

THE EFFECTS OF CLIMATE CHANGE ON THE TIMING
AND ABUNDANCE OF DIPTERA IN A SUBALPINE
MEADOW

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Abstract

Diptera play a critical role in alpine and subalpine ecosystems, though they are little studied in terms of what guides their timing and abundance. In order to reveal what cues dipteran timing this study was conducted for 24 years, using a Malaise trap to capture the insects, dipteran distributions were sampled once a week for 48 hours. Local climate changes have been observed at the study area at the Rocky Mountain Biological Laboratory in Gothic, CO. This along with the anthropogenic forcings that have been observed around the world indicate that a warmer climate is likely in the future. Changes in temperature and precipitation have shown to affect the phenology of many species in the Colorado Rocky Mountains but flies have been previously unstudied. In this study the Diptera order was studied as a whole along with the dipteran families of the syrphids (Syrphidae), tephritids (Tephritidae), and the crane flies (Tipulidae). The June temperatures appear to have the most effect on the timing of dipteran peak biomass, though snowmelt was also significantly related to peak timing.

Introduction

Changes in the global climate due to an influx of greenhouse gases are already altering the environments within which species must survive (Parmesan 2007; Vitousek, 1994). Plants and animals must adjust as the distribution of resources for organisms change as a result of climate change. How populations fluctuate as a result of changes will have broad reaching effects on our world.

In the western United States spring is coming earlier as a result of climate change this could lead to June temperature increases and earlier snowmelt (Cayan et al. 2001). This is reinforced by long-term studies in the Colorado Rocky Mountains at high elevations that indicate that the date of snowmelt has been occurring earlier in the year over the past 35 years (Miller-Rushing et al. in prep.). In the Rockies, the start of the growing season is dictated by when the snow melts (Inouye 2008). Once the snow melts, plants begin to grow and the insects increase in abundance as more food is available and the temperature rises. As the date of snowmelt becomes earlier, organisms that rely on snowmelt as a cue are appearing earlier as well (Inouye 2008). At the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA changes in the phenology of flowers and local climate changes have been documented in several long-term studies (Inouye 2008). However, absent from studies at the RMBL and elsewhere are data describing how insect phenology is changing. Inouye (2008) has documented that the phenologies of plants, though highly variable in their roles within ecosystems, are responding to similar climate cues, like snow melt, in predictable patterns. Insects are integrally linked to plants in their roles as pollinators, herbivores and decomposers, so it is possible that insects follow the same cues as plants at the beginning of the season and may be responding to climatic changes as well. A study, like this one of general insect abundance distributions in an ecosystem, could reveal trends and correlations that may inform what climatic variables effect the timing and abundance of insect populations.

In alpine areas, Diptera, in particular, have a high abundance and fill a range of ecological niches that at lower elevations are filled by other insect orders (Kearns 1992). Sampling of Diptera and other insect populations can pose challenges to researchers as their populations have a high amount of variability from year to year and appear to be

correlated with seasonal climatic fluctuations (Rossi et al. 2007, Harper & Peckarsky 2006). In studying insects of any type, long-term studies are helpful for extrapolating these year-to-year fluctuations from long-term trends and few, if any, studies have the opportunity to look at these fluctuations over a period >20 years. Fortunately at the RMBL, David Inouye and Michael Soulé have gathered data on the abundance and biomass of insects since 1984. They have set out a Malaise trap for 48 hours once a week from mid June to mid August, creating a unique data set that reflects temporal variation in insect abundance and biomass. These data, combined with the ongoing studies of the climate and plant phenology at the RMBL, will improve our understanding of the temporal dynamics of population fluctuations and relationships among species in a subalpine ecosystem and has the potential to provide insight on how communities may respond to a changing climate.

The Malaise trap captures mostly Diptera and Hymenoptera, with other insect orders occasionally represented due to the design of the trap and relative abundance of insect orders (Hughes 2000, Kearns 1992). In this study, I investigated the changes in the seasonal distribution of Diptera while also considering other insect taxa collected. The Malaise trap has proved effective in trapping a diversity of insects by many researchers in the Rocky Mountains and around the world (Hughes 2000, Kearns 1992, Kitching et al. 2004).

In this study, I analyzed David Inouye's data spanning the past two decades on insects trapped in a subalpine meadow at the RMBL and continued data collection using the same techniques. In analyzing the data, I investigated the number of insects collected on a weekly basis to determine the influences of climate change on insect abundance and phenology and also possible correlations between the timing of plant and insect abundances.

Methods

Study site

The study site is located in the Gothic Research Meadow, a subalpine meadow, at the Rocky Mountain Biological Laboratory (RMBL) in Gunnison County, Colorado (38° 57' N, 106° 59' W; elevation 2,912 m). The Malaise trap is located in a level area of the meadow.

Data collection

Starting in 1984, a Malaise trap was set out once a week for 48 hours from May until August. Michael Soulé collected data from 1984 to 1991, when David Inouye took over the project and continued it until 2008. The insects captured at the end of the 48-hour period were sorted into Diptera, Hymenoptera, and other. Then they were counted, dried for at least 72 hours, and weighed. Beginning in 1991, the insects were sorted to lower taxonomic unit when possible, so that data from this period on reflects numbers on the abundance of various families of flies.

A 20m square plot was established with the malaise trap in the center, and once a week in 2008 the flowering plants were recorded along with their relative abundance in the plot.

Weather data

Climatic data since for the study period (1984-2008) was obtained from the NOAA National Climatic Data Center, Asheville, NC. Snowmelt data for the study period was collected by billy barr at a site within 2 km of the research site and was recorded as day of first bare ground.

Analysis

For each identified group of insects, the seasonal distribution was quantified by determining onset, peak, and end. These measures were then compared across years using multiple variable regression analysis in the program R (R Development Core Team 2008). Dates for onset, peak, and end were converted so that they reflected the days after the vernal equinox of each year to account for shifts in the Earth's system (Sagarin 2001). Dates were also converted to reflect the time elapsed since last day of snowmelt. The two sets of days, those relative to vernal equinox and snowmelt, were the dependent variables in the analysis while the climatic variables were the independent variables. Climatic variables used included: June and July total precipitation and mean temperature, as well as snowmelt date.

Peak flower abundance and day was determined by data from David Inouye's wet meadow plots located within 1 km of the research site. Multiple regression analysis was run using this data relative to peak abundance and, when available, peak biomass. Regression was also run on peak amount relative to previous year's peak flower abundance.

When a sample first reached the minimum number of individuals it reached the onset cutoff and the season began. The season continued until the amount of individuals for a sample per week last fell below the cutoff number. For the tephritid and crane flies the distribution was said to begin when at least 2 individuals were found in a sample and end with the last week with 2 or more of that type of fly. For the syrphids the distribution was said to begin when 5 or more individuals were first found in a year and end on the last week that no less than 5 individuals were found. The duration of the season and number of individuals counted on the week with the highest abundance and biomass within a year also helped to quantify the distribution.

Results

Diptera

For every sample of Diptera collected per week in the Malaise trap, an average of 281 (SD = 255.8) individuals were collected with an average biomass of 0.56g (SD = 0.50). Data spanned from 1984-2007. The peak day of biomass for Diptera typically occurred on July 14 (SD = 11 days). The day of biomass peak transformed to reflect the number of days after vernal equinox was significantly correlated with the mean temperature in June ($p < 0.001$, fig. 1, Table 1.) and day of snowmelt ($p = 0.019$). Though, June temperatures best explained the differences among years (adj. $r^2 = 0.38$). For every degree that June temperatures increased, the day of peak Diptera biomass became 4.3 (SE = 1.1) days earlier.

It was assumed that snowmelt had an affect on the day of peak biomass, so dates were adjusted to account for day of snowmelt. The day of peak biomass relative to

snowmelt day was also significantly correlated to mean June temperatures ($p = 0.032$; adj. $r^2 = 0.16$) and snowmelt date ($p = 0.003$; adj. $r^2 = 0.29$), except snowmelt explained more of the variation over the years. As the snowmelt occurs a day later, the period between the biomass peak and snowmelt gets 0.6 days shorter. As the snowmelt occurs a day earlier, the period between the biomass peak and snowmelt gets 0.6 days longer.

Syrphid (Syrphidae)

On average, the onset of the syrphid fly season was July 1 (SD = 17 days), the peak occurred several days later on July 7 (SD = 14 days), and the end of the season occurred July 26 (SD = 13 days). The average duration of the syrphid season was 4.0 (SD = 3.0) weeks. On average the peak abundance of syrphid flies was 18 individuals (SD 26, fig. 2). In two years (1991, 1997) of the study period from 1991-2007, none of the samples reached the onset cutoff of 5 individuals and so were not represented in the analysis. As the day of the peak abundance relative to the vernal equinox abundance became later, the peak abundance decreased by 1.1 individuals per day ($p = 0.034$, Table 2). The peak abundance was also significantly correlated with the day of onset; that is, as the day of onset gets later the peak abundance decreases by 0.9 individuals per day ($p = 0.050$). When the date of peak abundance was adjusted to account for day of snowmelt, the resulting peak was significantly related to the peak abundance ($p = 0.038$) and snowmelt ($p = 0.006$; adj. $r^2 = 0.583$), as determined by multiple regression. When June temperature was substituted for snowmelt in the multiple regression model, peak date of abundance was related to peak abundance, June precipitation, and temperature ($p < 0.001$, 0.021 and 0.009; adj. $r^2 = 0.743$). The syrphid onset relative to snowmelt was significantly correlated with peak abundance ($p < 0.001$), June precipitation ($p = 0.021$) and temperature ($p = 0.037$; adj. $r^2 = 0.684$). Snowmelt also had a significant effect on the difference between snowmelt and onset ($p = 0.036$) and also on the difference between snowmelt and the end of the distribution ($p = 0.009$).

The duration of the syrphid season was not only significantly correlated with peak abundance ($p = 0.004$), but also July precipitation ($p = 0.009$; adj. $r^2 = 0.554$) as determined by multiple regression. Snowmelt and June precipitation and temperature were not significantly correlated to the duration of the syrphid season.

Tephritid (Tephritidae)

The onset of the tephritid fly season began on average on July 1 (SD = 16 days) and ended August 3 (SD = 10 days). The peak of the season typically occurred on July 11 (SD = 19 days) and the season lasted on average for 3.8 (SD = 3.4) weeks. The average peak abundance was 6 (SD = 4, fig. 2). Though, for five years during the study period from 1991-2007 the season never began (1996, 1997, 2002, 2003, 2004) because the onset cutoff was not reached, so onset and end dates are not available, and data was not available for two years (2000, 2001). The onset of the tephritid season relative to the vernal equinox was significantly correlated to the peak abundance ($p = 0.019$, Table 4) and the average temperature ($p = 0.014$) and precipitation in June ($p = 0.003$; adj. $r^2 = 0.767$). The peak and end of the tephritid distribution were not significantly correlated with any of the climatic variables tested.

The difference between the last day of snowmelt and the peak tephritid abundance ($p = 0.045$) and the difference between snowmelt and the end of the distribution were both

significantly correlated with snowmelt ($p = 0.008$). The peak abundance of individuals was significantly correlated to the day of snowmelt ($p = 0.009$) and the average temperature in July ($p = 0.017$; adj. $r^2 = 0.588$).

The tephritid flies were the only group of flies analyzed whose abundance was significantly correlated with peak flowering. The peak abundance of the tephritid flies was significantly correlated with the abundance of flowers from the previous year ($p = 0.002$), so that for every 100 flowers from the previous year's peak, there were 4 more tephritid flies collected on the week of peak abundance.

Crane fly (Tipulidae)

The onset of the crane fly season began on average on July 2 (SD = 14 days) and ended on July 28 (SD = 16 days). The peak typically occurred on July 15 (SD = 17 days), and the duration of the season lasted 4.0 (SD = 2.4) weeks. On average the peak abundance was 6 (SD=4, fig. 2). During two years (1992, 1995) in the study from 1991-2007, the crane flies never reached the onset cutoff, so the season never began, and for two years (2000, 2001), there were no data available. The peak abundance was significantly correlated with the last day of the season relative to vernal equinox ($p = 0.014$). The onset and peak days of the season had no significant correlations with any of the variables tested.

The day of the peak abundance of crane flies relative to snowmelt ($p = 0.0047$) and the onset relative to snowmelt ($p = 0.010$, Table 3) was significantly correlated with snowmelt. The end of the season relative to snowmelt was significantly correlated with peak abundance ($p = 0.022$) and snowmelt ($p = 0.008$; adj. $r^2 = 0.619$). The end of the season relative to snowmelt was also significantly correlated with July precipitation ($p = 0.035$). The duration of the season was negatively correlated with June precipitation ($p = 0.007$) and positively correlated with July precipitation ($p = 0.026$).

Discussion

All of the dipteran groups analyzed had a high amount of temporal and annual variability, reinforcing what others have said earlier that dipteran populations often fluctuate (Rossi et al. 2007, Harper & Peckarsky 2006). This study indicates though that much of this variation can be explained by climatic factors effecting the dipteran environment (Table 1).

Of the climatic variables analyzed June temperatures seem to be the best explanation for the variation in dipteran phenology (fig. 1, Table 1). Although snowmelt also explains some of the variability, June temperatures have a more significant impact. Inouye (2008) said that variations in flower phenology in alpine environments are attributed to date of snowmelt. If Diptera are following June temperatures and flowers are following snowmelt date this could lead to a potential ecological mismatch. Diptera rely on flowers and their prevalence at high altitudes in the absence of other pollinators indicates their significant role in alpine ecosystems (Kearns 1992). If snowmelt begins to occur earlier at a faster rate then June temperatures are adjusting, flower species that rely on Diptera for their proliferation may suffer reduced fitness. Conversely, Diptera can suffer reduced fitness as a result of not being able to get the nutrients from flowers, if their timing's don't match up.

While June temperatures best explained the variations in when the total peak dipteran biomass occurred, it is the day of snowmelt that best explains the difference between the day of the peak and the day of snowmelt. So, as snowmelt is occurring earlier the amount of days between snowmelt and peak biomass is getting longer. This indicates that Dipteran populations do not have the plasticity to adjust to the annual variations in snowmelt date, although they may be able to adjust to other climatic factors. The difference between snowmelt and day of peak abundance has a significant relationship for not just the larger dipteran order but also for the three families of dipteran studied as well further reinforcing the findings.

These results reinforce M.J.I. Briones et al. (1997), who found that soil-dwelling dipteran larvae are highly sensitive to temperature. Diptera go through a lifecycle that includes a larval, pupae, and adult form. In June and as the snow is melting many Diptera are still in their immature forms and would be susceptible to temperature fluctuations as Briones et al. have indicated.

These data were collected on a weekly basis throughout the summer and it is recognized that dates associated with Dipteran phenology are inherently inaccurate. The Malaise trap was set out for 48 consecutive hours per week and it is likely that the actual onset, end, and peak days were not captured. These phenological events could have occurred in between trapping samples. In the analysis, dates used were the first day of taking the sample and there was no way to extrapolate whether one day of sampling yielded a higher abundance than the other.

Much more still needs to be done to further this study. A further analysis of all the taxonomic groups recorded from each sample should be done. Along with, a further look into the relationship between flower phenology and dipteran phenology to determine how the dipteran species interact with flowers and effect their phenology, as well as vice versa.

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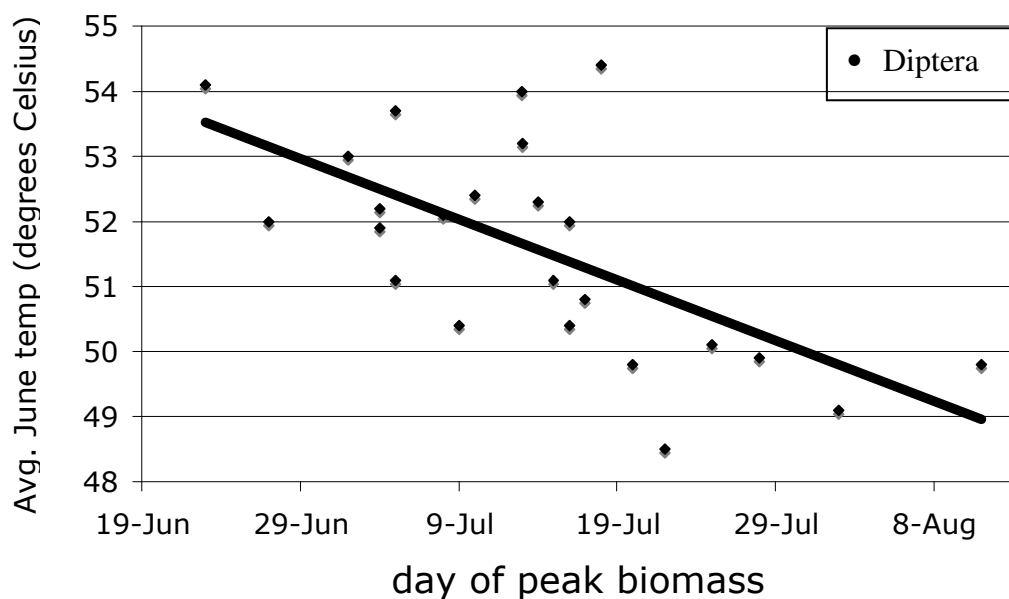


Fig. 1. The average June temperature for a year compared to the day of peak biomass of Diptera for a year. ($p < 0.001$, slope = -4.3, adj $r^2 = 0.377$, SE = 1.1)

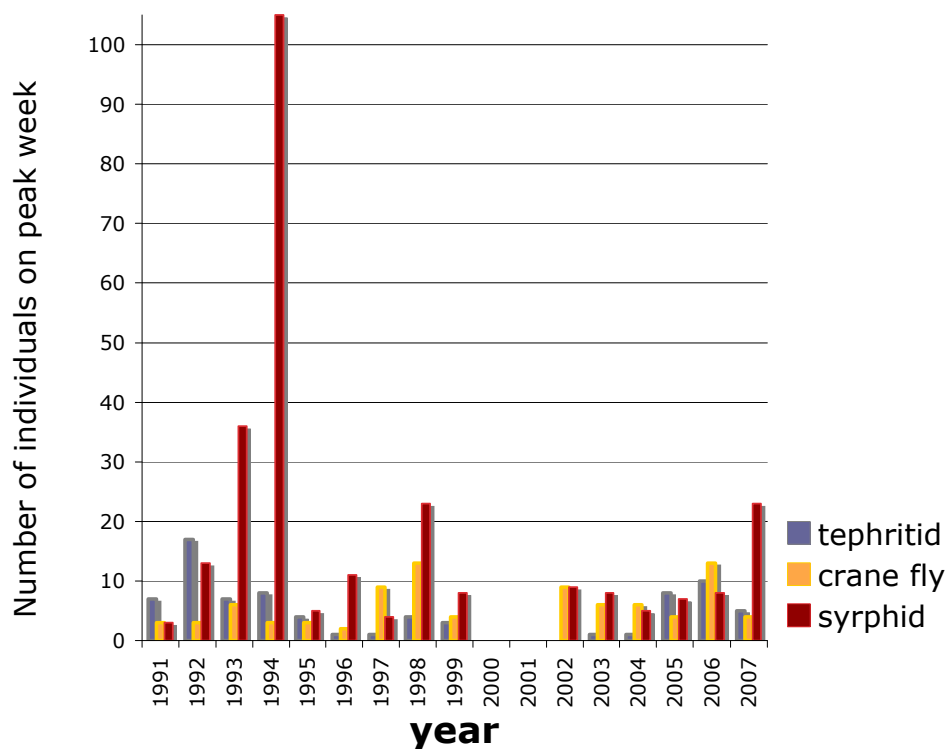


Fig 2. The peak abundance on the peak day of tephritids, crane flies, and syrphids across years.

Table 1.

DIPTERA ANALYSIS					
dependent	independent	estimate	std. error	p-value	adj. r squared
days between snowmelt and abundance peak	year	1.0717	0.5062	0.0477	0.1483
days between snowmelt and biomass peak	year	0.7691	0.3241	0.0268	0.1676
day of abundance peak					
	precip june			x	
	precip july			x	
	temp june	-7.055	1.999	0.002237	0.3643
	temp july			x	
day of biomass peak					
	precip june			x	
	precip july			x	
	temp june	-4.338	1.124	0.000846	0.3768
	temp july			x	
day of biomass peak					
	peak biomass			x	
	snowmelt	0.4372	0.1732	0.0193	0.1894
	precip july			x	
	temp july			x	
days between snowmelt and biomass peak					
	peak biomass			x	
	snowmelt	-0.5628	0.1732	0.00368	0.2936
	precip july			x	
	temp july			x	
days between snowmelt and biomass peak					
	precip june	-7.892	3.45	0.0321	0.1555
	precip july			x	
	temp june			x	
	temp july			x	

Table 2.

Syrphid analysis					
dependent	independent	estimate	std. error	p-value	adj. r squared
days between snowmelt and peak	year	2.1753	0.8696	0.0294	0.3046

days between snowmelt and onset					
year	2.1846	0.9403	0.0403	0.2682	
peak day					
peak abundance	-0.3083	0.1274	0.034	0.2882	
precip june			x		
precip july			x		
temp june			x		
temp july			x		
peak day					
peak abundance	-0.3083	0.1274	0.034	0.2882	
snowmelt			x		
precip july			x		
temp july			x		
days between snowmelt and peak					
peak abundance	-0.3125	0.1308	0.03801	0.583	
snowmelt	-0.8383	0.2397	0.00575	0.583	
precip july			x		
temp july			x		
days between snowmelt and peak					
snowmelt	-0.8654	0.2861	0.01155	0.4045	
precip july			x		
temp july			x		
days between snowmelt and peak					
peak abundance	-0.5838	0.1132	0.000599	0.7431	
precip june	-14.9636	5.3579	0.020957	0.7431	
temp june	5.6241	1.69	0.008829	0.7431	
precip july			x		
days between snowmelt and onset					
peak abundance	-0.3382	0.1533	0.0496	0.2436	
snowmelt			x		
days between snowmelt and onset					
peak abundance	-0.3382	0.1533	0.0496	0.2436	
precip june			x		
temp june			x		
days between snowmelt and onset					
peak abundance	-0.6101	0.1323	0.00127	0.6842	
precip june	-17.4689	6.2611	0.02105	0.6842	
temp june	4.825	1.9749	0.03717	0.6842	
days between snowmelt and onset					
peak abundance			x		
snowmelt	-0.7899	0.3314	0.03629	0.2806	
days between snowmelt and end					

	peak abundance snowmelt precip july temp july	-0.8294	0.2614	x 0.008882 x x	0.4303
duration					
	peak abundance snowmelt precip july temp july	0.08948	0.02359	0.00352	0.5537
		1.84658	0.57502	0.00931	0.5537
duration					
	peak abundance precip june precip july temp june temp july	0.08948	0.02359	0.00352 x 0.00931 x x	0.5537 0.5537

Table 3.

CRANE FLY ANALYSIS

dependent	independent	estimate	std. error	p-value	adj. r squared
duration					
	precip june	-1.7576	0.6788	0.0252	0.3222
end day					
	peak abundance temp june temp july precip june precip july	2.89	0.9911	0.014 x x x x	0.3847
end day					
	peak abundance snowmelt precip july temp july	2.89	0.9911	0.014 x x x	0.3847
days between snowmelt and peak					
	peak abundance snowmelt precip july temp july	-1.2962	0.3665	x 0.004661 x x	0.4895
days between snowmelt and onset					
	peak abundance snowmelt	-1.0906	0.3542	x 0.01048	0.4141

	precip july				x
	temp july				x
days between snowmelt and end peak	abundance	2.8466	1.0502	0.02192	0.6191
	snowmelt	-1.0838	0.3315	0.00844	0.6191
	precip july			x	
	temp july			x	
days between snowmelt and end peak	abundance			x	
	precip june			x	
	precip july	10.982	4.583	0.035472	0.2832
	temp june			x	
	temp july			x	
duration	peak abundance			x	
	precip june	-1.8526	0.551	0.007214	0.5554
	precip july	0.857	0.3294	0.026422	0.5554
	temp june			x	
	temp july			x	

Table 4.

TEPHRITID ANALYSIS

dependent	independent	estimate	std. error	p-value	adj. r squared
onset day	peak abundance	-2.1286	0.6663	0.01872	0.7674
	temp june	5.5594	1.6189	0.0139	0.7674
	precip june	19.7701	4.1564	0.00314	0.7674
days between snowmelt and peak	peak abundance			x	
	snowmelt	-1.1239	0.4739	0.0452	0.3394
	precip july			x	
	temp july			x	
days between snowmelt and end peak	abundance			x	
	snowmelt	-0.9065	0.2558	0.007582	0.5622
	precip july			x	
	temp july			x	
days between snowmelt and end peak	abundance	2.61	1.131	0.0499	0.3245
	temp june			x	
	precip june			x	
	precip july			x	

temp july		x			
peak abundance					
snowmelt	-0.24721	0.06987	0.00949		0.5884
precip july			x		
temp july	-1.4069	0.45035	0.01675		0.5884
peak abundance					
days between					
snowmelt and					
flower peak			x		
# peak flowers			x		
flower					
abundance of					
previous yr	0.004666	0.0009663	0.0019		0.7361