae	*Phycoides tharos*	25 - 27	Asteraceae	X	
L6	Pieridae	*Pontia occidentalis*, P. protodice*	37 - 45	*Cleome serrulata,* Brassicaceae	X	
L7	Pieridae	*Nathalis iole*	23 - 24	yellow Asteraceae	X	
L8	Pieridae	*Eurema mexicana*	35 - 37	*Astragalus, Lupinus,* and other Fabaceae	X	
L9	Pyralidae	*Aphomia sociella*	27 - 29	Develops in bee nests	X	
L10	Noctuidae	*Cucullia asteroides*	44	*Solidago* and other Asteraceae	X	
L11	Noctuidae	*Euoxa auxiliaris*	40 - 42	unknown	X	
L12	Noctuidae	*Schinia jaguarina*	28 - 30	unknown	X	
L13	Noctuidae	*Therasea augustipennis*	29 - 31	unknown	X	

* These species make up the majority of a given functional group, where multiple species are listed.

¥ Size measured as body length, excluding proboscis, antennae and non-scopa bearing hind tarsi, except in Lepidoptera, where size refers to forewing span as measured from spread specimen collection.

‡ Pile characteristics (for Coleoptera and Diptera): **SS**-short and sparse, **LD**-long and dense, **SD**-short and dense, **none**-no pile that could reasonably be assumed to contribute to pollen carryover

§ Scopa presence and type (for Hymenoptera): In this key, all descriptions use the term "scopa" to indicate a specialized area of pile used to dry-pack pollen for transport back to the nest. **Cor**-corbiculate bees, which mix pollen and nectar to form a putty that is packed into hind tarsal indentations; **Fe**-femoral scopa, which are close in to the body, usually on the hind legs; **Ta**-tarsal scopa, which are distal to the body, usually on the hind legs; **Met**-metasomal scopa, which are on the underside of the abdomen; **none**-no scopa of any type are indicative of males and parasitic and predatory groups that do not collect pollen for a brood.

† Sociality/life history characteristics (for Hymenoptera): **Eu**-eusocial, where one queen lays eggs for an entire colony of female workers. In this case, the only taxon to even loosely fit this definition is *Bombus*, which is actually primitively eusocial since only the queen overwinters; **Col**-colonial, where females collectively aggregate their nests, either with one main entrance or several individual entrances, but all still mate and lay eggs. Benefits include sharing of nest guarding duties against brood parasites and nest predators; **Sol**-solitary bees, which do not aggregate nests or share brood-raising duties; **Para(CDHL)**-parasitic wasps and bees, which lay their eggs in another species nest to develop, with order they are known to parasitize indicated as C-Coleoptera, D-Diptera, H-Hymenoptera, L-Lepidoptera; **Pred(CDHL)**-predatory wasps, which typically have solitary burrows (although some Vespidae can be colonial or even social). These wasps kill or parasitize a prey item and lay their eggs so that the brood consumes the prey item. Order of prey item they are known to utilize indicated.

Appendix A3. A table listing the component groups and characteristics of the functional-taxonomic grouping scheme used in 2004 and 2005 studies, discussed in Chapter 3. Also noted are which groups were observed on- and off- black-tailed prairie dog colonies.

COLEOPTERAN GROUPS

GRP	Family	Genera/Species	Size (mm)[¥]	Pile[‡]	ON	OFF
C1	Cantharidae	*Chauliognathus basilis*	11 - 12	None	X	X
C2	Cerambycidae	*Crossidus pulchellus**, *Typocerus sinuatus*	11 - 12	SD, none	X	X
C3	Meloidae	*Epicauta stuarti, Nemognathus piazatus, N. bicolor*	10 - 12	SD	X	X
C4	Meloidae	*Epicauta ferruginea*	6 - 8	SD	X	X
C5	Melyridae	*Collops bipunctatus*	6 - 7	SS	X	X
C6	Scarabaeidae	*Euphoria inda*	15 - 18	LD	X	

DIPTERAN GROUPS

GRP	Family	Genera/Species	Size (mm)	Pile[‡]	ON	OFF
D1	Acalyptratae	Various acalyptrate families	3 - 5	SS, none	X	X
D2	Bombyliidae	*Anastoechus* spp.*, *Bombylius* spp.	8 - 10	LD	X	X
D3	Bombyliidae	*Chrysanthrax* spp., *Exoprosopa decora, Poecilanthrax alcyon, Villa villa**	9 - 13	SD, SS	X	X
D4	Bombyliidae	*Phthiria* spp.	4 - 6	none	X	X
D5	Tabanidae	*Chrysops* spp.	10	SS	X	
D6	Syrphidae	*Copestylum caudatum**, *Eristalis stipator*	7 - 10	SD, none	X	X

HYMENOPTERAN GROUPS

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa[§]	Social[†]	ON	OFF
H1	Andrenidae	*Andrena gardineri*	11 - 14	Met/Fe	Sol/Col	X	
H2	Andrenidae (Panurgini)	*Panurginus beardsleyi*	8 - 9	Met/Ta	Sol/Col	X	X
H3	Apidae (Apinae)	*Bombus nevadensis, B. pennsylvanicus*	21 - 28	Cor	Eu	X	

GRP	Family (Subf/Tribe)	Genera/Species	Size (mm)	Scopa[§]	Social[†]	ON	OFF
H4	Apidae (Anthophorinae)	*Melissoides* spp.*, *Anthophora montana*	12 - 22	Ta/Met	Sol/Col	X	X
H5	Apidae (Anthophorinae)	*Melissoides* spp	8 - 10	Fe/Ta	Sol/Col	X	X
H6	Apidae (Anthophorinae)	*Nomada* spp.	7 - 8	None	Para(H)	X	X
H7	Braconidae	*Vipio* spp., *Chelarus* spp.	6 - 9	None	Pred(CL)		X
H8	Chrysididae	*Chrysis* spp.	6 - 7	None	Para(H)	X	X
H9	Colletidae (Colletinae)	*Colletes* spp.	6 - 8	Met/Fe	Sol/Col	X	X
H10	Colletidae	*Colletes* spp.	9 - 11	Met/Fe	Sol	X	
H11	Colletidae	*Tiphia* spp.	12 - 14	Met	Para(H)	X	
H12	Halictidae (Halictini)	*Agapostemon angelicus* and *texanus*	9 - 11	Fe/Ta	Col	X	X
H13	Halictidae (Augochlorini)	*Augochlora* spp.	6 - 7	None	Para(H)	X	
H14	Halictidae (Augochlorini)	*Augochlora* spp.	13 - 15	Fe/Ta	Sol	X	X
H15	Halictidae	*Dialictus* spp., *Halictus* spp, *Lasioglossum* spp., various DuPoureinae	5 - 8	Fe/Ta	Sol/Col	X	X
H16	Halictidae	*Nomia* sp.	9 - 11	Fe	Sol/Col	X	
H17	Ichnumonidae	*Agrypon* spp.	9 - 10	None	Pred	X	X
H18	Megachilidae	*Megilla* spp.	14 - 17	Met	Sol	X	
H19	Megachilidae	*Megachile* spp.	16	Met	Sol	X	
H20	Megachilidae	*Osmia* spp., *Anthidium* spp.	7 - 12	Met	Sol	X	X
H21	Pompilidae		15 - 20	None	Pred (spiders)	X	
H22	Sphecidae (Sphecinae)	*Ammophila* spp.*, *Chalybion* spp., *Prionyx* spp.	13 - 18	None	Pred (HL)	X	X
H23	Sphecidae (non-petiolate)	*Stizus* spp., *Tachytes distinctus*, *Bicyrtes* spp.	12 - 15	None	Pred	X	
H24	Sphecidae (Philanthini)	*Philanthus* spp.	8 - 10	None	Pred(H)	X	X
H25	Vespidae	*Stenodynerus* spp. *Euodynerus* spp.	8 - 13	None	Pred(CL)	X	X

LEPIDOPTERAN GROUPS

GRP	Family	Species	Size¥ (mm)	Larval Host Plant	ON	OFF
L1	Hesperiidae	*Hesperia uncas*	28 - 38	*Bouteloua gracilis*	X	X
L2	Hesperiidae	*Pyrgus communis*	25 - 35	*Sphaeralcea coccinea*	X	X
L3	Nymphalidae	*Vanessa cardui*		*Cirsium* spp., other Asteraceae	X	
L4	Nymphalidae	*Euptoieta claudia*	40 - 50	*Viola nuttallii, Portulaca oleracea*	X	
L5	Nymphalidae	*Phycoides tharos*	25 - 27	Asteraceae	X	
L6	Pieridae	*Eurema mexicana*	35 - 37	*Astragalus, Lupinus,* and other Fabaceae	X	
L7	Pieridae	*Pontia occidentalis**, *P. protodice*	37 - 45	*Cleome serrulata,* Brassicaceae	X	
L8	Pieridae	*Nathalis iole*	23 - 24	yellow Asteraceae	X	
L9	Lycaenidae	*Lycaena rubidus*	30	*Rumex venosus*	X	
L10	Lycaenidae	*Plebeius lupini*	22	*Eriogonum effusum*	X	
L11	Pyralidae	*Aphomia sociella*	27 - 29	Develops in bee nests	X	
L12	Noctuidae	*Cucullia asteroides*	44	*Solidago* and other Asteraceae	X	
L13	Noctuidae	*Euoxa auxiliaris*	40 - 42	unknown	X	
L14	Noctuidae	*Schinia jaguarina*	28 - 30	unknown	X	
L15	Noctuidae	*Schnia roseitincta*	16	unknown	X	
L16	Noctuidae	*Therasea augustipennis*	29 - 31	unknown	X	

* These species make up the majority of a given functional group, where multiple species are listed.

¥ Size measured as body length, excluding proboscis, antennae and non-scopa bearing hind tarsi, except in Lepidoptera, where size refers to forewing span as measured from spread specimen collection.

‡ Pile characteristics (for Coleoptera and Diptera): **SS**-short and sparse, **LD**-long and dense, **SD**-short and dense, **none**-no pile that could reasonably be assumed to contribute to pollen carryover

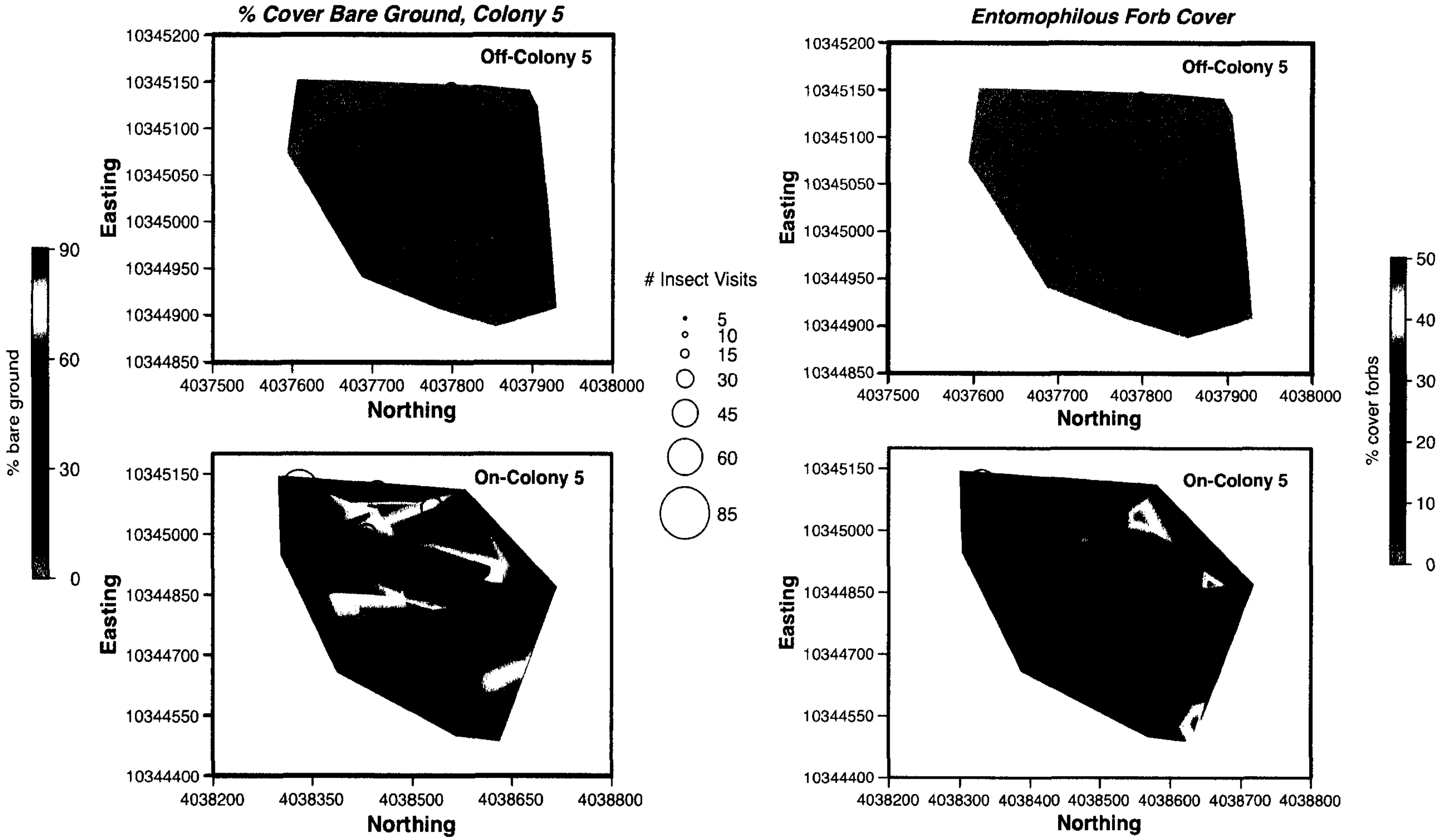
§ Scopa presence and type (for Hymenoptera): In this key, all descriptions use the term "scopa" to indicate a specialized area of pile used to dry-pack pollen for transport back to the nest. **Cor**-corbiculate bees, which mix pollen and nectar to form a putty that is packed into hind tarsal indentations; **Fe**-femoral scopa, which are close in to the body, usually on the hind legs; **Ta**-tarsal scopa, which are distal to the body, usually on the hind legs; **Met**-metasomal scopa, which are on the underside of the abdomen; **none**-no scopa of any type are indicative of males and parasitic and predatory groups that do not collect pollen for a brood.

† Sociality/life history characteristics (for Hymenoptera): **Eu**-eusocial, where one queen lays eggs for an entire colony of female workers. In this case, the only taxon to even loosely fit this definition is *Bombus*, which is actually primitively eusocial since only the queen overwinters; **Col**-colonial, where females collectively aggregate their nests, either with one main entrance or several individual entrances, but all still mate and lay eggs. Benefits include sharing of nest guarding duties against brood parasites and nest predators; **Sol**-solitary bees, which do not aggregate nests or share brood-raising duties; **Para(CDHL)**-parasitic wasps and bees, which lay their eggs in another species nest to develop, with order they are known to parasitize indicated as C-Coleoptera, D-Diptera, H-Hymenoptera, L-Lepidoptera; **Pred(CDHL)**-predatory wasps, which typically have solitary burrows (although some Vespidae can be colonial or even social). These wasps kill or parasitize a prey item and lay their eggs so that the brood consumes the prey item. Order of prey item they are known to utilize indicated.

APPENDIX B: SPATIAL MAPS

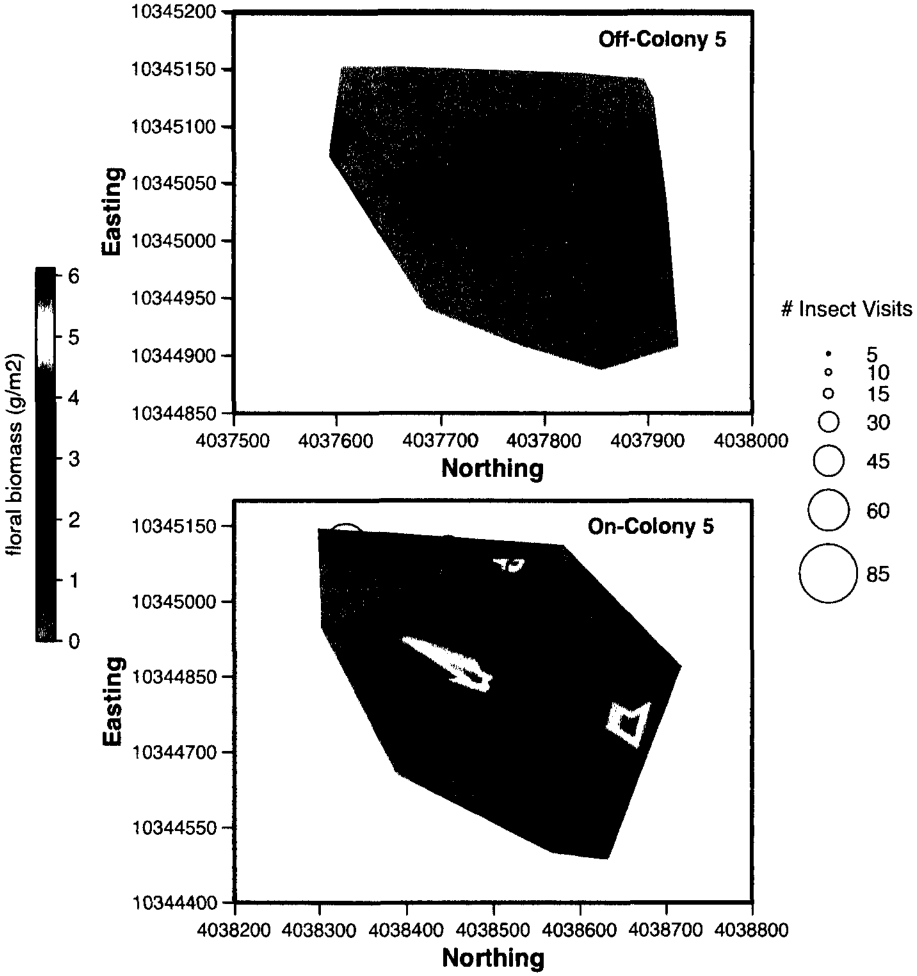
APPENDIX B: All maps were created from data taken in 56 1-m^2 vegetation plots, except mound density, which was recorded in 75 m^2 circular areas surrounding the 56 1 m^2 plots. Bubble size corresponds to the number of insects captured during each sample period, and does not indicate the area sampled for insects. This area was a constant 530 m^2.

Colony 5

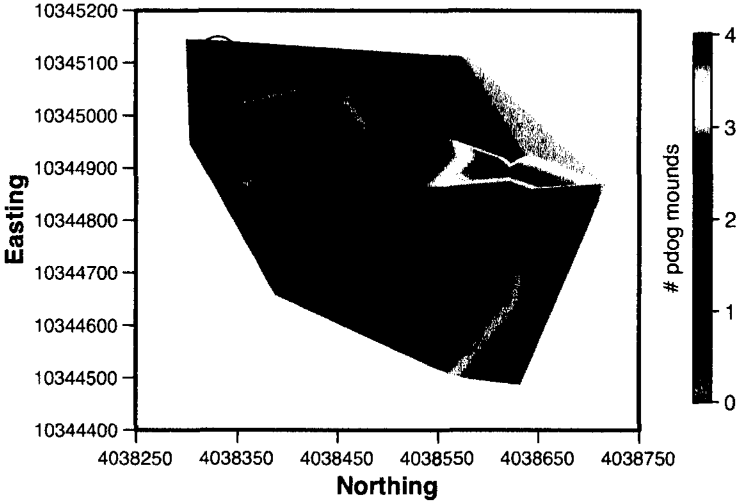

% Cover Bare Ground, Colony 5
Off-Colony 5
On-Colony 5
Entomophilous Forb Cover
Off-Colony 5
On-Colony 5
Easting
Northing
10345200
10345150
10345100
10345050
10345000
10344950
10344900
10344850
10344700
10344550
10344400
4037500
4037600
4037700
4037800
4037900
4038000
4038200
4038300
4038350
4038400
4038500
4038600
4038650
4038700
4038800
% bare ground
90
60
30
0
Insect Visits
5
10
15
30
45
60
85
% cover forbs
50
40
30
20
10
0

Colony 5

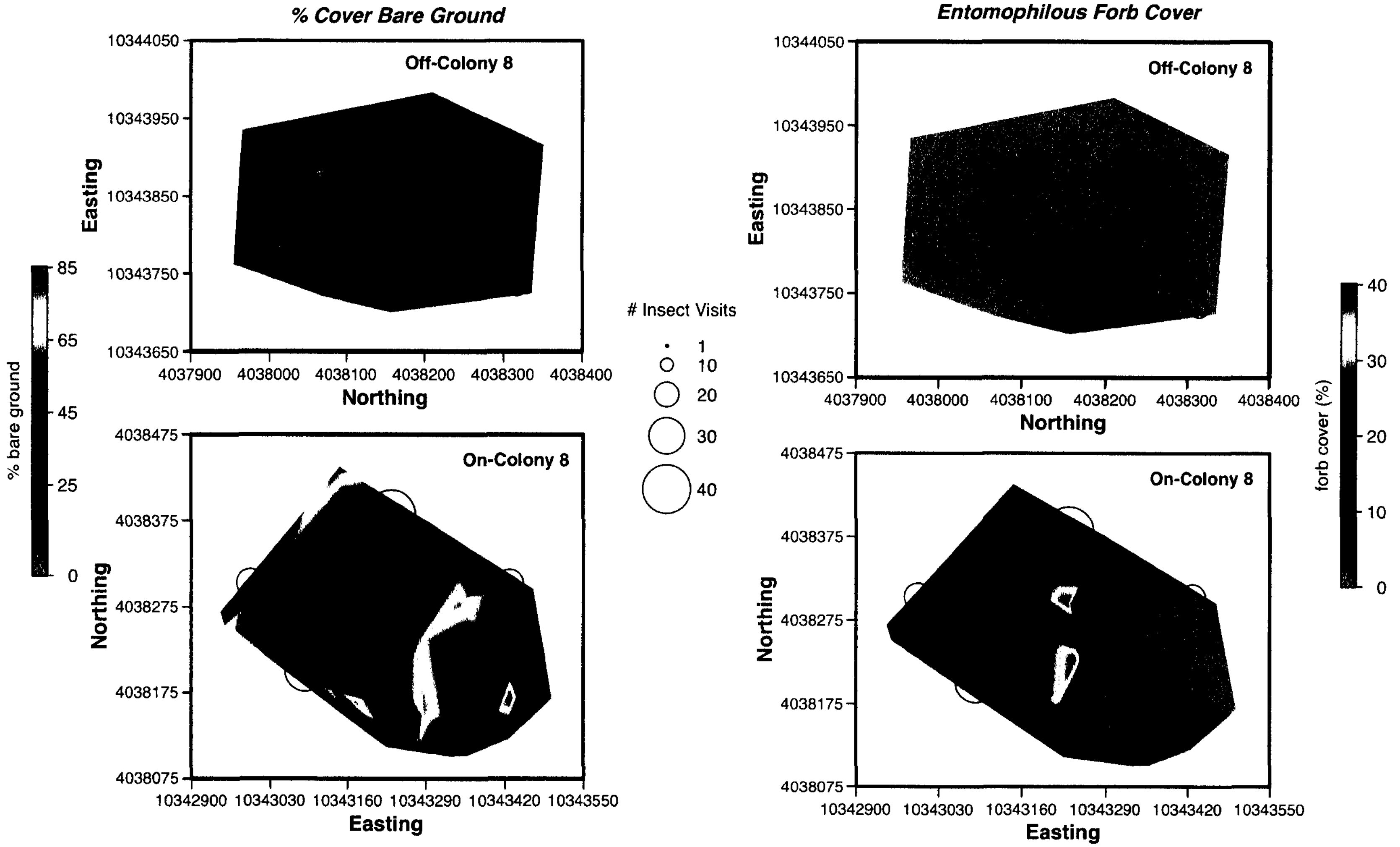
Floral Biomass for 16 Most-visited Plants (g/m²)



Mound Density, mounds/78 m² Colony 5

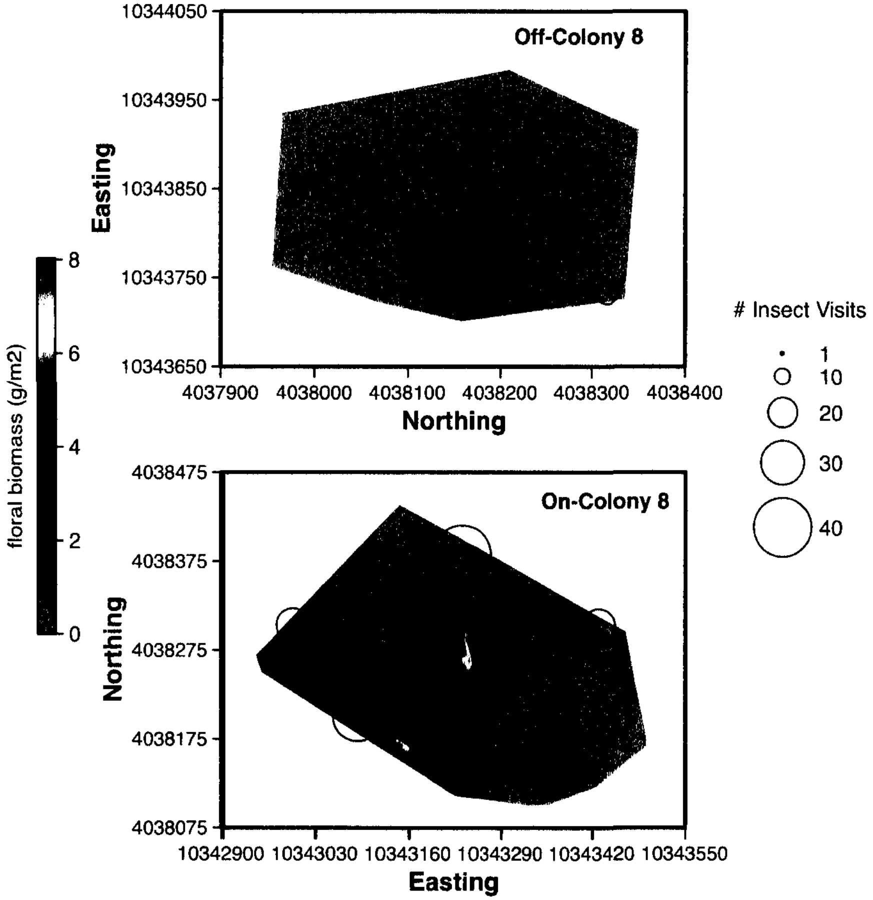


Colony 8

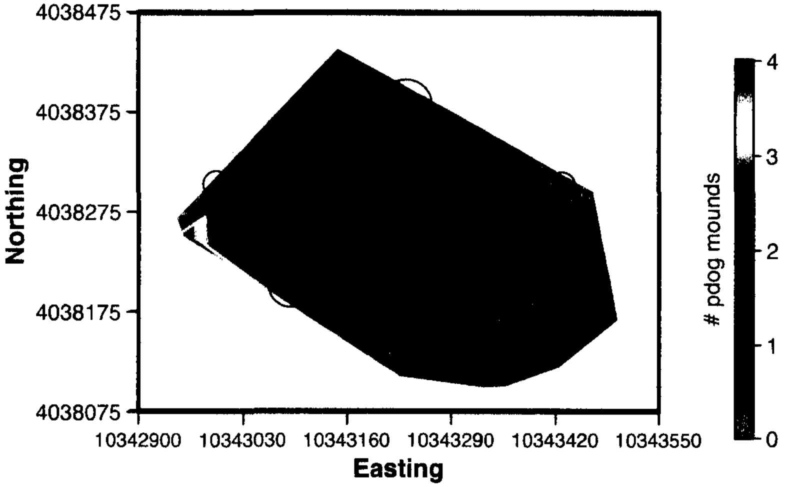

% Cover Bare Ground
Entomophilous Forb Cover
Off-Colony 8
On-Colony 8
Off-Colony 8
On-Colony 8
Easting
Northing
10344050
10343950
10343850
10343750
10343650
4037900
4038000
4038100
4038200
4038300
4038400
4038475
4038375
4038275
4038175
4038075
10342900
10343030
10343160
10343290
10343420
10343550
% bare ground
0
25
45
65
85
Insect Visits
1
10
20
30
40
forb cover (%)
0
10
20
30
40

Colony 8

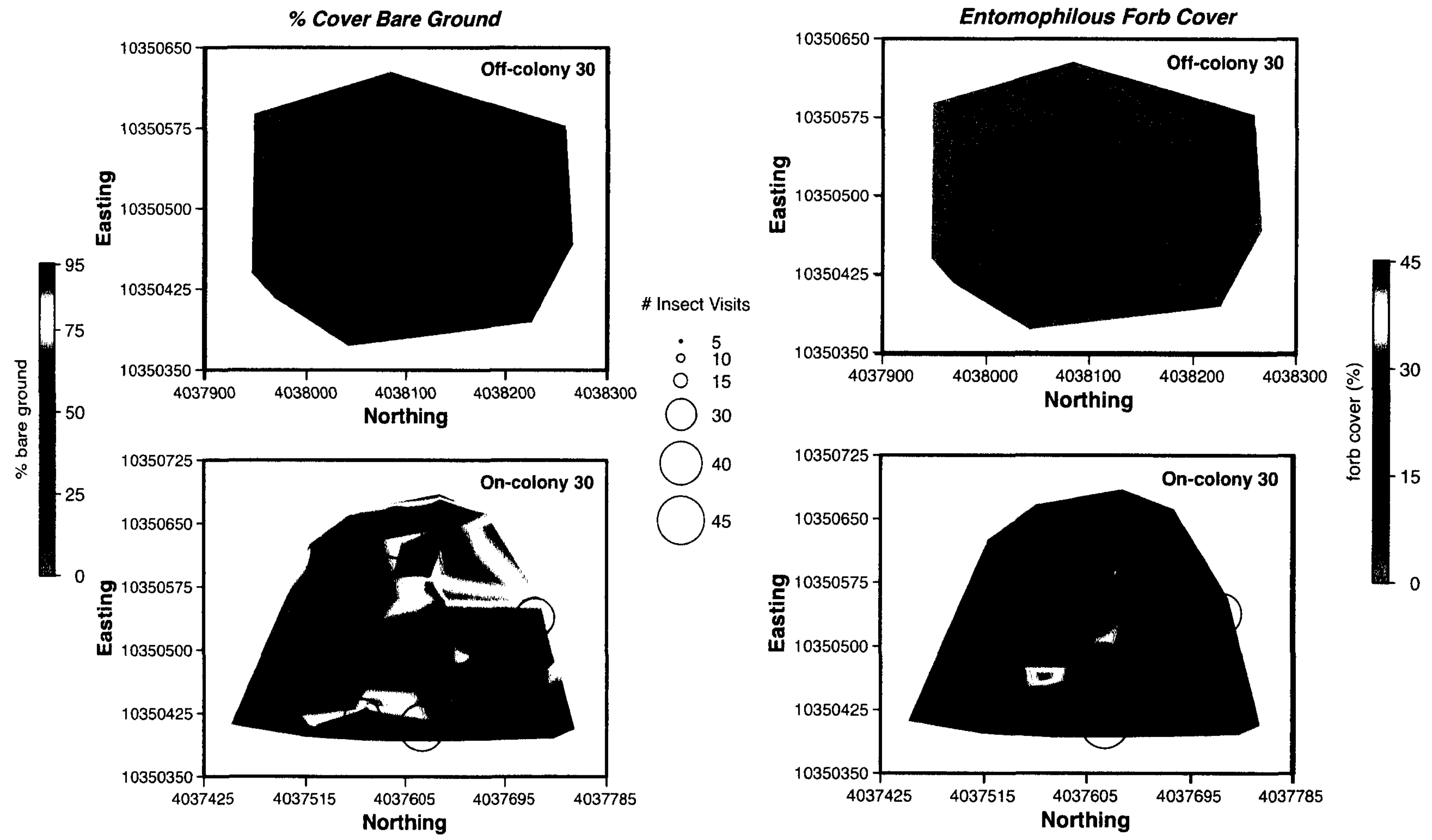
Floral Biomass of 16 Most-visited Plant Species (g/m^2)



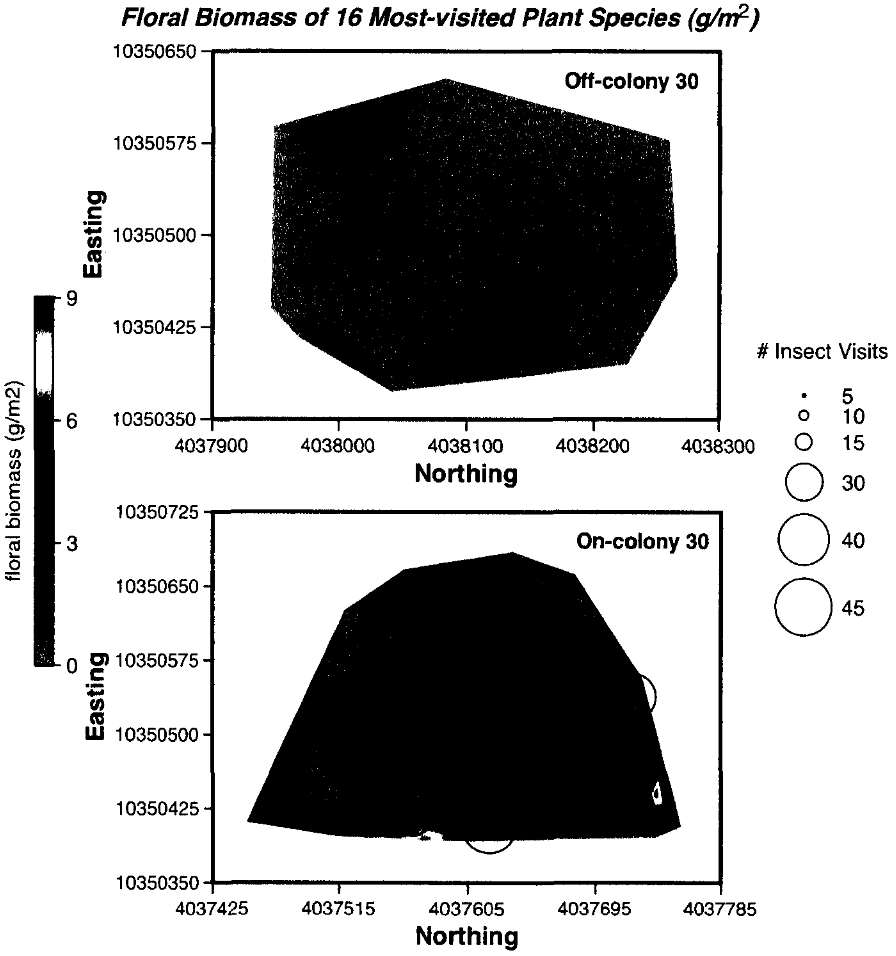
Mound Density (#/78 m^2), Colony 8

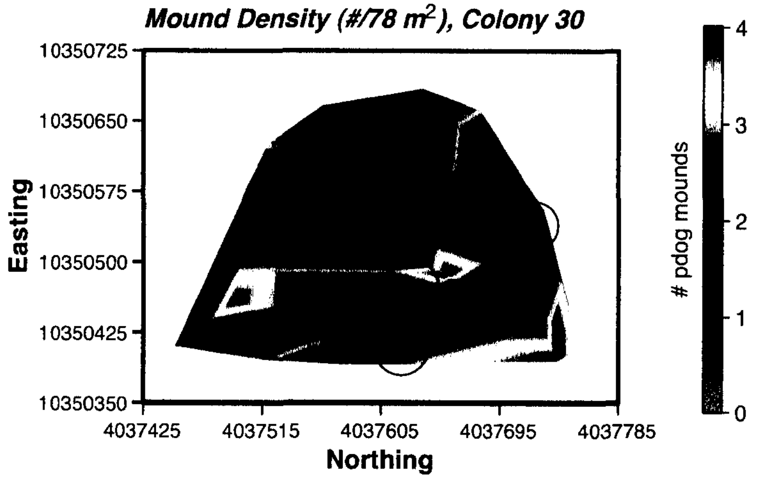


Colony 30

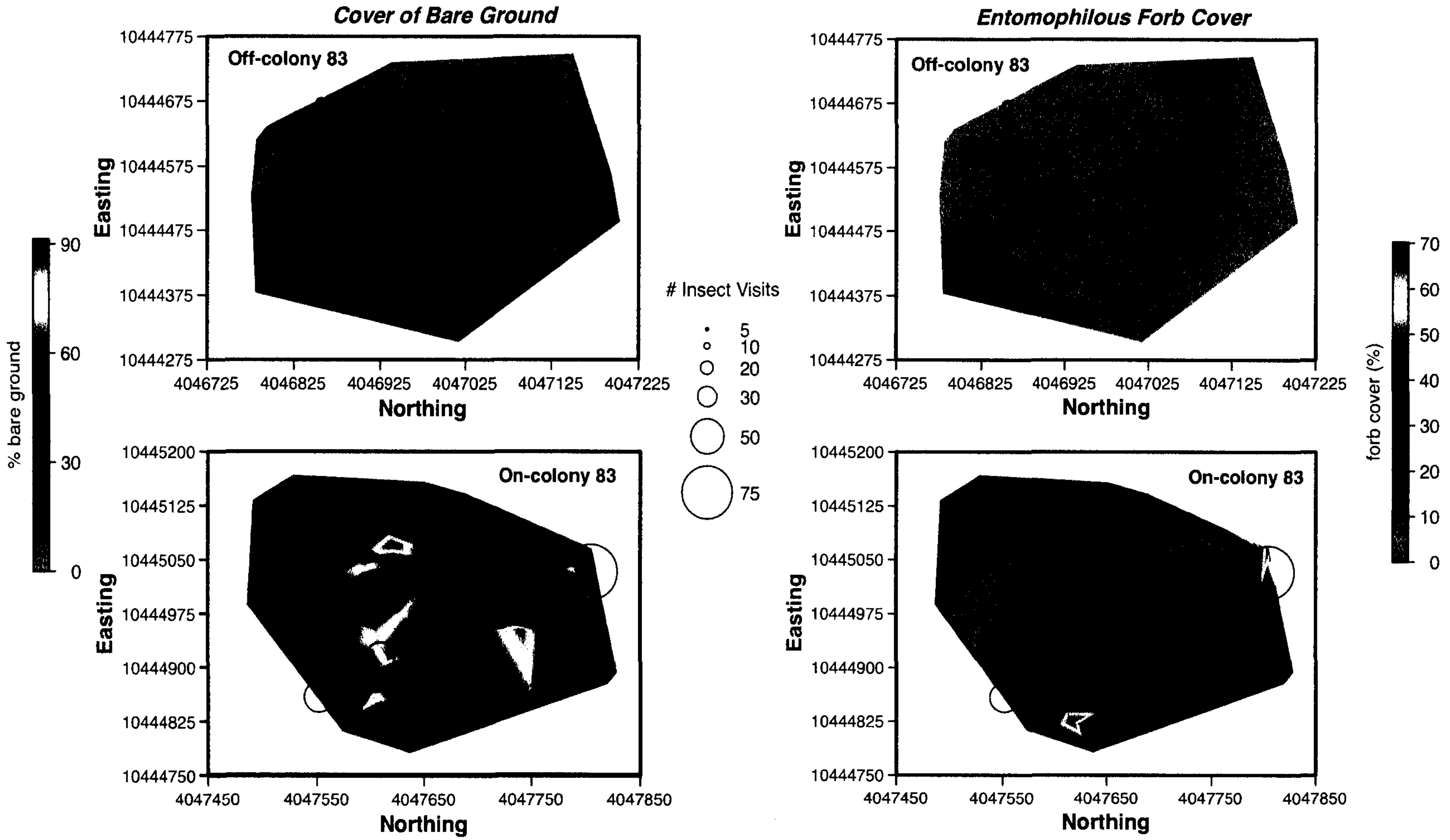

% Cover Bare Ground
Entomophilous Forb Cover
Off-colony 30
On-colony 30
Easting
Northing
10350350
10350425
10350500
10350575
10350650
10350725
4037900
4038000
4038100
4038200
4038300
4037425
4037515
4037605
4037695
4037785
% bare ground
0
25
50
75
95
Insect Visits
5
10
15
30
40
45
forb cover (%)
0
15
30
45

Colony 30

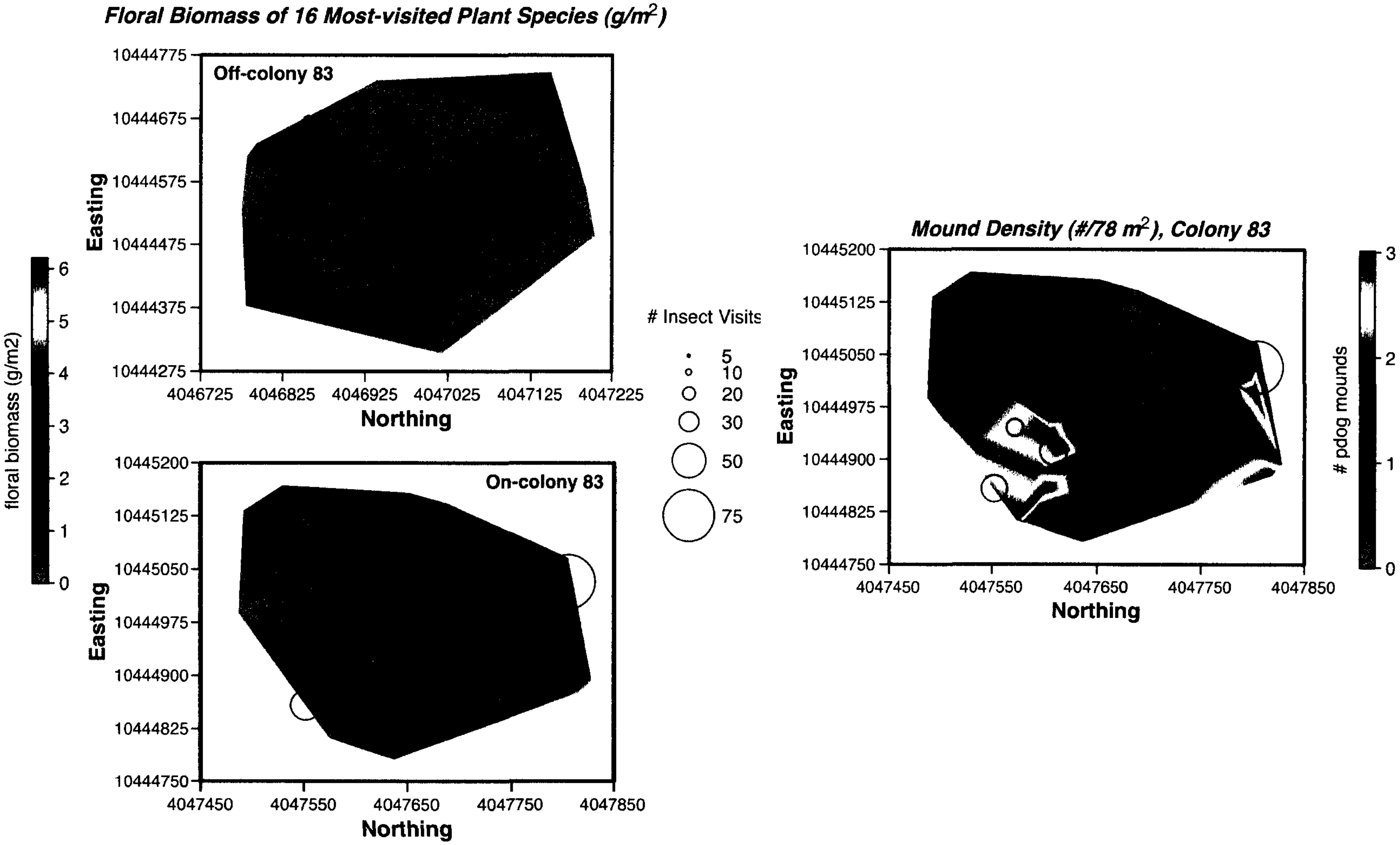

Floral Biomass of 16 Most-visited Plant Species (g/m²)


Mound Density (#/78 m²), Colony 30

Colony 83


Cover of Bare Ground
Entomophilous Forb Cover
Off-colony 83
On-colony 83
Easting
Northing
10444775
10444675
10444575
10444475
10444375
10444275
4046725
4046825
4046925
4047025
4047125
4047225
10445200
10445125
10445050
10444975
10444900
10444825
10444750
4047450
4047550
4047650
4047750
4047850
% bare ground
0
30
60
90
Insect Visits
5
10
20
30
50
75
forb cover (%)
0
10
20
30
40
50
60
70

Colony 83


Floral Biomass of 16 Most-visited Plant Species (g/m2)
Off-colony 83
On-colony 83
Easting
Northing
10444775
10444675
10444575
10444475
10444375
10444275
4046725
4046825
4046925
4047025
4047125
4047225
10445200
10445125
10445050
10444975
10444900
10444825
10444750
4047450
4047550
4047650
4047750
4047850
floral biomass (g/m2)
0
1
2
3
4
5
6
Insect Visits
5
10
20
30
50
75
Mound Density (#/78 m2), Colony 83
pdog mounds
0
1
2
3

APPENDIX C: Entomophilous plant species found at all on-colony and off-colony sites in 2003 to 2005 (including PNG colonies 5,8,30,35,62,66, and 83 and the paired uncolonized comparison site for each).

FAMILY	ENTOMOPHILOUS SPECIES	ON	OFF
AGAVACEAE	*Yucca glauca*	X	X
ALLIACEAE	*Allium textile*	X	
APIACEAE	*Lomatium orientale*	X	X
ASTERACEAE	*Chrysopsis villosa*	X	X
	Chrysothamnus nauseosus	X	
	Cirsium arvense	X	
	Cirsium ochrocentrum	X	
	Cirsium undulatum	X	X
	Erigeron pumilus	X	X
	Grindelia squarrosa	X	X
	Gutierrezia sarothrae	X	X
	Happlopappus spinulosus	X	X
	Helianthus petiolaris	X	X
ASTERACEAE	*Lactuca ludoviciana*	X	X
	Liatris punctata	X	X
	Lygodesmia juncea	X	X
	Machaeranthera tanacetifolia	X	X
	Nothocalis cuspidata	X	
	Picradeniopsis oppositifolia	X	X
	Ratibida columnifera	X	X
	Rudbeckia hirta	X	
	Senecio spartoides	X	X
	Senecio tridenticulatus	X	X
	Stephanomeria pauciflora	X	X
	Thelesperma megapotamium		X
ASTERACEAE	*Tragopogon dubius*	X	X
BORAGINACEAE	*Cryptantha crassisepela*	X	

FAMILY	***Species***	**ON**	**OFF**
BORAGINACEAE	*Cryptantha jamesii*	X	X
	Cryptantha minima	X	X
	Lappula marginata	X	X
	Lappula redowskii	X	X
	Lithospermum incisum	X	X
BRASSICACEAE	*Descurainia pinnata*	X	X
	Erysimum asperum	X	X
	Lesquerella ludoviciana	X	X
	Sisymbrium altissimum	X	X
	Thalspi arvense	X	
	Lepidium densiflorum	X	X
CACTACEAE	*Coryphantha vivipara*	X	X
	Echinocerus vidriflorus	X	X
	Opuntia humifusa	X	X
	Opuntia polyacantha	X	X
CAPPARIDACEAE	*Cleome serrulata*	X	X
	Pollanisia dodecandra	X	
CHENOPODIACEAE	*Chenopodium album*	X	X
	Chenopodium incanum	X	X
	Kochia scoparum	X	X
	Salsola iberica	X	X
COMMELINEACEAE	*Tradescantia occidentalis*	X	X
CONVOLVULACEAE	*Evolvulus nuttallianus*	X	
EUPHORBIACEAE	*Euphorbia fendleri*	X	X
	Euphorbia marginata	X	
FABACAEAE	*Astragalus bisculatus*	X	X
	Astragalus crassicarpus	X	
	Astragalus gracilis	X	
	Astragalus missouriensis		X

FAMILY	*Species*	**ON**	**OFF**
FABACEAE	*Astragalus shortianus*	X	X
	Dalea candida	X	
	Lupinus pusillus	X	X
	Melilotus officinalis	X	X
	Psoralea tenuiflora	X	X
	Sophora nuttalliana	X	X
	Vicia linearis		X
LILLIACEAE	*Leucocrinum montanum*	X	
LINACEAE	*Linum rigidum*	X	X
MALVACEAE	*Sphaeralcea coccinea*	X	X
NYCTAGINACEAE	*Abronia fragrans*	X	
	Oxybaphus linearis	X	X
	Tripterocalyx micranthus	X	X
ONAGRACEAE	*Guara coccinea*	X	X
	Oenothera albicaulis	X	X
	Oenothera caespitosa	X	
	Oenothera coronopifolia	X	X
	Oenothera harringtonii	X	
PAPAVERACEAE	*Argemone polyanthemos*	X	X
POLEMONIACEAE	*Ipomopsis laxiflora*	X	X
PORTULACACEAE	*Portulaca oleracea*	X	X
	Talinia parviflora	X	X
POLYGONACEAE	*Eriogonum effusum*	X	X
	Polygonum douglasii	X	
	Rumex venosus	X	X
RANUNCULACEAE	*Delphinium geyeri*	X	
SANTALACEAE	*Commandra umbellatum*	X	

FAMILY	***Species***	**ON**	**OFF**
SCROPHULARIACEAE	*Penstemon albidus*	X	X
	Collinsia parviflora	X	X
SOLANACEAE	*Solanum heterodoxum*	X	
	Solanum rostratum	X	
	Solanum trifolium	X	
VERBENACEAE	*Lippia cuneifolia*	X	
	Verbena bracteata	X	
VIOLACEAE	*Viola nuttallii*	X	