Species interactions across three trophic levels: *Cynomys ludovicianus* colonies increase floral visitation by insects.

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Abstract:

Black-tailed prairie dogs (*Cynomys ludovicianus*) change vegetation structure and composition on the mixed grass prairie and shortgrass steppe, with active colonies showing higher herbaceous dicot coverage, reduced canopy height, and an increase in bare ground, allowing for higher germination of flowering annuals. Extensive (> 40 ha) *Cynomys* colonies create large landscape patches within the prairie matrix, which pollinating insects should react to favorably if indeed floral resources are increased, and may perceive or utilize as a differing habitat type. In early summer 2003, and again throughout the entire growing season in 2004, floral resources were measured on a total of 6 colony sites on the SGS-LTER. Diurnal insect floral visitation was also measured at these same sites. Total abundance of inflorescences from all zoophilic species increased on colony sites in both years. Total frequency of insect visitation also increased on colony sites. The gross diversity of the community of diurnal insects by seems also to track the species diversity of the floral resources present in a given year. These findings show a clear link between three trophic levels on the shortgrass steppe.

Methods:

Sampling occurred on **4 colony sites** in **May-early July of 2003** (Towns 5, 8, 62, and 66). To increase statistical power, and due to the plague-out of Town 62 in 2004 as well as widely differing weather patterns during each year, sampling occurred on **5 colony sites** in **May-early September of 2004** (Towns 5, 8, 35, 66, and 83). Each site contained a colony and its paired, uncolonized control area (matching soil type, land-use history, aspect, and agricultural propagule rain) located as close together as possible. The basic sampling unit is termed a Floral-Resource-Visitor **(FRV)** plot. In each year, 12 FRVs were randomly placed on each colony site to determine floral resources: 6 on colony area and 6 on control area.

Floral Resource Sampling

FRV plots were designed to count floral resources at multiple spatial scales, because stochastic variance in spatial distribution of patchy resources, but also accuracy, decreases with increasing plot size. **In 2003, FRVs were 100 m^2 total** (for determination of species-area curves), and floral counts were collected from one 1 m^2 subplot and two 10 m^2 subplots located within the larger plot. **In 2004**, sampling was intensified in an attempt to reduce variance and better quantify the average floral resource density, so that **FRVs were 200 m^2 total**, with floral counts taken from five subplots within (two 1 m^2, two 10 m^2, and one 20 m^2 subplot).

Floral counts were done for both open flowers and inflorescences, for all zoophilic species. All counts were square-root transformed for statistical analysis.

OPEN FLOWERS give a measurement of the actual floral resources available to the insect community on the day of sampling.

INFLORESCENCES provide a less time sensitive measurement of floral resources, since they are visible both before flowers open as well as after fruit has set.

Above: *S. coccinea* flowers (top, two open flowers shown) and inflorescences (bottom, 9 late infl.)

Insect Visitor Sampling

I returned to FRV plot sites to quantify insect community composition and visitation rates. All sampling was done during sunny, calm, warm weather to minimize variation caused by weather. Sampling was always paired for day and time, with an FRV sampled from both the colonized and uncolonized area of a colony site within the same 100 minute period. Sampling of a FRV was **timed for 40 minutes** and all insects observed foraging for nectar and/or pollen were captured by sweep net for later identification, and I noted what plant species they had been foraging on when captured. **Four FRV pairs per colony site were sampled in 2003**, giving a total of 341 captures during 1280 minutes total sampling time. **Five FRV pairs per colony site were sampled in 2004,** giving a total of 725 captures during 2000 minutes total sampling time.

"Morpho-taxic" diversity categories for insects

As I am currently unable to identify all captured insects to species, a gross determination of diversity of the insect community was calculated by placing all samples into groups determined by both morphology as well as lowest possible identified taxon. This is based on the premise that ecological niche and function for a potential pollinator has in some way to do with its size and those life history characters common to its familial (or lower) taxon. For instance, the two bees below are both ground-dwelling bees in the family Halictidae. Yet the larger *Augochlora* individuals shown foraging on *Opuntia* on the left obviously move more pollen, forage differently, and preferentially visit certain flower sizes than the much smaller *Halictus* individual shown foraging on *S. coccinea* to the right. Also, the larger *Augochlora* are primitively social, with a worker caste. However, since many bees of differing genera look extremely similar to each of these specimens, they can be placed into the broad, morpho-taxic groups of **"large halictids" (left) vs. "small halictids" (right).** All captures fall into one of 30 such groups and diversity was assessed in this manner.

Comparison of typical vegetation for uncolonized (*above*) sites, dominated by anemophilic graminoids, vs.... colonized (*below*) sites, which appear to have greater floral resources and more visible flowers.

Rationale:

Or, why on earth would there be more flowers and potential pollinators on a prairie dog town? Don't they eat everything?

Prairie dogs *do* appear to decimate the vegetation, especially where colony growth remains unchecked and activity is intense. However, prairie dogs prefer anemophilic graminoids (wind-pollinated grasses) to most zoophilic flowering plants (insect-pollinated forbs). Over time, this changes the vegetation structure and composition by:

- increasing floral resource density above that of surrounding prairie
- affecting which species are present - some zoophilic plants are more prevalent on, or even restricted to, colony sites, and vice-versa
- lowering canopy height, making open flowers and inflorescences more visible to foraging insects

But what about all the disturbance from mound building, and all the bare ground on colony sites?

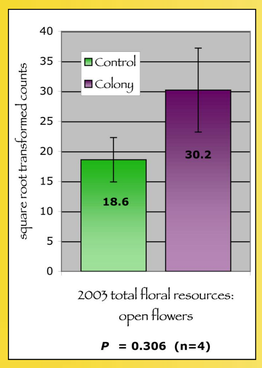
Mounds actually seem to act as refuges for certain flowering plants, and are often surrounded or even covered with flowers. Also, an increase in bare ground is actually favorable for most diurnal, flower-foraging insects on the SGS, because:

- native, ground-dwelling bees require bare ground for suitable nest sites
- bombyliids (bee flies) and meloids (blister beetles) parasitize these same bee nests, and so are also dependant on bare ground
- reflective surfaces created by bare ground allow for thermoregulatory activities, and open puddles on bare ground attract puddling Lepidoptera

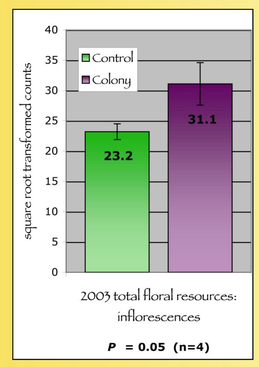
Results and Discussion:

NOTE: all *P* values were determined using colony sites as a random main effect, so that all conclusions can be drawn about "*Cynomys* colonies on the SGS" instead of only for these 6 towns. All t-tests are double-sided and paired. All graphs show means +/- one standard error.

2003 Floral Abundance



2003 Insect Abundance



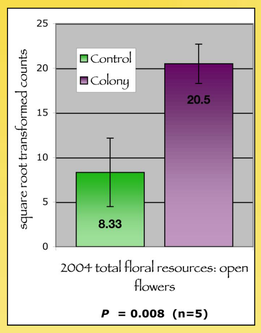
2003 FLORAL ABUNDANCE

While open flowers were not found to be significantly more abundant on colonies, this is probably due to the very large variance. Inflorescences of all zoophilic plant species, which had less stochastic counts, were significantly greater on colonies.

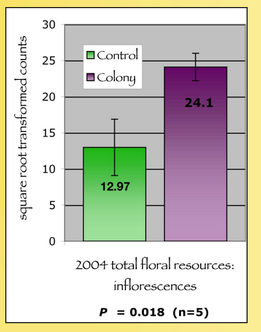
2003 VISITATION

There were significantly more insects foraging on colony sites compared to uncolonized areas. Data shown is the sqrt of the mean # captured per 40 minute sampling period. Insect abundance and activity seems to be predicted well by floral resource density.

2004 Floral Abundance



2004 Insect Abundance



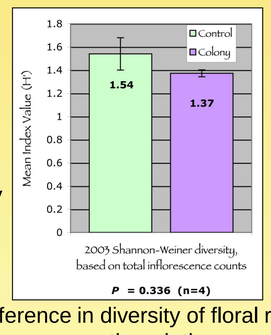
2004 FLORAL ABUNDANCE

Sampling intensity was increased in 2004, by adding an additional colony site, sampling over the entire growing season, as well as increasing total area sampled per site (see Methods). Variance in floral counts was successfully lowered, and both open flowers and inflorescences were significantly more dense on colonized areas.

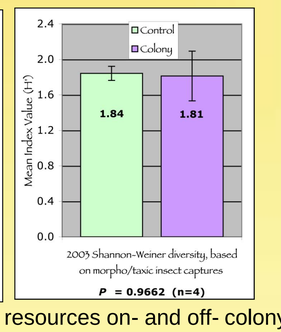
2004 VISITATION

Again, there were significantly more insects foraging on colony sites compared to uncolonized areas. Insect abundance and activity seems to be predicted well by floral resource density.

2003 Diversity (H')

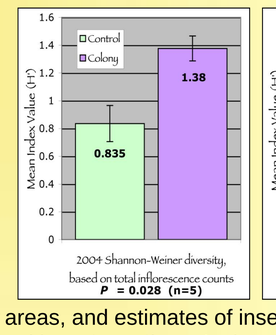


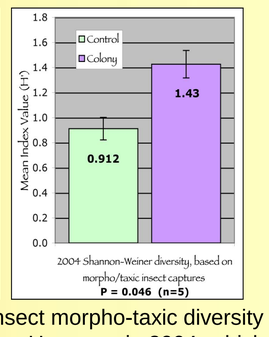
2004 Diversity (H')



Diversity (Shannon-Weiner)

H' was calculated for both years' data, using total inflorescence counts to determine diversity of floral resources, and using "morpho-taxic" categories (see Methods) to estimate gross diversity of the diurnal insect floral visitor community. Overall, diversity of the insect group appears to be closely related to diversity of the floral resources.





In 2003, there was no significant difference in diversity of floral resources on- and off- colony areas, and estimates of insect morpho-taxic diversity also was equal on both landscape types, even though there were both ***more*** inflorescences and insects on the colonies. However, in 2004, which exhibited very different weather patterns and prolific zoophilic species than those seen in 2003, diversity of both floral resources and insects was significantly greater on colony areas. Thus the insect community seems not only to track the overall density of floral resources, but the diversity of these resources as well. This conforms to *a priori* hypotheses regarding the connection between the two trophic levels, since different zoophilic species provide differing amounts of nectar and pollen, and are of differing shapes, sized, and reward-access difficulty. Different groups of insects, concomitantly, exhibit differing resource needs and foraging abilities.

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