University of Alberta

The Impact of Climate on the Population of Indiana Bat (Myotis Sodalis)

by

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Abstract

The Indiana Bat (Myotis sodalis) population had decreased by 56% between 1967 and 2006. In summer 2006, a mysterious disease called “White Nose Syndrome” was first identified. Since then, the disease killed almost one million bats in North America. Many Biologists believe that both the population decrease before the appearance of the disease and WNS are associated with climate. In a joined effort with Yellowstone Ecological Research Center (YERC), US Fish and Wildlife Service (USFWS) and NASA Terrestrial Observation and Prediction System (TOPS), our study is a partial population viability analysis which aims to establish a link between bat population dynamic and climate before the appearance of WNS.

Acknowledgement

First, I thank my supervisor Subhash Lele for his continuous support through my master program. Subhash was always there to listen and to give advice. He is responsible for involving me in the Indiana Bat project in the first place. Subhash educated me how the deal with a messy data coming from the real world. He taught me how to ask questions and express my ideas. He showed me different ways to approach a research problem and the need to be persistent to accomplish any goal. In one word, he taught me to love applied statistics and to use it to serve good purposes. I thank my advisors Bob Crabtree (YERC) and Lori Pruitt (USFWS). Bobs offered me the project, taught me how to think from biological point of view Bob also gave me several opportunities to present my work and discuss it with biologists in Montana. Lori Pruitt, the world expert in Indiana bat, was a great help through every step in the project. Working with Lori was a great opportunity to understand biological interpretation of statistical results . I thank the rest of the team who participated in the project including: Jennie Sheldon, Dan Weiss and Brandt Winkelman from YERK, Scott Pruitt from USFWS and Andy King from NASA.

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Chapter 1

Introduction

1.1. Problem Definition and Objective

Bats are a vital element to the ecosystem. They are pest controllers, seed dispersers, and pollinators. Bat history goes back at least 65 million years. They can be found in almost any environment. Indiana bats are a small species found in the Northeast and Midwest USA, where they once numbered in the millions. In the past 40 years their population has declined 56 percent to 387,000. In 2006, a mysterious disease named White Nose Syndrome (WNS) appeared in a New York cave. Since then, it has been spreading to other caves in both the USA and Canada and has killed more than one million bats. It is believed that this disaster has caused the most abrupt wildlife decline in the past century in North America. Experts in the fields of bat biology, fungal ecology and environmental modeling are working together to explore the disease and to develop solutions to manage it.

This study is a partial Population Viability Analysis (PVA) which aims to explore the association between bat population and climate covariates prior to WNS appearance in 2006 through:

1. Investigation of the growth rate in each of the 222 caves
2. Examining the growth rate in each cave to potential climate covariates

This connection may facilitate the understanding of the disease and how and under what conditions the disease might spread. Ultimately, the models would be used to help devise appropriate management strategies for controlling it.

1.2. Gathering Data

The Department of US Fish and Wildlife supplied a database of hibernacula survey population from 1950 to 2006. The database includes information on 450 Indiana bats caves. The dimension of the data matrices that will be analysed is

450*56. One of the challenging issues in this data was cleansing it by inputting missing values, removing duplicates and invalid entries, deleting caves with few observations and grouping nearby cave populations. The final clean data is reduced to 222 cave time series. The Ecological Forecasting Lab at National Aeronautics and Space Administration (NASA) provided the 145 climate covariates for each cave population using Terrestrial Observation and Prediction System (TOPS).

1.3. Analysis

The analysis consists of five steps. First, the model the growth rate of each of the 222 caves' population time series. For each cave, two models are fitted and compared to test for any association between the growth rate and the size of the cave population (density dependence mechanism). Second, after choosing the best fitted model, the average growth rate for each cave is estimated and plotted geographically. Subsequently, any geographical pattern is easily detected. Third, using Spline Smoothers, we fit a smooth curve to each cave growth rate time series in order to capture singular trends/behaviours over time. Next, the 222 trends are compared to detect any similarity across nearby caves. Finally, the last and most important step of the analysis consists of establishing a link between each cave population growth rate and the surrounding climate covariates for the time between 1982 and 2007. For each cave population, we regress the cave growth rate over 145 corresponding climate covariates supplied by TOPS, and then we select the minimum number of covariates that are highly correlated with the growth rate. The method is called automatic forward selection. Our aim is to choose the minimum number of covariates (2-4) that can predict the growth rate for a particular cave. For most caves, the set of selected covariates are not exclusive. Thus the next natural step is building frequency tables of the most selected climate covariates by region. The last step allows us to locate the most important climate factor associated with the bat growth rate for any region.

1.4. **Interpretation**

Our results and finding are communicated to Indiana bat specialists for biological interpretation. The result may be used as tool in species management planning, and probably shed some light in investigating the association between WNS and climate.

2. Chapter 2

Indiana Bat Population Decline and White Nose Syndrome

2.1. Introduction

Bats have been around for at least 65 million years. Their forelimbs are developed as wings and make bats the only true flying mammals. 1000 of the 4450 know species of mammals are bats (Fenton, 2003), and they are among the most successful and varied of all mammals. We can find them in almost every ecosystem, with the tropics home to the greatest density of bat species. The fastest bats can reach 25 km/h and some bats species weigh only 1.7-2 grams, smaller than many insects (Hill, 1984) .

Bats are vital to many ecosystems and human economies. Bat droppings are a natural fertilizer considered a major natural resource in many countries. They are vital for pest control. They are the only major predators of night-flying insects and seventy percent of bat species feed on insects and play an important role in environmental balance (Fenton, 2003). Many bat species that feed either on fruit or on nectar also perform the vital functions of dispersing fruit seeds or pollinating flowers. Many tropical plants depend entirely on bats for the distribution of their seed (Hill, 1984).

2.2. Indiana Bat

The Indiana Bat is a mid-sized bat (6-9 grams) of the genus Myotis (Indiana Bat (Myotis Sodalis), 2010), with brown hair and pink lips, and a life expectancy of 5 – 10 years. In the US this bat lives in the forest and caves of the Northeast, Southeast and Midwest. Indiana Bat feeds on flying insects along shorelines, and in the trees of forests and floodplains (Indiana bat, 2010)

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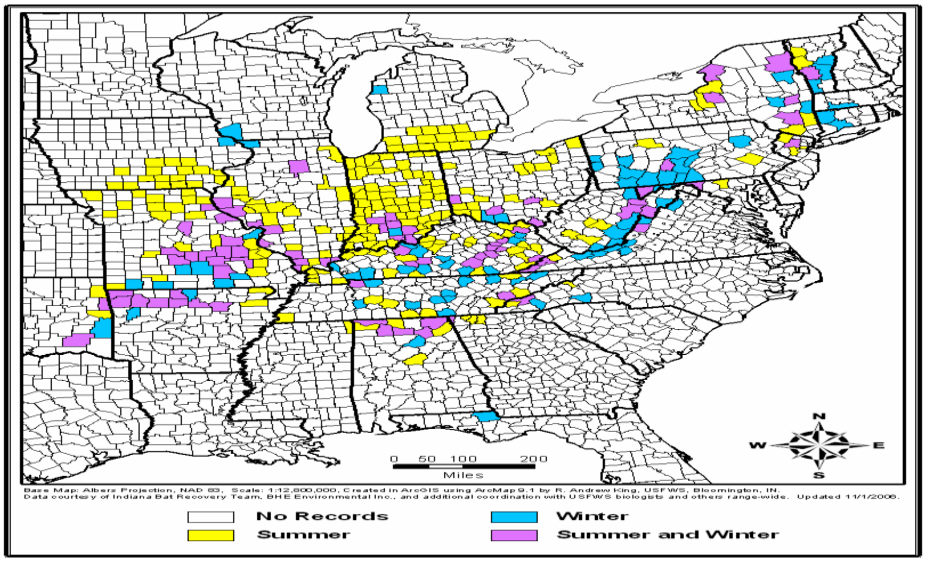

Figure 1: Counties that have Summer and Winter records for Indiana Bat (Pruit, 2007)

A social animal, the Indiana Bat migrates in spring to congregate in summer colonies where it roosts in trees and feeds on insects in preparation for winter, and again in fall to congregate in winter colonies where they hibernate in caves called hibernacula. It has strong homing instincts to its hibernacula. In experiments where biologists released 500 Indiana Bats 200 miles from their hibernacula, more than two-thirds returned (Pruit, 2007). This instinct seems much stronger along a north-south axis, the direction for migrating to and from summer roosts, than along the east-west direction. Winter hibernacula and summer roosts may be as much as 300 miles apart (Pruit, 2007).

The Indiana Bat migrates to the hibernacula from late July to early October for mating. The adult female Indiana Bat stores sperm through the winter, with fertilization only occurring after spring emergence from hibernation. During fall, Indiana Bats stock up fat supplies as they forage in the neighbourhood of the hibernacula (Barbour, 1964).

Indiana Bats hibernate in the same cave that they swarm. They hibernate in the same cave every year. Most enter hibernation by the end of November, usually in large, dense clusters ranging from 300 to 500 per square foot (Pruit, 2007). During hibernation, Indiana Bats may arouse naturally to move to a different spot in the cave depending on cave microclimate factors. Even small changes in the temperature, barometric pressure, and humidity of a hibernacula can make it unsuitable for bats (Pruit, 2007).

In spring the Indiana Bat emerges from hibernation. The female Indian Bat migrates hundreds of kilometres from her hibernacula to their maternity sites, although shorter migrations are known to occur (Pruit, 2007). Little information is available to determine habitat use and needs for Indiana Bats during migration.

Reproductive females arrive at their summer habitats as early as mid-April (Fenton, 2003). Upon arrival, female Indiana Bats form maternity colonies which can vary greatly in size. It was documented that maternity colonies may contain 100 or fewer adult females (Harvey 2002). Maternity colonies are widely dispersed and difficult to locate. All efforts have found only a fraction of the maternity colonies presumed to exist based on population estimates. The 269 maternity colonies identified only represent 6 to 9 percent of the 2,859 to 4,574 maternity colonies assumed to exist. Therefore the geographic locations of the majority of Indiana Bat maternity colonies remain unknown (Pruit, 2007).

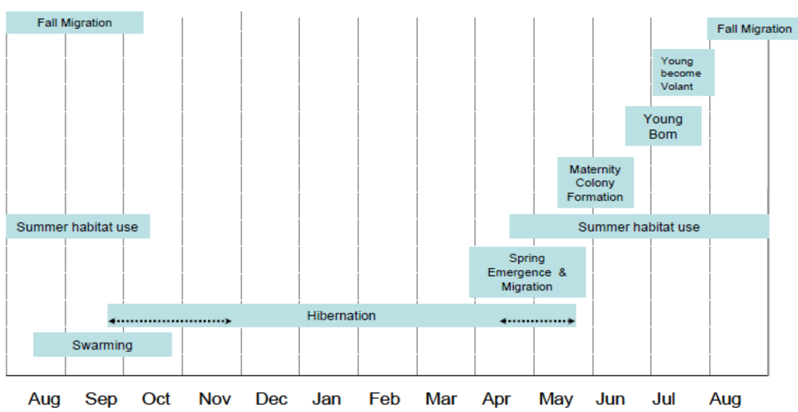

Figure 2: Indiana Bat Chronology (Pruit, 2007)

Female bats and their pups are poor thermo regulators Their growth may be controlled by the rate of metabolism and body temperature (Whitaker, 2004). Thus, it is believed that roost temperature is essential in the growth and development of young Indiana Bats. Kurta and Lacki suggest that roost microclimate is the primary selection factors of the roosting site where bats feed on insects (Micheal J. Lacki, 2007). Indiana Bats forage in forested stands, along forest edges and hedgerows, and near or along open water and wetlands.

2.3. Decline in Indiana Bat Population

The Indiana Bat population is in decline. In the past 40 years, it has been reduced from 883,300 to 387,300, a reduction of 56 percent (Pruit, 2007). Human disturbances, vandalism, killing and unsuitable attempts to protect bats in their winter hibernacula contributed to this decline. However, even after these problems were addressed, populations continue to decline. Biologist looked at the I-Bat’s summer colonies, and found loss and degradation of habitat may be contributing to population decline (Indiana bat, 2010). Some biologist believed that climate change may be a determining factor.

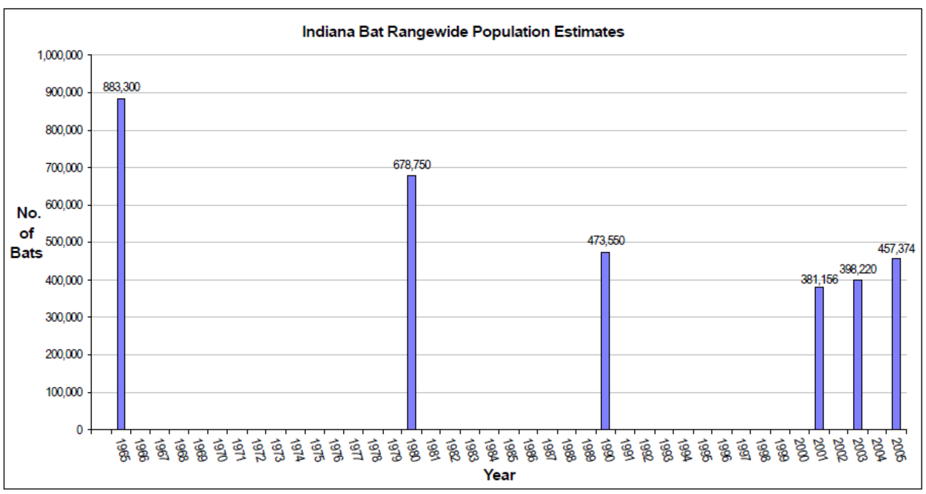

Figure 3: Indiana Bat Population Estimate (Pruit, 2007)

2.4. White Nose Syndrome

Since 2006, White Nose Syndrome (WNS) has been associated with the deaths of more than a million different bats (White-Nose Syndrome in Bats, 2009). The affected animal has a distinctive ring of fungal growth around the muzzle and on the wings.

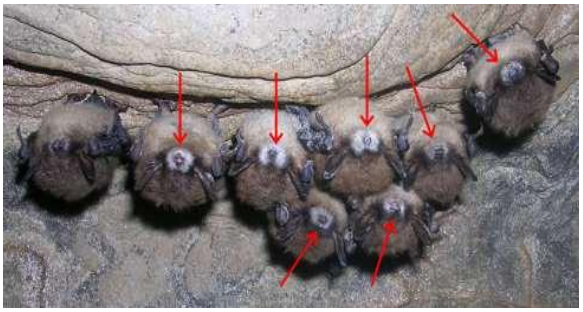

Figure 4: White Nose Syndrome ((White-Nose Syndrome in Bats, 2009))

Originating in New York, in the last 4 years it has spread to Vermont, Massachusetts, Connecticut, New Hampshire, New Jersey, Pennsylvania, West Virginia and Ontario. Mortality rates have approached 100 percent at some sites. According to biologists, the disease has caused the steepest wildlife decline in the past century in North America (What We Do/ White-Nose Syndrome, 2010). Ultimately, bats across North America are at imminent risk.

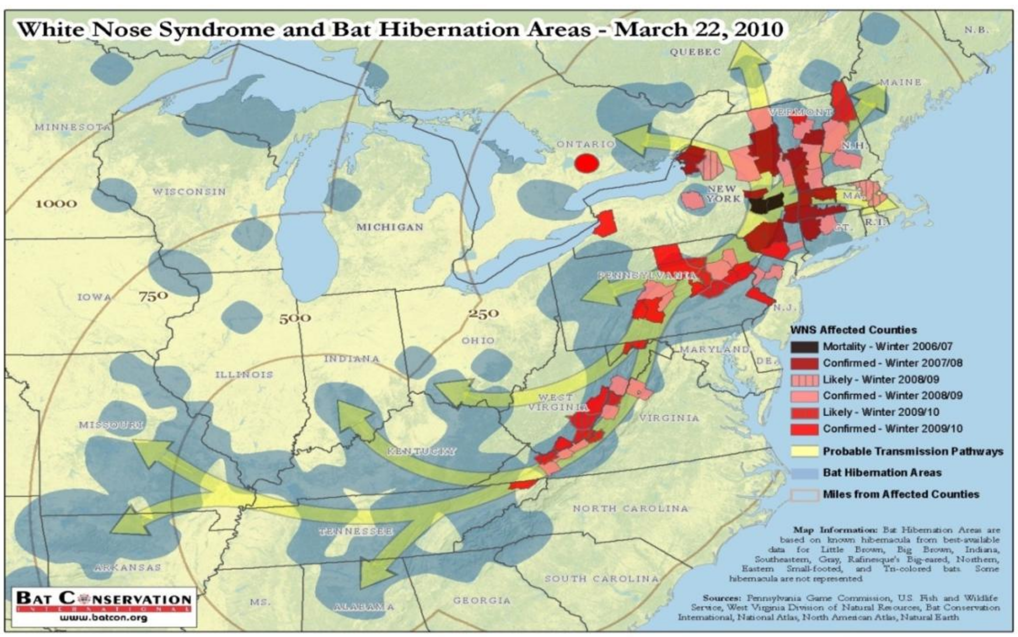

Figure 5: Path of the Spread of WNS (Cryan, 2010)

Bat experts, biologists, and environmental scientists have been working to understand Indiana Bat population decline and to solve the mystery of WNS. Our study is an effort to explore the relationship between Indiana Bat population and climate prior to WNS.

3. Chapter 3

Modeling Each Cave Population Time Series

3.1. Introduction

In ecology, population viability analysis (PVA) is used to estimate the likelihood of a population's extinction and study the factors that may affect population dynamics. PVA output is used to develop recovery plans. As bat biologists believe that climate is a key factor in understanding Indiana Bat population dynamics, this study aims to establish a link between the population dynamics and climate variables.

The key to this analysis is the modeling of each cave population's per capita growth rate. Per capita growth rate is the change in population size over time per individual, and it regulates the population size change over time. Assuming no migration, the population size can only be changed by birth or death. Population annual per capita growth rate is positive when more individuals are added than removed, negative when more individuals are removed than are added, null when the annual numbers of death and births are equal (Taper & Dennis, 1994).

Biologists have developed mathematical models to study the per capita growth rate. The simplest model of population growth is the exponential growth model which assumes that the per capita growth rate stays constant independent of the population size (a Density Independent Growth Model). Because a population growing exponentially will continue to grow infinitely, this model is usually not realistic.

On the other hand, the logistic growth model allows the per capita growth rate to vary with population size. In fact, it assumes that the per capita growth rate is negatively proportional to the population size.

For each cave population time series, we will check which of the two models isthe best fit. A better fit of the exponential model may suggest the effect of climate on Indiana Bat population decline. Such a hypothesis needs to be confirmed by investigating the existence of similar patterns in the growth rate across nearby caves using spatial or temporal plotting. If evidences support the climatic effect approach then the final step is linking each cave growth rate to surrounding climate.

3.2. USFW Cave Population Data

The data provided by the USFW consisted of 450 records, one for each hibernaculum, each containing the population estimates from 1950 to 2006. For each hibernaculum, the population estimate was taken either annually or biennially. Many of the values for the population estimates were missing. After removing hibernacula with fewer than three values for population estimates, 222 hibernacula remained. The missing values for the remaining hibernacula were imputed using linear interpolation.

3.3. Models

Exponential Growth Model (Density Independent Growth Model)

To model the per capita growth rate we will use a discrete version of the exponential and logistic growth models. To build the two models, we start by a simple version of the exponential: the continuous case

Continuous Case

Let:

- *N: The density of the population*
- $\frac{dN}{dt}$: *Rate of change*
- $\frac{dN}{dt.N}$: *Per capita rate of change(Per capita growth rate)*
- *b: Per capita birth rate is constant*
- *d: Per capita death rate is constant*

We assume that all changes in this population result from births and deaths and that b and d stays the same. We also assume that births are happening in a short time interval (dt)

$r = b - d$: *Intrinsic rate of growth (*stays constant)

$\dfrac{dN}{dt.N}$: ***Per capita growth rate for continuous case*** (1)

$\rightarrow \dfrac{dN}{dt\,.N} = b - d = constant\ (r)$

$\rightarrow \dfrac{dN}{dt\,.N} = r$

Discrete Case

For many organisms, birth occurs in well defined *breeding seasons*. Consequently, Dennis and Taper (Taper & Dennis, 1994) modified the per capita growth rate definition slightly to incorporate discrete time births. Indeed they approximate *(1/n) dN/dt by d(ln N)/dt*:

Let:

- N_t: Population Abundance at time t (censused, estimated) where t is discrete (0,1,2...)
- We assume that the population is observed at the same time each year
- $X_0 = \ln(N0)$
- $X_t = \ln(Nt)$
- The definition of the per capita growth growth rate $Ln(N_t/N_{t-1})$ is analogue to that of continuous time d(ln N)/dt
- The per capita growth rate over time is taken to be constant independent of the population size:

$$ln(N_t/N_{t-1}) = b_0$$

$$ln(N_t) - ln(N_{t-1}) = b_0$$

$$N_t = N_{t-1} . e^{(b0)} \quad \textit{(first order difference equation)}$$

- Integrating stochastic effects due to element of chance such as: Fire, storms.

$$ln(N_t / N_{t-1}) = b_0 + E_t \qquad (4)$$

$$N_t = N_{t-1} . e^{(b0 + Et)} \qquad (5) \qquad \textit{(Discrete time Markov process)}$$

- $E_t \sim$ normal $(0,\sigma^2)$: random shock due to unspecified stochastic forces
- E_1, E_2...are independent,
- N_0, N_1,...are dependent under this model.
- The stochastic process Nt is a <u>Markov process:</u> Given population size attained N_t, the future distributions of the population depend only on N_t and not past sizes of the population.

Logistic Growth Model (Density Dependent Growth Model)

The per capita growth rate is changing linearly with the population size (Taper & Dennis, 1994)

$$ln(N_t/N_{t-1}) = b_0 + b_1 N_{t-1}$$

$$ln(N_t / N_{t-1}) = b_0 + b_1 N_{t-1} + E_t \qquad (6)$$

$$N_t = N_{t-1} . e^{(b0+ b1 Nt-1 + Et)} \qquad (7) \qquad \textit{(Discrete time Markov process)}$$

- $E_t \sim$ normal $(0,\sigma^2)$: random shock due to unspecified stochastic forces
- E_1, E_2...are independent,
- N_0, N_1,...are dependent under this model.
- The stochastic process Nt is a <u>Markov process:</u> Given that population size attained N_t, the future distributions of the population depend only on N_t and not on past sizes of the population.

3.4. Analysis

Testing Exponential Model vs. Logistic Model for Each Cave Population Time Series

For each cave population time series we fit both the exponential model and the logistic one. Then we test the best fitted model using the likelihood ratio test proposed by Dennis and Taper (Taper & Dennis, 1994). The null hypothesis is that the population is undergoing stochastic exponential growth/decline. The alternative hypothesis is that the population is experiencing stochastic logistic growth/decline. The distribution of the test statistic under both hypotheses is obtained through ***parametric bootstrapping.*** The testing methodology used is illustrated by an example of three cave populations (Annex 1).

The exponential model seems to fit better each cave population. In fact, the data shows enough evidence that individual cave population per capita growth rates are density dependent.

Investigating Cave Per Capita Growth: Rate Spatial Correlation

To investigate the existence of any spatial correlation trends among different cave population growth rates, it is essential to plot the average growth rate of each population for the time period 1982-2007 in the specific geographical location on the map, the check visually for any possible trend. The procedure is detailed in the following steps.

Procedure

1. Fitting the exponential model for each of the 222 cave time series
2. Estimating b_0: average per capita growth rate population per cave
3. Average b_0 for the caves that belongs to the same county
4. Discretize the parameter b_0 to simplify the plotting:
    - $b_0 < 0$: Decreasing Population over Time
    - $0 < b_0 < 0.3$: Slightly Increasing Population over Time
    - $0.3 < b_0 < 0.6$: Moderately Increasing population over Time
    - $0.6 < b_0 < 1$: Increasing Population over Time
    - $1<b_0$: Highly increasing Population over time
5. Plotting b_0 geographically per corresponding county

6. Grouping counties per state for a total of 17 states where Indiana Bat resides

Estimating Each Cave Population Growth Parameters

The estimated average per capita growth rates for Missouri caves are illustrated in the following table. The names and codes of caves and counties are removed. The rest of the tables corresponding to other 16 states are (Annex 2).

Table 1: The Estimated Average Per Capita Growth Rates for Missouri Caves

Cave	State	County	County FIPS	Name	b0	Bo average per county	sigma
122	MO(29)				0.503677928		0.119
123	MO				0.464253909	0.483965919	0.096
124	MO				0.847918981		0.059
125	MO				0.101644944	0.474781963	0.923
126	MO				-0.08748		0.343
127	MO				-0.11853763	-0.103008815	0.263
128	MO				-0.03456613		0.260
129	MO				-0.06842984		0.241
130	MO				0.272494969	0.056499667	0.494
131	MO				0.44854562		1.453
132	MO				-0.03050378	0.209020921	0.751
133	MO				0.164702675		0.087
134	MO				0.35692367		0.759
135	MO				-0.02713032	0.164832009	0.143
136	MO				0.443918364		0.946
137	MO				-0.21684672		0.140
138	MO				-0.00353738		0.164
139	MO				0.144130088		0.210
140	MO				-0.05662024		0.507
141	MO				-0.14916298		1.081
142	MO				-0.0225223		0.259
143	MO				-0.26826431		0.214
144	MO				-0.08731484		0.723
145	MO				-0.23669369	-0.099648043	0.225
146	MO				-0.2752901		0.493
147	MO				0.463307569		0.255
148	MO				0.159391284		0.231
149	MO				-0.68899486		1.118
150	MO				0.048173021	-0.058682617	0.154
151	MO				-0.77642159		1.498
152	MO				-0.07354407		0.367
153	MO				-0.08874113		0.172
154	MO				0.047360974		1.111
155	MO				-0.27569475	-0.105691632	0.188
156	MO				-2.74367935		0.929

Plotting the Average Per Capita Growth Rate (b_0) per County

Plotting of the average per capita growth rate is illustrated for Missouri. Similar plots are made for the other 16 states (Annex 3).

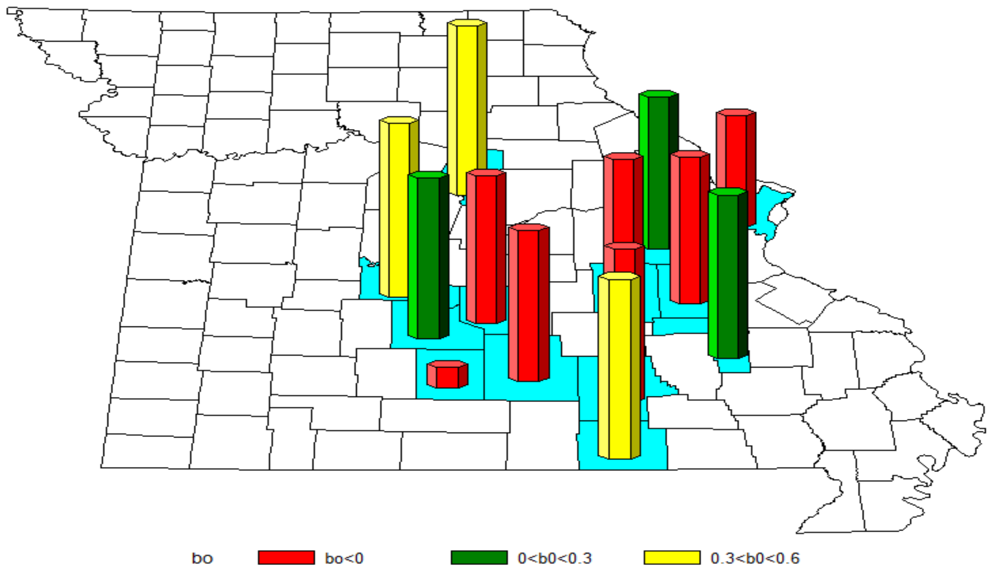

Figure 6: Plotting of the Average Per Capita Growth Rate (b_0) for Missouri

Comment

Plotting the average per capita growth rate per county using bars plot reveals a systematic pattern in the growth rate values across space in Missouri. Negative growth rates are presented in red, whereas positive growth rates are either in green or yellow depending on their strength.

The plots show that counties with declining populations are clustered in the interior (red), while those with increasing populations are located on the edge (green and blue). It also shows that the further the caves are from the cluster center , the healthier the population is. Similar patterns are seen in the other 16 states (Annex 3).

Investigating Temporal Trends in Per Capita Growth Rates across Cave Populations

In a second exploratory analysis, we use spline smoothers to capture the overall trend in each cave population per capita growth rate over time. The objective is to investigate any similar trends in neighbouring caves

Spline smoothers are non-parametric curves. They are defined as piecewise polynomial. We will use penalized splines (Marx & Eilers, 1996) to fit a smooth curve through each cave per capita growth rate. The best smoother curve for each cave is selected through minimizing cross validation criteria (CV).

We applied the smoothing method to each population time series across the 222 hibernacula. The technique is illustrated below using three neighbouring caves from Missouri. Two of the caves belong to the same county, while the third belong to a neighbouring county. First, the actual three cave population time series are plotted. Then, each cave's per capita growth rate over time scatter plot is smoothed. Finally the smoothers curves are compared to check for trend similarities.

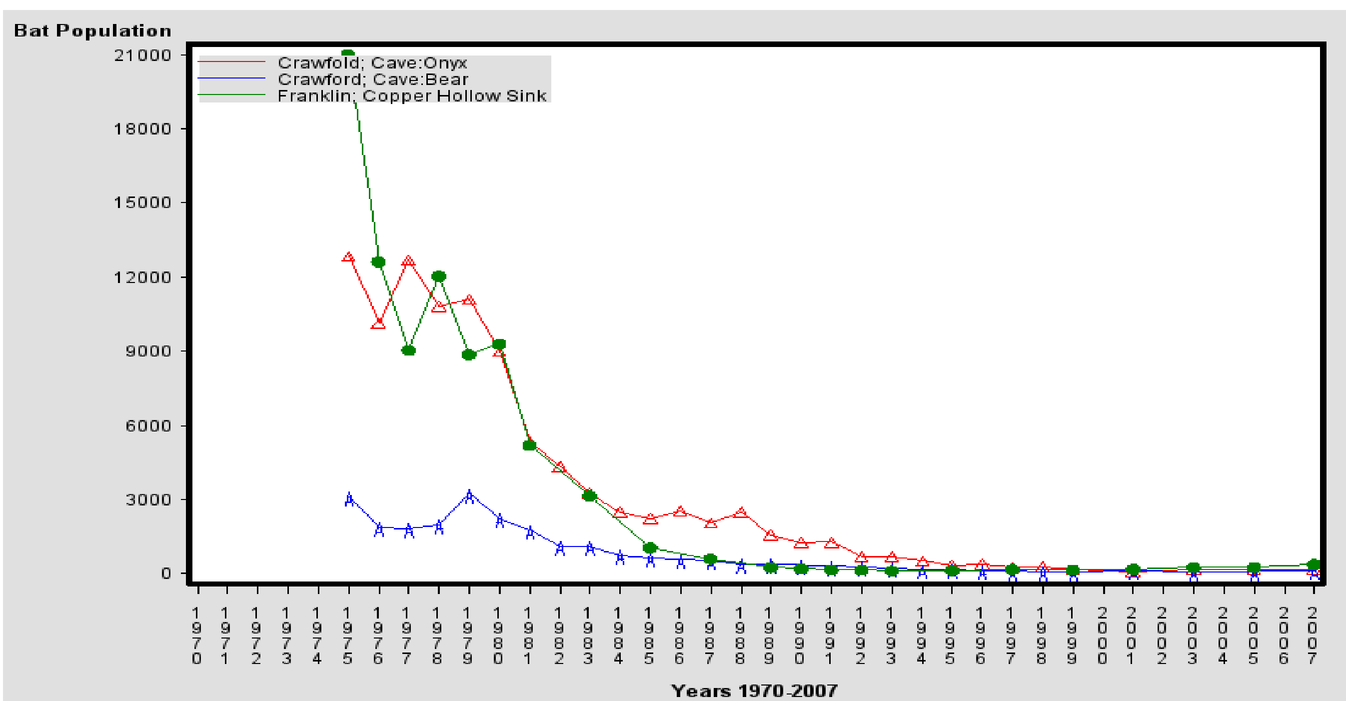

Figure 7: Populations vs. Time for the Three Complete Missouri Caves

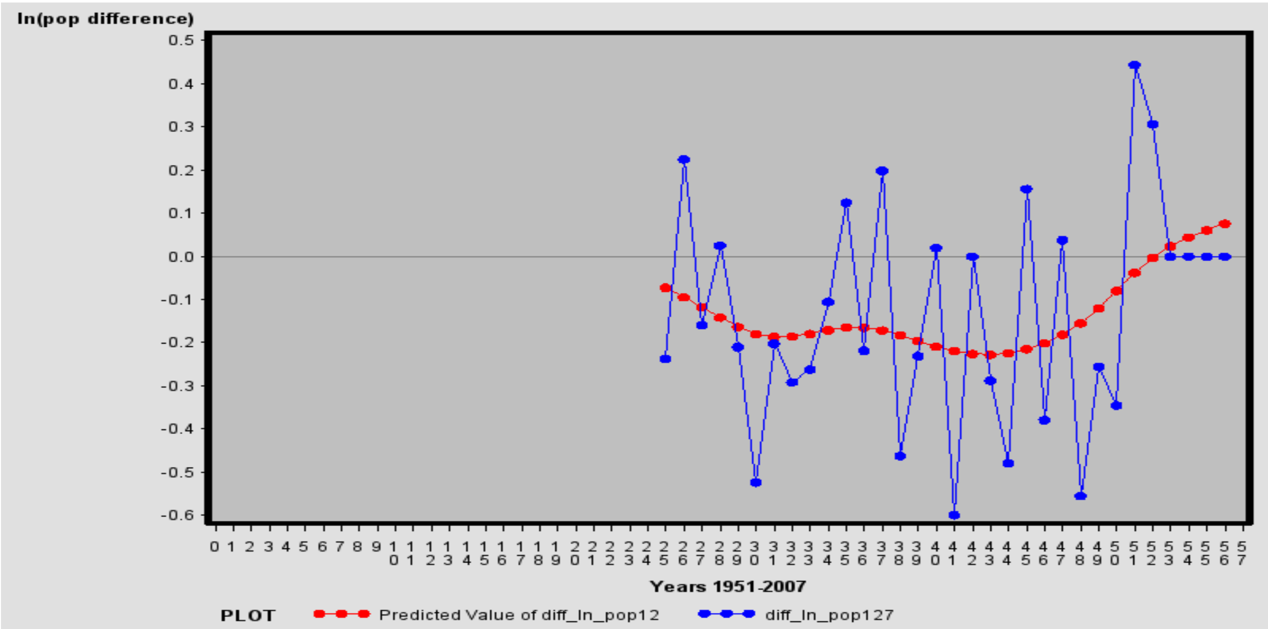

Figure 8: B-Spline Smoothing for First Cave (Pop 127); the per capita growth rate ($\ln(N_t) - \ln(N_{t-1})$) trend over time.

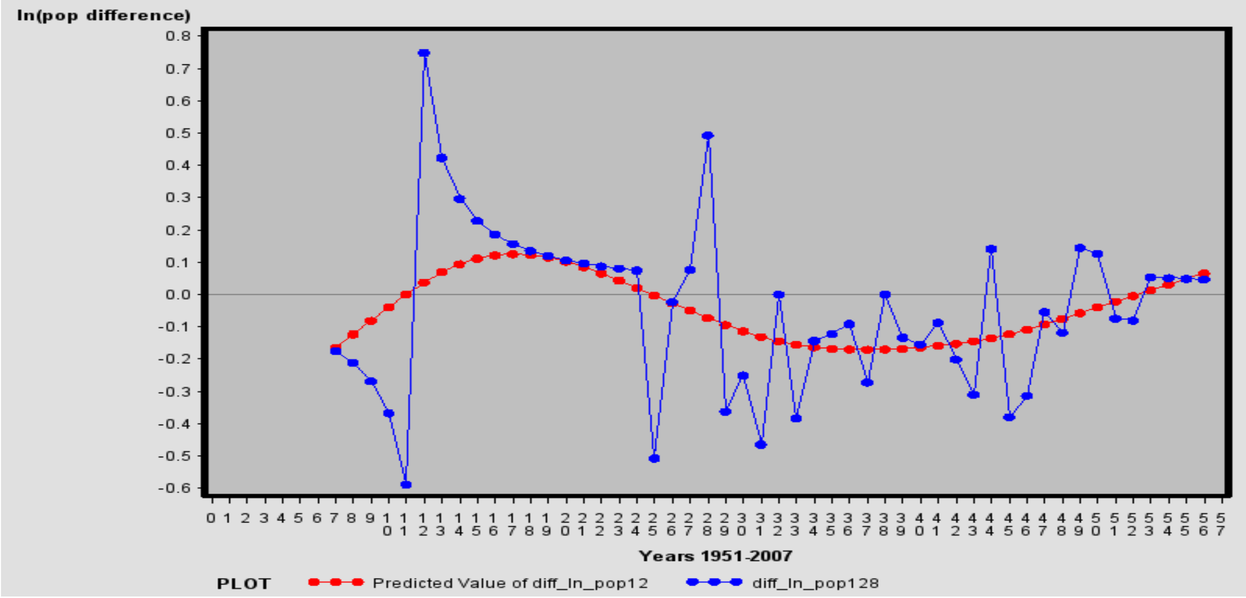

Figure 9: B-Spline Smoothing for Second Cave (Pop 128); the Per Capita Growth Rate ($\ln(N_t) - \ln(N_{t-1})$) Trend Over Time is Smoothed.

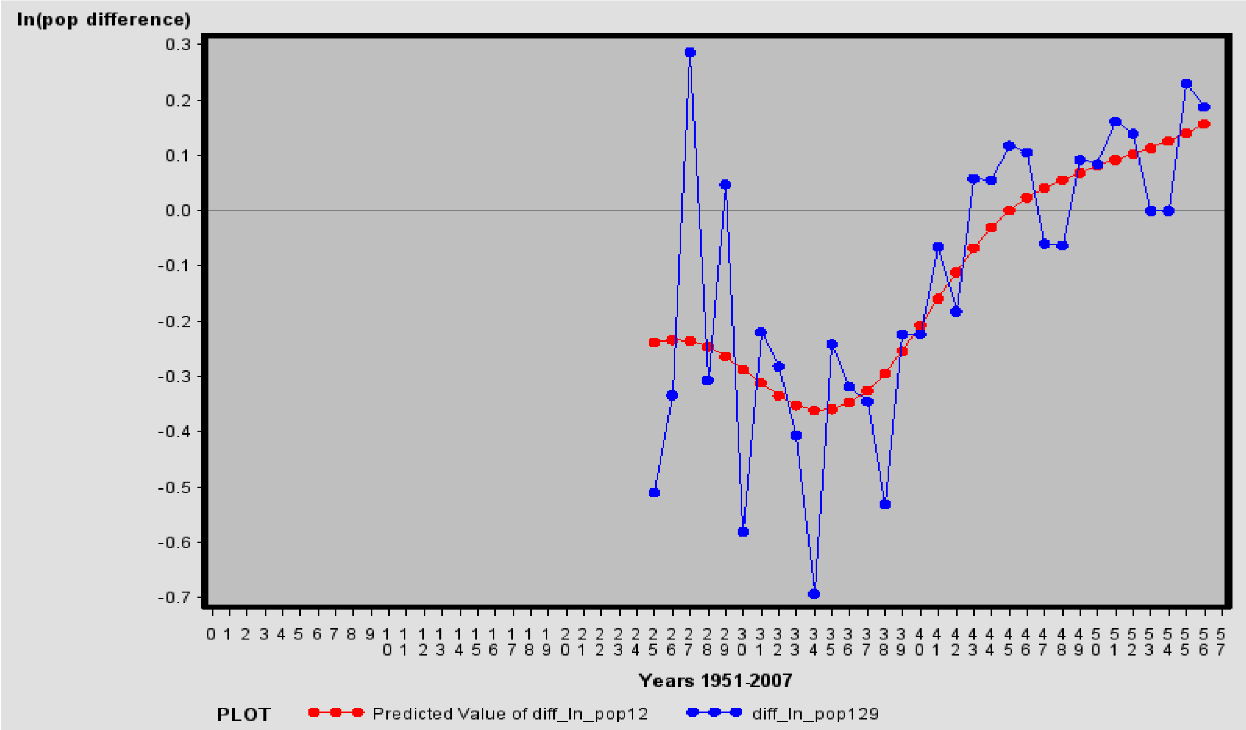

Figure 10: B-Spline Smoothing for Third Cave (Pop 129); the Per Capita Growth Rate ($\ln(N_t) - \ln(N_{t-1})$) Trend Over Time is Smoothed.

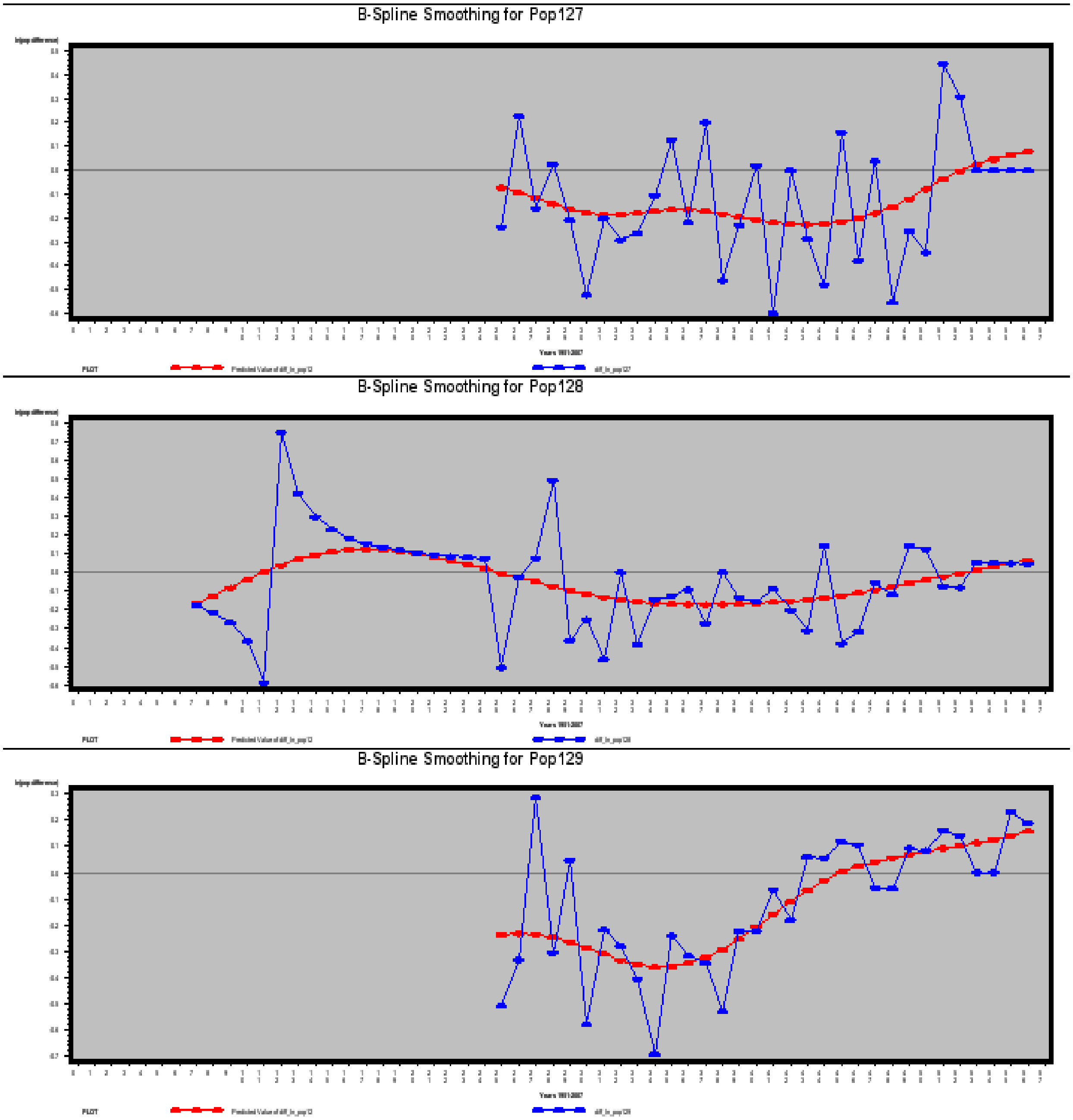

Figure 11: Graphical Comparison of the Three Population Growth Trends; the Per Capita Growth Rate ($\ln(N_t) - \ln(N_{t-1})$) Trend Over Time is Smoothed.

Comment

The blue curves represent annual per capita growth rates for each of the three caves. The red curves are the B-Spline smoothers. The smoothers show that the three populations had been declining prior to 1997 (negative per capita growth rates), then starting from around 1998, their population started to increase (positive per capita growth rates). Furthermore the imputed values are clearly distinguished in Figure10 between years 1962 and 1973. The trends comparison for these 3 populations is made only for the most recent years where the population values are real. For other populations with too many missing values, the comparison is ineffective.

3.5. Conclusion

In the current chapter, we investigated the behaviour of Indiana Bat population dynamic over time. First, modeling the per capita growth rate for each of the 222 cave populations showed that the exponential growth model holds. Second, plotting per capita growth rates per corresponding counties revealed spatial cluster. Third, comparing the per capita growth rate over time for complete data set population shows similar trends. In the next chapter, we will investigate a possible link between each cave per capita growth rate and surrounding climate covariates.

4. Chapter 4 Exploring Potential Link between Indiana Bat Per Capita Growth Rate and Climates Covariates

4.1. Objective

Establishing a potential link between climate and Indiana Bat population dynamic is the core of this study. According to Indiana Bat experts, I-Bat survival and reproduction may be affected by several climate covariates such as: Temperature, Precipitation, sunlight, etc. For instance, in winter, Indiana Bats hibernate in caves that have specific climate conditions. In fact, they need cool caves with temperatures of around 40 degrees Fahrenheit and relative humidity between from 66% to 95% (Indiana Bat-Myotis Soladis, 2010). In summer, Indiana Bat roost in sunny areas. The sun seems an important factor for Indiana bat summer habit (First Descriptions of Indiana Bat Maternity Roosts in the Southern U.S, 2010)

Our objective is to link each cave population per capita growth rate to potential surrounding climate covariates, then investigate if there a particular climate covariate that is associated with all or most of the cave populations per capita growth rate. Firstly, Indiana Bat biologists define a set of possible climate covariates for each cave population. Then, NASA Terrestrial Observation and Prediction System (TOPS) provides the requested covariates based on the cave geographical coordinates. Next, among the suggested covariates, we use automated forward selection technique to select only the highly associated covariates with the per capita growth rate for the given cave. Next, a frequency table summarizes climate covariates that are associated with most of the 167 caves. Such a step is necessary to explore the possible effect of a global climate variable on all the cave populations. Finally, a frequency table summarizes climate covariates that are associated with most of the caves state.

4.2. TOPS Climate Covariates

USFW Indiana Bat biologists suggested five essential climates covariates that may be associated with the variation in each cave's population.

- tmax (average daily maximum temperature, unit C)
- tmin (average daily minimum temperature, unit C)
- srad (average daily shortwave solar radiation, unit w/m^2)
- vpd (average daily vapor pressure deficit, unit Pa)
- prcp (average daily precipitation , unit mm)

For a given cave population, due to the migratory nature of the species (see Introduction - Indiana Bat Chronology), the major challenge is for which areas these covariates should be measured. For instance, in winter, the entire cave population hibernates in the cave. Therefore, the area around the cave is the target. However, in summer, each cave population disperses into smaller groups of hundreds, and establishes summer colonies hundreds of kilometres from the cave. The exact locations are unknown. To capture the climate covariates affecting these summer colonies, measurement need to be taken at distances from the cave that cover all probable areas in which these colonies may exist.

Based on the Indiana Bat annual cycle, for each cave, USFW biologist and YERK ecologists came to a consensus to investigate the 5 essential covariates during 11 time periods of the year, within 4 radii. According to the biologists, the 11 time periods correspond to important cycles of activities for the Indiana Bat. Similarly, the 4 radii correspond to the probable locations of the bats during these time periods.

NASA TOPS provided the requested climate data for each cave based on the geographical coordinates. TOPS data goes back only to 1982, and the data they provided covered the period 1982 – 2006. The following table describes the name of the data files provided, the time periods, radii and their corresponding climate covariates for each cave:

Table 2 TOPS ASCII: File Nomenclature, Periods, Radii and Number of Covariates

Tops ASCII Files (11 files per location)	**Period** **mm/dd-mm/dd**	**Radius** **r1= 16 km** **r2= 80 km** **r3= 160 km** **r4= 460 km**	**Number of Covariates** **(tmax, Tmin, Srad, Vpd, Prcp)**
1-Fall1 (swarming and mating)	0815-0914	r1	5
2-Fall2	0915-1014	r1	5
3-Fall3	0815-1014	r1	5
4-Winter1 (hibernation)	0101-0131	r1	5
5-Winter2	0101-0228	r1	5
6-Spring (Emergence /Migration)	0401-0430	r1 to r4	5*4 radiuses= 20 total covariates
7-Summer1 (Reproduction)	0401-0430	r1 to r4	5*4= 20
8-Summer2	0401-0531	r1 to r4	5*4= 20
9-Summer3	0501-0630	r1 to r4	5*4= 20
10-Summer4	0501-0831	r1 to r4	25*4= 20
11-Summer5	0701-0831	r1 to r4	5*4= 20
			Total number of covariates per location = 145

In total, 145 potential climate covariates are suggested for a single cave population. Each covariate has one value per year from 1982 to 2006. The following algorithm summarize the procedure followed by TOPS to generate each cave population climate covariates

```
For each year
  average between year-day-x and year-day-y
     for each point of interest(Cave)
      get closest 8km pixel
```

```
      take all pixels in the given radius
      average them within the radius
      output the average to ascii file as one value
   end for points
end for years
```

The output file is described as follows:

Table 3 TOPS ASCII: File Data Structure

```
The ascii files internal structure is as follows:

year tmax_r1  tmin_r1  prcp_r1  vpd_r1  srad_r1  year  tmax_r2
tmin_r2 ..
1982 10.0      9.0     1.0      600.0    300.0   1982   10.0
9.0     ..
1983 11.0      9.5     2.0      700.0    400.0   1983   11.0
9.5     ..
```

4.3. Methodology

Our aim is to link a given cave annual per capita growth rate (1982-2006 time period) to the corresponding 145 potential climate covariates (same time period), then use forward selection procedure to select only highly associated climate covariates with the growth rate. Only the selected climate covariates are included in the linear model. In other words, we are interested to relate USFW population time series data to NASA TOPS climate data, then use the forward selection technique to choose the smallest set of climate covariate (maximum 4 variable) that best predict the growth rate for a particular cave.

The link is based on the exponential model described in the third chapter. In fact, for each individual cave population, the annual per capita growth rate can be described as a response of the corresponding climate covariates.

Model

Let :

N_t : Population size of cave (i) at year (t)

N_{t+1}: Population size of cave (i) at year (t+1)

Then, for a given cave population (i), the annual per capita growth rate is taken to be a linear combination of the potential climate covariates.

$$\ln(N_{t+1}/N_t) = bo + b_1\, Cov_1 + b_2\, Cov_2 + \ldots + b_{145}\, Cov_{145} + Error$$

$$Error \sim N(0,\sigma^2)$$

Cov1: The first climate covariate

Cov2: The second climate covariate

...

Cov145: The last climate covariate

Selecting Significant Climate Covariates using Forward Selection

Given the outnumbered potential climate covariates suggested for each cave, forward selection algorithm is used to choose only statistically significant climate covariates. Forward selection is a data driven model approach. At each step, each climate covariate is tested for inclusion in the model. Thus, we begin by including the climate covariate most highly associated with variation in the per capita growth rate, and continue adding less associated covariates until none of the remaining variables are statistically "significant". A sequence of F-tests is used to control the inclusion of variables into the linear model. Finally, the final list of climate covariate is confirmed by evaluating the model R^2(the % of variation in the per capita growth rate explained by the chosen climate regressors), and C(p) (equivalent to AICC). The desired model has to have a high R^2 and a low C(p).

For clarification, the following example illustrates the steps followed in model selection using forward selection procedure, applied to cave-1. The example includes also a table of cave-1 data records for elucidation:

1. Use USFW data to estimate the annual per capita growth rate for cave-1 from 1982 to 2006. The per capita growth rate is denoted by Y and placed in the last table column
2. Match the annual growth rate to the corresponding annual value of the 145 climate covariates provided by NASA TOPS. The 145 covariates are labelled “x1” to “x145” to simplify SAS coding. (see Annex 4 for key to all the covariate labels)
3. Regress Y on each of x1-x145, then select only the statistically significant climate covariates to be included into the final model
4. Verify the final list of climate covariates incorporated in the model using the model R^2 and C(p)

Cave-1 Data Records

Table 4 Cave 1 Data: USFWS and TOPS Data

year	***"x1"*** **Tmax** within 16km radius (Aug-Sep**)**	***"x2"*** **Tmin** within 16km radius (Aug-Sep**)**	***"x3"*** **Srad** within 16km radius (Aug-Sep)	***"x4"*** **Vpd** within 16km radius (Aug-Sep)	***"x5"*** **Prcp** within 16km radius (Aug-Sep)	**....**	***"x145"*** **Prcp** within 460 km radius (May)	***Y*** **Per CapitaGrowth Rate**
1982	23.449	11.677	4.565	664.95	352.684	....	281.720	-0.279
1983	27.092	14.399	3.071	909.02	374.929	....	297.865	-0.388
1984	23.994	11.224	2.237	662.94	378.806	....	298.834	0.013
1985	24.860	12.525	1.518	761.88	367.968	....	305.268	0.025
1986	23.372	11.088	2.694	686.43	363.244	.....	317.692	0.025
1987	25.212	12.672	5.286	881.46	367.836	....	293.490	-0.031
1988	25.234	12.165	5.004	904.04	380.248	.....	313.284	-0.032
....						.....		

4.4. Analysis

For each cave, the forward selection technique is used to link its per capita growth rate to a set of highly associated climate covariates. The resulting model can be used to predict the cave annual growth rate base on the chosen set. This forward selection technique is applied to each of the 167 caves population. The output shows that each cave population per capita growth rate is associated with a distinct set of climate covariates. Such a result was anticipated due to the geographical dispersion of Indiana Bat population. To demonstrate the finding, the analysis of 4 caves from three different states is presented.

4.4.1. The Four Caves Population Time Series Data (USFWS)

Table 5 Population Time Series Data for Four Caves (Source USFWS)

	Cave-1	Cave-2	Cave-3	Cave-4
Code	29	84	249	(255-260),262
State	AR	IN	MO	MO
1982	2785	11822	4350	1100
1983	2500	13475	3250	4250
1984			2500	750
1985	1850	16200	2250	1706
1986			2550	575
1987	1660	22990	2050	1131
1988			2500	400
1989	1400	28581	1575	674
1990	2300		1250	550
1991	1700	41854	1275	466
1992	1580		700	425
1993	1370	38386	700	359
1994	1450		525	165
1995	1280	41157	325	333
1996	1180		380	130
1997	1210	51365	260	270
1998			270	90
1999	1530	62464	155	237
2000	1070			0
2001	1045	48219	85	290
2002	1107			12
2003	729	50941	180	340
2004	614			0
2005	745	54325	180	350
2006				0
2007	938	77687	180	490

4.4.2. Fitting the Model for Each of the Four Caves

Applying the forward selection procedure for each of the 4 caves, the final model has a higher R^2 and lower C(p).

Table 6   Forward Selection for Four Caves

	Significant Covariates	Coeff. Estimate	Partial R^2	Model R^2	C(p)
Cave-1	Sum2_prcp_r4 Fal1_srad_r1 Fal1_vpd_r1	-0.081 -0.006 0.00034	0.2269 0.1260 0.0983	0.2269 0.3529 0.4512	5.4038 3.1016 1.7456
Cave-2	Fal3_srad_r1 Fal3_tmin_r1 Sum1_vpd_r3	-0.0016 0.0376 0.00023	0.4090 0.1154 0.0815	0.4090 0.5244 0.6059	14.902 5 9.8946
Cave-3	Sum3_tmin_r1 Sum1_tmin_r1 Sum4_prcp_r4	-0.12061 0.06661 0.14323	0.1745 0.1174 0.1190	0.1745 0.2920 0.4110	9.6160 7.2606 4.8456
Cave-4	Win2_srad_r1 Sum5_tmax_r4 Sum3_tmin_r4	0.10087 -0.87346 0.81122	0.2665 0.1142 0.0726	0.2665 0.3807 0.4533	7.5388 5.0952 4.2694

Comment

For Cave 1, Sum2_prcp_r4 which is April precipitation within 460 km around the cave seems to be highly associated with variations in the cave per capita growth rate. The covariate explains 22 % of that variation. The covariate estimate is negative. It implies that Cave 1 population decreases with any increase in the precipitation.

For Cave 2, the highly associated covariate with the per capita growth rate is Fal3_srad_r1. It is the solar radiation within 16 km radius from the given cave, in the time period 0815-1014. The covariate explains 40 % of the variation in per capita growth rate. The solar radiation seems to have a negative effect on the cave population growth rate.

For Cave 3, summer temperature seems to be a key factor. Both minimum and maximum temperature within r1 and r3 in the time periods 0501-0630 and 0401-0430 consecutively, seems to affect the growth rate.

For Cave 4, solar radiation in winter time and temperature in summer time may be the key.

To summarise, the four cave growths seem to be associated with different climate covariates. Each cave selected covariates by the model explain between 40 and 60% of the variation in the per capita growth rate. The difference in climate covariates selected may be due to geographical and climate variation among the 4 caves that are located in 3 different states or simply to the forward selection technique limitation. Also the high number of covariates made it easy for the procedure to select different covariates across distinct caves.

4.4.3. Comparing Actual vs. Predicted Per Capita Growth Rates Based on the Selected Model for Each of the Four Caves

One way of checking the goodness of fit of the chosen model for each cave population is plotting the actual per capita growth rate over time and the predicted per capita growth rate by the model. The plot of the actual per capita growth rate over time for the time period 1982-2006 is in blue, while the predicted one is in red.

Cave1

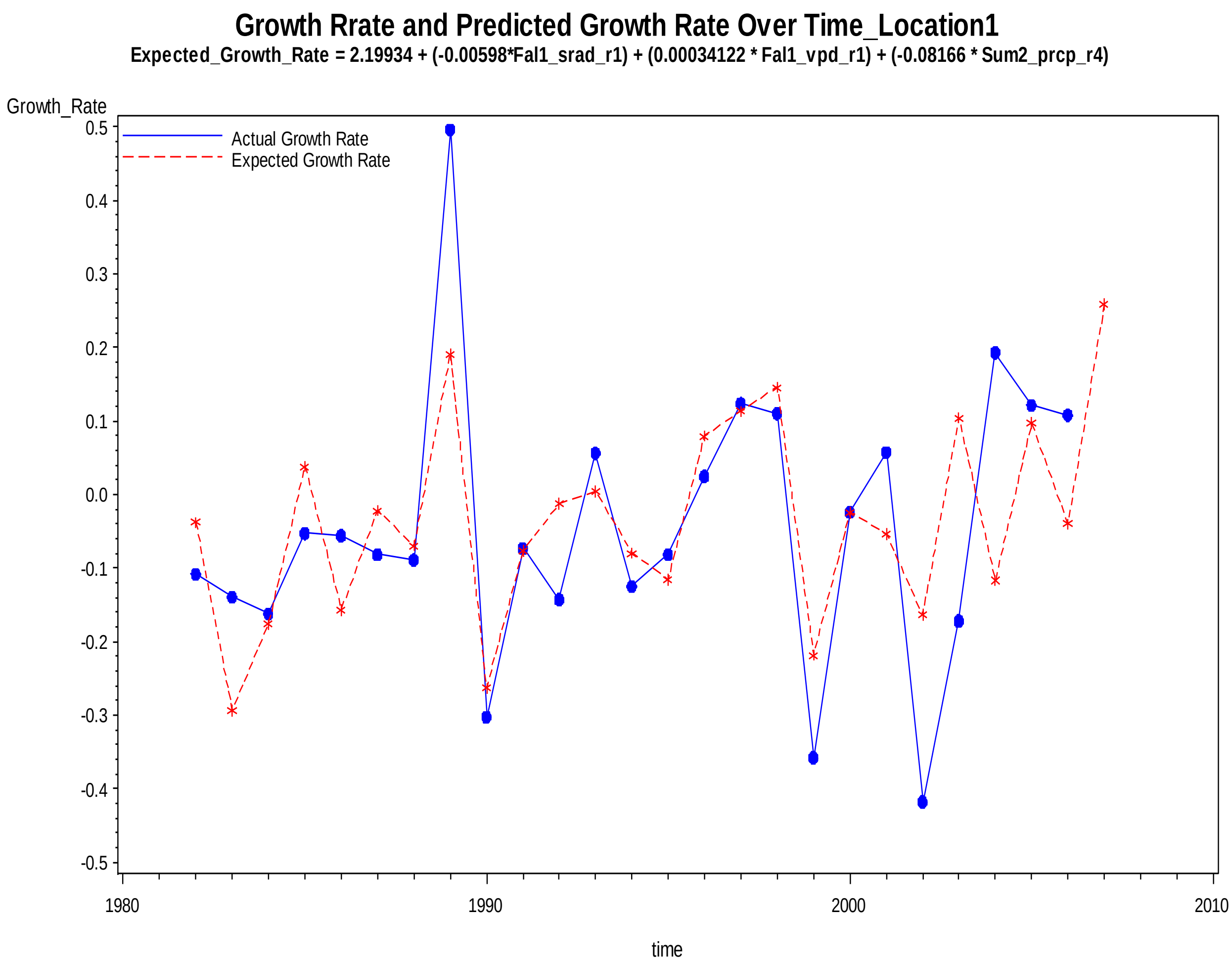

Figure 12: Cave 1 - Growth Rate and Predicted Growth Rate over Time

Cave 2

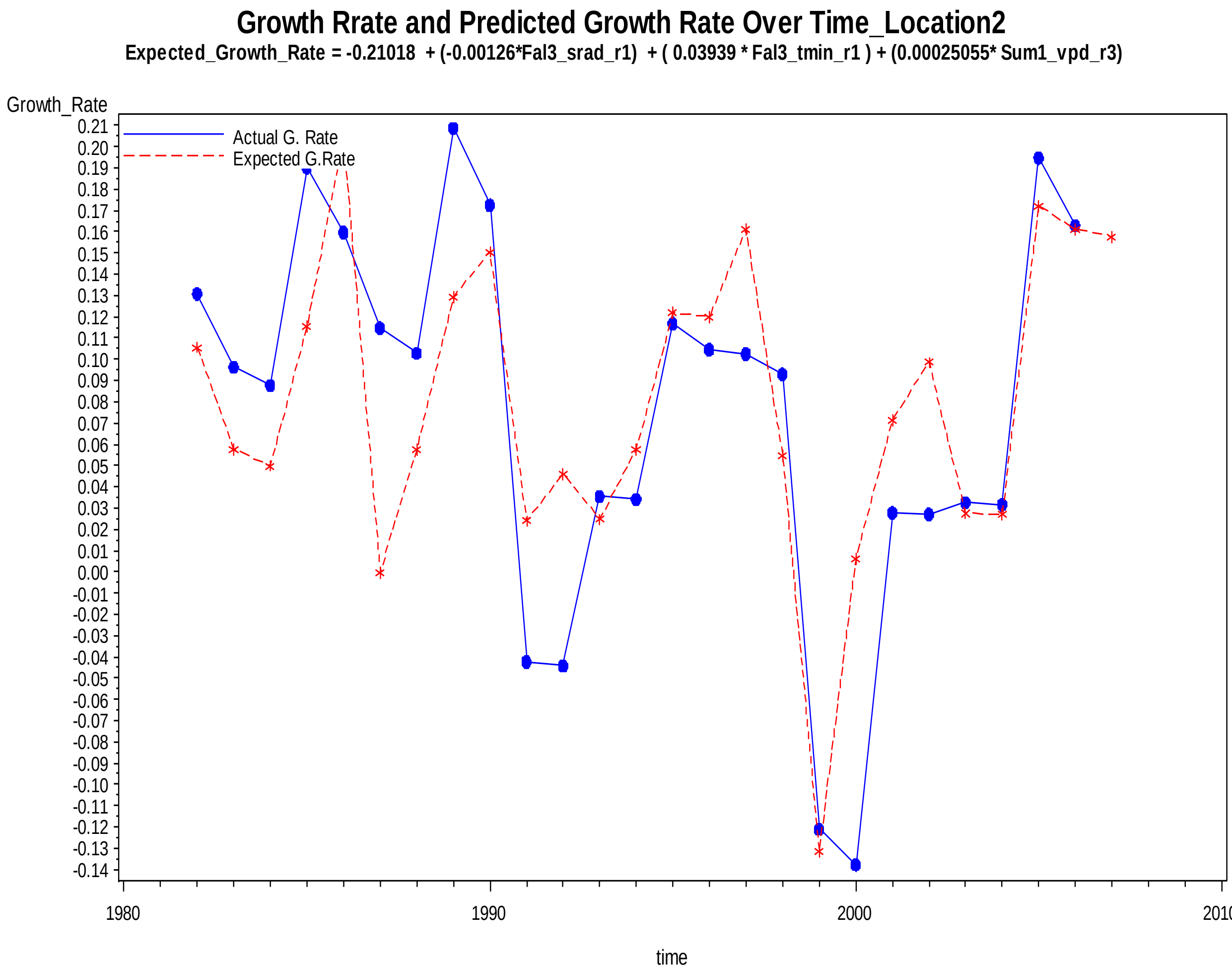

Figure 13: Cave 2 - Growth Rate and Predicted Growth Rate over Time

Cave3

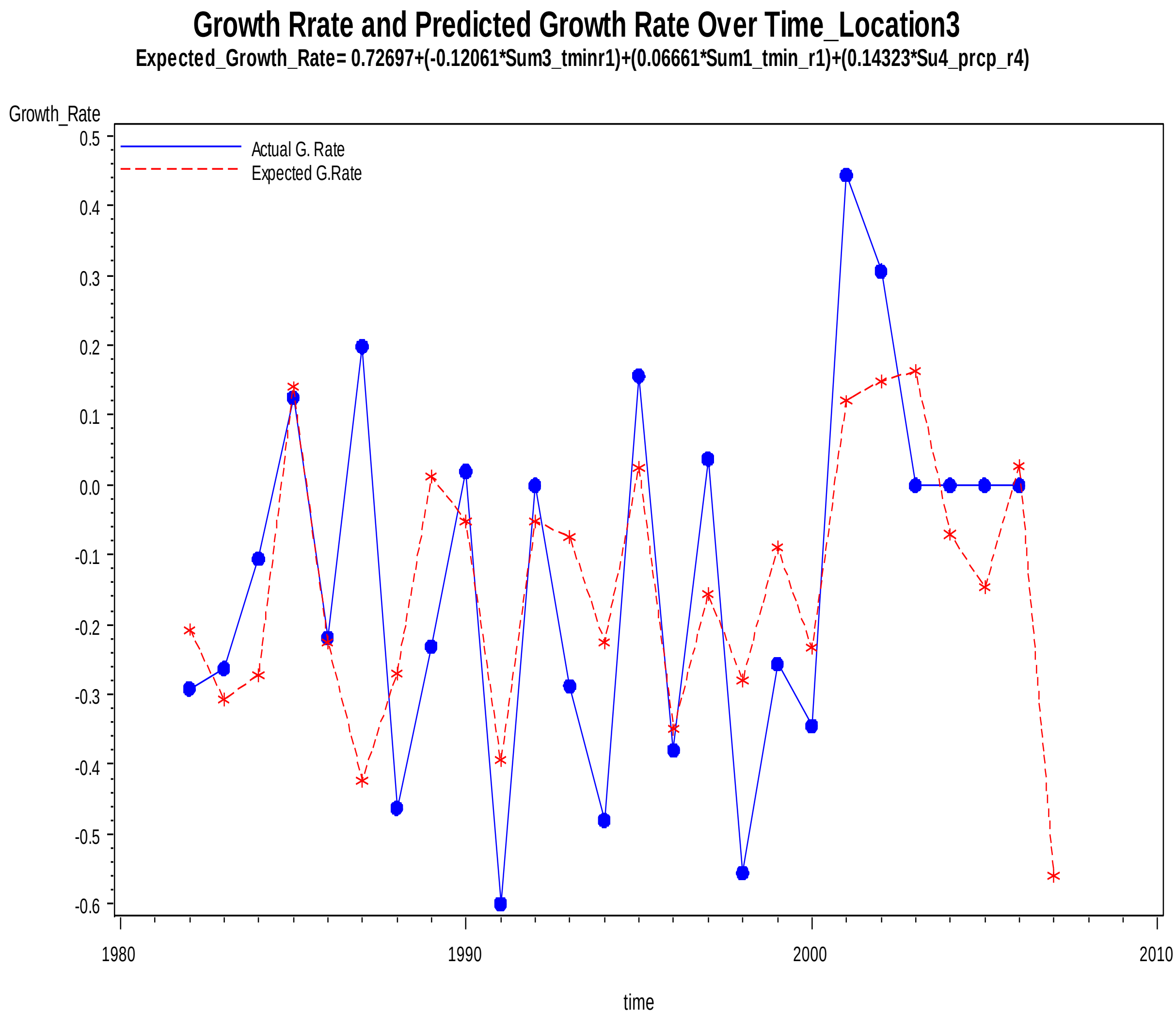

Figure 14: Cave 3 - Growth Rate and Predicted Growth Rate Over Time

Cave – 4

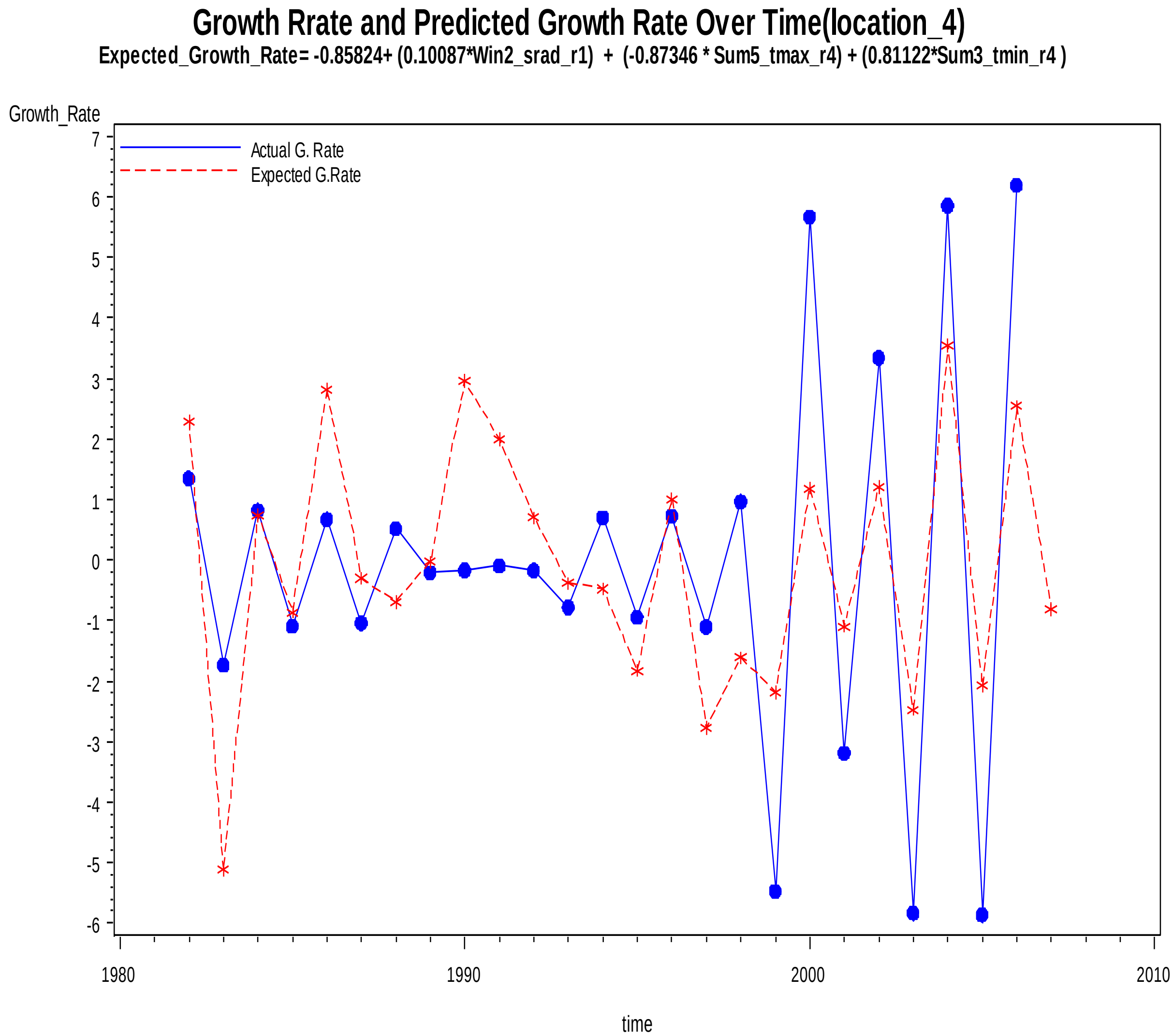

Figure 15: Cave 4 - Growth Rate and Predicted Growth Rate over Time

Comments on the 4 plots

- The 4 charts show that the per capita growth rate predicted values and the actual values are very close
- The graphs demonstrate that the predicted models based on the selected climate covariate are able to capture the variation trend of the actual population per capita growth rate over time. In fact, the 2 trends are similar over time.
- Caution should be made about the models. The R^2 values and the similarity between the predicted and the actual data may be due simply to over fitting the training data set. In the presence of 145 covariates, overfitting is a potential issue. Moreover, in the absence of an independent test set, it is difficult to test the adequacy of the proposed model.

d- Summarizing the Output for all 167 Caves

The Indiana Bat population is geographically dispersed, therefore it was anticipated that the associated climate covariates would vary from cave to cave. After checking for strongly associated covariates with individual caves, we are interested in covariates that are associated with most of the caves. The following table illustrates the most frequent covariate and their frequencies.

Table 7 Most Frequent Climate Covariates

Variable	**Total Count** (number of caves where the variable occurs)
x23	14
x2	15
x211	15
x212	16
x5	16
x215 : Solar radiation within 16 km around the cave in winter (Jan-Feb)	18
x3: Precipitation within 16 km around the cave in fall (Aug 15- Sep 14)	21
x213: Precipitation within 16km around the cave in winter (Jan-Feb)	25

Comment

- X213 is associated with 25 cave population growth rates out of 167 caves
- X3 is associated with 21 cave population growth rates out of 167 caves
- X215 is associated with 18 cave population growth rates out of 167 caves

The frequency table shows that precipitation by the cave in both winter and fall are associated with a large number of cave growth rates. Also, it shows that solar radiation by the cave in winter is a climate factor that is associated with the growth rate. Other climate factors are associated with other caves. We noticed also, while running the frequency tables, that caves in a given geographical area tend to share similar climate factors. Therefore we decided to group the significant covariates by state.

f-Frequency of Significant Climate Covariates by State

Based on the above analysis, it seems that some significant covariates are more common in a particular geographical area than others. Therefore, grouping climate covariate by state is the next step. To illustrate the output, Missouri caves are used. Missouri has 19 caves. The other states frequency tables are in Annex 5.

Table 8 Significant Climate Covariates for Missouri

Variable	Total Count
x188	3
x190	3
x2	3
x24	3
x3	3
x213	4

5. Chapter 5

Limitation of the Study

While linking Indiana Bat Population to climate seems to shed some light on I-Bat population dynamics between 1982 and 2007, it is imperative to emphasize the *exploratory* nature of the study. Indeed, the analysis suggests a possible association between Indiana bat population and local climate covariates. However, the weakness of the USFW data and the limitation of the applied forward selection technique do not allow establishing a definitive association.

5.1. Issues with USFW Data

Due to limited surveying, Most of Indiana Bat population time series contain a limited number of time points, giving rise to short-time-series data, which imposes challenges for extracting meaningful information. In fact the longest cave time series has 25 observations, while the shortest has 3 observations. Moreover, missing values constitute up to 50% of some of the time series. Loss of information due to artificially replacing missing values in most Indiana Bat caves population using linear interpolation may weaken any analysis conclusions. Also, surveying has been done in different caves by different samplers and using dissimilar techniques which may have introduced biases and measure errors.

5.2. Forward Selection Algorithm Limitation

When we have to choose among a large pool of covariates (145) for a large number of population time series, the forward selection technique is a suitable technique. Like any other statistical tool, forward selection has it shortcoming. For instance, Harrell (2001) states that "Forward variable selection has been a very popular technique for many years, but if this procedure had just been proposed as a statistical method, it would most likely be rejected because it violates every principle of statistical estimation and hypothesis testing.".

One problem in forward selection is that it is based on sequential testing with specified entry (SLE) significance levels. A single selection step does not represent one hypothesis test but, rather, involves a large number of tests. The "*F*" -to-enter" statistics do not follow an "*F*" distribution as we may think(Draper, Guttman, and Kanemasu 1971). Hence, the SLE cannot be considered a probability.

A second problem is that the order of parameter entry affects the selected model. This issue is particularly acute where the predictors are correlated (Grafen & Hails 2002) which is the case in our study. On the one hand, the 6 different climate covariates are correlated with each other, on the other hand, each covariate covering a specific radius is highly correlated with itself in the 3 other radii. If we are dealing with 145 covariates, depending on the order of entry, the algorithm can lead to different final models. Only one model will be presented as an answer to biologists, which may give the false impression that only this selected model explains the relationship between climate and a Indiana bat population dynamic for a specific cave.

A third issue is the difficulty to interpret significance due to the correlation of explanatory climate covariates. Interpreting a single coefficient as the amount by which the mean response changes when a given covariate changes by one unit, holding other climate repressors fixed, is senseless. A specific climate covariate does not change in isolation.

5.3. The Research Question Limitation

A precise hypothesis is the key element in any successful scientific research. Due to limited foreknowledge of the relationship between I- Bat population and climate, scarce literature about the topic and the absence of previous work on the subject, it was difficult to formulate a well-defined and focused research question. Instead, a more general and board-based one was proposed by the biologists: Among 145 possible climate covariates, what is the best set that can explain well each cave population time series data? Such an *exploratory* question can lead to different answer for each cave. In fact, the final selected model is not the best model; rather, it is a good one among other possible fine models.

Since, forward selection in our case is used for exploration, rather than for dressing a specific question, great caution should be used in interpretation the result (Ramsey, 2002):

- Biologists should investigate each cave final model to detect any biological significance or suggest adjustments.
- The chosen explanatory variables are not necessary unique. They depend on the correlation between the 145 climate covariates and the order of entry into the selection process
- Because of large number of covariates, a selected climate covariate may be a result of pure chance

To summarise, despite modeling difficulties, this preliminary exploratory analysis is valuable in shedding light over a presumed association between Indiana bat population dynamics and climate. The study could be used as a platform to generate a more elaborated hypothesis such as: Is August average maximum temperature, within 80 km radius, around cave 'x" a key factor in increasing the per capita growth rate for that cave, while controlling for the other 5 known possible confounders within the same radius? Moreover, a selected model for a cave "x" can be used to predict the per capita growth rate for cave "y" if the 2 caves are geographically close. This algorithm can test the goodness of the model, and therefore prove if the selected climate covariates are indeed associated with Indiana bat per capita growth rate for the 2 caves.

6. Chapter 6

Summary

6.1. Discussion

Key to understanding the in decline in Indiana bat population is climate. Indiana bats are selective for their habitat. In winter, they hibernate in lime stone caves with very specific climatic conditions. Stable, low temperatures, favourable relative humidity, and optimal air flow conditions are all need to conserve fat reserves during hibernation. In summer, they roost in warm habitats, preferring forests that have old trees and sunny openings. They also prefer river shorelines for their reliable supply of insects.

All attributes of the bat's hibernation and migration are mediated by ambient light regimes, temperature, and food resources or a combination of these factors. The bat's ability to build up energy stores, and therefore survive both the long hibernation and the long migration, depends on the interplay of these factors. Any small change in climate of the cave affects the bat's hibernation, and depletes its energy supplies, and thereby affecting its survival. Furthermore, any climatic change its summer habitat affects the roosting habits by altering its food supply or plant phenology.

As exploratory analysis, plotting the per capita growth rate per county and comparing the per capita growth rate over time among nearby caves then linking each cave growth rate to climate covariates *suggest* that different climate covariates are affecting cluster of caves at different geographical area. In other words, the possible association between climate and Indiana bat population dynamic varies depending on the geographical area. For instance, while most caves in Minnesota are associated with winter precipitation within 16 km radius from the caves, most caves population in Ohio are associated with maximum temperature in spring within a large radius from the caves (460 km). The analysis suggest that Indiana bat populations are associated with specific regional climate instead of global climate.

The regional effect of climate may be due to global climate change. Indeed the impact of potential change might be affecting the Indiana bat ecosystem such as: the climate covariate, the landscape cover, rivers and lakes, forests in ways that varies from area to area. For instance, it may be increasing the temperature in some region, while decreasing it others. While such hypothesis need deeper investigation, earlier biologist observations propose it. In fact, Clawson's summary reveals a clear division in population trends between northern regions of the states versus southern range. (2002). He documented that while the southern population has declined by 74% since 1960, the northern States population has been an overall increase in population of 50% over the same time. It is probable that suitable temperature may be a key to understanding such regional disparities since the northern region are colder than the southern ones.

This exploratory study suggests a possible relationship between climate and the Indiana bat population. Due to the weakness of the data, the large number of covariates and the limitation of forward selection tool, the results are suggestive, not final.

As a part of monitoring effects of climate, it is particularly critical to continue to assemble information on climate covariate inside the cave and around it, as well as at known summer colonies of the species. Such precise information would be critical in further investigating causal relationships between climate and I-Bat population, especially for priority 1 and priority 2 caves. The 2 priority are the key stone in any recovery plans due to their large populations. Also, the specific data may help avoid controversies about any management plan that can arise as a result of decisions based on incomplete information.

6.2. Conclusion

Bats are a fundamental component in the environment. Indiana bat have populated North America for centuries before man invade their habitat and spoil it. The

Indiana bat population has been decreasing dramatically in the past half a century before WNS immerged in 2006 and start driving the species to extinction. Our work is a step in exploring possible relationship between I-Bat population growth and climate before the appearance of WNS.

The low quality of the I-Bat data required intense work with bat biologist to clean and input missing values. A useful, but smaller, data set was produced where the number of caves was reduced from 450 to 222, then later to 167 and the first of time series was 1982 instead of 1950.

The adequate fit of the exponential growth model versus the logistic to the 222 population time series suggested the absence of the density dependent mechanism. In fact, independently of their size, many caves population are decreasing. This result proposes the possibility of existence of external factors regulating I-Bat population growth, such as weather, habitat limitation or natural disaster.

Plotting the growth rate for each population geographically, and over time reinforced the hypothesis of possible climate effect. First, the geographical plotting of caves growth rates shows spatially clustering patterns. Indeed, I-Bat population appear to be increasing in some areas while declining in others. Second, smoothing each cave growth rate reveals astonishing similarities in growths behaviour over time. In fact, closer the caves, more similar are the trends.

To come to the point, the absence of density dependence, the spatial correlation of growth rates and the existence of similar patterns in the growth rate over time for adjacent caves suggest the idea of possible effect of climate on the bat population decline

Finally, discussing previous results with USFW bat biologists and YERC ecologists leads us to the core of our analysis: Exploring the potential link between each cave growth rate and the climate. The analysis is done in the following steps: 1- Defining which climate covariate may be affecting I-Bat survival

2- Depending on I-Bat annual cycle, define which radiuses around the cave

3- Request the covariate from TOPS for each cave based on caves spatial coordinate

4- Use forward selection to extract the associated climate covariate for a given cave then for a given geographical area

To summarize, the study suggest a possible effect of local climate on Indiana bat population decline. However, the limitation of the study method does not permit establishing a solid and direct link. The study is exploratory and can be used as a base to more elaborate research.

It should be noted that :

- This preliminary results are being interpreted by biologist
- USFW and YERK biologists are reducing substantially the number of covariates to 1 raduis and probably few seasons to deal with the many covariates issue
- YERC is currently gathering data about the landscape change in the period time 1982-2006 in counties that have Indiana Bat caves. Such data will be incorporated in our model.

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Annex 1

Density Dependence Testing for 3 caves population

We tested the density dependence mechanism for all the 167 caves. We choose 3 caves to illustration the procedure

Cave-1

State: Missouri

County: Franklin

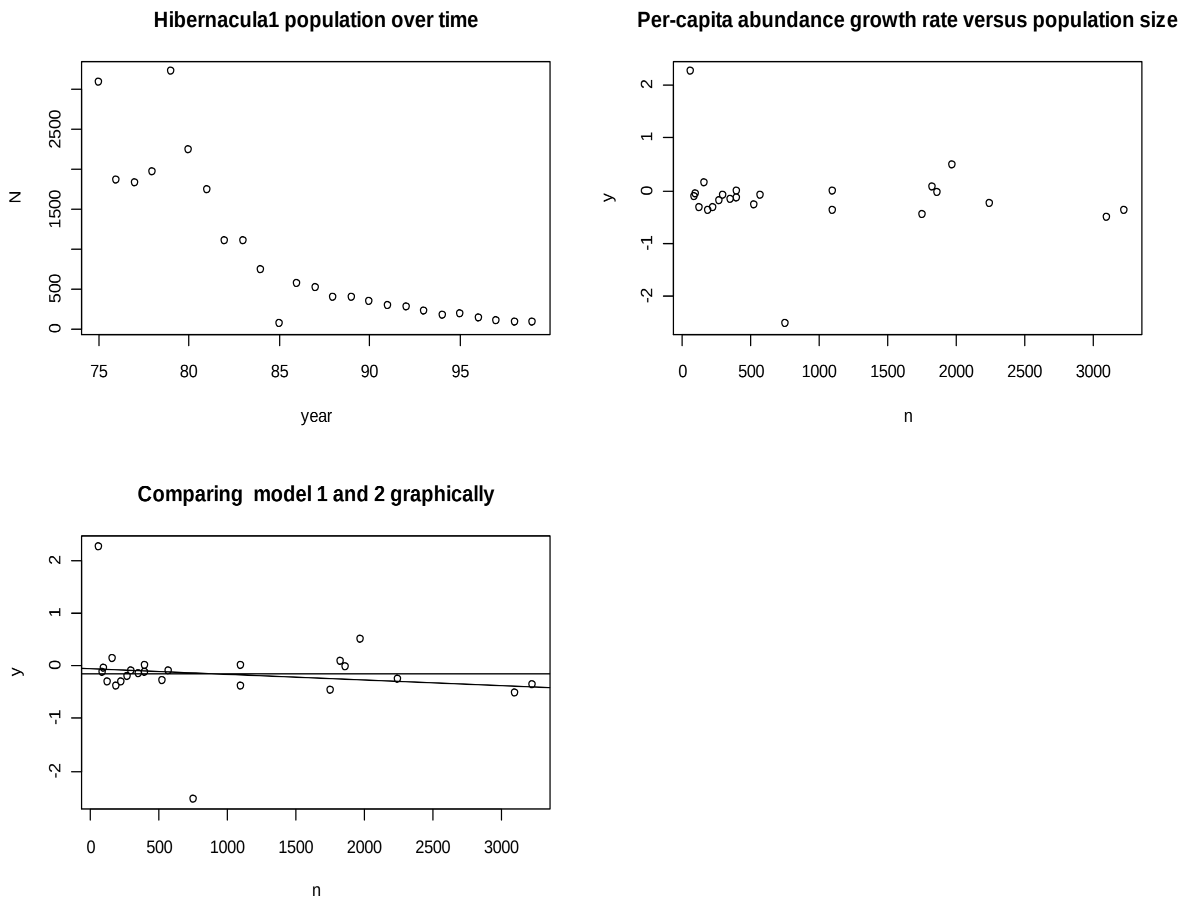
Data row number: 258

Cave-1 Population Time Series

Year	Population size
1975	3100
1976	1867
1977	1825
1978	1972
1979	3229
1980	2247
1981	1750
1982	1100
1983	1100
1984	750
1985	650

1986	575
1987	525
1988	400
1989	400
1990	350
1991	300
1992	275
1993	225
1994	165
1995	190
1996	130
1997	95
1998	90
1999	80

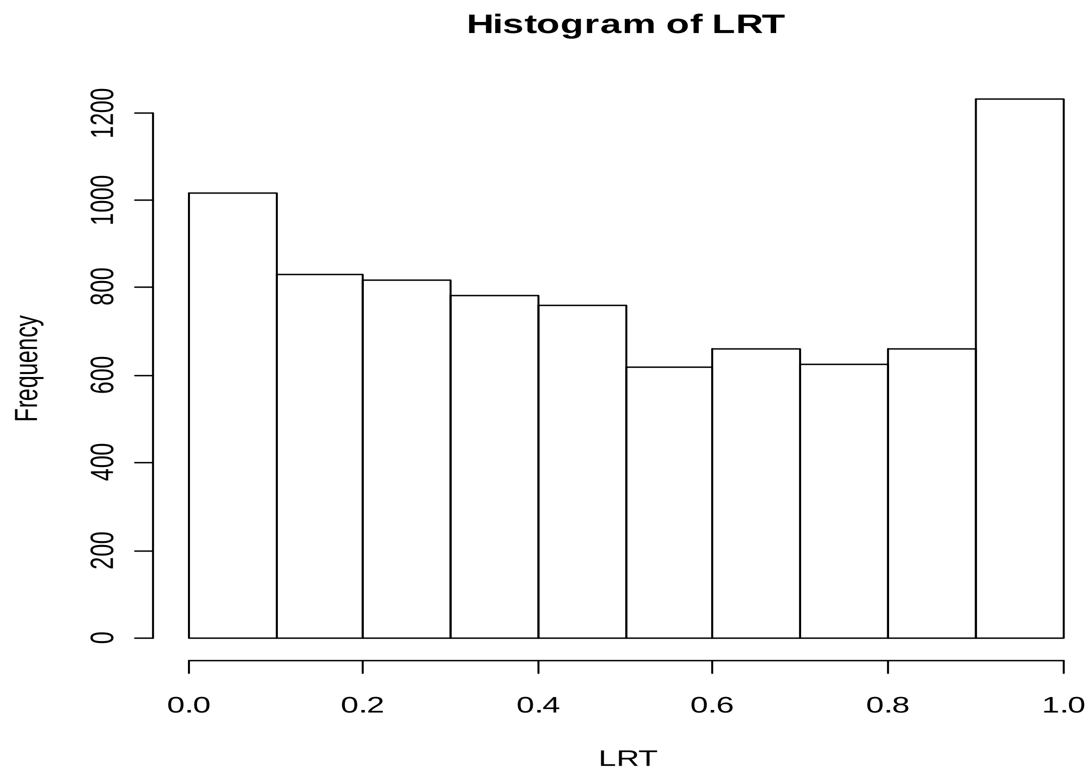
Comparing the 2 Fitted Models (Exponential and Logistic) Graphically



Comment

Comparing the 2 models graphically suggested no difference in the fitting quality. We may expect that the simplest model (exponential) is the best fit. We will quantify the difference in the next step by using bootstrapping.

8000 Bootstraping Generated LRT's Distribution Graph



P-value

P-value= 0.74

As it was expected from the graph, there is no evidence against the null hypothesis. Therefore, there is no evidence of an effect of the population density on the the growth rate in
hibernacula 2.

Cave-2

State: *Kentucky*

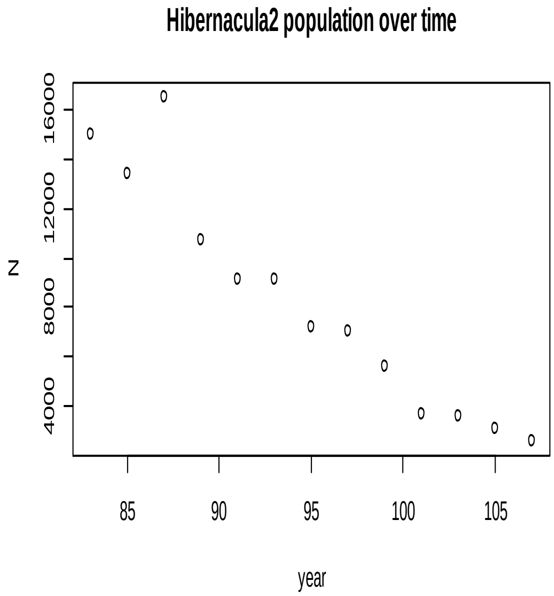
County: *Edmonson*

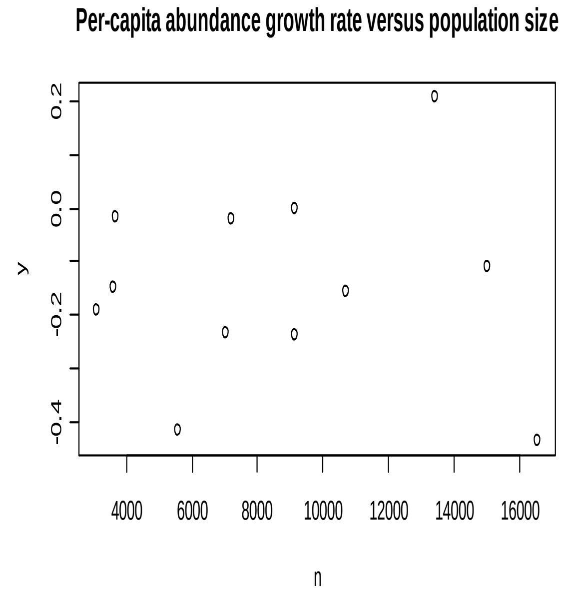
Data row number: 134

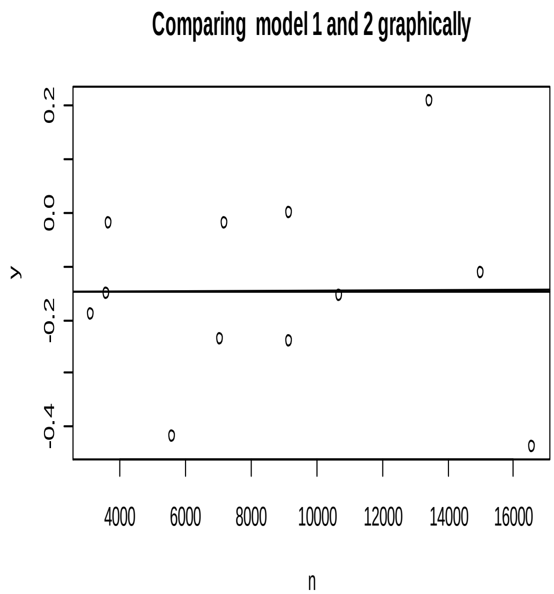
Cave -2 Population Time Series

Year	Population size	Per Capita Growth Rate
1983	15000	-0.11
1985	13425	0.209
1987	16550	-0.436
1989	10700	-0.156
1991	9150	0
1993	9150	-0.239
1995	7200	-0.021
1997	7050	-0.234
1999	5575	-0.418
2001	3670	-0.019
2003	3600	-0.149
2005	3100	-0.19
2007	2563	NA

Comparing the 2 Fitted Models Graphically



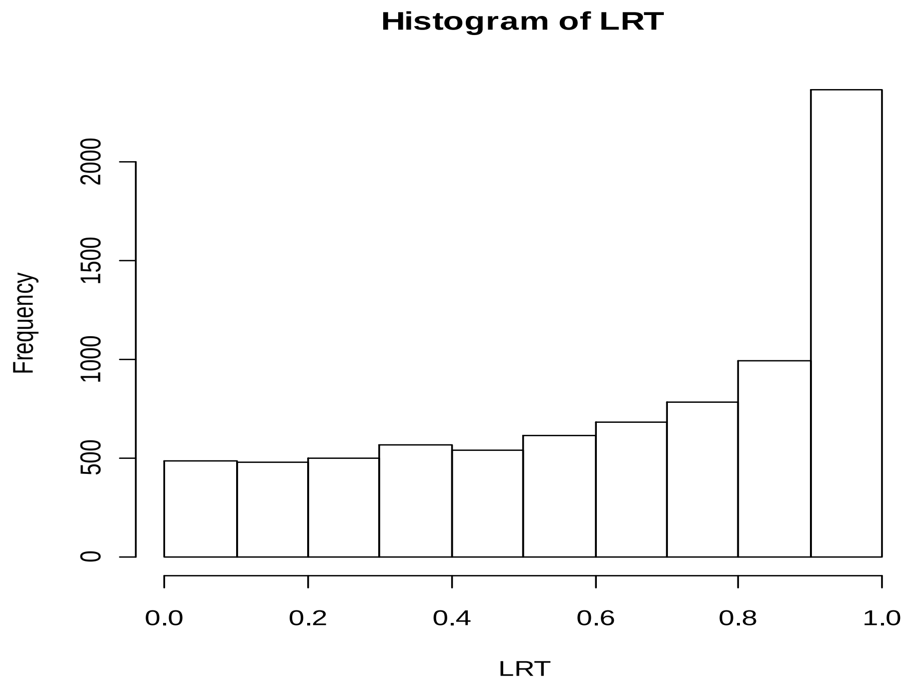




Comment:

The exponential model is overlapping literally with the more complicated model (logistic). Hens, we may expect the absence of the density dependence effect. Next, bootstrapping should confirm this result

8000 Bootstraping Generated LRT's Distribution Graph



P-value

P-value= 0.99

The null hypothesis is not rejected as we expected from the graph. Bootstraping confirmed the exact result by a high P-value. Therefore, we conclude that there is not enough evidence for density dependence in this particular cave population.

3. Cave-3

State: *Missouri*

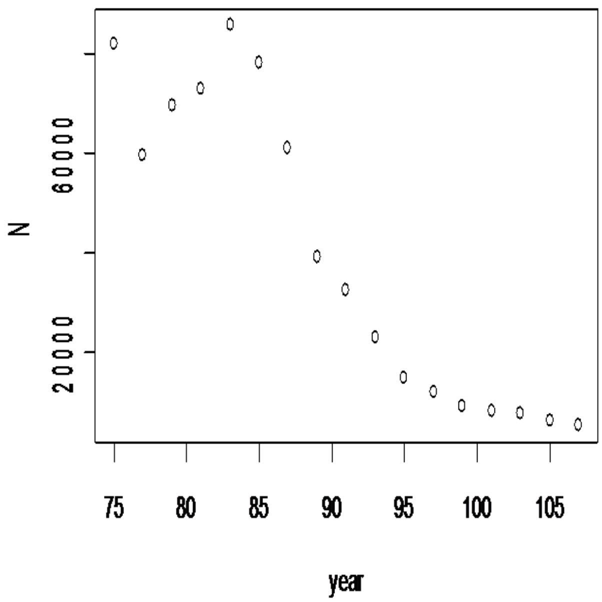
County: *Washington*

Data row number: 298

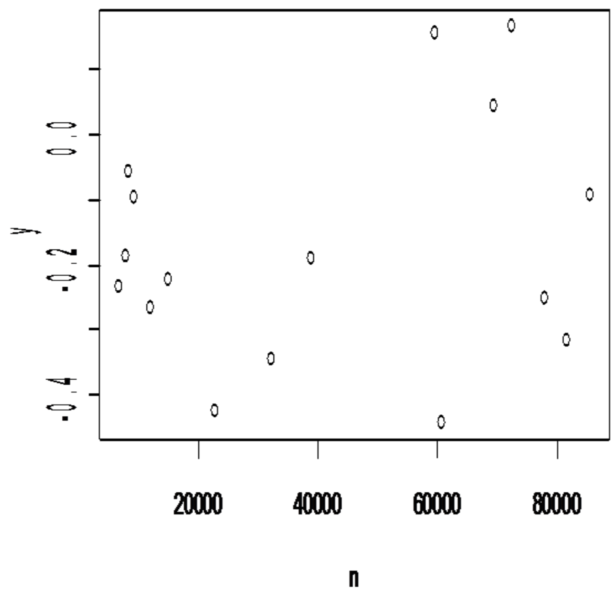
Year	Population size
1975	81800
1977	59515
1979	69387
1981	72500
1983	85700
1985	77950
1987	60650
1989	38875
1991	32125
1993	22750
1995	14850
1997	11875
1999	9100
2001	8250
2003	7775
2005	6450
2007	5100

Comparing the 2 Fitted Models Graphically

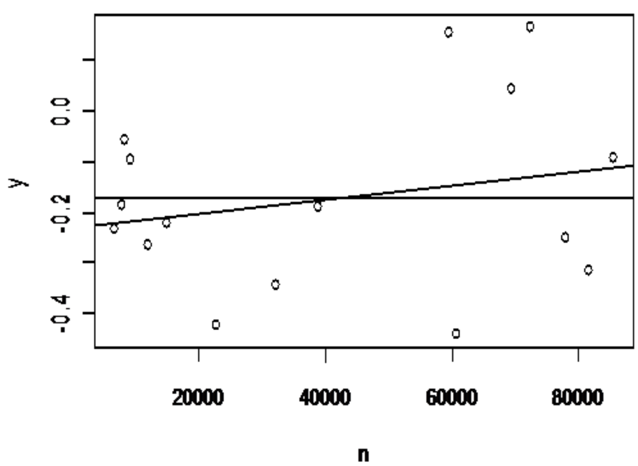
Population Size over Time



Growth Rate vs



Comparing the 2 Fitted Models



P-value= 0.71

It appears that the third cave population growth rate is also independent of the size of the population.

For the 3 caves we:

1. Fitted both exponential and logistic growth model.

2. Used bootstraping technique to simulate the test statistic distribution under the null.
3. Concluded, based on the P-value, that there is strong evidence for the exponential. growth model and hens the absence of the effect of density dependence on the per capita growth rate.

We conclude that these 3 populations may be heading to extinction since their growth rate is negative and sensity independent.

For the total number of caves(222 caves)

1. Checked density- independence for all the 222 caves
2. Same result as above

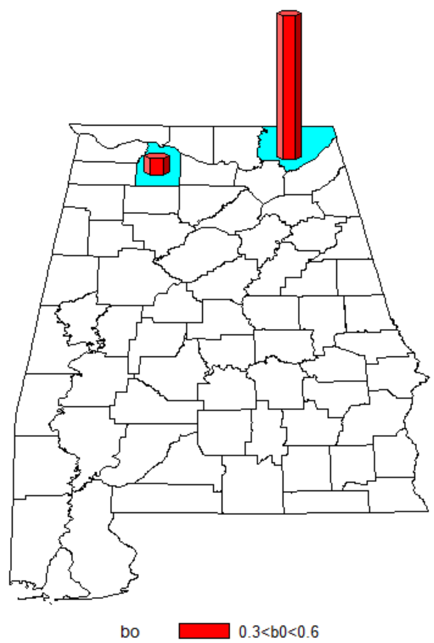
Annex 2

The per capita growth rate estimate per county

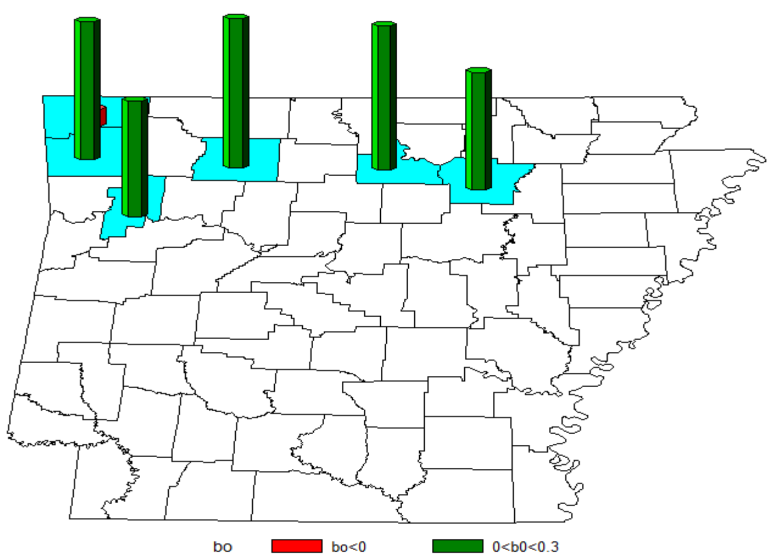
Hiberna	b0	bo Average Fc	sigma			
	0.5896		0.1913			
	0.3018		0.7413			
	0.6796	0.490709873	0.5449			
	-0.494		0.3385			
	0.0493		0.2174			
	0.0675		0.4654			
	0.1899		0.9688			
	0.1686		0.3458			
	0.1644		0.1757			

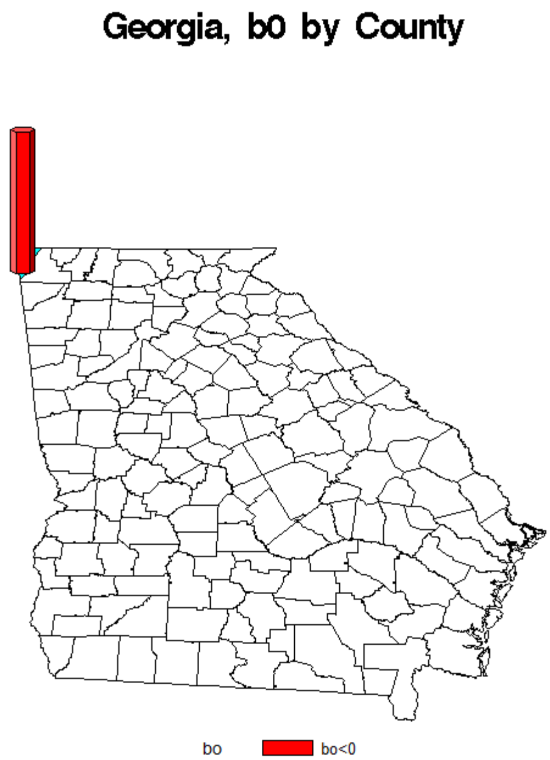
Annex 3

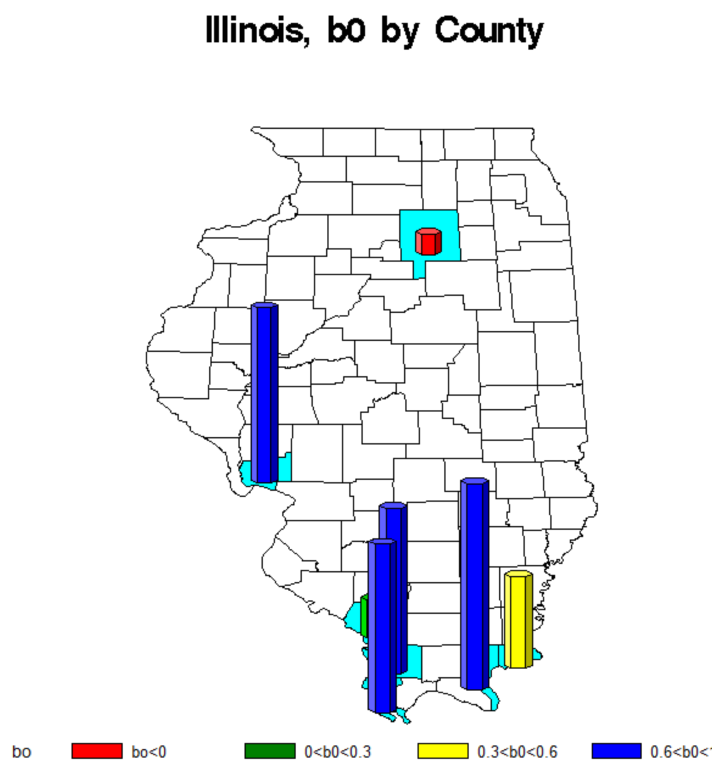
Alabama, bo by County



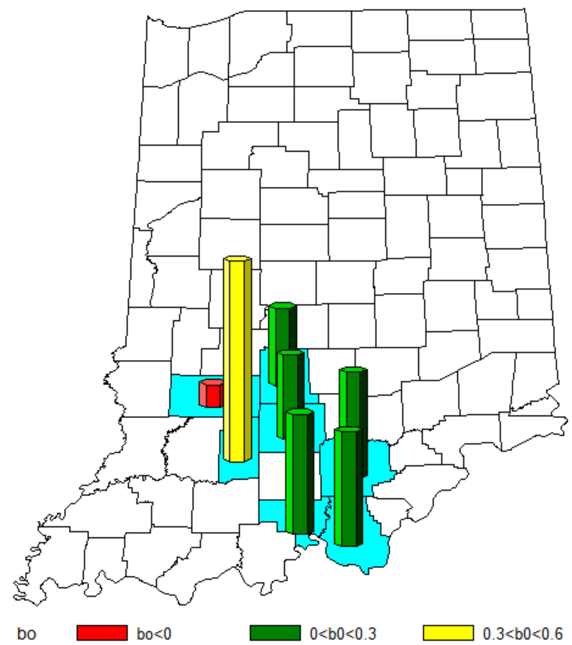
Arkansas, b0 by County



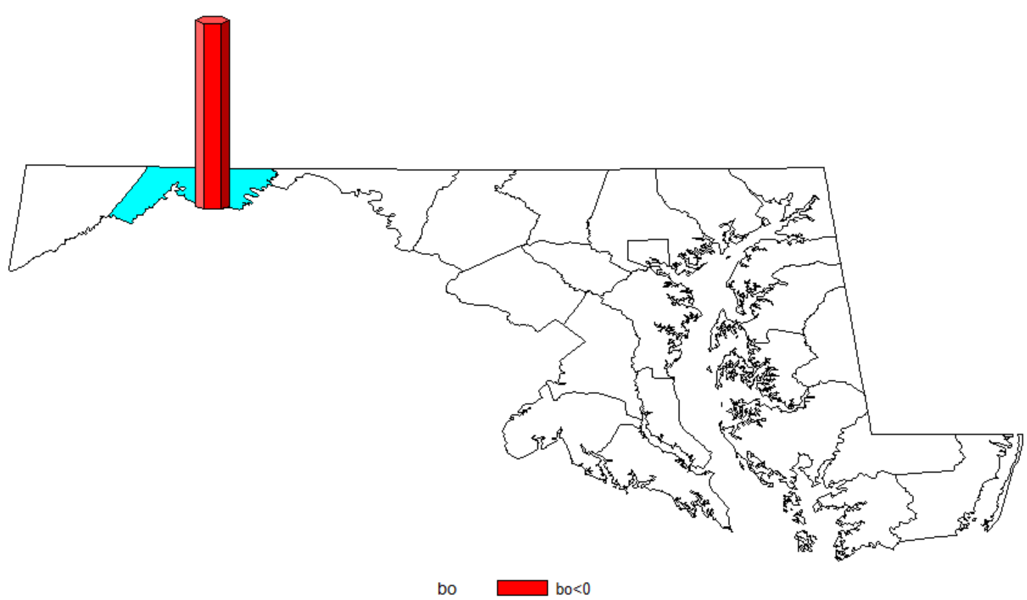

Georgia, b0 by County
bo
bo<0

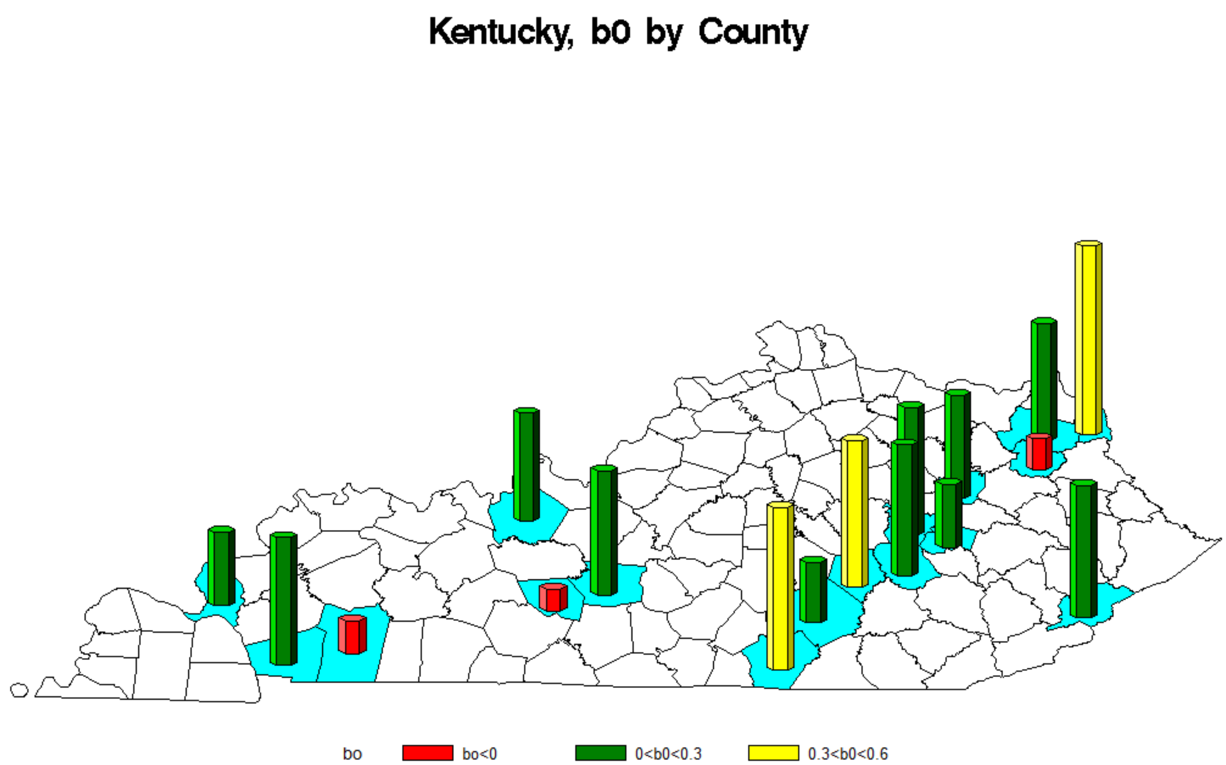

Illinois, b0 by County
bo
bo<0
0<b0<0.3
0.3<b0<0.6
0.6<b0<1

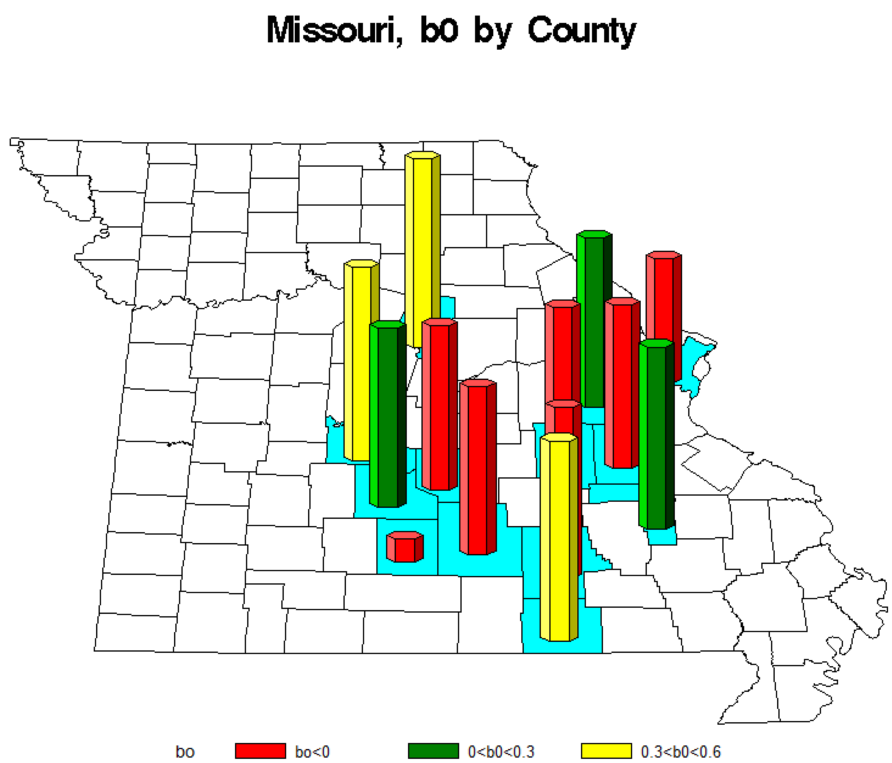
Indiana, b0 by County



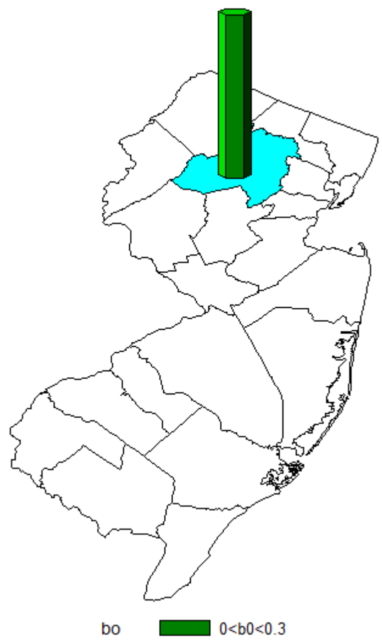
Maryland, b0 by County



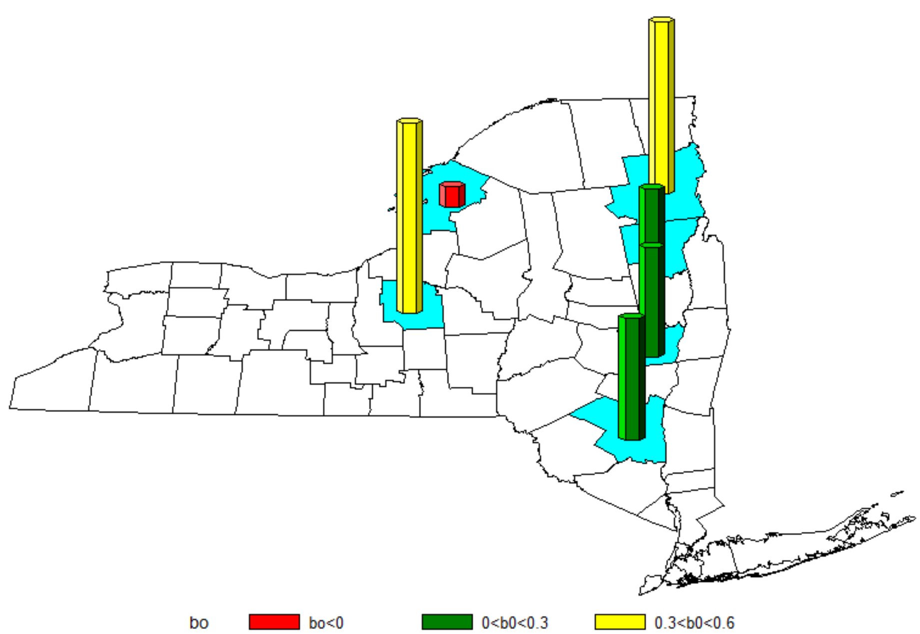

Kentucky, b0 by County
bo
bo<0
0<b0<0.3
0.3<b0<0.6


Missouri, b0 by County
bo
bo<0
0<b0<0.3
0.3<b0<0.6

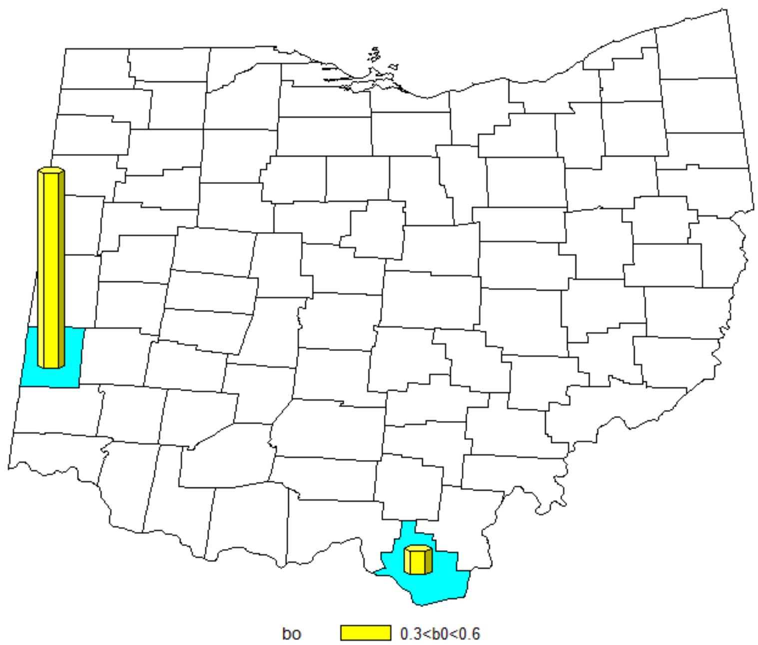
New Jersey, b0 by County



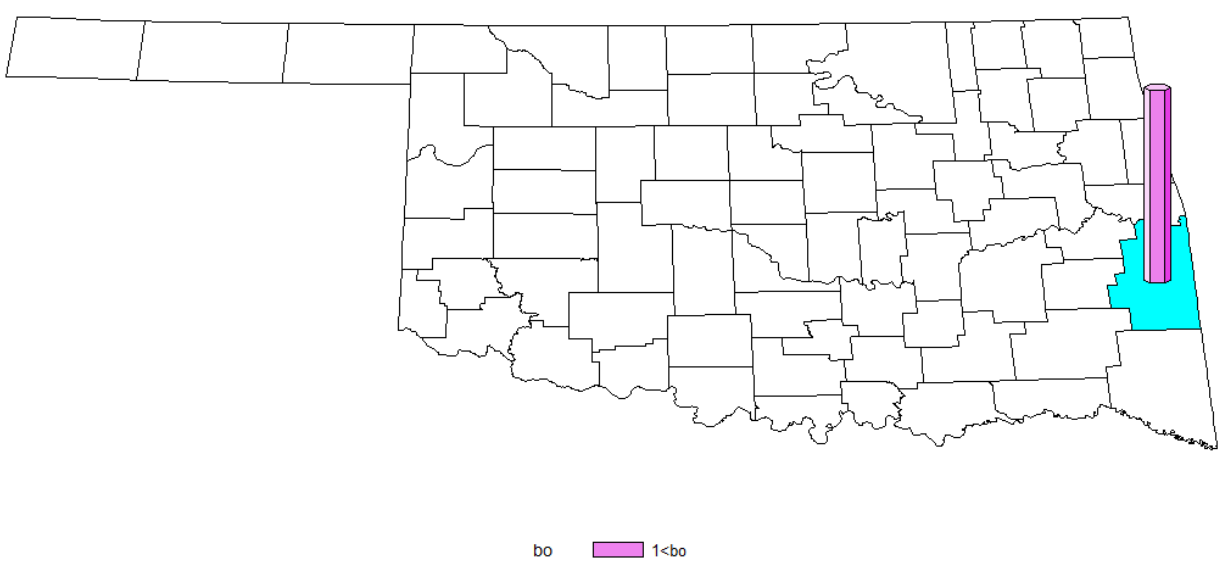
New York, b0 by County



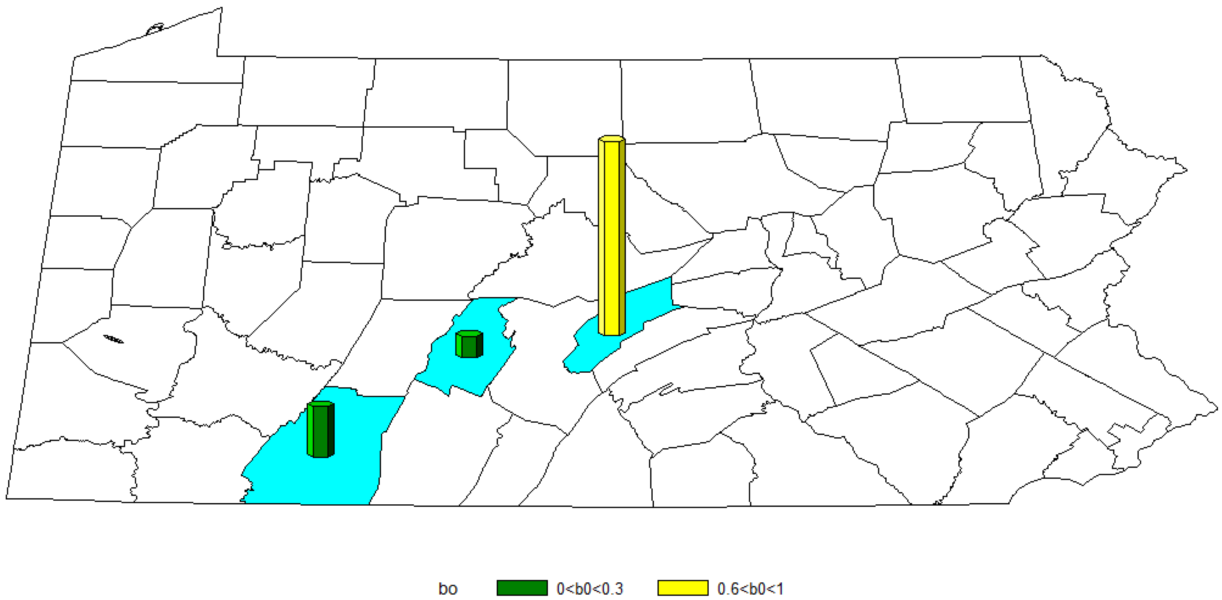
Ohio, b0 by County



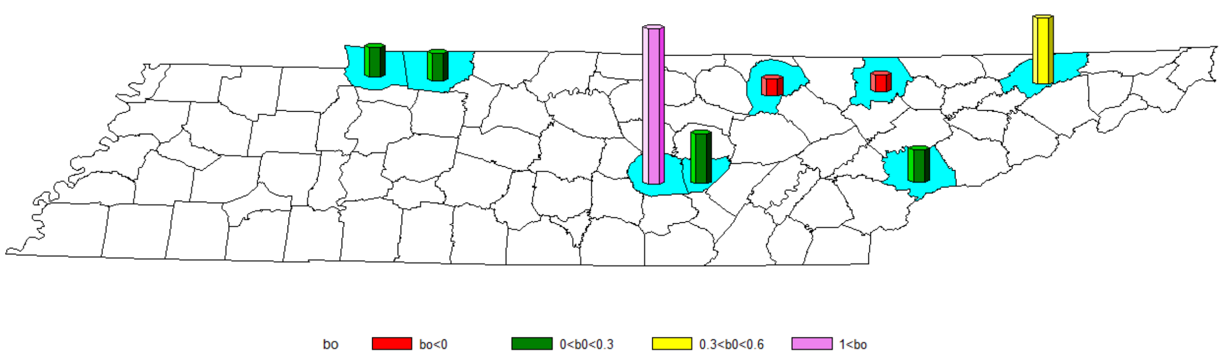
Oklahoma, b0 by County



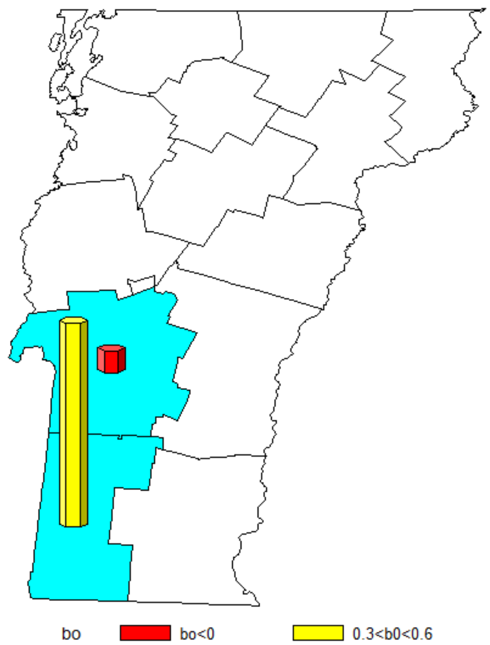
Pennsylvania, b0 by County



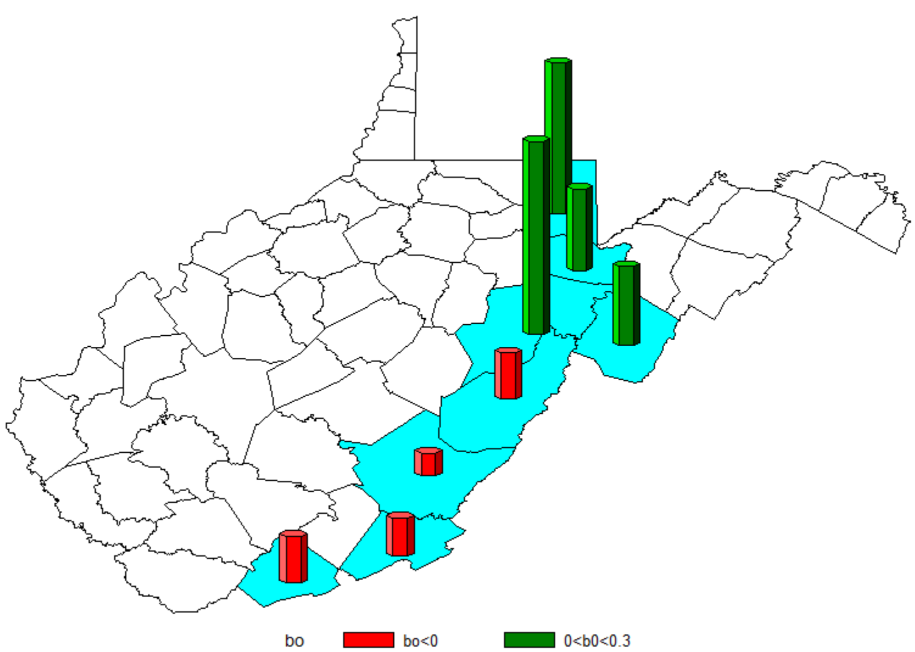
Tennessee, b0 by County



Vermont, b0 by County



West Virginia, b0 by County



Annex 4

To facilitate the programming macro, we denoted the covariates by x1-x127. These nomination correspond to the 5 main covariates consecutively: tmax, tmin, prcp,vpd, srad for the following seasons and radii:

Climate variables key is presented in the following excel file:

Table 9 Covariates Labels Key

x190	winter1 dates?	16km	tmax			
x191	winter1 dates?	16km	tmin			
x192	winter1 dates?	16km	prcp			
x193	winter1 dates?	16km	vpd			
x194	winter1 dates?	16km	srad			
x211	winter2 1/1-2/28	16km	tmax			
x212	winter2 1/1-2/28	16km	tmin			
x213	winter2 1/1-2/28	16km	prcp			
x214	winter2 1/1-2/28	16km	vpd			
x215	winter2 1/1-2/28	16km	srad			

Annex 5

Table 10. Covariates Frequency for West Virginia - 18 Caves

Variable	Total Count
x180	2
x192	2
x2	2
x212	2
x215	2
x22	2
x24	2
x3	2
x65	2
x87	2
x5	4

Table 11 Covariates Frequency for Virginia - 10 Caves

Variable	Total Counts
x167	2
x213	2
x215	2
x3	2

Table 12 Covariates Frequency for Tennessee - 9 Caves

Variable	Total Count
x139	2
x142	2
x23	2
x24	2
x75	2

Table 13 Covariates Frequency for Pennsylvania - 3 Caves

Variable	Total Count
X98	2

Table 14 Covariates Frequency for Ohio - 2 Caves

Variable	Total Count
x121	2

Table 15 Covariates Frequency for New York - 7 Caves

Variable	Total Count
x102	2
x124	2
x23	2

Table 16 Covariates Frequency for Kentucky - 53 Caves

Variable	Total Count
x192	5
x211	5
x212	5
x214	5
x22	5
x23	5
x3	6
x45	6
x2	7
x5	8
x215	9
x213	12

Table 17 Covariates Frequency for Indiana – 14 Caves

Variable	Total Count
x103	2
x122	2
x123	2
x137	2
x191	2
x211	2
x25	2
x45	2
x46	2
x87	2
x66	3

Table 18 Covariates Frequency for Illinois - 9 Caves

Variable	Total Count
x98	1
x1	2
x150	2
x180	2
x188	2
x44	2
x80	2
x82	2
x211	3
x3	3
x67	3

Table 19 Covariates Frequency for Arkansas - 13 Caves.

Variable	Total Count
x130	2
x163	2
x181	2
x212	2
x25	2
x78	2
x124	3