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I am submitting herewith a dissertation written by Paula Federico entitled “Bat Population Dynamics: An Individual-based Model Approach.” I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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Bat Population Dynamics:
An Individual-based Model Approach

A Dissertation
Presented for the
Doctor of Philosophy Degree
The University of Tennessee, Knoxville

Paula Federico

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To my children, Victoria and Federico.

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ABSTRACT

Temperate zone bats are subject to serious energetic constraints due to their high surface area to volume relations, the cost of temperature regulation, the high metabolic cost of flight, and the seasonality of their resources. To my knowledge, there are no individual-based mathematical models for any bat species. The model developed here for a female bat is primarily based on life history and energetics. It describes the growth of an individual female bat using a system of differential equations modeling the dynamics of two main compartments: storage (lipids) and structure (proteins and carbohydrates). The model is parameterized for the little brown bat, *Myotis lucifugus*, because of information available on energy budgets and changes in body mass throughout its life history. However, with appropriate modifications the conceptualization might be applied to other species of bats with similar life histories.

The dynamic estimates of daily energy budgets resulting from the model reasonably compare to previous estimates obtained through different methodologies. Sensitivity analysis using statistical screening design techniques identifies the individual parameters driving the model output and indicates the individual characteristics that might play an important role in survival, reproduction, and consequently in population dynamics. The individual model is used to test hypotheses related to strategies used by temperate bats to meet their energy demands. A complete corroboration of the model is not possible due to the lack of a data set independent of that used to construct and calibrate the model.

The individual model is integrated into a structured population model. Characteristics of the individuals determine the structure and, subsequently the dynamics of the population. This methodology uses and integrates the information on bat biology and physiology that has been collected primarily at the individual level. Survival and reproductive rates estimated from simulated populations under varying density dependence are comparable to those reported in the literature for natural populations of *M. lucifugus*. The population model provides insight into possible regulatory mechanisms of bat population sizes and dynamics of survival and extinction. A better understanding of population dynamics can assist in the development of management techniques and conservation strategies, and to investigate stress effects.

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CHAPTER I
INTRODUCTION

1.1 Motivation

Bats account for nearly one fourth of living mammal species, they are unique among mammals in their ability to fly. The evolution of flight and echolocation in bats have played a major role in the diversification of feeding and roosting habitats, reproductive strategies, and social behaviors (Kunz 1982). Bats are highly beneficial, playing key roles in many ecosystems as insect predators, seed dispersers, and pollinators (Kunz and Fenton 2003). They have become the focus of large research efforts in almost every field of biology. As a result of new technologies, observational techniques, and analytical methods, there have been enormous advances in the study of bats during the past three decades (Fenton, Racey et al. 1987; Kunz and Racey 1998). However little is yet known about population dynamics of bats. For most species, status assessments are hindered by the lack of realistic population estimates and lack of knowledge of the effect of coloniality on minimal viable population size (Racey and Entwistle 2003). Studying population dynamics of bats presents particular challenges but bats are essential in some areas of concern in conservation and disease ecology that demand immediate investigation.

Bats have colonized all continents but Antarctica and are most abundant in the tropics. Forty-five bat species representing four families are native to the United States. Most of these bat species are insectivorous. Because insects are not generally available as food in winter in temperate regions, these bats survive by either migrating to warmer regions where insects are available, or by hibernating (Harvey, Altenbach et al. 1999).

Temperate zone insectivorous bats are subject to serious energetic constraints due to their high surface area to volume relations, the cost of temperature regulation, the high metabolic cost of flight, and the seasonally of their resources. Numerous studies have focused on energy budgets, diet and prey selection, thermoregulation strategies, and flight and echolocation physiology. Most provide valuable empirical data and a few of them attempt to explain patterns or processes based on some kind of mechanistic model. However, to my knowledge, there is no physiologically structured population model for any bat species.

The main goal of this research is to develop quantitative methodology to investigate the dynamics of bat populations. The approach to be used consists of a mathematical model for bat population dynamics that employs physiological information at the individual level (Hallam,

Lassiter et al. 1992). This requires the development of a mathematical model of relevant physiological processes of the individual, determination of the parameters in the individual model that can lead to variation among types of individuals in the population, and formulation of the population model (Hallam, Lassiter et al. 1992).

The integration of an individual model into a dynamic population model can assist understanding in many areas of bat biology and ecology. By modeling individual and population dynamics we may be able to improve understanding of the strategies used by bats to meet their energy requirements, to generate population dynamics leading to the development of conservation strategies, and to investigate stress effects like loss of suitable habitat or chemical insults.

1.2 Biological Background

Only three families of the order Chiroptera (Vespertilionidae, Rhinolophidae, and Molossidae) occur in temperate regions for extended periods of time (Koopman and Cockrum 1967). This subset of bats is composed entirely of insectivorous species that must deal with seasonally fluctuating food supplies (Raesly and Gates 1987) and decreased ambient temperature that increases the thermoregulatory energy costs. Bats have adapted to temperate zones mainly by hibernating during the colder months (Davis 1970). Vespertilionidae and Rhinolophidae are hibernators while within the Molossidae family some species may be capable hibernators (Cowan 1945; Jewett 1955) and others migrate.

In this section I will describe in general the main life history characteristics of temperate zone insectivorous bats in order to provide the biological background for the mathematical model and to determine key processes to be included in the model. Available information is employed to identify questions that the models developed here can help to answer.

1.2.1 Hibernation

In hibernating bats, males and females generally hibernate together in caves or mines where mating takes place during fall and winter. Bats undergo a rapid fattening during the fall with fat reserves amounting to more that 25% of the body mass at the onset of hibernation (Baker, Marshall et al. 1968; Ewing, Studier et al. 1970; Kunz, Wrazen et al. 1998). Depending on latitude and local temperatures, these fat reserves must fuel metabolism for periods up to 200 days (Speakman and Thomas 2003). Individual bats vary in the amount of fat stored before hibernation (Speakman and Racey 1989; Kunz, Wrazen et al. 1998). In general, young bats enter hibernation weighing significantly less than adults (Fenton 1970) and suffer high mortality (Keen and Hitchcock 1980). Because starvation at the end of hibernation is a cause of mortality in some

bat populations it has been suggested that bats entering hibernation with a large energy deposit are more likely to survive (Davis and Hitchcock 1965). This hypothesis implicitly assumes that mass losses throughout hibernation are independent of the body mass at the start. This assumption may be invalid (Speakman and Racey 1989) since energy costs of hibernation probably increase with increases in body mass (Hook 1951), and the regulated body temperature and the microclimate elected by the bats may vary among individuals (Beer and Richards 1956).

During hibernation, torpor metabolic rate (TMR) is so low that even the smallest fat reserves could sustain animals throughout the winter if they remained in continuous torpor. However, all hibernators arouse periodically, an action that represents a high thermoregulatory cost (Thomas, Dorais et al. 1990; Humphries, Thomas et al. 2002; Speakman and Thomas 2003). Thomas et al. (1990) estimated that roughly 308 mg of fat could sustain a 6.58g little brown bat (*Myotis lucifugus*) for 193 days of continuous torpor. An extra 1,618.5mg fat would be necessary to cover the cost of 15 arousals. Arousals account for about 85% of fat depletion for Myotis lucifugus, and the same pattern has been found for other hibernators (Kayser 1961; Wang 1978). This leads to the question “Why do animals expend so much energy on arousals that may risk their over winter survival?”

There are many theories explaining arousals (Thomas and Geiser 1997). One of the main explanations for arousals has been "feeding" (Speakman and Thomas 2003). Observations have confirmed that some species do feed in winter (Swanson and Evans 1936; Ransome 1971; Avery 1985). Avery (1985) formulated an energy cost-benefit model to better understand the choice of torpor or feeding during hibernation for pipistrelles in England. The model predicted that feeding is only worthwhile if capture rates are as high as 2.92 captures per minute, which tend to occur on warmer and calmer nights. For little brown bats, *M. lucifugus*, and northern bats, *Myotis septentrionalis*, it was demonstrated that these species were not feeding when flying outside in winter in Indiana (Whitaker and Rissler 1993). Moreover, other studies suggest that on some occasions bats may leave the hibernacula without feeding (Whitaker and Rissler 1992; Whitaker and Rissler 1993) or they may arouse without leaving the hibernacula (Thomas 1995). Speakman and Racey (2003) conclude that "feeding may occur during arousals in some species, but it does not appear to be the underlying cause for arousals."

Three other hypotheses have been proposed to explain the occurrence of arousals in hibernators. The "metabolism hypothesis" proposes that the reduction of energy substrates or the accumulation of metabolic wastes forces animals to arouse to reestablish intra- and extra-cellular conditions (Lyman, Willis et al. 1982). The "biological clock hypothesis" proposes that torpor-

arousal rhythm is determined by an endogenous biological clock that may or may not be dependent on the body temperature (Tb) of the organism (Willis 1982). Finally the "water balance hypothesis" postulates that hibernators face a water deficit due to excessive evaporative water loss (EWL), which results in the concentration of electrolytes and forces animals to arouse to drink (Thomas and Cloutier 1992). Recent studies support this last theory (Thomas and Cloutier 1992; Thomas and Geiser 1997; Speakman and Thomas 2003). Thomas and Cloutier (1992) measured EWL for *M. lucifugus* and argued that metabolic water production will not compensate for EWL except at relative humidities greater than 99.3% at normal hibernating temperatures. Torpor durations predicted on the basis of their net EWL model correspond closely to those observed in laboratory and field studies. Also Thomas and Geiser (1997), who modeled water losses for hibernating *Spermophilus lateralis*, found that the rate of EWL predicts arousals frequency far more accurately than did either Tb or TMR at normal hibernation temperatures (-2^{o}C to 8^{o}C). These studies suggest that the water balance hypothesis should not be disregarded when considering factors that determine duration of torpor-arousal bouts.

Even though hibernating bats normally are able to balance their energy expenditures during the winter, human disturbances can dramatically increase their energy demand by causing extra arousal, which affects overwinter survival (Speakman, Webb et al. 1991; Thomas 1995). It is well accepted that handling and banding activities stimulate hibernating bats to arouse and fly (Speakman, Webb et al. 1991). However, Thomas (1995) found that even brief visits involving non-tactile stimuli (light, sound, and increase in temperature) provoked arousals in a portion of the hibernating population. This result has important practical implications for the conservation and management of hibernating bats.

1.2.2 Migration

Fleming and Eby (Fleming and Eby 2003) define migration as a seasonal, usually two-way, movement from one place to another to avoid unfavorable climatic conditions and /or to seek more favorable energetic conditions. The tendency to migrate and the scale of migration vary within and between species; partial migration and sex-biased migration are possible. Partial migration is common in several species which have populations that migrate substantial distances and also have sedentary populations in some parts of their range (Fleming and Eby 2003). Mexican free tailed bat (*Tadarida brasiliensis*), one of the most abundant species in the United States, it is a well-known partial migrant (Cockrum 1969). Migratory populations travel south from the southwestern United States into the warmer subtropical and tropical climates of Mexico where they remain active through the winter (Tuttle 1992). Other examples of migratory

insectivorous species in United States include northern populations of big free-tailed bat (*Nyctinomops macrotis*), which is of special concern because it is very uncommon throughout its range and may be proposed for listing as endangered in the future, and northern populations of the hoary bat (*Lasiusus cinereus*) (Harvey, Altenbach et al. 1999).

1.2.3 Sexual maturity, Mating and Fertilization

In the majority of bat species males and females reach sexual maturity at one or two years of age (Racey 1982; Tuttle and Stevenson 1982). However, within a species, time to sexual maturity varies geographically, typically being delayed at higher latitudes (e.g. *Myotis lucifugus*, (Schowalter, Gunson et al. 1979)). Some females of vespertilionid species attain sexual maturity in their first fall, i.e. when they are about 4 months old (Racey 1974).

Most bats that live in temperate zones are monoestrous. In hibernating bats, mating can take place before and/or during hibernation during temporary periods of arousal. Females store sperm in the uterus and oviduct. Ovulation and fertilization are delayed for months until about 1 to 3 days after arousal (Neuweiler 2000). Successful ovulation appears to depend on stored fat reserves, quantity and quality of the fat deposited and on the amount that remains at the end of hibernation (Kunz, Wrazen et al. 1998). Delayed implantation also may occur. In that case copulation and fertilization occur in the fall, but implantation of the blastocyst is delayed until the end of hibernation.

Bats are generally monotocus, meaning that only one egg per cycle matures and is released for fertilization. However, three families of bats also include polytocous members. The vespertilionids *Pipistrellus pipistrellus*, *Nyctalus noctula*, and *Vespertilio murinus* tend to give birth to twins in climates with harsh winters, whereas those that live in mild climates usually give birth to only one offspring. *Lasiurus borealis*, a North American vespertilionid, give birth to one to four young (Harvey, Altenbach et al. 1999). Big brown bats, *Eptesicus fuscus*, usually bear twins in the eastern US and usually one young in the western US (Harvey, Altenbach et al. 1999).

For temperate-zone bats reproductive cycles are forced into a relatively short time span that is controlled by climate conditions (Wilson 1976). Just one litter per year is possible, and the timing of parturition is highly synchronous (Tuttle and Stevenson 1982).

1.2.4 Length of Gestation

Prenatal growth rates in bats vary in response to environmental conditions with temperature and food availability the most influential factors. In temperate species development is delayed when bats fall into torpor (Tuttle and Stevenson 1982). Thus gestation lengths vary

widely, both among (44 days-11 months) and within (56-100 days) species (Carter 1970; Orr 1970).

For *Pipistrellus pipistrellus*, Racey (Racey 1969; Racey 1973) found that the gestation length could be "profoundly affected by environmental conditions." Bats deprived of food and subjected to 11-14^{o}C for 13 days enter torpor and showed a mean delay in parturition of 14.5 days relative to the control group fed regularly and kept at 18-26 ^{o}C. And those pipistrelles provided with all the food they could eat at temperatures ranging 10-25 ^{o}C, did not differ from controls in mean lengths of pregnancy and remained homoeothermic.

Bats may use behavioral thermoregulation either to increase or to reduce rates of embryonic development (Kunz 1982). Bats remaining heterothermic during late gestation would consequently have longer pregnancies than would those changing regulation strategies. For *Plecotus auritus*, Speakman and Racey (Speakman and Racey 1987) suggested that bats which gave birth in early July, weaned their young in mid August during peak insect availabilities. Young bats born later would have to learn to feed and sustain their apparent heavy energy demands during the dearth of insects in September, which would presumably reduce their chances of survival. However, in *Miniopterus schreibersii* and *Myotis grisescens*, after a period of homeothermy during mid-gestation, near-term females were found to be heterothermic as a possible attempt to synchronize parturition (Dwyer and Harris 1972; Tuttle and Stevenson 1982).

1.2.5 Development of the Young and Lactation

Bats are born with very large feet and thumbs, but beyond their ability to cling tenaciously to their mothers or the roost substrate, all are highly dependent upon their mothers (Orr 1970). Relative to many other mammals, bats are enormous at birth (Leitch, Hytten et al. 1959); they weight approximately 15-30% of the mass of the postpartum mother (Wimsatt 1960; Orr 1970; Kleiman and Davis 1976). The young of other small mammals are typically 7-8% of the mother's weight (Neuweiler 2000). One of the most important factors affecting the growth of the young is temperature (Tuttle and Stevenson 1982); they have a limited ability to regulate their body temperature. An important aspect of parental care is the selection and maintenance of a favorable thermal environment (Kunz and Hood 2000). Most temperate-zone bats form maternity colonies, where they may cluster in order to reduce thermoregulatory costs. Pups are raised in the nursery colony until they are old enough to fly and to be weaned. Insectivorous species produce highly nutritious milk and nurse the young for 4 to 8 weeks (Neuweiler 2000). Young bats are weaned when they reach about 71% of adult body mass while other mammals are weaned at nearly 40% of adult body mass (Barclay 1994; Barclay 1995). Thus, lactation is associated with

an important increase of energy demand on the mother. In Mexican free-tailed bat females the average nightly energy intake ranges from 57 $\left[\text{KJ d}^{-1}\right]$ in early lactation to 104 $\left[\text{KJ d}^{-1}\right]$ in mid-lactation (Kunz, Whitaker et al. 1995).

Flight and echolocation capabilities of the young start developing before weaning, and progress is made rapidly. In the case of *Myotis lucifugus* young bats progress in 7-10 days from first flights, where the bat is attentive to large stationary objects, to a complex integration of moving signal source and to moving targets (Buchler 1980). At this point the juvenile bat's flight and echolocation parameters became close to those of adults. About 3 weeks after initial flights, juvenile's maneuvers become indistinguishable from those of adults, they emerge with adults, and fly and forage along traditional adult routes that were avoided initially for being acoustically complex environments. Racey and Swift (Racey and Swift 1985) also reports a 3 week period over which flight ability and foraging increases progressively in juvenile *Pipistrellus pipistrellus*.

1.3 Objectives of Research

1.3.1 General Objective 1

Develop a life history based, integrated dynamic energy budget for a generic individual in a nonspecific bat species.

Rationale for Objective 1

Energy budgets of bats have been developed for life history processes (e.g. hibernation) and for daily life events (such as maintenance, echolocation, and flight). The discrete integration of aspects of the energy budget has been accomplished but temporally dynamic integrated energy budgets have not been formulated and validated for any bat species.

Methodology to Achieve Objective 1

I will develop a generic physiologically-based, individual model for a bat that takes into account the main processes occurring at the individual level during its life history and perturbations of these processes caused by environmental change.

The individual model will be first parameterized for a temperate-zone insectivorous bat, the little brown bat, *Myotis lucifugus*. Then by changing parameters and modifying processes, such as hibernation if the species of interest does not use this strategy, the model could be used to study and simulate the population dynamics of other bat species. Species such as the Mexican free-tailed bat, *Tadarida brasiliensis*, which plays an important role as a predator of the bollworm *Helicoverpa zea*, a corn and cotton consumer in Texas; and bat species whose populations have

been declining in recent decades (e.g. Indiana bat, *Myotis sodalis*) would be interesting candidates to be modeled and parameterized in the future.

Questions addressed with the individual model

Several hypotheses and questions have been formulated concerning strategies used by bats to meet their energy requirements (see Section 4.3). More insight on these questions can be gained by performing simulations of the individual model under particular scenarios. The questions are:

- What are the physiological characteristics that contribute most significantly to the individual's energetic, survival, and reproduction?
- Is the body condition of young females appropriate to survive hibernation and cope with a following gestation if they mated in their first Fall?
- How does the body condition at the end of hibernation affect reproduction?
- How does use of torpor help females to afford pregnancy and lactation costs?
- What might be the behavioral and physiological mechanisms that promote pre-hibernation fat deposition?
- How does the foraging learning process in juveniles influence their survival and readiness for hibernation?
- Do lactating females need to feed selectively on more high-density prey to produce the proper amount and quality milk for their pups?
- How does temperature in hibernacula affect winter survival and reproduction?
- How much do arousals caused by human disturbances change winter survival?

There are other questions that would be interesting but need further modifications of the individual model developed here to provide answers. Some of the modifications or additions to the model include: mechanistic modeling of an aqueous component, modeling of calcium component, and modeling dynamics of timing of events. Questions of interest are:

- Is calcium a limiting resource for reproduction?
- Is the need of water the cause of the costly periodic arousals during hibernation?
- Is there an optimum number of arousals during hibernation?
- How does the timing of reproduction affect winter survival?
- How does ambient temperature and food supply affect the timing of hibernation?

1.3.2 General Objective 2

Describe the temporal dynamics of bat populations through physiological and behavioral characteristics of individual bats and their relationship with the environment.

Rationale for Objective 2

There are no long-term birth rate and death rate data for any bat species. There are no reliable long-term estimates of population numbers for any bat species, in part because of the difficulty in determining population size in bats and documenting changes over time. The need for these data is fundamental for ecology and applied sciences such as conservation and integrated pest control. The existence of a dynamic theory to couple with current field laboratory research is necessary to understand dynamics of bat populations.

Moreover, generating population dynamics not only will give us a better understanding of the population dynamics of bats, but it can lead to the development of management techniques and conservation strategies, and can be used to investigate stress effects like loss of suitable habitat or chemical insults.

Methodology for Objective 2

The population model to be developed will have a foundation built on the individual model. Several lines of reasoning suggest this approach. From a population perspective, demographic processes of birth, growth, and death occur at the individual level; these processes are functions of the individual characteristics. Thus, characteristics of the individuals ultimately determine the structure and, subsequently the dynamics of the population. Also this methodology uses and integrates the information on bat biology and physiology that has been primarily collected at the individual level. To my knowledge, there is insufficient data at the population level to develop a viable population model.

Questions addressed with the population model

- How lipid dynamics at the individual level influences survival and reproduction and ultimately population dynamics?
- How are populations regulated in abundance?
- How does density dependence pressure affect population dynamics and persistence?
- What are the forces that drive a population to extinction?
- What are the dominant ecotypes in a population?

CHAPTER II
INDIVIDUAL MODEL OF A TEMPERATE ZONE INSECTIVOROUS FEMALE BAT

2.1 Life History Summary

Key maturational and reproductive characteristics that define the life course of an individual describe its life history. Notable characteristics include size at birth and maturity, age at weaning, age of sexual maturity, time of first reproduction, length of gestation, litter size, and inter-birth intervals. Because resources and their consumption are limited, individuals allocate them differently to competing life functions, especially growth, body maintenance, and reproduction. Thus the life history traits and trait boundary conditions arise from an individual's schedule of investment in growth, maintenance, and reproduction.

The life history of temperate bats is particularly interesting because of their resource allocation priorities. These bat species must confront seasonally fluctuating food supplies (Raesly and Gates 1987) and decreased ambient temperature that increases the thermoregulatory energy costs. Endotherms may adopt three strategies, which are not necessarily mutually exclusive, to cope with the difference in energy supply and demand during cold weather (Speakman and Racey 1989). They may emigrate, they may store energy during summer and fall to subsidize reduced intake during winter or they may reduce energy expenditure by changes in activity, coupled with physiological modifications including increases in insulation and adaptive hypothermia (Speakman and Racey 1989). Bats have adapted to temperate zones mainly by hibernating during the colder months (Davis 1970). Vespertilionidae and Rhinolophidae are hibernating species while within the Molossidae family some species may be capable of hibernation (Cowan 1945; Jewett 1955) and others may migrate. In the majority of the species males and females reach sexual maturity at one or two years of age (Racey 1982; Tuttle and Stevenson 1982). Most bats that live in temperate zones are monoestrous. In hibernating bats, mating takes place before and during the hibernation period during temporary intervals of arousal. Females store sperm in the uterus and oviduct. Ovulation and fertilization are delayed for months until about 1 to 3 days after arousal from hibernation (Dale Buchanan 1987; Neuweiler 2000). Successful ovulation appears to depend on the stored fat reserves, the quantity and quality of the fat deposited and on the amount that remains at the end of hibernation (Kunz, Wrazen et al. 1998). In general, bats give birth to one offspring in the spring or summer. Pups have a limited ability to regulate their body temperature; hence an important aspect of parental care is the selection and maintenance of a

hospitable thermal environment (Kunz and Hood 2000). Most temperate-zone bats form maternity colonies, where they may cluster in order to reduce thermoregulatory costs. Pups are raised in the nursery colony until they are volant and weaned. Insectivorous species produce highly nutritious milk and nurse the young for 4 to 8 weeks (Neuweiler 2000). Young bats are weaned when they reach about 71% of adult body mass while other mammals are weaned at nearly 40% of adult body mass (Barclay 1994; Barclay 1995). Thus, lactation is associated with an important increase of energy demand for the bat mother.

The individual model described in this chapter is built upon the characteristics of the life history of a hibernating female bat. Life history attributes determine the processes to be modeled at different stages or periods during the course of a female bat's life. The model presented here is generic for temperate zone bats and is first parameterized for the little brown bat, *Myotis lucifugus*. Based in the species characteristics and in modeling needs, I defined three consecutive age stages in the life of the bat: "pup", "juvenile" and "adult". The "pup" stage corresponds to newborn individuals whose only source of food is mother's milk. The "juvenile" stage follows the "pup" stage and individuals remain under this category until beginning their first hibernation. "Juveniles" feed on their mother's milk and insects until they are weaned, and then forage only on insects. They are assumed to forage and behave as "adult" individuals but might be less efficient than adults in foraging activities over a certain period of time, which I call the "training period". Females that were born in June mate before their first hibernation, as they usually are sexually mature at that time. The next age stage, "adults" contains sexually mature females and, once in the adult stage, remain there until they die. Also I defined five physiological categories: "hibernation", "pregnancy", "lactation", "post-lactation", and "pre-hibernation". These categories correspond to very different energetic requirements, behavioral strategies, and allocation of resources. The physiological categories repeat each year for adult individuals. The model requires that if in a particular year a female does not ovulate, or has a miscarriage, it transitions directly from hibernation to post-lactation or from pregnancy to post-lactation. If lactation ends earlier due to pup loss the female transitions at that time to the post-lactation category. Juveniles go through the pre-hibernation category their first Fall. One more condition defined is "migration". Under this condition energetic demands might increase significantly due to increased flying activity. Migration occurs at the beginning of pregnancy and the bat travels from hibernacula to summer roost and at the end of post-lactation from summer roost back to hibernacula. Even though the transitions through the age stages, physiological categories and migration condition occur synchronously over a few weeks for individuals in the same region,

individuals are influenced by environmental conditions and body condition. Because this is the first individual modeling approach developed for bats, this initial version of model is kept as simple as possible to obtain parameters from available literature, to compare results with data, and to analyze results in a meaningful manner. Therefore, the transitions through the life history stages are implemented as simple rules determined by calendar days and average lengths of periods obtained mainly from Davis and Hitchcock (Davis and Hitchcock 1965) who performed a detailed mark and recapture study on a *Myotis lucifugus* population that hibernates in Aeolus Cave in south western Vermont.

A schematic life history diagram and summary of the rules is depicted in Figure 1. In the computer code associated with the model each individual has a variable that indicates its present stage and each state is updated daily. When a transition occurs a switch takes place in the equations or some of the parameters involved. In a later version of the model these rules could be defined more realistically to study the effects and relationships among the variables affecting the transitions in the life cycle.

As expected from the description of the life history and confirmed by studies in body composition (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000), the lipid profile of a female bat is very dynamic over and within its life stages and may play an important role in population dynamics. An objective of this work is to examine these dynamic fluctuations at the individual level to study their implications on survival and reproduction and ultimately on population dynamics.

2.2 Conceptual Model

2.2.1 Mini-Review of Lipid, Protein and Carbohydrate Metabolism

Metabolism is the sum of all the chemical reactions within a biological system related to the management of the supply of energy to power cellular activity and the generation of molecules for cellular syntheses. Metabolism is divided into catabolism, the oxidation of biological fuels to produce energy in the form of ATP, and anabolism, the synthesis of molecules using energy supplied in the form of ATP. Three groups of biological molecules are considered to be "fuels" for the body and therefore the main materials of life (Kooijman 2000). They are fats, proteins and carbohydrates. The individual model developed here aims to describe the dynamics of these components in terms of resource intake and energetic demands. A brief and very general description of the metabolic pathways of fats, proteins, and carbohydrates is presented below as the conceptual foundation of the mathematical model.

Lipids (fats) in the diet are the major fuels used as a source of bond energy for the synthesis of ATP. Fat may be oxidized immediately following absorption from the gut or stored as triglycerides in the adipose tissue and used later. Fat is the most important form of energy storage. Because of the absence of water, triglycerides are compact, light, and can be stored in a relatively small space compared to glycogen. Hence the relative energy yield from fat and carbohydrate is approximately 40kJ/g triglyceride and approximately 18kJ/g glycogen. If the energy value of the food intake exceeds that required by the body, fat is stored. This may result by synthesis either from preformed fatty acids furnished by the food or by the generation of fatty acids from carbohydrate and indirectly from protein. Also, lipid functions as a regulator of certain metabolic functions, as a threshold trigger and essential component of reproduction, and as a thermo insulator in certain organisms.

The dietary proteins ingested are not the proteins required by the body, nor can large molecules be absorbed from the gut. Therefore, these proteins are digested and their component amino acids absorbed into the blood stream. Amino acids are used for synthesis of new proteins and other compounds, and as a biological fuel. The synthesis of new proteins is very important during growth. In adults, protein synthesis is directed towards replacement of proteins as they are constantly being supplanted. In humans, about 10% of the energy production comes from amino acids. This percentage can be as high as 90% in carnivores, whose diet is almost entirely protein. Amino acids can be converted to carbohydrate and fat.

Carbohydrate in the diet is converted to monosacharides in the digestion process; the monosacharides are then transported to the liver and converted in glucose. The liver has a central role in the storage and distribution of all fuels, including glucose, within the body. Glucose in the body has three metabolic fates. Glucose can be catabolized to produce energy (ATP) stored as glycogen in the liver and muscles, and can be converted to fatty acids. When muscle and liver glycogen stores are saturated, the glucose is not excreted or wasted. It is converted to the fuel storage form which has an unlimited capacity, i.e. triglycerides stored in adipose tissue.

2.2.2 Model Compartments and Flows

The model represents the individual by featuring two major compartments one called lipid and the other called structure, which aggregates protein and carbohydrates. Each compartment consists of a labile and non-labile portion. Protein and carbohydrate are aggregated in the same compartment to maintain the model in a simple representation but this union is complex enough to serve the model purposes including synthesis of lipids. This aggregation is justified in an energetic model by the fact that the energy equivalents per unit mass of protein and

carbohydrate are nearly equal, both compounds are ultimately converted to fat under positive energy balance, and in the particular case of bat's diet, carbohydrate comprises a small portion of the diet (Kurta, Bell et al. 1989).

Figure 2 presents the conceptual model recording associated compartments and the flow chart for an adult female bat. The dynamics of an individual are determined by the rates of change of the lipid and structure compartment, which are expressed as ordinary differential equations. The rates of change are given by the difference between the input flows and the output flows of the compartments. These two components have been used to describe individual dynamics of aquatic organisms in previous models (Hallam, Lassiter et al. 1990; Hallam, Lassiter et al. 1992; Hallam, Lassiter et al. 2000) and the conceptual model presented here is based on them.

Ingested and assimilated food is partitioned to the lipid and structure compartments. The structure compartment primarily represents proteins, and is composed of labile and nonlabile portions of protein and carbohydrates. The nonlabile portion is structure bound to somatic tissue and cannot be mobilized to meet energetic needs. The lipid compartment is also divided into a nonlabile portion, which is associated with protein in cell membranes and other fine subcellular structures and is not available to the organism even under starvation conditions, and a labile portion. Both labile structure and labile lipid can be integrated to support the energy demands of the individual. The energy integrator compartment functions as a processor that takes the mass input from both lipid and structure, converts it to energy, and supplies the demands of the individual (maintenance and work). The energy integrator acts as a switching mechanism that supplies the energy demand unless the energy demand is greater that the energy available in the compartment. Under this situation the energy integrator supplies all available energy. One important assumption of this model that differentiates it from previous related models (Hallam, Lassiter et al. 1990; Hallam, Lassiter et al. 2000) is the conversion of protein and carbohydrate in the structure compartment to lipid that takes place under "energy available greater than energy demand" condition and active periods (i.e. it does not occur during hibernation). This assumption is absolutely necessary to represent the dynamics of an individual with a relatively low fat diet and the need to store lipids over a short period of time before hibernation. Under various formulations different from the one presented here, synthesis of lipid has been modeled using other energetic models (Kooijman 2000).

During pregnancy and lactation lipid, protein and carbohydrate are allocated to the neonate and milk production. The mass allocated to the offspring is represented as a discrete loss that takes place on the day of the birth of the pup. Milk is produced only after basic energy

demands (maintenance and work) are met the milk components are then directly taken from the constituent compartments.

2.3 The Individual Model Equations

The mass of lipid and the mass of protein and carbohydrates are denoted by m_L and m_S [g] (all weights in the model are dry weights) respectively. The mass of protected structure, m_{PS} [g], is assumed to be non-decreasing with age and is a constant proportion of mass of structure, i.e. $m_{PS} = \alpha m_S$. Non-labile lipid is given by εm_{PS} [g] where ε is a dimensionless parameter that gives the ratio of non-labile lipid to non-labile structure. Given these representations, the mass of labile lipid is given by $\left(m_L - \varepsilon m_{PS}\right)$ and the mass of labile structure by $\left(m_S - m_{PS}\right)$.

On a continuous time scale, the individual model of an adult female bat or weaned juvenile consists of two ordinary differential equations representing the rates of change of m_L and m_S. These rates are determined by the differences in the inputs and outputs shown in the conceptual model. The first input terms in the equations correspond to assimilated lipid and protein and carbohydrate components of the resource obtained from feeding whereas the first output terms are the losses due to maintenance (basal metabolism and thermoregulation costs), activity (flight cost), and reproduction (allocation to neonate tissue and milk production). The general equations are given by:

If $E_D < E_A$:

$$\frac{dm_L}{dt} = A_L X_L F - M_L\left(m_L - \varepsilon m_{PS}\right)\frac{E_D}{E_A} + e\,S\,M_S\left(m_S - m_{PS}\right)\left(1 - \frac{E_D}{E_A}\right) \tag{1}$$

$$\frac{dm_S}{dt} = A_S X_S F - M_S\left(m_S - m_{PS}\right)\frac{E_D}{E_A} - S\,M_S\left(m_S - m_{PS}\right)\left(1 - \frac{E_D}{E_A}\right)$$

If $E_D \geq E_A$:

$$\frac{dm_L}{dt} = A_L X_L F - M_L\left(m_L - \varepsilon m_{PS}\right) \tag{2}$$

$$\frac{dm_S}{dt} = A_S X_S F - M_S\left(m_S - m_{PS}\right)$$

The proportions of lipid and protein and carbohydrates of the resource are denoted by X_L and X_S. The amount of resource that can be converted into viable energy is based on the assimilation efficiencies of the lipid and structure, represented by A_L and A_S [dimensionless]. And $F\ [\text{g d}^{-1}]$ represents the feeding rate which takes the form of a type II functional response $F(x)=\frac{Mx}{x+i}$, with maximum feeding rate M [g d^{-1}], and half saturation constant i [g volume^{-1}]. The resource x [g volume^{-1}], is a function of time that reaches a maximal peak in abundance on Julian day P=198 (July 17th). This function takes the general functional form of a Cauchy density function $x(t)=C\frac{1}{s\pi\left(1+\left((t-P)/s\right)^2\right)}$ where s is the scale parameter, P is the location parameter, and C is a constant multiplying the probability density function. In equations (1) and (2) the terms $A_L X_L F$ and $A_S X_S F$ represent the gain of mass of lipid and mass of structure per unit time coming from food. The second terms of the equations represent the loss of labile mass of lipid and labile mass of structure per unit time necessary to meet the energy requirements. The coefficients M_L and $M_S\ [\text{d}^{-1}]$ are the labile lipid and labile structure mobilization rates. The energy available $E_A\ [\text{KJ d}^{-1}]$ is given by $e_L M_L\left(m_L-\varepsilon m_{PS}\right)+e_S M_S\left(m_S-m_{PS}\right)$, where e_L and $e_S\ [\text{KJ g}^{-1}]$ are the energetic contents of one gram of lipid and one gram of structure respectively.

The energy demand is denoted by $E_D\ [\text{KJ d}^{-1}]$, and is a function of the individual physiology, morphology, and temperature as an environmental variable/parameter. During the hibernation period $E_D=E_{hib}(t,T_a,m)$ is a function of time, temperature in the cave and total body mass of the individual. During active periods in spring, summer, and fall, the energy demand for adults and juveniles is $E_D=E_{roost}(t,T_a,m)+E_{flight}(m)$, which account for the energy spent at the roost (day and night) and flying. A detailed description of the formulation of these functions is given in the next section.

The individual is assumed to die if $E_D>E_A$ for 3 consecutive days. In this case the simulation ends. A reason this rule needed to be implemented is because equation (2) implies that the individual continues to forage at the same rate as in the case $E_D>E_A$. In general, if an individual is not able to meet its energetic needs over several consecutive days it enters in a lethargic state, it is not able to forage, and eventually dies of starvation. Thus, this rule tries to

represent this condition in a simple form. The 3-day period also gives time for the lipid and structure labile portions to be mobilized, a process that is not instantaneous. Simulations performed at the model parameterization stage showed that individual dying under this rule had reached the protected levels of lipid and structure. Moreover, a period of 3 days is consistent with relevant data for vampire bats (Altringham 1996).

The above equations are slightly modified for individuals in pup and juvenile stages. In the case of pups the input terms correspond to milk provided by the mother with specific lipid, carbohydrate and protein content. After peak lactation the young individuals are assumed to start foraging as milk supply decreases, during this short period two input terms from food (milk and insects) are represented in the equations. I assume juvenile individuals are not as efficient as adults when foraging (Racey and Swift 1985; Hamilton and Barclay 1998) and they go through a "training" period of T days. During this training the feeding rate F is multiplied by a linear function of age that increases from φ to 1 over the T day period.

The energy demand for pups as kJ per gram per day is assumed to be a constant and it was estimated from growth data and assuming a particular food intake. The energy demand for juveniles takes the same formulation as the one for adults with the appropriate parameter values. But over the training period an adjusting factor similar to the one multiplying the feeding rate is included for the time spent flying.

The model does not contain a water compartment in the individual; however, water is an important component accounting for about 60% of the body weight. The functions involved in the E_D term depend on the wet body mass, so it is necessary to estimate the wet body mass, $m(t)$. For weaned juveniles and adults I assume a constant proportion of water, w, relative to the structural mass because lipid is stored without or with very little water. Hence wet body mass is estimated as $m(t) = m_L + m_S + m_S w$. Data on body composition (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000) show the ratio of water content to lean dry mass, w, varies less over the life cycle ($\overline{w} = 2.74$, $sd = 0.21$, Range $= 0.55$, $n = 5$) than the proportion of water with respect to total body weight which decreases from 69% during pregnancy, lactation, and post-lactation to 52% in pre-hibernation. For pups and lactating juveniles data (Reynolds and Kunz 2000) show that the ratio of water to lean dry mass decreases from birth to the end of the lactation period. Hence w is assumed to be a linear decreasing function of time during this period.

As described in the conceptual model, when there is an energy excess (energy demand less than energy available), it is stored as fat. The third terms in the equations correspond to the

flow from the structure to lipid compartment. The function $S = S(m_S)$ represents the fraction of the energy excess to be stored as lipid and e represents the efficiency of the conversion. The metabolic pathways through which carbohydrate and protein are converted to lipid differ and the conversion efficiencies might also differ. However, because this model represents the lipid synthesis in a generic form based on energetics, the efficiency of the conversion is assumed to be the same for protein and carbohydrate given that they have nearly equal energy equivalents. Once adult size is reached, the structural component of organisms does not vary much. If there is energy excess, organisms grow fatter even if they are on a very high protein/low fat diet. In order to represent this process I assumed the following formulations for the function S. In the case of non-pregnant and non-hibernating females:

$$S(m_S) = \begin{cases} 0 & m_S \le m_{S\min} \\ \dfrac{(m_s - m_{S\min})^2}{(m_{S\max} - m_{S\min})^2} & m_{S\min} < m_s \le m_{S\max} \\ 1 & m_S > m_{S\max} \end{cases} \quad (3)$$

In the case of pregnant females:

$$S(m_S) = \begin{cases} 0 & m_S \le m_{S\min} \\ \dfrac{(m_s - m_{S\min})^2}{(m_{S\max P} - m_{S\min})^2} & m_{S\min} < m_S \le m_{S\max P} \\ 1 & m_S > m_{S\max P} \end{cases} \quad (4)$$

These forms assume that the structural component of the individual is within a certain range given by $m_{S\min}$ and $m_{S\max}$ for non-pregnant individuals and given by $m_{S\min P}$ and $m_{S\max P}$ in the case of pregnant females. During hibernation I assume there is no synthesis of lipids.

Several parameters at the individual level may vary in terms of the age stage of the bat (pup, juvenile, adult) and/or the physiological category (hibernating, pregnancy, lactation, pre-hibernation, and migration). These variations among stages and/or categories are indicated in Table 1 through Table 7 by indicating a different value of a parameter for each stage and/or category it corresponds to. For example lipid mobilization rate, M_L, takes different values at the different stages and categories, being the lowest at pre-hibernation when lipid reserves are being built and highest at pregnancy and lactation when energy demand is highest. As was mentioned before, transitions through the life history generate switches in fluxes of the equations or in the parameters involved.

2.4 Energetic Demands and Production Loses

2.4.1 Maintenance

The energy requirement for maintenance of the body is taken into account under the basal metabolic rate parameters involved in the formulations described below for hibernation, summer roosting, and flight.

2.4.2 Energetics during Hibernation

Hibernation in mammals is a temporary suspension of euthermia allowing endotherms to undergo reversible hypothermia and generate significant savings in energy expenditures.

The formulation for the energy demand during hibernation is related to a model proposed by Humphries et al. (2002) that predicts the feasibility of mammalian hibernation under different climate conditions. They parameterized the model for the little brown bat *M. lucifugus*, given its well-quantified hibernation energetics. The formulation distinguishes three phases of hibernation: torpor, arousal, and euthermic phase. The energetic cost of being in these phases is a function of ambient temperature inside the cave and parameters related to the individual physiology.

Torpid Phase

Torpor is characterized by low body temperature, low metabolic rate, and absence of food and water intake. A lower ambient set-point temperature, $T_{tor\_\min}$ of 2°C is set for this bat species. When ambient temperature T_a is above $T_{tor\_\min}$ body temperature T_b is not defended and fluctuates more or less parallel with T_a, thus oxygen consumption increases exponentially as temperature increases due to the Q_{10} effect. The temperature coefficient, Q_{10}, expresses the thermal dependence of a reaction rate (e.g. metabolic rate) and is defined as:

$$Q_{10} = \left(\frac{\text{rate af a reaction at temperature } T_2}{\text{rate af a reaction at temperature } T_1} \right)^{\frac{10}{T_2 - T_1}} \qquad T_1 < T_2$$

When ambient temperature T_a drops below $T_{tor\_\min}$, animals increase metabolic rate to defend body temperature, and they exhibit the same thermoregulatory characteristics as homeotherms. At $T_{tor\_\min}$ the metabolic rate is minimized, taking on the value $TMR_{\min}$ $\left[\text{ml O}_2\,\text{g}^{-1}\text{hr}^{-1}\right]$. If heat needs to be produced to maintain body temperature, the rate of heat gain equals the rate of heat loss and the increase in the metabolic rate. The rate of heat loss is equal to the difference in temperatures (body and ambient) times a thermal conductance

coefficient C_t $\left[\text{ml O}_2\,\text{g}^{-1}\text{hr}^{-1\,o}C^{-1}\right]$. The factor 0.01998 represents energy demand in kJ per milliliters of oxygen consumed. Thus, the energy demand E_{tor} $\left[\text{kJg}^{-1}\text{hr}^{-1}\right]$ during the torpid phase of hibernation is given by:

$$E_{tor} = \begin{cases} TMR_{\min} Q_{10}^{\frac{T_a - T_{tor\_\min}}{10}} 0.01998 & T_{tor\_\min} \le T_a \\ \left(TMR_{\min} + (T_{tor\_\min} - T_a)C_t\right)0.01998 & T_{tor\_\min} > T_a \end{cases}$$

The temperature coefficient, Q_{10}, is expressed as a function of ambient temperature by adjusting a quadratic form to data on metabolic rate at different temperatures (Hook 1951) giving the following expression:

$$Q_{10}(T_a) = -0.0058T_a^2 + 0.3059T_a + 0.4305.$$

Arousal and Euthermic Phase

As mentioned before, torpor is not maintained throughout the period of hibernation. The animal must awake periodically for reasons that are not yet well understood. An increase in heart rate and breathing rate marks the beginning of the arousal process, which takes about 45 minutes in *M. lucifugus* (Thomas, Dorais et al. 1990). The energetic cost of an arousal E_{ar} $\left[\text{KJg}^{-1}\right]$ is a function of the required increase in body temperature from torpor T_{tor} to euthermic levels T_{eu}, and the specific heat capacity S $\left[\text{ml O}_2\,\text{g}^{-1\,o}C^{-1}\right]$ of the hibernator's tissues:

$$E_{ar} = 0.01998(T_{eu} - T_{tor})S$$

$$T_{tor} = \begin{cases} T_{tor\_\min} & T_a \le T_{tor\_\min} \\ T_a & T_a > T_{tor\_\min} \end{cases}$$

During the euthermic phase, high body temperature has to be maintained at the low ambient temperature in the hibernacula. The energy expenditure of this phase E_{eu} $\left[\text{KJg}^{-1}\text{hr}^{-1}\right]$ varies according to the well-described metabolic response curve: $E_{eu} = \left(RMR + (T_{eu} - T_a)C_{eu}\right)0.01988$, wherein RMR $\left[\text{ml O}_2\,\text{g}^{-1}\text{hr}^{-1}\right]$ is the resting metabolic rate, and C_{eu} $\left[\text{ml O}_2\,\text{g}^{-1}\text{hr}^{-1\,o}C^{-1}\right]$ is the euthermic thermal conductance. This euthermic thermal conductance may be higher than the torpid thermal conductance because during torpor a reduction in peripheral blood flow acts to reduce convective heat transfer through the tissues, increasing tissue resistance and decreasing heat flux for a given temperature gradient (Speakman and Thomas 2003).

Hibernation Daily Energy Demand

Let t_{ar} [.] and t_{eu} [.] be the proportions of the day spent in arousing and in euthermic phase respectively on a day with an arousal. Hence the daily energy demand per individual bat $E_{hib}(t)$ [kJ day^{-1}] is given by the following equation:

$$E_{hib}(t) = \begin{cases} \left(24(1 - t_{ar} - t_{eu})E_{tor} + E_{ar} + 24t_{eu}E_{eu}\right)m(t) & t \text{ within a day with ONE arousal} \\ 24E_{tor}m(t) & t \text{ within a day with NO arousal} \end{cases}$$

A model flag variable indicates whether an arousal event occurs in a particular day. It is not completely clear yet for bat biologists what triggers the periodic arousal and several hypotheses such as the “biological clock hypothesis”, the “water balance hypothesis”, and the “metabolism hypothesis" have been proposed (see Section 1.2.1). In order to keep the model simple in relation to mechanisms that are not completely clear, in the model an arousal occurs every certain number of days indicated by D_{tor}. Later, a more elaborate function could be formulated to indicate a day with an arousal that could be used to study the trigger mechanisms that might be involved in periodic arousals.

2.4.3 Thermoregulation during Active Season

Data on oxygen consumption of *Myotis lucifugus* at various ambient temperatures (Studier and O'Farrell 1976) show great variability indicating that at a given temperature some bats are regulating body temperature and others are conforming to ambient temperature. Bats frequently can shift from regulating to conforming and vice versa depending on environmental and physiological conditions. Roosting energy demand is considerably reduced in conformers compared to regulators (Studier and O'Farrell 1972; Studier and O'Farrell 1976). They can cut energy costs during roosting in half by shifting to thermo-conforming at temperatures below 16ºC.

There exist several explanations and hypothesis related to thermoregulatory patterns and agreement among studies is not uniform (Studier and O'Farrell 1976). It has been shown that torpor in pregnant vespertilionids prolongs gestation (Racey 1973). Delays in fetal and juvenile growth contribute to a poor survivorship during young bats’ first hibernation period (Kurta, Johnson et al. 1987). In late summer the tendency might be directed towards heterothermy (conform to ambient temperature) in preparation for hibernation and for reduction of energy demand, which would enhance pre-hibernation fat deposition.

I propose a model that allows for some flexibility about the “choices” made by an individual bat regarding thermoregulation. The temperatures during this period in the roosting

spot are assumed to be above 2°C. Two ambient temperatures are defined, an average daytime temperature, T_{aD}, and an average nighttime temperature, T_{aN}. Both temperatures can be defined as functions of time to reflect seasonal changes or can assumed to be constant. At a given temperature, during any time of the day, the bat can enter torpor and conform to ambient temperature or remain active and regulate its body temperature. The energy expenditure, $\left[\text{kJhr}^{-1}\right]$, is given by the expressions below for each case, where T_a, corresponds to T_{aD} or T_{aN}.

Bat is torpid and conforming to ambient temperature:

$$E_{conf}\left(T_a\right) = TMR_{\min} Q_{10}^{\frac{T_a - T_{tor\_\min}}{10}} 0.01998\, m$$

Bat is active and regulating its body temperature:

$$E_{reg}\left(T_a\right) = \begin{cases} \left(RMR + (T_{eu} - T_a)C_{eu}\right)0.01998\, m & T_a < T_{eu} \\ RMR_{\min} Q_{10}^{\frac{T_a - T_{eu}}{10}} 0.01998\, m & T_{eu} \le T_a \end{cases}$$

In general, studies about the daily energy budget of bats are based upon diel fractional commitments and existing data on number of hours per day spent in different activities (day roosting, night roosting, and foraging) and the oxygen consumption at each of those activities (Burnett and August 1981; Kurta, Johnson et al. 1987). In order to use these kinds of data and to evaluate in a simple way different thermoregulatory strategies at different status in the life history of a female bat (pregnancy, lactation, post-lactation, pre-hibernation) I propose simple linear or constant functions to represent the proportion of the day regulating and the proportion of the night regulating. These functions depend on the time and physiological status of the individual. For pregnant females the proportion of the daytime regulating increases linearly from $P_{regD\min}$ (pregnant) to $P_{regD\max}$ (pregnant) over the 60 days pregnancy period. Similarly the proportion of the night regulating increases from $P_{regN\min}$ (pregnant) to $P_{regN\max}$ (pregnant). Lactating females are assumed to spent constant proportions of the day and night regulating their body temperature, P_{regD} (lactating) and P_{regN} (lactating) respectively over the 27-day lactation period. In the case of females in the post lactation category constant proportions are also assumed, P_{regD} (post lactating) and P_{regN} (post-lactating), if they enter to this category around peak of insect availability or after lactation. Females that fail to ovulate as they come out from hibernation enter the post-lactating category when food resources are still low. Hence high constant values for P_{regD} (post-lactating) and P_{regN} (post-lactating) are assumed since with after real lactation values they could not survive. Thus, in this particular case the proportions of the day

and night regulating are defined as linear increasing functions similar to those defined for pregnant females. The proportions increase from $P_{regD\min}$ (post lactating) and $P_{regN\min}$ (post lactating) to P_{regD} (post lactating) and P_{regN} (post lactating) respectively over a period of 60 days. Juveniles are assumed to spend a constant proportion of the day and night regulating given by P_{regD} (juvenile) and P_{regN} (juvenile). During pre-hibernation the proportion of time regulating decreases for both adults and juveniles from P_{regD} (post lactating/juvenile) and P_{regN} (post lactating/juvenile) to zero over period. Hence the daily energy demand from roosting at any given time is given by:

$$E_{roost}(t) = D\left(P_{regD}E_{reg}(T_{aD}) + (1-P_{regD})E_{conf}(T_{aD})\right) + N\left(P_{regN}E_{reg}(T_{aN}) + (1-P_{regN})E_{conf}(T_{aN})\right)$$

where D and N are the number of hours of daytime and nighttime roosting respectively. The proportions of the daytime hours and nighttime hours that the bat spends regulating are given by P_{regD} and P_{regN} respectively, linear or constant functions described above.

2.4.4 Flight and Foraging

Mathematical aerodynamic models of different degrees of complexity have been derived to predict the power consumption of flying as a function of flight speed and of bird or bat morphology (Rayner and Ward 1999). The mechanical power output P_{mech} consists of the sum of four components:

Parasite Power: P_{par} the power needed to overcome the resistance caused by friction between the body and the air.

Induced Power: P_{ind} the power induced by the wing beat that creates lift and propulsion.

Profile Power: P_{pro} the power to overcome the resistance caused by friction between the wings and the air.

Inertial Power: P_{in} power needed to move the wings up and down. At medium and high flight speeds P_{in} is in general considered negligible. However, during slow horizontal flight and hovering in the air, P_{in} is a significant part of the animal's energy expenditure.

The expressions for each of the components of the mechanical power (Norberg, Kunz et al. 1993) are given below with the corresponding description of the variables and parameters in Table 6. All known aerodynamic models predicting P_{mech} in flapping flight have similar U-shaped relationships as a function of flight speed (Rayner and Ward 1999).

Body shape relationships and basal metabolic rate:

$$S_d = \pi \left(\frac{w}{2} \right)^2 \text{ [m}^2\text{]}$$

$$S_b = 8.13 10^{-3} \ m^{2/3} \text{ [m}^2\text{]}$$

$$BMR = RMR \, 0.01988 \, m$$

Parasite power is represented as:

$$P_{par} = \frac{\rho V^3 S_b C_{D\,b}}{2} \text{ [W]}$$

Induced power is represented as:

$$P_{ind} = \frac{k(mg)^2}{2 S_d V \rho} \text{ [W]}$$

Profile power is represented as:

$$P_{pro} = \frac{\rho V^3 S_d C_{D\,pro}}{2} \text{ [W]}$$

Inertial power is assumed to be negligible (Neuweiler 2000).

Mechanical power is represented as:

$$P_{mech} = P_{par} + P_{ind} + P_{pro} \text{ [W]}$$

Metabolic power is represented as:

$$P_{met} = C \left[\frac{P_{mech}}{E_{FM}} + BMR \right] \text{ [W]}$$

Fight muscle efficiency, E_{FM} is defined as the ratio between P_{mech} and metabolic power consumed by the flight muscles. Muscular efficiency is approximately 20%, and roughly 80% of the energy required for flight is lost as heat (Speakman and Thomas 2003). The term BMR corresponds to basal metabolism and the factor C (1.1 in general) accounts for the 10% extra costs of respiration (5%) and circulation (5%) during flight (Ward, Moller et al. 2001).

The metabolic power is a function of several morphological and physical parameters and two variables, mass of the individual and the speed at which it is flying. The mass is a dynamic function of time that is updated every time step as the sum of the different components in the model. The speed is assumed to be constant but can differ at different parts of the flight trajectory: commuting to foraging ground, active foraging, and long distance migration. I assume the bat spends a specific amount of time commuting and foraging during the day (or equally certain distance covered when commuting and foraging at a given speed). During the migration

period a specific time is spent or a specific distance is traveled at migration speed per day. Taking into account these probable differences in average speeds we calculate the energy demand due to flight activity [KJ d^{-1}] by the following rules:

$$E_{com} = P_{met}(V_{com})t_{com}\,3.6 \quad [\text{kJ d}^{-1}]$$

$$E_{for} = P_{met}(V_{for})\,t_{for}\,3.6 \quad [\text{kJ d}^{-1}]$$

$$E_{mig} = P_{met}(V_{mig})t_{mig}\,3.6 \quad [\text{kJ d}^{-1}]$$

$$E_{fligth}(t) = \begin{cases} E_{com} + E_{for} & t \text{ within a day outside migration period} \\ E_{com} + E_{for} + E_{mig} & t \text{ within a day during migration period} \end{cases} \quad [\text{kJ d}^{-1}]$$

The factor 3.6 represents the conversion from W to kJ h^{-1}.

As in the case of feeding rate, I assume that juveniles do not fly when young for as much time as their mothers (Racey and Swift 1985; Hamilton and Barclay 1998). Hence over a training period of T days the foraging time, t_{for}, is multiplied by a linear function of time that increases from ψ to 1.

2.4.5 Reproduction

Mammals do not have a huge increase in parental reproductive tissue to support reproduction. The female, whose uterine and mammary tissue increase, has the largest investment in tissue, but this is only a small fraction of the total amount of protein and energy necessary for reproduction. Fetal growth is the next stage of reproduction with a significant cost. The majority of fetal growth occurs in the last 40% of gestation. The cost of reproduction can be estimated from the composition of the fetus. The proportions of water, fat, protein, and minerals in the fetus vary between species; however, once these are known, the energy and protein cost of the fetal tissue can be calculated. Most mammalian neonates have very little fat (2-5%). Protein in neonates ranges from 10-20% and ash from 1-4%. (Kurta, Bell et al. 1989) estimate the cost of pregnancy for *Myotis lucifugus* from body composition of neonate. A newborn weights 2.3 g and consist about 18% of protein and 3% of fat. Hence the total energy content is 12.5 kJ per neonate (2.3 0.03 39.5 +2.3 0.18 23.6).

In the model a female becomes pregnant at the end of hibernation only if her lipid reserves are enough to promote ovulation; if not the female transitions to the post-lactating status. All pregnant females are assumed to complete their pregnancy if they survive through the period, i.e. no miscarriages are allowed. The pregnancy cost is considered as a discrete loss at the moment of birth. The weight of the neonate is a proportion, β, of its mother's weight. The fat,

and protein and carbohydrate content of the pup are subtracted in a discrete way from the corresponding compartments describing the mother body composition.

2.4.6 Lactation

Most of the costs of reproduction in mammals occur during lactation. By determining the volume and composition of milk produced by the female we can then estimate the nutrient cost of lactation not including increased metabolism in making milk.

Milk production increases from an initial volume at beginning of lactation until it peaks at time L_P around the 17th –19th day, then decreases until lactation ends at time L_T around day 27th (Kurta, Bell et al. 1989). Composition of the milk also varies throughout the lactation period (Kunz, Stack et al. 1983; Kunz, Oftedal et al. 1995). With fat concentration increasing from about 10% at the beginning of lactation to 18% at peak lactation, and with carbohydrate and protein concentrations remaining relatively low and stable through the period (Kunz, Oftedal et al. 1995).

The mammary gland is very well supported with blood vessels, arteries and veins. The primary function of the arterial system is to provide a continuous supply of nutrients to the milk synthesizing cells. Milk synthesis takes place in the alveoli where the milk secreting cells in the mammary gland are provided with a continuous supply of nutrients from the blood stream. Milk fat consists mainly of triglycerides, which are synthesized from glyceroles and fatty acids. Long chained fatty acids are absorbed from the blood. Short-chained fatty acids are synthesized in the mammary gland from the components acetate and beta hydroxybutyrate, which have their origins in the blood. Milk protein is synthesized from amino acids also with origin from the blood, and consists mainly of caseins. Lactose is synthesized from glucose and galactose within the milk secreting cells. Vitamins, minerals, salts and antibodies are transformed from the blood across the cell cytoplasm into the alveolar lumen (Linzell and Peaker 1971). Even though the mammary gland synthesizes the milk components from the blood nutrients it is reasonable to assume that lipids in milk come from lipids in the mother, and carbohydrates and protein come from the structure compartment in the mother.

Hence lactation is represented by direct losses in lipid and protein and carbohydrate compartments that correspond directly to the amount of these components in the milk. A two-piece linear function, $Vol(t)$, is used to estimate the volume of milk in grams per day that should be produced as a function of the day of lactation. Then another two-piece linear function, $R_L(t)$, is used to estimate lipid requirement as a percentage of the milk produced. The protein and carbohydrate requirement, R_S, is estimated as a constant percentage of the milk volume.

$$Vol(t)=\begin{cases}\left(\frac{v_{\max}-v_{\min}}{L_P-1}\right)t+v_{\min}-\left(\frac{v_{\max}-v_{\min}}{L_P-1}\right) & 1\le t\le L_P\\ \left(\frac{-v_{\max}}{L_T-L_P}\right)t+\left(\frac{v_{\max}}{L_T-L_P}\right)L_T & L_P<t\le L_T\end{cases}$$

$$R_L(t)=\begin{cases}\left[\left(\frac{K_{LP}-K_{L0}}{L_P-1}\right)t+K_{L0}-\left(\frac{K_{LP}-K_{L0}}{L_P-1}\right)\right]V(t) & 1\le t\le L_P\\ K_{LP}V(t) & L_P<t<L_T\end{cases}$$

$$R_S(t)=K_S Vol(t)$$

The losses to the lipid and protein compartments are given by the functions $P_L(t)$ and $P_S(t)$, which are equal to the requirement when labile lipid and protein are sufficient or to whatever is available in other cases. Milk is produced after all other energetic needs have been met, these losses only take place if $E_D < E_A$. Hence during the lactation period, the system of equations (1) is modified to systems (5) and (6) defined below:

If $E_D < E_A$:

$$P_L=\begin{cases}R_L & R_L<M_L(m_L-m_{PL})\left(1-\frac{E_D}{E_A}\right)\\ M_L(m_L-m_{PL})\left(1-\frac{E_D}{E_A}\right) & R_L\ge M_L(m_L-m_{PL})\left(1-\frac{E_D}{E_A}\right)\end{cases}$$

$$P_S=\begin{cases}R_S & R_S<M_P(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right)\\ M_S(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right) & R_S\ge M_P(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right)\end{cases}$$

$$P_S<M_S(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right)$$

$$\frac{dm_L}{dt}=A_L X_L F-M_L(m_L-m_{PL})\frac{E_D}{E_A}-P_L+eS\left[M_S(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right)-P_S\right] \quad (5)$$

$$\frac{dm_S}{dt}=A_S X_S F-M_S(m_S-m_{PS})\frac{E_D}{E_A}-P_S-S\left[M_S(m_S-m_{PS})\left(1-\frac{E_D}{E_A}\right)-P_S\right]$$

$$P_S \geq M_S\left(m_S - m_{PS}\right)\left(1-\frac{E_D}{E_A}\right)$$

$$\frac{dm_L}{dt} = A_L X_L F - M_L\left(m_L - m_{PL}\right)\frac{E_D}{E_A} - P_L \qquad (6)$$

$$\frac{dm_S}{dt} = A_S X_S F - M_S\left(m_S - m_{PS}\right)\frac{E_D}{E_A} - P_S$$

If $E_D > E_A$, then no milk is produced and the system is represented by equations (2).

2.5 Parameter Estimation

The model has 93 parameters that can be grouped as 82 parameters related to individual characteristics, 8 constant environmental factors, and 3 conversion coefficients. It is important to note that in some cases a parameter related to a process takes different values depending on the age stage or physiological category of the individual. For example "Lipid mobilization rate" takes different values for pups, juveniles, juveniles pre-hibernating, adults hibernating, pregnant, lactating, post-lactating, and pre-hibernating. All these values are considered 8 different parameters, even though only one parameter is used in the equations at a given time and they appear as a group in the parameters' tables.

Some parameter values were directly extracted from the literature or the value used was within a certain range proposed in the bibliography. In these cases the references are noted in Table 1 to Table 9. Other parameters were estimated using linear or quadratic regression for a related set of data. The parameters in this group are indicated as "fitted".

There are a number of parameters for which I had no option but to assign a value because of no or insufficient data available for estimation. In some cases, hints from the literature were used. In such situations the parameters are indicated with the word "hint" and the corresponding references are indicated in the tables. There are also parameters for which I did not have a clear hint; those are indicated as "created". Some detail is given below on particular "hint" and "created" parameters.

No information was available for parameters related to Lipid and Structure mobilization rates. This adds 15 parameters in the "created" category; however some biological facts were taken into consideration when choosing the value of one parameter relative to the other parameter values in the group. For example, due to the fact that lipids are the main fuel during hibernation (Dark 2005) a higher rate was assigned to Lipid mobilization rate during hibernation when

compared with Structure Mobilization rate during hibernation. The opposite relationship was assumed during the pre-hibernation period when fat deposition occurs. Keeping these relationships among the parameters was also necessary to generate the main lipid cycles observed in hibernators.

The other large group of parameters without much empirical support to which values were assigned is that of the proportions of the day and night that a bat regulates its body temperature. These 11 parameters are based on the assumption that bats spend part of the day regulating temperature and the remaining part of the day conforming to ambient temperature. For the periods in which I assumed a increasing or decreasing linear function for the proportion of the day/night regulating as a function of days spend in that particular period two parameters are used: a minimum and maximum. Bats may use behavioral thermoregulation either to increase or to reduce rates of embryonic development (Tuttle and Stevenson 1982). Pregnant females might increase the time regulating their temperature as they get closer to parturition in order to increase fetal growth; hence, values assigned follow this hypothesized strategy. In the case of lactating females the proportion is constant over the lactation period but the assumed strategy is that they save on thermoregulation costs during the day (low value for proportion of day regulating) and they regulate temperature to enhance milk production during the night when most of the nursing occurs (Wilde, Knight et al. 1999). It has also been suggested that during pre-hibernation bats cease thermoregulation in partial preparation for hibernation (O'Farrell and Studier 1970). I think that it is feasible and it would be very interesting to test these hypotheses through field studies in maternity roosts and to provide a quantitative measurement of the thermoregulatory strategies adopted by bats at different times.

There are parameters related to foraging and resources available that have been assigned without empirical information. As described earlier, the ingestion rate takes the form of a type II functional response $F(x) = \frac{Mx}{x+i}$, with maximum feeding rate M [g d^{-1}], and half saturation constant i [g $volume^{-1}$]. For maximum feeding rate a value of 7 grams per night was assumed based on estimates in the literature (Kurta, Bell et al. 1989). However I found no data available that could be used to estimate i or to estimate the abundance of resources in a number of insects or grams of insects per volume of air scale. Hence the distribution of insects [grams/volume unit] is theoretical. Once *M* is fixed the resulting feeding rate [g d^{-1}] is intrinsically related to *x* and *H*, and different combinations of these two can produce the same numerical results. Given the distribution of insect abundance is theoretical; the value for i used in this model should not be

interpreted as an estimate with real biological value by itself. If the distribution of insect availability were changed the current value of i may need to be reset to produce reasonable values for feeding rate. Note that the total time foraging is fixed independently of insect abundance.

In the process of reviewing data I have realized most field or laboratory experiments fail to provide good information in a format that could be used to determine appropriate functional responses for different processes. For example, it would be very useful to have time series data for several variables such as time spent regulating temperature, time that a juvenile bat spent foraging, food consumed by juveniles and adults. Also temperature and food availability should be provided at the same times.

2.6 Model Implementation

The model is implemented through a computer code written in the C programming language and compiled with gcc. A 365 day simulation with a single cohort takes 37 CPU seconds when the program is run on a SUN Blade 100 300 MHz UltraSPARC III.

A second order Runge-Kutta method with step size of 45 minutes is used to solve the differential equations in the individual model. This step size was chosen after solving the system for larger and smaller step sizes. As the step size decreased no changes were observed in the behavior of numerical solutions of the system, leading to the choice of time step. Because there was no evidence of numerical problems such as negative solutions or values out of reasonable ranges and simulation time was acceptable, there was no need to use a more complex numerical scheme to solve the equations.

The age, age stage, physiological category, migratory condition, counters for pregnancy, lactation, and days under negative energy balance are updated daily. Mass values and other variables such as energy demand, energy assimilated, milk production, etc, are reported daily for analyzing and plotting results.

2.7 Summary of Individual Model Assumptions

Life History

- The model only represents females.
- Individuals go through three consecutive age stages: “pup”, “juvenile” and “adult”. The “pup” stage corresponds to newborn individuals whose only source of food is mother’s milk. The “juvenile” feed on theirs mother’s milk and insects until they are weaned, and then

forage only on insects. These individuals move to the "adult" stage at the beginning of their 1st hibernation and are assumed to be sexually mature.

- Juveniles go through a training period during which their feeding rate and time flying increases progressively (linear) until adult levels at the end of the training.
- Adult females go through five physiological categories: "hibernation", "pregnancy", "lactation", "post-lactation", and "pre-hibernation". These categories correspond to very different energetic requirements, behavioral strategies, and allocation of resources. The physiological categories repeat each year for adult individuals. Pregnancy and post-lactation categories overlap with "migration" condition between hibernacula and summer roost.
- Transitions through these stages and categories occur at fixed calendar dates. Transitions are independent of environmental variables, or body condition of the individual.

Body Components

- The individual is composed of three major compartments: lipid (dry mass), structure (dry mass), which aggregates protein and carbohydrates, and water. The model describes the dynamic over time of lipid and structure compartments at the individual level.
- The water compartment is assumed to be a constant proportion of structure compartment.
- Wet weight of individual is equal to the sum of the mass of each compartment (lipid, structure, and water). The wet weight is used in several formulations to calculate individual energetic requirements.
- Labile portions of lipid and structure components can be mobilized to meet energy requirements. However the rates at which each component is mobilized vary depending on the age and/or physiological stage of the individual.
- The structure compartment in adults is assumed to be between minimum and maximum thresholds determined by two model parameters.
- Lipid synthesis occurs when the energy demand is below energy available during active periods (i.e. it does not occur during hibernation). Protein and carbohydrate in the structure compartment is converted to lipid. The proportion converted depends on the structure level and minimum and maximum structure thresholds. The process is not 100% efficient.

Feeding and Resource

- The feeding rate (Type II functional response) is a saturating function of resource available and individual foraging ability (maximum feeding rate and half saturation constant).

- The resource available to each individual is assumed to be a humped function over the active season reaching its maximum at the time of peak lactation. The resource level is independent of what it is consumed by the individual.

Energy Demand

- An individual dies if its energy demand is above its energy available for 3 days.
- The cost of deep torpor during hibernation is a function of individual parameters (minimum body temperature, Q10, minimum torpid metabolic rate, etc), total body weight, and ambient temperature. The cost of deep torpor increases as ambient/cave temperature departs from an optimal temperature at which metabolic cost is minimum. The cost of torpor increases with body mass.
- The cost of a periodic arousal during hibernation is a function of body parameters (euthermic body temperature, thermal conductance, euthermic metabolic rate, etc), total body weight, ambient temperature, and the time awake. The cost increases as ambient temperature decreases. The cost of an arousal increases with body mass and elevated euthermic body temperature.
- Periodic arousals occur in a prescribed number of days. This frequency is independent of ambient temperature or individual physiology.
- Hibernacula's temperature is assumed to be constant during hibernation period.
- Roosting cost during the summer is a function of individual parameters (euthermic temperature, resting metabolic rate, etc), ambient temperature (average during day, average during night), the number of hours roosting during the day and during the night, and the proportion of the day/night regulating body temperature (vs. conforming to ambient temperature). This cost increases with lower ambient temperatures, with high proportion of the day thermo regulating, and with body mass.
- Roost temperature during the day and night are assumed to be constant during the active period.

CHAPTER III
INDIVIDUAL MODEL SENSITIVITY ANALYSIS

3.1 Sensitivity Analysis

Sensitivity analysis is the study of how variation in an observed response can be associated with different possible sources or factors. In the case of a mathematical or/and computer models the "observed response" is a state variable or a computer output, and the "factors" are the parameters in the model or inputs to the computer code. Sensitivity analysis is an essential tool of a good modeling application. It can be used to determine the quality of the model, factors that contribute the most to output variability, the region in space of factors for which the model variation is maximized, optimal regions in the factors' space, and interactions between factors (Saltelli et al., 2000).

In this application sensitivity analysis is used to:

- assess the variation of the model output
- ascertain how the model output depends upon the input parameters
- identify parameters (individual characteristics) that might play an important role in survival and reproduction of individuals
- investigate interaction between environmental and individual parameters
- detect important processes that need further empirical studies
- based on a small number of important parameters define ecotypes, groups of individuals with the same characteristics, that will structure the population model

3.1.1 Methodology

Factors and Responses

The model has 82 parameters (factors) directly related to the individual characteristics (Table 1 to Table 7) and a total of 13 parameters considered environmental and external variables, and conversion coefficients (Table 8 and Table 9).

The first 82 parameters were considered for the sensitivity analysis and previously relabeled as depicted in Table 10. The model output provides the body composition of the individual over a desired period of time. In order to perform the analysis several response variables were defined in terms of the output from a model run. A list of the response variables defined and their description is presented in Table 11.

Experimental Design

The experimental design is determined by the selection of inputs at which the output of the model is computed. The multidimensional region corresponding to the values of the inputs over which the model response is studied is called the experimental region.

When an experimental design is selected in the case of "physical experiments" *replication* and *blocking* are two techniques used to estimate and control the magnitude of random error. A "computer experiment" that produces the outputs of a deterministic model differs from a traditional "physical experiment" in the sense that repeated observations at the same set of inputs produce identical responses. Hence replication is unnecessary. Uncertainty arises because the functional form used to investigate the relationship between response and factors is an approximation (e.g. linear or quadratic) of the functional forms and/or rules implemented in the computer code. Hence only the differences observed between the observed responses and estimated values from the fitted model are the source of error (Santner, Williams et al. 2003). This error can be referred as lack of fit error or model bias. Based on this particularity of deterministic computer experiments, the experimental design should not take more that one observation at any set of inputs, it should allow one to fit a variety of models, and provide information about all portions of the experimental region (Santner, Williams et al. 2003).

For this experiment given a center/baseline set of parameter values for the model (see Table 1 to Table 7), $\{x_1, x_2, \ldots, x_{82}\}$, the experimental region was defined as the multidimensional region $\prod_{i=1}^{82}\left[x_i - 0.05x_i, x_i + 0.05x_i\right]$ except for a few parameters (parameters marked as * in Table 10 whose baseline value was already set at the maximum of the range. Given the great number of factors and assuming the factors have a monotonic effect on the response over the experimental region I decided to start with a fractional factorial design with 82 factors and 256 runs (sample size) automatically generated by the statistical package JMP 6.0.0 (Statistical Discovery ^{TM} from SAS). This software generates a fractional factorial given number of factors and level of resolution desired. In the case of big designs JMP uses a Hadamard matrix that is either a power of two or a multiple of 4 in sample size. If necessary, the algorithms remove the last columns of the matrix so that the "design matrix" only has as many columns as there are factors (Kathleen Kiernan, JMP Technical Support Statistician, personal communication). If there are not missing data this design is resolution IV, which means no main effects are confounded with 2-factor interactions and some of the 2-factor interactions can be estimated (Montgomery 2005).

Given a set of parameters a simulation experiment starts with the development of a newborn individual bat and continues until the end of its third hibernation. The initial conditions are the same for all experiments. Because several individuals die under the chosen parameter combinations there are missing values in the generated data. This lowers the resolution of the design and in some cases affects the analysis of the results.

Analysis

If a relatively simple functional form explicitly described the responses or state variables in a mathematical model, the partial derivatives of the state variable respect to each of the parameters involved would indicate the sensitivity of the response respect to each parameter. When mathematical models became more complex, or are a sequence of rules implemented through a computer code, the traditional differentiation approach cannot be applied. A detailed description and discussion of current methods to carry out sensitivity analysis when the traditional approach is not applicable can be found in Saltelli's et al. works (Saltelli, Chan et al. 2000; Saltelli 2004).

The sensitivity analysis performed here is based on regression modeling. The general technique consists of fitting regression models to the response variables and assessing the importance of the input parameters (factors) by their regression coefficients. These approaches are most effective when the design is orthogonal or nearly orthogonal (Santner, Williams et al. 2003). When the overall fit of the regression model is poor the model does not adequately describe the relation between the output and input, therefore the response might not be most sensitive to the factors included in the regression model and the interpretation of the results is not valid.

The method chosen for constructing the regression model to assess sensitivity in this work is *stepwise regression*. In stepwise regression one variable is entered at each step, following the order of the most influential. The procedure continues until the amount of variation explained through addition of further variables is not considered meaningful according to some criteria previously selected. The criterion can be based on statistics such as the mean squared error, the coefficient of determination R^2, the adjusted R^2, or F-statistic for testing whether the addition of another variable significantly improves the model. For this particular application the criterion chosen is to include factors as long as they increase the R^2 more than 5%. Also the change of R^2 as a function of the number of parameters included in the model was checked by plotting R^2 at each step of the regression versus the number of parameters entered.

3.1.2 Sensitivity Analysis Results

Survival

After performing the 256 runs the first thing noticed is the high number of missing values (95 missing out of 256) for lipid and structure mass before hibernation 1, indicating that several individuals have not survived to reach adulthood and enter hibernation. Even though this is not yet a population model, the runs could be assumed to represent a new cohort of a population. Thus this result indicates a high mortality during pup and juvenile stages (~37%) for this particular set of 256 runs. The response variable "*Survived Juvenile*" is used to identify the parameters that have contributed the most to determine pup and juvenile survivorship. The package was not able to handle the 82 parameters in a Nominal Logistic model. Hence important parameters were identified assuming the response was continuous and doing a stepwise regression. Then the Nominal Logistic model was fitted indicating that the parameters identified were significant ($P<0.01$) and that lack of fit was not significant. Using the same procedure the parameters that had the greatest effect on survival during 1st hibernation were identified. The parameters included in both models are shown in order of the magnitude of their effect in Table 12.

The parameters involved in both responses are different, which represent the differences in most relevant factors at two different stages of the life history. Factors that contribute the most to survivorship during the pup and juvenile period are more related to growth and energy expenditures during the first months of life. The greater the *proportion of non-labile structure* (X20) the smaller the chances of surviving to adulthood. A high *ratio of water to dry structural mass* (X22) implies an overall heavier individual, which basically translates to higher maintenance cost and consequently indicates a smaller probability of surviving. Both higher *euthermic body temperature* (X34) and *proportion of the day that the juvenile regulates its body temperature* (X47) increases energetic costs and decreases survivorship. The factor X44 that represents the *metabolic rate for pups* was expected to appear but with the opposite sign. This factor was at the limit of the cut off, increasing R^2 by 4.8%, and was included because relative increments in R^2 were rounded to the 2nd decimal place. By exploring the effect of factors that ranked below X44 I also discovered that they appeared with a sign that contradicts biological sense or had no reason to affect juvenile survivorship. These contradictions added to the fact that the R^2 is relatively low indicate that the model is not a very good approximation of the response variable and results may not lead to correct conclusions.

In the case of "*Survived Hib 1*" the fitted model is again not very good. But at least all the factors included in the model and sign of their effect are biologically relevant. However, when comparing the resulting important factors they are related also to the amount of lipid before hibernation. There are factors related to feeding efficiency (X28, X27) and flight (X68, X71, and X65). "Bigger individuals" as characterized by high *maximum structure* (X24) and heavier individuals as consequence of high *ratio of water to dry structural mass* (X22) have greater maintenance cost and consequently less chances of surviving hibernation. I think it is interesting that the *maximum structural size* (X24) appears as an important factor affecting survival during hibernation therefore showing an advantage for "smaller individuals".

It was not possible to repeat the analysis on the survival for the following periods' response variables. Due to high survival in all following periods there was not enough information to determine the parameters that have a significant effect on survival. For the following periods the number of individuals/runs surviving are: 101 out of 111 (~91%) for "*Survived Adult*", 97 out of 101 (~96%) for "*Survived Hib 2*", 94 out of 97 (~97%) for "*Survived Adult 2*", and 94 out of 94 for "*Survived Hib 3*".

Lipid before Hibernation

The "*lipid before hibernation*" response variables were analyzed. The plots of the distributions of values (Figure 3) show that an important number of runs produce individuals whose lipid mass is above what we would expect as maximum lipid content before hibernation for *M. lucifugus*. Even though I do not have data indicating the maximum lipid content ever observed for this species previous to hibernation, I think that values above 3g could be considered very rare or unrealistic based on records of body composition before hibernation (Kunz, Wrazen et al. 1998).

Even if the ranges for each of the 82 parameters might be realistic and varying one parameter at a time over that range may produce reasonable values, it is evident from these distributions that several combinations with all parameters at one of their limits produce values of lipid content higher than expected. It is not possible to say that 4.19g is the upper limit for lipid content before hibernation for the model predictions. The observations that led to the distribution are a small sample of all 2^{82} possible combinations of parameters.

The parameter X2, *protein assimilation*, is the one contributing the most to produce these "fat bats", around 73% of the runs with lipid values above 3g correspond to a combination of parameters in which X2 is set in the upper limit as indicated by the following counts:

31 out of 43 are in high X2, and 24 of the 31 are in high X27

29 out of 39 are in high X2, and 22 of the 29 in high X27

Having these results that are out of the range would not compromise the analysis performed to detect the significant parameters to the lipid mass response variables if we just translate their importance to the model output. However when interpreting the significant parameters identified through the model and the statistical analysis as important parameters in the real individual life history, we should do it with care. For example, in this case, it could be that X2 is really important in determining lipid before hibernation or it leads to results important just in the statistical analysis as a result of many runs above 3g that are set at high X2 contribute to make X2 significant. An option to solve this possible problem is to apply a transformation (e.g. natural log, inverse, square root) to the response variable. This reduces the importance of high observations and amplifies the importance of those with low observations. Thus for the analysis presented below, stepwise regression for the untransformed and transformed response variable was performed. If the two analyses show different parameters to be significant both results will be presented and discussed; if not, only the results using the untransformed variable are presented. Also once the parameters of a linear model are identified, a model including order two interactions was fitted. The purpose of this is to explore the possibility of a more parsimonious model, i.e. less number of factors, including order two interactions. In many cases the desired 2-factor interactions cannot be estimated because of the resolution of the design and the missing values for several simulation experiments. If a satisfactory 2^{nd}-order model is found, it will be reported along with the linear model.

I consider the regression models fitted to these responses good approximations with R^2s greater that 70% and random residuals that allow me to draw reliable conclusions. In all cases the results did not vary much when fitting the model to the transformed response variables, and neither did the quadratic models proved to provide better fits. All the parameters identified make biological sense as well as the sign of their relationship with the response variables.

Many factors are identified as important from this analysis for all the response variables. In general, these factors rank at the top of the lists. As expected, parameters related to feeding efficiency (X27 and X28) and flight (X65, X68, X70, X71) appeared important in determining fat deposition before hibernation. *Assimilation efficiencies of lipid* (X1) and *protein* (X2) also contribute positively to fat stores. The *temperature of a euthermic bat* (X34) and *basal metabolic rate* (X36) are associated with thermoregulation energy costs and therefore have an inverse linear relationship with the amount of lipid. The *percentage of body lipid in neonate* (X76), which represents a lipid loss for the mother, appears only important before Hibernation 2 and

Hibernation 3. The reason for this is that individuals before Hibernation 1 are juveniles that have not reproduced yet, while most reproduce after the 1st hibernation.

Lipid after Hibernation

First the distributions of the differences between lipid before and after hibernation are shown in Figure 3. These distributions show the amount of lipid spent by the bats during the hibernation period.

Most of the parameters that were identified as important for "*lipid before hibernation*" appear again as factors influencing the most on "*lipid after hibernation*" (see Table 13). The only factors exclusively related to hibernation and that are detected here are the *time a bat spent euthermic during periodic arousals* (X38), the *euthermic temperature* (X34), and the *euthermic conductance* (X37). The former appears in the 3 responses while the latter only in the first one. The only parameters that are not relevant are X44, *metabolic rate for pups*, in "*Lp bf Hib 2*" and X45, *number of hours roosting during summer*, in "*Lp bf Hib 3*". However they appear at the bottom of the lists.

Regression models were also fitted to the difference in lipid. These models are slightly better in terms of describing the relationship between response variables and factors, with higher R^2s and all showing random residuals.

Structure before Hibernation

The distributions of the structure component of the individual are shown in Figure 4. Because the structure component is explicitly bounded in the formulation of the model (see Section 2.3), the values for protein and carbohydrates fall within the expected ranges.

The regression models fit the data with fewer factors (when comparing to lipid responses) explaining 80% or more of the variation (see Table 14). As in the previous variables *maximum feeding rate* (X27) and *protein assimilation efficiency* (X2) are important factors. However factors that are more specifically related to the structural component are detected. The *non-labile proportion of the structural compartment* (X20), and the *minimum and maximum structural masses* (X23, X24) are definitely factors to consider when defining ecotypes and that characterize the structural size of an individual.

Structure after Hibernation

The factors that contribute the most to the variation in structure after hibernation (Table 14) are mainly the factors that were identified as relevant for "*structure before hibernation*" (X2, X20, X23, X24). Even though some structure can be mobilized to meet energetic requirements during hibernation; most of the demand is met by the use of the lipid stores. The *euthermic body*

temperature of the bat (X34) is physiologically important because the major energetic demand during hibernation comes from the periodic arousals when the bat spends time regulating its body temperature. At this time protein may need to be mobilized to meet the demand. This factor was not important for "*structure before hibernation*".

Contrary to the case of the lipid related responses after hibernation, the models fitted to the differences between structure before and after hibernation explain less variation and involved more factors.

Reproduction

The model assumes that every female with lipid content above a certain threshold given by parameter X74 ovulates and gives birth to her pup 60 days later unless the female bat dies before the end of this time interval. From this computer experiment I can tell if a female reproduced after her 1st, 2nd, and 3rd hibernation based on the lipid content after hibernation. At the individual level only the mother bat is tracked through its life history; hence, it is not possible to know whether she produced a viable pup that at least reaches weaning. Hence we cannot have an indication from these data about successful reproductive events. This information is obtained from the population model (see Chapter 5).

From these numerical experiments, the number of females that ovulate in the 3 consecutive years and reproduced after their first, second, and third hibernation respectively are 60 out of 111 (54%), 73 out of 97 (75%), and 78 out of 94 (83%). Also note that any combination of occurrences of ovulation can occur, i.e. a female can have enough lipids in the first year and not the following years, or not enough lipids in the first 2 years and be able to reproduce in the third, etc. This is an important dynamic to investigate with a longer computer experiment following individuals over several generations and investigating the impact on population dynamics. The biological literature (Schowalter, Gunson et al. 1979; Crichton and Krutzsch 2000) indicates that some females may reproduce in their first summer and that most reproduce every year from the second summer. However, it is hard to obtain field data to validate this preposition because in general only reproductive females aggregate at the summer maternity roosts where information is collected and almost nothing is known about the non-reproductive females that might behave as solitary males.

It was not possible to fit a good nominal logistic model to the "*Ovul Year 1*", *Ovul Year 2*", and "*Ovul Year 3*" variables as it was in the case of the response variables related to survivorship.

Reproduction will be better analyzed from an individual perspective in Section 4.3.1 and under the population model context in Chapter 5.

3.1.3 Interactions with environmental factors

The model includes environmental constant factors that play an important role in the individual dynamic because they are directly related to energy intake and energy expenditures. To assess possible interactions between these factors and the individual parameters the same sensitivity analysis described above was repeated under different scenarios for the environmental factors. The simulations used for the sensitivity analysis performed above were run under a "Baseline Scenario". Then another 6 scenarios were considered. The values for the parameters for each case are shown in Table 15.

Following the same methodology used for sensitivity under the baseline scenario the individual parameters that are significant for each response were identified when possible. Then these parameters or factors were compared with those that were significant under the baseline scenario. As a means to easily compare with previous results, the following tables with the rank of significant parameters should be interpreted as parameters in plain font are significant under the baseline and new scenarios (however the rank order may have changed), parameters highlighted in bold indicate results that are significant only under the new scenario, parameters significant only under the baseline case are listed at the bottom of the tables, the sign beside a factor represents the sign of the relationship between the factor an the response variable.

I searched for patterns in the newly identified significant parameters and in those discarded. I gave more importance to new parameters appearing and/or parameters being discarded that were at the top of rank rather than at the bottom. High mortality in either of the two first periods in the life of the individuals (Juvenile, Hibernation 1) resulted in a high number of missing values for the 256-runs computer experiment under scenarios of unfavorable environmental conditions (scenarios 2, 3, and 6). For these scenarios, it was not possible to estimate the parameters of a regression model with 40 runs or less for some of response variables. Or else the regression model was possible to obtain but the results make no biological sense and the model is not reliable. Hence the information obtained from the analysis originally proposed is less than what it was anticipated.

To be able to compare the effect of important parameters under the Baseline Scenario with the Scenarios 2, 3, and 6, I decided to re-do the experiment but starting with adult individuals instead of newborn pups. However this experiment did not gave enough information to estimate good regression models because many individuals died under these scenarios during

the first two periods (summer and hibernation). The high number of individuals or ecotypes not surviving the first two periods indicates that many combinations of parameters do not characterize individuals that could cope with the proposed scenario. This percentage of mortality in the 256 runs cannot be compared with data on population mortality because we do not know the composition in terms of ecotypes of the population. The results from these simulations are not presented here.

Scenario 1: Warmer summer and warmer winter

As in the case of the baseline scenario, Scenario 1 does not provide much information for survival response variables because the fitted models are unreliable, and because of the lack of information to perform the analysis when the nominal data is not balanced (Table 16). However, it was observed that warmer temperatures considerably increased the number of surviving individuals to the juvenile stage (from 63% to 82%) in our sample of 256 individuals/runs.

In the case of lipid contents before and after the hibernation periods 2 and 3 (see Table 17) the factor X76 (*percentage of lipid in neonate*) is absent from the list of important parameters. This suggests that a more favorable situation (e.g. warmer temperatures) yields an impact where of reproductive cost represented by X76 is less important. This effect is also noticed under other favorable scenarios. In "*lipid content after hibernation*" responses, X38 that represents the *time that hibernating bat spends awake during periodic arousals* is absent from the list of important parameters. A higher temperature in the cave reduces the cost of regulating temperature during arousals; however there is a trade off because it increases the costs during the torpid phases. There is another set of mixed factors that are added to the lists, in general at the bottom, to "*Lipid before hibernation 1 and 2*" and to "*Lipid after hibernation 1, 2, and 3*". This set is formed by X20 –, *non-labile structure proportion*, X36 –, *resting metabolic rate*, X71 –, *time foraging*, and X65 +, *flight efficiency*. Because bats under this scenario tend to weigh more than in the baseline scenario, these factors might be associated with the increasing cost of maintenance and flight of bigger individuals. The factors related to structural response variables did not change under this scenario (Table 18).

Scenario 2: Colder summer and colder winter

A colder summer decreased winter juvenile survival significantly (from 63% to 36%) while did not affect survival over the other periods. However this effect produces experiments with a high number of missing values for the response variables, which causes poor performance of regression models in identifying parameters important in describing the response variables (see Table 19, Table 20, and Table 21). The R^2s of the fitted models can be high and residuals can be

suitable but factors included in the model might not make sense based on model formulations or based on biological reasons. For example, factors that are only associated with pup and juvenile stages (X29, X30, X21, X44) appear significant in determining "*Lipid before hibernation 2*", a response that represents the lipid content of adult individuals. Hence, no further suitable conclusions should be drawn from these results derived from responses related to lipid. The results for the structure component before and after hibernation are difficult to interpret since there is no clear pattern of factors that are present. For "*structure before hibernation*" it seems there is no difference between the factors important under the baseline scenario. For "*structure after hibernation*", X27 (*maximum feeding rate*) and X34 (*euthermic body temperature*) dropped from the list of significant factors. This is somewhat counterintuitive for X34 because when a bat is subject to colder temperatures, maintaining body temperature is an important cost. Moreover, new factors such as X25, X44, X47, that entered the rankings do not make sense biologically and were placed at the bottom of the lists. This suggests a poor performance of the model in describing the response. Hence, reasonable conclusions about interactions were not derivable from these results.

Scenario 3: Low resource availability

The situation encountered under Scenario 3 is similar to that for Scenario 2, where high mortality at the beginning produces too few data points to produce adequate regression models to describe the response variables (see Table 22, Table 23, and Table 24). However the biggest effect of low resource availability is not on juvenile survival (decreased from 63% to 60%) but on survival to 1st hibernation (decreased from 69% to 26%). This is evidence of how insufficient resources during the summer affect winter survival because fat deposition is not enough to fuel winter energetic demands. Due to experiments with a high number of missing values, no models were fitted to most of the responses.

Scenario 4: High resource availability

Results for this scenario are presented in Table 25, Table 26, and Table 27. As opposed to its complementary scenario (Scenario 3) these environmental conditions considerably increased survival to 1st hibernation period (from 69% to 92%) without having other important effects on the other periods of the life history.

The patterns for those factors dropped and added to the rankings related to lipid response variables are similar as those observed under Scenario 1. The impact of reproductive cost represented by X76 loses importance. Factors X38, *time that a hibernating bat spends awake during periodic arousals*, and X70, *time commuting*, are also dropped from the lists in the

responses related to "*lipid after hibernation*". There is set of mixed factors that are added to the lists, in general at the bottom, to "*Lipid before hibernation 2*" and to "*Lipid after hibernation 1, 2, and 3*". This set includes X20 –, *non-labile structure proportion*, X36 –, *resting metabolic rate*, X71 –, *time foraging*, and X65 +, *flight efficiency*. Because bats under this scenario tend to weigh more than in baseline scenario, these factors might be associated with the increasing cost of maintenance and flight of bigger individuals.

No significant changes are observed on the factors contributing the most to structure response variables in the baseline scenario.

Scenario 5: Low energy density diet

A diet with lower percentage of lipid and higher content of protein and carbohydrates decreases both juvenile (from 63% to 52%) and 1st hibernation survival (from 69% to 56%) (see Table 28).

Again the large number of missing values in the response variables after the 1st hibernation produces regression models that do not perform well in describing the responses and results are not considered for discussion (see Table 29 and Table 30). These regression models not only have low R^2s and 8 or more factors but also include factors that do not make biological sense (X45, X32, X44, X21, X5) for the particular response variable. The models fitted to "*Lipid and Structure before hibernation 1*" (fitted with sufficient number of runs) do not show any important changes when compared with the models fitted under the baseline scenario. Hence, no further conclusions are drawn from these results.

Scenario 6: High energy density diet

The results for this scenario are very similar to those for Scenarios 1 and 4. Results are shown in Table 31, Table 32 and Table 33. Survivorship is increased for juvenile (from 36% to 69%) and 1st hibernation (from 69% to 79%) periods.

In the case of "*Lipid before and after the hibernation periods 2 and 3*" the factor X76 (*percentage of lipid in neonate*) drops from the list of important parameters. In "*Lipid after hibernation 1 and 2*" responses, X38 which represents the *time that a hibernating bat spends awake during periodic arousals*, loses its effect. The same set as before formed by X20 –, *non-labile structure proportion*, X36 –, *resting metabolic rate*, X71 –, *time foraging*, and X65 +, *flight efficiency* is added to "*Lipid before hibernation 2*" and to "*Lipid after hibernation 1, 2, and 3*".

The factors related to structure response variables do not change under this scenario.

3.1.4 General Conclusions from the Sensitivity Analysis

Eighty-two parameters were included in the screening sensitivity analysis of the individual model. Using a fractional factorial design, 256 simulations were performed to assess the sensitivity of model output with respect to the model parameters. The conclusions from the analysis performed are summarized below.

The response variables related to individual lipid content ("*Lipid before and after hibernation 1, 2, and 3"*) showed greatest variation, including the values for certain runs that are above biologically reasonable levels. This is not a desirable feature in the individual model. However, there is an explanation for these values. First it was verified that, even when mass values obtained are above normal ranges, the model variables are not unbounded. If a female continues in post-lactating state under constant energy demand per unit mass and at maximum constant resource level, both lipid and structure components level off resulting in an individual of approximately 11 g wet weight for the parameter values chosen. Therefore, individuals do not grow unboundedly. On one side, these high values for lipid content result from combinations of parameters set at the end of their ranges that might not occur in nature. On the other side, the model does not represent any feedback mechanism that limits the lipid content by adjusting the intake rate and energy demand accordingly. This limitation of the model is further discussed at the end of this chapter. The response variables related to structure component remain within the ranges set in the model formulation.

On the average, 78% of variability in lipid content before hibernation can be explained by 10 or 11 factors or parameters. The following 7 factors appear significant in the 3 responses for "*Lipid before hibernation*": *maximum feeding rate* (X27+), *half saturation feeding rate* form (X28-), *lipid* and *structure assimilation* (X1+, X2+), *euthermic temperature* (X34-), *water to structure ratio* (X22-), and *foraging speed* (X68-). In the case of reproductive females ("*Lp bf Hib 2 and 3*") the *lipid composition of offspring* (X76-) is significant. "*Lipid after hibernation*" is influenced in general by the same factors affecting lipid content before hibernation except for the time that the bat spends active during periodic arousals.

Approximately 84% of the variation in the structure component before and after hibernation is explained by 5 to 8 factors. Some of these are directly related to the structural mass of the individual: *non-labile portion of structure compartment* (X20+), *minimum* and *maximum structural masses* (X23+, X24+). Again factors related to feeding efficiency (X27+, X28-) are significant. It is important to note that for most of the cases, the factors included in the regression models had the expected sign describing a direct or inverse relation with the response.

The methodology used here failed to identify parameters that might play an important role in survival and reproduction because of the high number of missing data points (individuals/runs that die) and the unbalanced characteristic of the results. When the majority of individuals survive from one stage to the next or reproduce, both categorical responses (survival and ovulation) took the value 1. Under this situation there is not sufficient information to identify parameters affecting one of the two fates (survival vs. death, ovulations vs. not ovulation). Survival and reproduction will be studied again at the population level in Chapter 5.

Regarding the problems to identify parameters for survival response, Maria Weese, a doctoral student in the Statistics Department at University of Tennessee did a class project using the data from these simulations and investigated other approaches to deal with the problem of missing data points due to a bat dying in a earlier stage of life. She suggested modeling the responses as the joint probability of death instead of the conditional probability approach used here. With this approach all missing data points are transformed to zeros and the logistic regression models converge allowing fitting a model for all the survival responses. The "joint probability model" identifies the same factors for "*Juvenile Survival*" and "*Survived Hib 1*" as the model presented here. For the remaining survival responses, "*Survived Adult*", *Survived Hib 2*", *Survived Adult 2*", and *Survived Hib 3*", most of these factors remain in the models and new factors are added as significant. Factors X47, *proportion of day regulating temperature for juvenile*, and X44, *pup metabolic rate*, only appear important in the juvenile stage. The factors added are X76, X1, X36, X37, and X55; and all of them make biological sense as being important. Also the use of an ordinal logistic regression model was investigated coding the response variables as ordinal values. However the "proportional odds" assumptions of this model is violated and the approached was discarded.

To investigate possible interactions between the individual characteristics and the constant environmental factors the analysis was repeated assuming six different environmental scenarios representing favorable (Scenarios 1, 4, and 6) and unfavorable (Scenarios 2, 3, and 5) conditions. In the case of unfavorable scenarios there were insufficient data points to fit appropriate models to the responses in most of the cases or the fitted regression models did not explain the variation well. Because of this deficiency, interactions between individual characteristics and environmental variables were difficult to identify. However a few conclusions were drawn from the experiments.

Warmer temperatures increased considerably the number of surviving individuals to the juvenile stage (from 63% to 82%) in the sample of 256 individuals/runs. Low resource

availability decreases survival but its effect is not on juvenile survival (decreased from 63% to 60%) but on survival to 1st hibernation (decreased from 69% to 26%). This is evidence indicating how insufficient resources during the summer affect winter survival because fat deposition is not enough to fuel winter energetic demands.

In the case of "*Lipid before and after the hibernation for periods 2 and 3*" the factor X76 (*percentage of lipid in neonate*) drops from the list of important parameters in the favorable scenarios (1, 4, and 6). This suggests that under more favorable situations (e.g. warmer temperatures, high resources, high lipid diet) the impact of reproductive cost represented by X76 loses importance. In "*Lipid after hibernation*" responses, X38 that represents the time that the hibernating bat spends awake during periodic arousals loses effect.

Overall, the most influential parameters in the model output were:

X1 lipid assimilation efficiency

X2 protein and carbohydrates assimilation efficiency

X20 non-labile structure proportion

X22 water to structure ratio

X23 minimum structure size

X24 maximum structure size

X 27 maximum feeding rate

X28 half saturation constant in feeding rate formulation

X34 euthermic body temperature

X36 resting metabolic rate

X65 flight efficiency

X70 time commuting

X71 time foraging

X76 lipid percentage in neonate

For some of these factors/parameters there was not field nor laboratory information to set the values to be used in the simulations as described in Section 2.5. Based on the sensitivity analysis I would suggest further studies to investigate a functional response for feeding rate based on insect availability. Flight efficiency is another important parameter for flight energetics that needs to be estimated for bat species. Flight efficiency not only is identified here as important but also when comparing the estimates for flight energetics from different studies or models in Chapter 4.

A few factors from the previous list of the most influential, were used to generate individual ecotypes to create a heterogeneous population. The ecotypes definition is described in Chapter 5.

3.2 Model Limitations

In the process of formulating a mathematical model to represent a given system one continuously faces the question of what to include and what not to include. The model should be kept as simple as possible but needs to include enough detail to be relevant to the objectives proposed. Computer models can be very complex. Many rules and parameters can be implemented to represent various and complex mechanisms as desired by the user. However, as more detail is included, testing, analysis and interpretation of results generally become more difficult.

The model presented here is the first model of this kind used to represent the individual dynamics of a bat. Even though the energetic flow and components (lipid and structure) modeled might be generic for other organisms, the particular life history of a temperate hibernating bat adds complexity to the formulation of the energetic demand. Several assumptions were made to represent the energetic demand for the different activities (thermoregulation/roosting, flight) at the different life history periods (hibernation, pregnancy, lactation, migration, etc). The resulting model represents a first quantitative methodology to study in a dynamic and integrated approach the energetic and lipid cycle of a hibernator bat. The model allows one to answer and/or test several questions related to the strategies that the bats use to meet their high energetic requirements. However, several other interesting questions cannot be addressed with the model as it is. Limitations in this model are mainly related to those processes that I decided not to include or were included under very simple assumptions.

Bats get too fat!

One result observed from the sensitivity analysis is that the model bats easily gain weight by increasing their lipid content when they are subject to certain combinations of parameters values or favorable environmental conditions. This is a feature of the model that is not particularly attractive but it is based on the assumptions and formulations made, which are controllable. The lipid content of an individual results mainly from the balance between energy input and energy output. In the natural system several feedback mechanisms may act to maintain this balance within observed ranges. Two important mechanisms are:

- changing the thermoregulatory strategy to compensate for changes in temperature and/or food availability
- appetite (and consequently insect consumption) is regulated by hormones as a function of lipid content (Mercer 1998; Frisch 2002, Mercer 1998; Rousseau, Atcha et al. 2003)

The thermoregulatory strategies assumed in the model are fixed, depending on the physiological category of the individual; for example, pre-hibernating bats are assumed to increase time in torpor as hibernation day gets closer (it is a function of time). I consider this to be a reasonable assumption because both insect resources and temperature are expected to decrease as the summer ends. But if environmental conditions in a particular year continue to be favorable, bats probably do not need to enter daily torpor as much.

In the individual model, the feeding rate is assumed to be a type II functional response depending only on the insect density. This function saturates at maximum feeding rate when insect density is high. In reality the bat may not necessarily feed at this maximum capacity at high insect densities if it is not hungry. But in the model, there is no regulatory mechanism of appetite assumed depending on current energy demand and/or lipid content.

These feedback mechanisms can be implemented in the model. However, more field information is needed to provide some evidence about the functional responses involved in the processes mentioned. Defining and assuming a feedback mechanism at this stage would just add more parameters and complexity when more simple processes have yet to be understood.

Timing of the events

The model assumes that the transitions of individuals through their life history stages occur at fixed calendar dates independently of any other important factors that might be involved (see Section 2.1). Moreover the transitions occur to all individuals at the same time, the parameters used to define the rules updating the stage/condition of an individual are the same for all kinds of individuals, and sensitivity analysis of model output to changes in these parameters has not been performed.

The timing of events such as parturition, and beginning and ending of hibernation and their relationship with environmental factors might play an important role in population dynamics and geographic distribution of the species. The model developed is not flexible enough at this stage to answer questions related to these issues. However it could be modified to include more dynamic rules related to transitions through the life history of individuals.

Temperature profiles and thermoregulation

The ambient temperatures to which the bat is exposed are constants over a fixed period; a fixed cave temperature, a fixed portion of day summer roosting, and a fixed portion of night summer roosting. Also the energetic requirement for thermoregulation is calculated based upon a constant proportion of the day regulating temperature that varies with the physiological category (e.g. pregnant, lactating, pre-hibernating, etc). In most instances, the portion of the day the bat thermoregulates is a function of the ambient temperature. Hence it would be interesting to link both temperature and thermoregulatory strategy chosen by the bat to study in more detail the effects of temperature on the energy budget of the individual.

CHAPTER IV
INDIVIDUAL MODEL RESULTS AND APPLICATIONS

4.1 Individual Dynamics

Given the parameter values that characterize a particular individual or ecotype, the parameter values that describe environmental conditions and physical constants, and a set of initial conditions for the state of the individual at the initial time of the simulation, the individual's lipid and structural component dynamics is generated over time. The dynamic generated for both components reflect the modeled age stages and the physiological status of the individual according to its life history. The aqueous component of the individual is estimated as a proportion of the structural component and the total mass (wet weight) is estimated as the sum of lipid, structure, and water content.

It would be ideal to have time series of body composition for the same individuals over their life history to compare with the dynamics generated by the model. However such data are not available. The most relevant field studies showing data related to the dynamics of lipid and lean mass in pups and adult pregnant females are Kunz, Wrazen et al. (1998) and Reynolds and Kunz (2000). The data published are summarized in Table 34 in Appendix A. These data represent average body mass and/or body composition for several individuals caught at different points of their life history. Even though these are not time series, the data provides a good idea of the patterns in body composition through the life history of female bats and support the lipid cycle patterns expected for hibernators (Dark 2005). In an effort to more clearly show the patterns in the body composition and mass dynamics I plotted the data from both studies in a time series fashion in Figure 5 (juveniles) and Figure 6 (adult pregnant female). However, it is important to note that the time coordinate was not always described in terms of calendar day; hence, the time location of the data points might be shifted and/or stretched along the horizontal axis. Parts of these data sets were used to fit some parameters in the model or used as goal values when the value of a parameter was completely unknown.

The dynamics shown in Figure 7 correspond to the numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. The figure also depicts the events in the life history associated with the observed changes in the dynamics. Growth that is almost linear in both lipid and structure is observed during the first 2-3 weeks of life until peak lactation. This kind of growth has been observed in field studies (Baptista, Richardson et al. 2000; Hood, Bloss et al.

2002). Then the model predicts a decrease in mass over a short period of time as the pup starts to lower milk intake and begins to forage. Data available (Reynolds and Kunz 2000) related to pup growth do not exactly follow this dynamic (Figure 5), however it is an expected result from the rules in the model during the transition from purely milk diet to an insect diet. A more detailed analysis of the dynamic of this transition will be presented in the applications section later in this chapter. After another period of increase there is a slight decrease in mass associated with migration costs. Then, the pre-hibernation period starts with the expected increase in lipid stores, while the structure component remains relatively constant for fully-grown individuals. During hibernation, lipid is used preferentially to fuel the cost of torpor and periodic arousals (marked drops); however, proteins are also mobilized to meet energetic requirements (Esher, Fleischm.Ai et al. 1973) and consequently this compartment also decreases.

Figure 8 corresponds to the resulting dynamics for an adult pregnant female starting at the end of hibernation. A female's mass increases with an increased resource intake due to additional insect availability. There is a discrete drop in structure and lipid associated to parturition. Then mass continues to decrease, mainly to decrease in the lipid component, until peak lactation. After that lipid and structure grow again. As described above there is a decrease in mass associated to migration and after that an important increase in lipids as the individual builds its reserves for the winter stresses. During hibernation, lipid and structure components decrease. In the case of a female whose lipid level at the end of hibernation is not enough to trigger ovulation, the dynamic shows an increase in mass that peaks with maximum food availability, then decreases during migration, and increases during pre-hibernation. An example of this dynamic is shown in

Figure 9 that corresponds to an individual that does not reproduce after its 1st hibernation but reproduces after its 2nd hibernation. Even though the data and the model dynamic are not completely independent, the data provide support for the model's ability to capture the main dynamic patterns in body composition through the life history of an insectivorous hibernating bat.

4.2 Comparison with Previous Estimates of Daily Energy Budgets for *Myotis lucifugus*

The purpose of this section is to check for consistency between previous estimates of daily energy requirements for little brown bats and those generated by the individual model presented in this dissertation. I do not necessarily want nor expect the estimates of this model to match the previous ones. However, given that there are other estimates available but calculated using different methodologies, I believe it is important to compare the results produced with the

individual model. A degree of agreement among estimates would lend confidence to the methods used.

Each of the methods used for estimating energetic demand have their advantages and disadvantages, and their own potential errors. Hence a better understanding of energy expenditure and allocation by free ranging animals can be gained when several approaches are used concurrently (Kunz and Nagy 1988). When comparing results coming from different methodologies it is important to note the assumptions involved in the procedures. This checking does not intend to be a formal validation nor a corroboration of the model (Gross 1994), rather is a check on the consistency of the model with other estimation approaches.

First, I briefly describe the main methods that have been used to estimate the daily energy budgets for bats, and then I highlight the main results obtained in studies that used these methods applied to *M. lucifugus* including a very short description of assumptions and methodology for each study. Later I present the results from the individual model and highlight the differences in methodologies and results with previous estimates of the energy budget.

The term "daily energy budget" (DEB) is described in a review paper on the subject by Kunz (1980) as "the amount of energy for a bat to satisfy daily energy requirements of maintenance, reproduction, and productive processes". Four methods or models that have been applied to estimate the daily energy budget of bats are described in this section. For a more detailed description of these and other methods of energy budget analyses, see Kunz and Nagy 1988.

4.2.1 Methods for Estimating DEB

Time budget method

Time-budget studies record the amount of time the animals spend in various activities during the day. For bats these activities are mainly roosting, flying, and feeding. When the appropriate time-budget data are available, then assuming that the concurrent physiological events are additive, an estimate of the daily energy budget can be obtained by multiplying the time spent in each activity by the energy equivalent to that activity (Kunz 1980). Time spent and metabolic costs associated with major activities of bats are additive. However, these activities may occur simultaneously with behaviors such as grooming, clustering, or predator surveillance and cannot be compartmentalized in general. Kunz (1980)(eqn.3) has proposed the following generalized time-budget model for bats:

$$DEB = \left[\mu\left(T_{dr} M\right) + \mu\left(T_{nr} M\right)\right] + \left(1 - T_{dr+nr}\right) M_f .$$

In this equation M represents the roosting metabolic rate, μ is a coefficient to modify the roosting metabolic rate for clustering, T_{dr} and T_{nr} are the proportions of time spent in the day and night roost respectively, and M_f is the metabolic cost of flight. In this formulation, roosting metabolic rate includes the basal metabolic rate, metabolic increments resulting from thermoregulation, and various roost activities.

*In*gesta *method*

The *ingesta* method utilizes data on food consumption obtained from free-living animals and requires laboratory estimates of digestibility and energy equivalents of food consumed. Thus the energy consumed, *E*, can be expressed by the following equation:

$$E = \sum_{i=1}^{n} C_i \lambda .$$

The food consumed, C_i, over each feeding period *i* is multiplied by its caloric value and then summed over the *n* feeding periods. C_i can be calculated by measuring changes in body mass over a span of time in which an individual feeds. Then the *DEB* is determined as the product αE, where α is the digestibility coefficient.

Egesta Method

The *egesta* method utilizes feces production from free-living bats and a laboratory derived relationship between consumption and feces production. Using this method, the energy consumed, *E*, is given by the following expression:

$$E = \sum_{i=1}^{n} F_i \left(\frac{1}{1-\alpha}\right)\left(\frac{1}{1-\beta}\right)\lambda .$$

In this equation F_i represents the dry weight of feces for each period of feeding, α the digestibility coefficient, β the percent water in food eaten, and λ the caloric value of the food. Again, the daily energy budget is determined as the product αE. Due to high gut clearance rates in some species of bats, some fecal loss can occur during foraging flights and before bats return to their roost.

Doubly labeled water method

Originating in the late 40's and early 50's at the University of Minnesota, the doubly labeled water (DWL) method is the first genuinely non-invasive method for measuring energy expenditure in free-living organisms and the method has become an established important tool for investigating energy metabolism. The DWL method works by measuring CO_2 production via the

differential washout rates of injected isotopes of hydrogen and oxygen (Kunz and Nagy 1988). Then CO_2 production can be converted to units of energy metabolism (field metabolic rate) using an appropriate equation and corrections made for diet composition and digestibility (Nagy 1980).

4.2.2 Estimates available from previous models and experiments

The main relevant assumptions and methods corresponding to each study are briefly described. Results have been summarized in tables and transformed to common units to make comparisons easier. The first 5 studies correspond to active bats, some are pregnant, lactating or juveniles. The last work corresponds to hibernating bats.

Anthony and Kunz 1977 – Ingesta and Egesta Methods combined

The authors estimated food consumption for the little brown bat in southern New Hampshire by comparing pre-feeding body weights with post-feeding weights. Feces were also collected and analyzed. It is noted that food consumption might be underestimated due to a very high gut clearance rate. Wet weight of food consumed was estimated from dry weights of feces collected, assuming 88% assimilation efficiency and 60% water content of insect eaten. The energy value of wet weight to fresh stomach content was estimated to be 8.7 kJg^{-1} (equivalent to 21.77 kJg^{-1} dry mass). DEB estimates are presented in Table 35.

Kunz 1980 - Time Budget Method

In this case the DEB was estimated using the time budget observed the same night as Anthony and Kunz 1977 and roosting metabolism reported for pregnant bats by Studier and O'Farrel (1976) based on the temperatures recorded in the day and night roosts. The metabolic rates for the first 5 h of the day roosting and the 5 h of night roosting were corrected for specific dynamic action (SDA) by multiplying the average temperature-dependent metabolic rate for that period by a factor of 1.2. The cluster coefficient in the time budget model, μ, was assumed to be 0.5 because both at day and night roosts the bats were tightly clustered. Energy cost of flight was estimated from the allometric equation in Thomas (1975). The estimates obtained for each of the components of the energy budget are not reported; the overall estimate is 3.1 $kJg^{-1}day^{-1}$.

Burnet and August 1981- Time Budget Method

From direct observation of time budget and temperatures at a maternity colony of *Myotis lucifugus*, the authors applied a modification of Kunz's (1980) time-budget model. Basically, they considered a different term for activities other than resting and proposed the following formulation:

$$DEE = \left[T_{dr} M_t (\mu + A)\right] + \left[T_{nr} M_t (\mu + A)\right] + (24 - T_{dr+nr}) M_f .$$

In this formulation DEE is the daily energy expenditure, M_t is the temperature dependent resting metabolic rate, T_{dr} and T_{nr} are the hours spent day roosting and night roosting, respectively, μ is a coefficient to modify M_t for clustering behavior, and A is the coefficient to account for the increased metabolic cost of activities other than resting (i.e. moving, grooming). The temperature dependent metabolic rate, M_t, was estimated from multiple regression equations fitted to experimental data by Studier and O'Farrel (1976). The metabolic cost of flight M_f was estimated from the allometric equation of Thomas (1975). Calculations shown in Table 36 assume an 8.24 g bat.

Kurta et al 1987 – Time Budget Method

The authors monitored oxygen consumption of captured little brown bats throughout the day and night roosting periods under simulated roost conditions. Then they applied a time budget model using their observed estimates of metabolic rates during day and night roosting. The metabolic cost of flight M_f was estimated from the allometric equation of Thomas (1975). In pregnant females not all energy expenditure is reflected in oxygen consumption because small amounts of energy go into storage in the form of fetal growth and maternal tissue. They estimate this cost from previous work (E. Pierson and T.H. Kunz, unpublished data). In lactating females a significant amount of energy is exported as milk and it is not recorded in the oxygen consumption measurements. They used Kunz's (Kunz 1987) estimated value of milk energy output at peak lactation using an isotope dilution technique. Calculations assume an 8.34g pregnant bat and 8.30g lactating bat. Estimates are shown in Table 37.

Kurta et al 1989 – Doubly Labeled Water Method

In this study CO_2 production rates of 10 pregnant (average body mass 9.02 ± 0.28g) and 14 lactating (average body mass 7.88 ± 0.14g) females were measured using DLW method. The authors assumed a diet of insects consisting of 70% water, 17.8% protein (23.6kJg^{-1}), 4.6% fat (39.5 kJ g^{-1}), and 2.2% carbohydrate (17.7 kJg^{-1}). It was also assumed that 95% of ingested protein, fat and carbohydrate are assimilated, and then 15% of assimilated protein is lost as urea. Hence, the fresh insects ingested had an energy density of 7.25 kJg^{-1} (24.17 kJg^{-1}dry mass) and provided 5.51 kJg^{-1} of metabolizable energy. Because metabolic rates obtained with DLW do not include chemical energy stored as new tissue or exported as milk, they estimated these values from previous works. The energy stored in the fetus represents 78% of the total energy stored in the fetus, placenta, uterus, and mammary glands (Migula 1969; Kurta and Kunz 1987). They

assumed a 2.3g neonate equivalent to 2.5 kJ (Burnett and Kunz 1982, Stack 1985, Fujita 1986). Hence the total production during pregnancy was estimated to be 16 kJ and was uniformly distributed over the last 30 days. The daily milk-energy production was estimated from field measurements of juvenile metabolic rate using DWL and the composition of *M. lucifugus* milk (Kunz, Stack et al. 1983); T.H. Kunz unpublished data). Estimates from this study are presented in Table 38.

The authors also partitioned the maintenance daily energy demand into the three components used in time budget models: day roosting, night roosting, and foraging/flight. They assumed the model below for daily-metabolized energy budget, E_D:

$$E_D = P_{DR} t_{DR} + P_{NR} t_{NR} + P_F t_F ,$$

where the subscripts *DR*, *NR*, and *F* represent the day-roosting, night-roosting, and foraging periods, respectively; and *P* and *t* represent power requirement and duration, respectively, of those periods. They assume the power requirement for roosting periods from Kurta et al (1987) and solved for P_F. They obtained that a 9g *M. lucifugus* requires 4.46kJ h^{-1} (0.5 kJ $g^{-1}h^{-1}$); which is 13% lower than that predicted by equation (36) of Thomas (1975).

Thomas et al 1990 – Time budget method during hibernation

In this study oxygen consumption was measured during the warming and homeothermic phases of a bat in torpor at 5 ^{o}C in a metabolic chamber. Estimates at the different phases are depicted in Table 39.

4.2.3 Comparing with Dynamic Individual Model Estimates

As mentioned at the beginning of Section 4.2, when comparing the results presented here with the results summarized above it is necessary to have the methodological considerations in mind. Table 40 summarizes the methodology used in each case, including the individual model presented here.

In the individual model the daily energy demand also takes the form of a time budget model but the per hour energy costs for each of the components are neither constant parameters obtained from data nor values estimated from linear regression to data. The formulations for these costs try to use a more mechanistic representation of the thermoregulation and flight processes. The estimates are calculated daily since the mass of the individual is a dynamic variable and other aspects vary as a function of time. A detail description of these terms is given in Chapter 2 of this dissertation.

It important to mention that the parameter values selected to compute the estimates were not chosen to fit any of the values of energy demand presented in the papers reviewed above. However the times spent day roosting, night roosting and foraging or flying were those assumed/observed in Burnet and August (1981). The data from Hook (1951) was used to estimate most of the parameters in the roosting formulations. The evidence from Studier and O'Farrell (Studier and O'Farrell 1972; Studier and O'Farrell 1976) of bats regulating and conforming suggested the idea for bats adopting one of these strategies throughout the day. The proportions of the day and night conforming and regulating were 'created' on basis of some biological evidence and hypothesis (see Section 2.4.3 for details) but no data to support the values of the parameters were found. Here the opportunity is open to bat biologists to generate field data to validate the model presented. If more data were available a more realistic rule to determine the strategy chosen by the bats could be formulated, instead of the proportion regulating being selected as linear function of time.

Another important difference is that the costs of pregnancy and lactation were not expressed as a component of the daily energy budget but were subtracted directly from the constituent components (see Sections 2.4.5 and 2.4.6). The discrete mass loss at parturition in the individual model assumes the same neonate mass and body composition as Kurta et al (1987). The cost of lactation as given by Kurta et al (1987) was coupled with milk composition data and used to estimate the daily losses of mass of lipid and mass of structure during lactation in our model. Hence these costs can be considered close in magnitude to those in the model presented here even though they are expressed in different units.

Except for Kurta et al (1989), all estimates reviewed used the allometric formula from Thomas 1975 to estimate flight cost. From empirical data on oxygen consumption during flight for different bat and bird species, allometric relationships for power input have been derived. This frequently used (Kunz 1980; Burnett and August 1981; Kurta, Johnson et al. 1987) allometric equation for power is that derived by Thomas during horizontal flight:

$$P = 58.4m^{-0.21}.$$

Here P $\left[\mathrm{W\ kg^{-1}}\right]$, is the power input during level flight and $m\left[\mathrm{kg}\right]$ is the mass of the animal. It is assumed that the bat or bird flies in nature at a speed where the cost of transport is minimal in value for the species under consideration. The cost of transport $[.]$ is the ratio of power input to the product of body weight $\left[\mathrm{N}\right]$ and speed $\left[\mathrm{m\ s^{-1}}\right]$. Data for three species of birds with mean body mass ranging from 0.035 to 0.321kg and two species of bats, *Phyllostomus hastatus* (0.093kg)

and *Pteropus gouldii* (0.78kg), were used for the least-squares fit. A more recent allometric equation was proposed by Speakman and Thomas (Speakman and Thomas 2003) eqn.5 from mask respirometry studies made at a range of flight speeds for flight costs at the minimum power speed (13 bats and 9 birds):

$$P = 0.23m^{0.794}.$$

In this equation P is in Watts and m is in grams. When units are transformed to $\left[\mathrm{W\ kg^{-1}}\right]$ for P and kg for *m*, the equation scales to

$$P = 53.9m^{-0.21}.$$

This equation gives flight costs about 7% lower than Thomas 1975. Both equations and similar ones must be applied with extreme caution in estimating flight energy budgets in different conditions and for different species. Extrapolating estimates beyond the range of masses of the data points used in the fitting and for bats under different bat situation leads to unreliable results.

In order to make comparisons easier, all estimates were transformed to units of kJ $g^{-1}d^{-1}$. In this way the changes in energy demand that occur due to dynamical changes in individual mass in the individual model are normalized. The estimates of daily energy demand per unit time calculated with the individual model assuming the baseline set of parameters and constant environmental factors are shown in Figure 13. The total DEB (kJ $g^{-1}d^{-1}$) varies temporally as a result of time and physiological stage dependent thermoregulatory strategies (proportion of roosting time regulating vs. conforming). Literature available (Studier and O'Farrell 1972; Studier and O'Farrell 1976) suggests that a pregnant bat might increase the proportion of its roosting time thermoregulating as pregnancy progresses. A lactating bat might save energy conforming most of day roosting but mainly regulates temperature during the night roosting to enhance milk production and nurse the pup (Studier and O'Farrell 1972; Studier and O'Farrell 1976). Data from Studier and O'Farrel (1972) also suggest that post-lactating bats tend to regulate their temperature; hence, high constant proportions of roosting time thermoregulating regulating were assumed. To store fat and cope with decreasing insect resources the strategy adopted by pre-hibernating bats is to spend more of the roosting time in torpor (or conforming) as they approach the hibernation period (Speakman and Rowland 1999). By changing the values of the constants involved in the thermoregulatory strategy functions described above and formulated in Section 2.4.3, and by changing the values for average ambient temperature constants assumed for day (25^{o}C) and night (17^{o}), the estimates of energy demand for day and night roosting could be easily modified to match previous results. But as was mentioned, this was not the conceptual idea and by doing that this approach would have not been independent of the estimates in the literature.

Overall I think that all the estimates for day and night roosting, including the ones presented here, give a valid approximation to roosting expenditures. Moreover, the use of a thermoregulation strategy function allows future testing of thermoregulation strategies that have been hypothesized.

The energy allocated to flight [kJ $g^{-1}d^{-1}$] predicted by the individual model fluctuates around 0.76 kJ $g^{-1}d^{-1}$. The sharp increase over a 3 day period corresponds to migration from the maternity colony to hibernacula. Small fluctuations occur in the "mass specific" energy demand because the flight power function is a non-linear function of the total mass of the individual. The flight component is the one where greatest differences in estimates are found when different methods to estimate the energetic demand are used. Kurta et al 1989 estimate is 13% lower than the prediction using Thomas (1975) allometric equation. Estimates using the classical mechanical flight models are much lower (De la Cueva Salcedo, Fenton et al. 1995). The calculated energy requirement for flight presented here is approximately one third of the estimate using the Thomas (1975) equation. This low energy requirement for flight contributes the most to lower estimates of DEB when compared to previous estimates. Both the allometric models and biomechanical models' estimates should be interpreted with care. Several of the parameters used in these models come from bird literature and have not been validated for bats (e.g. flight efficiency). Moreover most of them come from experiments in wind tunnels that differ considerably from conditions of flight in the field. One parameter that is particularly important because it has a big effect on model estimates and has not been independently estimated for bats is flight efficiency. This parameter was set at 15% efficiency in this model, however Speakman and Thomas (2003) suggests that small bats fly with efficiencies of only 4%, while larger bats fly at efficiencies of about 20-25%. By setting the flight efficiency to 4%, and assuming a 8.34g bat, Thomas' (1975) formulation gives a power estimate of 1.33 W; Speakman and Thomas' (2003) estimate would be 1.24 W, and the formula used in the model here produces estimates between 1.15 to 2.48 W for speeds between 3 to 5 m s^{-1}. It is obvious that the efficiency parameters play an important role in determining the energy allocated for flight. Currently, Jonathan Reichard, a graduate student at Boston University, is measuring radiative and convective heat fluxes from Brazilian free-tailed bats, *Tadarida brasiliensis*, in flight (personal communication). His work could provide a more realistic estimate of flight efficiency in the near future.

The DEB estimates corresponding to hibernation are consistent with the previous estimates. In Figure 13 the peaks during hibernation correspond to days with an arousal and the estimated energy demand is 0.714kJ $g^{-1}d^{-1}$. For days without an arousal the energy requirement is 0.014kJ $g^{-1}d^{-1}$. The cave temperature assumed in the calculation is 2^{o}C, which gives the minimum

estimated energy demand under the formulated model. Hence, these are minimum values. Even though the cost estimated in Thomas et al 1990 assumes a temperature of 5^{o}C, both results are close.

Figure 14 shows the curve for DEB per bat in kJ d^{-1} and the energy assimilated from the ingested insects. It is important to remember that the model assumes a modal distribution of insects and type 2 functional response feeding rate. When the energy assimilated curve is above the DEB the individual gains mass (e.g. pre-hibernation) except during lactation because the cost of lactation is not included in the DEB estimate. When the energy assimilated curve is below the DEB the individual uses its reserves to meet the demand, as occurs at the end of post lactation when insects start to decrease and during migration.

4.3 Model Results and Applications

4.3.1 Reproduction

As mentioned in Section 2.4.5 an adult female reproduces only if her lipid content at the end of hibernation is above a certain threshold given by the parameter $m_{L\min}$ (Table 7). This idea comes from a number of studies initially published by Rose Frisch in 1974 that suggested that fat is the primary factor that contributes to reproductive success of females (Frisch 2002). In 1994 the hormone leptin was identified. This hormone is secreted by fat cells and informs the brain how much fat the body has in storage and thus regulates appetite (Frisch 2002). Evidence has been found that the hormone leptin acts as a biochemical trigger for the Frisch hypothesis. Studies have been performed recently on leptin levels on bats during pregnancy, lactation and pre-hibernation (Kronfeld-Schor, Richardson et al. 2000; Kronfeld-Schor, Zhao et al. 2001). However there is no data available to estimate the threshold level of lipid/leptin at the end of hibernation to ensure successful ovulation and reproduction. This is a study that Dr. Kunz at Boston University expects to conduct in the future (personal communication).

Maternity colonies, the subjects of most field studies, are almost exclusively limited to reproductive females. Adult males and non-reproductive females spend the active season in smaller ‘shelters’ (Fenton 1970). Hence, it is difficult to study non- reproductive females and very little is known about the generalities and roosting behavior of non-reproductive females during the summer time. To my knowledge there is no specific information on energetic requirements, their behavior, their mass, and body composition. Non-reproductive females do not have the burden of pregnancy and lactation. As has been suggested for adult males (Keen and Hitchcock

1980), one could expect that these females are free to become torpid on a daily basis to minimize daily energy expenditures. In the case of males, Kurta and Kunz (1988) present data that indicate that male *M. lucifugus* do not use torpor during the day-roosting period under average environmental conditions and that day-roosting maintenance costs for males are actually greater than lactating females. The authors suggest that males apparently maintain higher body temperature and spend considerable more energy in day roosts than what was previously assumed. They hypothesize that this strategy may be related to spermatogenesis and testicular development.

In the individual model presented here females that fail the rule to ovulate enter post-lactating status and, as a consequence of this status, the parameter indicating the proportion of the day and night regulating body temperature is set to be close to 1. However, it was necessary to assume a gradual increase in the proportion of day spent regulating temperature at the beginning of the season when insect resources are low to allow survival of the non-reproductive female. Under these assumptions the mass of a female that did not ovulate increases and decreases following insect availability (

Figure 9). Because the total mass predicted by the model is above expected from literature reports (males in Kurta and Kunz 1988 males averaged 7.67g), it is possible that the model is underestimating the energy costs of these females in different ways. If most of these females were roosting under solitary conditions the energy expenditure may be higher due to lower ambient temperature and the lack of a beneficial cluster effect in the maternity roost. The higher body condition maintained by these females during a summer when they do not reproduce translates into a better physiological condition at the beginning of hibernation and, consequently, increases their chances to reproduce the following season.

The literature indicates that most of the females reproduce in their first year at southern and mid-latitudes within their distribution and females at northern latitudes which results in a shorter growing season delay reproduction until their second year (Fenton 1970; Humphrey and Cope 1977; Schowalter, Gunson et al. 1979). However, because most non-reproductive females do not roost in the maternity colonies, it is very difficult to quantify the actual number of reproductive females in a population and the reproductive history of an individual if it is not recaptured in a field study. Through the individual model we learn the reproductive events in the life history of a female bat can differ depending on individual characteristics and environmental conditions. Through the simulations performed for the sensitivity analysis that cover 3 reproductive periods, I observed several distinct patterns of reproduction. As presented in Section

3.1.2, the proportions of females that ovulate in the 3 consecutive years from these simulations are 54%, 75%, and 83% after their first, second, and third hibernation respectively. These proportions support the fact that many females do not reproduce in their first summer and indicates that it may take a female two no-reproductive years to start reproducing every year. More interesting to me was the observation that any combination of occurrence of ovulation can occur, i.e. a female can have enough lipid in the first year and not the following years, or not enough lipid in the first 2 years and be able to reproduce in the third, etc. Even though the environmental conditions remain the same over the years and no density dependence factors apply at this level of the model, once a female starts to reproduce it will not necessary continue to do so every year. I performed simulations including more than 3 reproductive seasons to explore the reproductive patterns in the long term. Sets of parameters that yield a female that reproduces every year after its second hibernation (Figure 10), a female that reproduces every other (Figure 11), and a female that never reproduces (Figure 12) were identified. In general, most of the females that survive reproduce every year after variations in the patterns in the initial years. This shows that under favorable constant environmental conditions and no density dependence effects, less fit individuals can survive. But under a changing environment and/ or density dependence pressure these individuals will die off within the population. The proportions indicated above cannot be interpreted as the reproductive rate at a population level. The population reproductive rate, proportion of females in the population reproducing each year, will be analyzed using the population model developed here in Section 5.2.

Life history theory predicts that in species such as bats, in which adult survival is higher than that of juveniles, foregoing reproduction when conditions are unfavorable maximizes fitness. Thus if a female is in poor body condition, the optimal strategy is to allocate resources to self-maintenance rather than reproduction. Females should enhance their own chance of survival and future reproduction rather than investing in young that have a relatively low chance of surviving to reproduce (Barclay, Ulmer et al. 2004). The model provides a good tool to test this hypothesis. By lowering the threshold parameter that triggers ovulation/reproduction it is possible to force a female to reproduce under poor body condition and to observe the fate of this female and its young. Even though I consider and present these results as a part of the individual model, the simulations were performed under the population model (see Chapter 5), assuming one initial female, which allows me to follow the fate of pups. If simulations were performed under just the individual model framework I would only know if the female reproduces and/or survives but I could not assess pup/juvenile survivorship. I started with a simulation under conditions in which

the female does not reproduce because her lipid content at the end of hibernation was not above the ovulation threshold $m_{L\min}$ (Figure 15). Then I decreased $m_{L\min}$ sufficiently to force the female to ovulate/reproduce with very low lipid content. The female in the latter case dies at the beginning of pregnancy only if the difference in the cost associated to the pregnant female and the non-reproductive (Figure 16) at the initial stage of pregnancy when food resources are still low is sufficiently large. Females might face higher energy demands during pregnancy because of the thermoregulatory strategy chosen or an increased migration distance to the appropriate maternity roost. Because the beginning of pregnancy coincides with an individual ending hibernation with low lipid reserves and non-abundant resources, even slight changes in energy demand can have an impact in survivorship. In the case of this model if the minimum proportion of the day or night that the female spends regulating its body temperature when pregnant is higher than when non-pregnant (post-lactating) it is advantageous not to reproduce under low body condition. Entering pregnant status with a very low lipid level would cause death of the female at an initial stage of pregnancy. A female with low reserves at the end of hibernation might ovulate but might need to use torpor as an energy saving strategy. Torpor is known to prolong gestation in female vespertilionids (Racy 1982). A late parturition might lead to a juvenile that enters hibernation without sufficient lipid reserves and does not survive. However, the model developed here does not represent a variable gestation length related to time spent in torpor nor to other variables. I was not able to generate a scenario in which negative consequences (e.g. death of mother during late pregnancy or lactation, death of pup/juvenile during lactation or following hibernation) of reproducing under very poor body condition appear in a later stage in the life of the mother or the offspring. To explore if density dependence has any effect on the dynamic I repeated the simulations changing the values for the parameters $m_{L\min}$, and $P_{regD\min}$ (pregnant) but assuming a high number of individuals in the initial population (1 ecotype, 1 cohort) that diminish the resources available per bat (as describe in Section 5.1.3) during the entire active season. Under these circumstances and a ovulation threshold of $m_{L\min} = 0.25g$ of lipid a female that started hibernation with low lipid reserves does not ovulate at the end of winter but it is able to produce a viable offspring that survives its first hibernation in the following year but the offspring will not ovulate (Figure 17). When $m_{L\min}$ is reduced to 0.05 g the female ovulates at the end of hibernation but her female offspring dies at the end of winter ovulation because of the low parameter value set for $m_{L\min}$. Consequently even a slightly higher energy cost of pregnancy

and limited resources due to density of bats kills the offspring who has less lipid reserves than her mother (Figure 18).

4.3.2 Thermoregulatory Strategies

It has been suggested that the principal mechanism for energy conservation during lactation in bats appears to be torpor (Wilde, Knight et al. 1999). For small bats, reserves of maternal fat are insufficient to cover milk production. However, because of its presumed non-specificity, torpor may result in the interruption of milk synthesis and secretion (Wilde, Knight et al. 1999). A study conducted on *Pipistrelluus pipistrellus* bat mammary tissue suggests that periods of torpor are likely to produce pronounced diurnal variation in the rate of milk secretion (Wilde, Knight et al. 1999). Variation in milk synthesis during the day has been observed in other small mammals related to scheduled feeding (Carrick and Kuhn 1978; Wilde, Knight et al. 1999). The authors conclude that lactation in the pipistrelle bat depends on the temporal relationship between suckling, foraging, and torpor. Henry et al. (Henry, Thomas et al. 2002) argue that the majority of nursing is likely to occur during the night, forcing females to reconcile nursing and foraging. Considering these indications, the model assumes a strategy in which the female enters torpor more often during the day to save energy and chooses to regulate during the night to enhance milk production at the same time that feeding and nursing occur. Assuming all parameters set at the values specified in Table 1 to Table 9 and changing P_{regD} (lactating) the effects of this strategy can be explored. It is important to note that the increase in torpor only translates to an energy saving and not to a reduction in milk synthesis. The model formulation prioritizes the basic energetic needs of the female and what is left is used for milk (see Section 2.4.6). Thus, if the energy demand of the mother increases over a certain threshold level her milk production decreases affecting the pup and the lactating juvenile intake. If P_{regD} (lactating) is set to 0.5 (the bat spends 50% of the day regulating temperature) the offspring's body composition increases to values close to data available (Table 34). When the proportion of the day that the lactating female regulates body temperature increases the offspring's lipid and structure content remain significantly lower than those suggested by the data (Figure 19). However the offspring does not die, as one might expect. It requires changes in other parameters to increase energy demand of the pup/juvenile to cause its death under the assumptions of the model. This indicates that several factors combine to contribute to pup/juvenile survivorship and it is possible that the model parameters need additional tuning and/or the model is somehow misrepresenting some

processes. However, the effect of the use of torpor as an energy saving strategy to produce milk in sufficient quantity to support appropriate development of offspring is clear and significant from the model simulations. Moreover the savings by using day torpor are sufficient to eliminate the need of going into torpor during the night when higher levels of milk synthesis and nursing would occur.

During the fall, temperate zone bats must deposit fat to cover their energetic needs during the hibernation period. Fat reserves are built throughout the pre-hibernation period that takes place from late August to mid October. During this period increased food intake, reduced energy expenditure, and lipogenic factors may combine to assure adequate fat deposition in hibernator species. But, for the case of temperate bats, by this time of the year insect density has already declined from its peak in mid summer, and consequently food intake is reduced. Hence it has been hypothesized that behavioral changes that reduce significantly the energy demand can account for the mass increase despite the reduced energy intake (Krzanowski 1961). Several studies support this hypothesis, in particular (Speakman and Rowland 1999) shows that: brown long-eared bats (*Plecotus auritus*) in the pre-hibernal period preferred colder temperatures to roost, (about 10^{o}C), they enter torpor for up to 14 hours at a time, and the extent of the saving was sufficient to positively affect their mass balance. Simulations with the individual model show that under the assumed decreasing insect density at the end of the active season, bats are forced to save energy by gradually spending more time conforming to ambient temperature until hibernation starts. But this strategy by itself may not be enough to account for the observed levels of fat stores observed in the field or levels sufficient to survive winter and reproduce. This indicates that fat deposition during pre-hibernation is not simply the result of decreased metabolic rate or gradual increase in torpor, but rather represents a programmed change in the preferred level of WAT (white adipose tissue) lipid reserves as indicated by (Dark 2005). A neural mechanism appears to control or regulate the deposition and mobilization of lipid stores around a preferred level (Mauer, Harris et al. 2001). In the model presented here there are only two parameters that can represent the changes resulting for such mechanisms. These parameters are the lipid and structure mobilization rates M_L and M_S. During the initial phase of the model development these parameters were assumed to take the same values at all points of the life history, but later it was indispensable to set them to different values at different stages such as post-lactation, pre-hibernation, and hibernation (Table 1) in order to generate the observed lipid dynamic of bats. But the values of these parameters were set at the different stages without any filed/laboratory data indication because I was not able to find studies providing such information.

Nevertheless, the model allows exploring the implications of changing the fuels of metabolism during different periods by changing the rates at which lipid and structure are mobilized. I assumed that changes in these rates result from mechanisms regulating lipid reserve levels. Most probably changes in these rates occur gradually and not in discrete switches as the model describes. However this was the simplest approximation for a mechanism that is not fully understood nor explicitly modeled under this representation. Simulations were performed to test the hypothesis that changes in mobilization rates of lipid and structure components are required for the individual to reach adequate lipid reserves. I started by assuming that the mobilization rates do not change from post-lactation to hibernation, and then I started to decrease the lipid mobilization at pre-hibernation. Results are presented in Table 41. For the particular set of parameters chosen, by decreasing the lipid mobilization rate to almost zero, lipid content at the beginning of hibernation increases to approximately 13%. Moreover, the female survives winter and does not reproduce the following summer in the first case and survives and reproduces in the second case. The lipid mobilization rate cannot be set below a certain threshold because the individual would die immediately after migration when energetic savings through torpor are still not important and lipid mobilization is needed to meet the daily energy demand. By increasing the mobilization rate of structure at the same time the resulting lipid reserves increase even further.

I was not able to find in the literature data or values to directly estimate the mobilization rates either for bats or for other small mammals. Data on respiratory quotient could be related to these rates. The respiratory quotient (RQ), the ratio of the volume of carbon dioxide produced to the volume consumed, indicates which substrate is being used for energy production; and an RQ of 1 suggests carbohydrates as the source of energy, whereas an RQ of 0.7 suggests lipids. Values in between 0.7 and 1 can reflect either use of protein or mixed fuel use (Kleiber 1975). Realization of other laboratory experiments that could provide information on the rates at which energy reserves are used would give useful insight into the mechanisms regulating lipid levels and metabolic strategies.

As the model assumes food resources decrease gradually at the end of the season and bats need to enter torpor more frequently to save energy and deposit fat, a similar scenario is assumed to occur at the beginning of the active season/pregnancy. Food resources increase gradually when bats end hibernation and are insufficient to support the daily requirements of a completely homothermous bat. However, because torpor is known to prolong gestation in female vespertilionids (Racy 1982), the model assumes that by the end of gestation the female bat

regulates its body temperature most of the day. The length of gestation and proportion of day regulating temperature are not related in the model so it is not possible to test hypotheses regarding the thermoregulatory strategies during pregnancy.

Studies on different bat species roosting in natural roosts will help determine if there are general patterns in the thermoregulatory strategies.

4.3.3 Young Training Period

As described in Section 2.3, the individual model contains a "training period" for the young bats. It is assumed that at peak lactation juveniles (not weaned) start incorporating insects in their diet as they learn to fly, and their echolocation and foraging abilities develop. At the same time milk intake starts to decrease until complete weaning occurs about a week later. Three parameters in the model describe the training process; the length of the training period, T [d], the initial percentage of adult maximum feeding rate, φ, and the initial percentage of total adult's flight time, ψ. Under this formulation, by the end of the training period the juveniles forage like adults. In a more descriptive way, this kind of gradual development is supported for several studies (Buchler 1980; Hamilton and Barclay 1998; French and Whitaker 2002). The mass dynamics resulting with the given parameter values shows a decrease in mass after peak lactation. Mass reaches a minimum at weaning and then starts to increase until migration (Figure 7). Even though this decrease in mass is not observed in the data presented here (Figure 5) it is not an unexpected dynamic. Juvenile flying animals, including bats, often cease increasing, or even decrease in body mass after the onset of flight (Hamilton and Barclay 1998). The decrease in mass after peak lactation can be more or less abrupt depending on the parameters values. However mass increase can result if the training period is very short and/or the initial percentage of adult maximum feeding rate is close to one. Results from selected simulations are given in Table 42 and Figure 20. The simulations show that long T values combined with low φ values cause the death of the juvenile due to food shortage at the end of lactation. This result is obtained even under a scenario of high insect availability because φ sets a maximum for amount of insects ingested independent of the insect density. Thus, juvenile bats that learn too "slowly" and start with a very inefficient foraging ability compared to adults die independently of availability of food supply. If T is long and φ is high enough the bat can also die but at the end of hibernation instead at the end of lactation. This happens because the cost of being heavier (maintenance and flight) does not allow the juvenile bat build up sufficient lipid reserves to survive the entire hibernation period.

Even though it is unrealistic to think that there is no learning process or it takes only a day or two for the bat to be foraging as an adult, the model allows exploring the consequences of this scenario. The juveniles that learn too "fast" get big and fat quickly which translates into higher maintenance and flight costs that they may not able to afford when food supply starts to decrease. In these cases lipid reserves before hibernation are insufficient to support them throughout the winter. If resources were equally available through the year with no need for hibernation these bats would survive and their mass would stay at the leveling off levels.

The idea of the cost of being "too big" as a trade off for survival first appeared in this work in the sensitivity analysis where bats with bigger limits for structural mass were less likely to survive. Simulations 14 to 16 in Table 42 show how for bigger bats the range of values for T at which the bat survives narrows. The work by Hamilton and Barclay (1998) test the hypotheses that low body mass of juveniles may be a result of stress associated with the initiation of flight, or may be an adaptation to reduce flight cost. Under their study conditions the authors found support for the latter. The results of their study suggest that juvenile bats maintain a low body mass even under conditions that permit adults to accumulate greater fat deposits. Juveniles do not forage earlier or for longer periods to compensate for poor foraging ability and increased energy expenditures resulting from the onset of flight. The bats in their study did not show a decrease in mass at the onset of flight or weaning, however they did not do sequential captures of the same bats. The results from the individual model simulations presented here add a possible mechanism to explain decrease of mass or lower mass of juveniles when compared to adults. The limiting mechanism to mass accumulation in juveniles may result from the characteristics of the foraging learning process despite the food availability. I argue that not only does the fact that flight costs increase as mass increases play an important role in the energy budget, maintenance costs are also considerable. Juvenile bats may need to maintain high metabolic rate to enhance growth. If quantitative data were collected on the characteristics of the onset of flight and foraging it would be possible to provide support for this mechanism.

4.4.4 Diet Composition during Lactation

Lactation is the major component of early care and the most costly part of female reproduction in mammalian species. It has also been shown that offspring survival and growth are correlated with milk quality, the rate of milk transfer, and length of lactation period (Altmann, Altmann et al. 1978; Oftedal 1984; Loudon 1985).

The model allows studying the extent and circumstances under which the female is able keep an adequate milk supply for her young. Based on actual field data on milk composition and some information on milk volume a “required” amount of lipid, protein, and carbohydrates is estimated. Then based on the availability of lipid and structural components in the individual, the actual “supplied” amount is calculated over time. In optimal conditions this “supplied” amount equals the “required”, but it is possible that at some point during the lactation period the female is not able to produce nor to supply the desired or required amount. Because milk production has second priority after maintenance and flight costs (see Section 2.4.6), an increase in these costs can cause a deficit on the milk supplied with respect to the required amount. Also reduced food intake and/or energetically low quality food (e.g. low lipid content) can contribute to inadequate milk quality and production. It has been shown that females increase food ingestion during lactation (Anthony and Kunz 1977) and the possibility exists for selective feeding on more profitable insects (Anthony and Kunz 1977; Kurta, Bell et al. 1989; Kurta and Whitaker 1998) during this time. Because of the speculations on diet during lactation, I decided to explore the effects of food ingestion and diet composition on milk production by using the model.

Assuming the parameter values indicated in Table 1 to Table 9, Figure 21 shows daily estimated “required milk lipid” and “required milk protein and carbohydrates” in solid lines, and “supplied milk lipid” and “supplied milk protein and carbohydrates” in dotted lines. If dotted lines are not visible the corresponding supplied amount overlaps with the required amount, as is the case for protein and carbohydrate component during the entire period and for lipid at the beginning and at the end of the period. Dietary lipid, protein and carbohydrate assimilated are shown in the same figure. Under the assumptions of the model and defined parameter values a deficit in milk lipid content is observed around peak lactation (supplied lipid is below required lipid). Also for about 50% of the period the dietary lipid assimilated is below the required milk lipid. This indicates the need for synthesis of lipid from protein, which is an inefficient process when compared to using dietary lipids. It is important to note that at this time the individual is feeding at its maximum feeding rate because of the resource distribution function assumed. Thus increasing food availability would not ameliorate the lipid deficit in milk. Any change increasing daily energetic demands would accentuate the observed low lipid supplied. However a slight increase in diet lipid content, which would represent a switch in diet composition during lactation, can result in adequate milk lipid supply. Results in Figure 21 assumed a diet of 4.6% fat and 20% protein and carbohydrates. Figures Figure 22 and Figure 23 show the results assuming a diet composition of 6% fat and 19% protein and carbohydrates and 7% fat and 18% protein and

carbohydrates respectively. If the fat diet content is 7% or higher not only can the bat produce milk with the desired amount of lipid but also the need of lipid synthesis for milk lipid is eliminated, which translates into a more efficient use of the energy sources.

The increase in diet fat content may need to be higher than the one presented in these particular cases depending on the daily energetic demands of the individual and the quantity of food ingested. Because an ingestion rate of 7 g per day as is assumed for these simulations is a value that is most probably at the top of the range of what is possible for little brown bats to eat, the 6% fat content in the diet can be considered a minimum threshold to be able to produce the high fat milk required. As the ingestion rate decreases the fat content of the diet should increase during lactation to ensure appropriate quality milk production. Given the flexible thermoregulatory abilities of temperate bats, also an increase in energy savings could compensate for low intake and/or low fat content of the resource. Two studies that have been already briefly described in Section 4.2.2 provide an example of how estimates for ingestion and energy budgets can be affected by different assumptions on energy density of the resources. (Anthony and Kunz 1977) measured food consumption for pregnant (2.5g/night) and lactating females (3.7g/night), assumed and energy equivalent of stomach content of 8.7 kJ/g wet weight and estimated a daily energy budget of 32.19 kJ/day for lactating females. (Kurta, Bell et al. 1989) estimated daily energy budget of lactating females using DWL method plus energy exported as milk from milk composition. They estimated a demand of 41.3 kJ/d. They assumed an insect diet of 4.6% of fat, 17.8% protein, and 2.2% carbohydrates (approximately 6.4 kJ/g wet weight) and estimated a feeding rate of 6.7 g of insects per day.

The study by Anthony and Kunz (1977) is interesting because it provides support to more selective feeding during lactation, which coincides with the period of higher insect abundance. However small sample sizes to perform appropriate statistical comparisons do not allow for strong conclusions. The switch in diet they observed shows an increase in Coleoptera (23.6 kJ/g), Hephemeroptera (22.7 kJ/g), Hymenoptera (19.37 kJ/g), and Neuroptera; along with decrease in Culicidae (21.83 kJ/g) and Lepidoptera (21.25 kJ/g). I was not able to find fat content at family level for these families of insects that would allow me to provide support for a switch for a higher fat content diet. The energetic values between parentheses are from a recompilation in (Kunz 1988). From these energetic equivalents, which do not present huge differences, I consider it is not possible to conclude a switch to a higher energy content diet either from the data in (Anthony and Kunz 1977). Results from two studies in Indiana bat *Myotis sodalis* also present somewhat conflicting results. (Belwood 1979) reported a significant increase (from 31% to 70%) in moth

(Lepidoptera) consumption and a significant decrease (from 41% to 16%) in fly (Diptera) consumption during lactation compared to pregnancy. The author hypothesized that the shift to moths during lactation was an effort by females to obtain energetically more rewarding prey. A report on energetic content of invertebrates by (Robel, Press et al. 1995) indicates a fat content of 11.4% for Diptera and 17.7% for Lepidoptera. Moreover, calcium, which has been suggested to be a limiting factor during lactation (Barclay 1994), is reported to be higher in Lepidoptera (2560 ppm) than in Diptera (1292 ppm) (Robel, Press et al. 1995). A study done by (Kurta and Whitaker 1998) on the same species found the opposite pattern, significant increase in fly consumption with a decrease in moth consumption during lactation in Michigan. The authors suggest that the differences might arise from different availability of insects at different locations instead of from a selective switch towards more profitable insects.

An ideal study to strongly support the idea of a diet switch toward more energetically rewarding diet with higher fat content and selective feeding in lactating insectivorous bats should include measuring factors such as food consumption, diet composition in terms of insects and energetic content, insect availability, individual energetic demands, and milk composition.

4.4.5 Winter Survival

As it was described in Section 2.4.2, the winter energetics module is based on Humphries et al (2002) so the character of the results produced are similar. However it is important to note that in the representation used in this work, the mass of the individual changes dynamically with time as the individual depletes its reserves. This decrease in mass causes a decrease in thermoregulation costs. During deep torpor the decrease is almost insignificant; however, during arousals the difference becomes more important. For example, an arousal at the beginning of the hibernation at 2^{o}C for an individual with 2.49 g of lipid reserves and 1.83 g of structure costs 6.46 kJ, while the cost for the same bat at the end would be 4.6 kJ (assuming 193 days hibernation and 12 arousals, parameter values as in Table 1 to Table 9). These differences in costs may became important and allow an individual to survive under a wider range of temperatures or lower lipid reserves that those predicted by Humphries et al 2002. Another difference is that the representation presented here allows for mobilization of structural component to meet the energetic requirements as has been indicated in laboratory studies (Dodgen and Blood 1956). For the parameter values assumed, lipid would account for 94% of total winter budget and protein and carbohydrates for approximately 6%.

Lipid reserves are not only important in assuring survival but also reproduction in the following summer. Given an amount of lipid reserve and structure at the beginning of the hibernation the model can estimate minimum and maximum temperatures that allow survival and reproduction for that specific body composition and individual parameters. From the temperature ranges, predictions about geographic distributions of hibernating locations can be made as done in Humprhies et al (2002). Figure 24 shows such temperature ranges from the model predictions. The northern range is more restricted than the southern limit. Doubling lipid reserves only allows survival up to approximately 1.2 ^{o}C less than the optimal 2 ^{o}C. Even though deep torpor cost increases as temperature increases above 2 ^{o}C, the cost of periodic arousal decreases significantly. Thus slight increases in lipid reserves allow survival under increasing maximum temperatures, indicating more flexibility of the species at the southern range or dealing with higher temperatures. The upper temperatures could be even higher if we assume that would be correlated with locations of shorter winters. In the simulations performed to generate Figure 24 the length of the winter was assumed to be constant, 193 days, with a total of 12 arousals, one occurring every 16 days. The same kind of graph is presented in (Humphries, Thomas et al. 2002) and (Humphries, Speakman et al. 2006) just for survival conditions based on the model developed by these authors. Direct comparison of numeric values between this graph and the one presented here is not possible because of the mentioned differences among models. However the model presented here allows for a wider range of temperatures that yield survival. The minimum lipid reserve to survive at 2 ^{o}C is 1.52 g in this model compared to 1.2 g in (Humphries, Speakman et al. 2006). Moreover, in the model presented here the minimum lipid reserves that lead to survival and the minimum lipid reserves that allow survival and reproduction are suitable for a range of cave temperatures and not just for a single optimal temperature value as in (Humphries, Speakman et al. 2006). These results suggest that the changes made in the model allow for increased thermal flexibility of the individual to cope with winter temperatures given certain initial lipid reserves.

It is reasonable to assume that bats experience a relatively constant temperature during hibernation because of thermal properties of the cave or bat movement inside the cave looking for optimal temperature. However, other bat species that hibernate in rock crevices, trees, or other structures might be exposed to more variable temperature profiles. Thus, given the possibility of simulating a dynamic temperature profile with minimum temperatures at mid winter I explored the effects on the lipid reserve and survival relationship depending on minimum temperature reached during the winter. A quadratic form, $T(t) = a\left(t - \frac{193}{2}\right)^2 + M$, whose minimum is reached

at the middle of the hibernation period described the temperature profile inside the cave. The difference between maximum and minimum temperature during the period is given by $a\left(\frac{193}{2}\right)^2$ and was supposed to be 4.5 ^{o}C (Karst 1997; Craig 2003); hence, the parameter a was set to 0.0005. The minimum temperature given by M was varied to find the minimum value that allowed survival given an initial lipid reserve. The minimum temperatures are also plotted in Figure 24. These temperatures are on average 1.2 ^{o}C degrees lower than the minimums found when constant cave temperature was assumed. Hence this experiment shows that up to some limit, days with warmer temperatures during the winter in which arousal costs decrease can compensate for colder days at mid-hibernation where low temperature increases both deep torpor and arousal costs. Thus under variable temperature conditions the minimum temperatures that bats can survive are lower if they are combined with warmer days, which gives more flexibility when determining the northern geographical range of the species. Moreover these results show the feasibility of hibernating in environments subject to fluctuating temperatures that are chosen by other temperate species. Even though the temperature range was assumed to be constant at a reported level for caves, simulations varying the range of temperatures were performed as well. By decreasing the parameter a, the minimum temperature to survive is increased (in Figure 24 the cyan line would move up towards the blue line). Increasing a sufficiently causes the death of the bat because of increased costs of deep torpor at the beginning and ending of the hibernation period due to the Q_{10} effect at temperatures higher than 2 ^{o}C.

The model presented here assumes a constant torpor bout length and, consequently, a constant number of periodic arousals given a constant hibernation length. Increasing the number of arousals by decreasing torpor bout length or increasing winter length leads to higher energetic demands. Consequently, more lipid reserves and/or hibernating temperatures close to optimal are needed for individuals to survive and reproduce. In Humphries et al. (2002) a function form is proposed for the length of the torpor bout depending on cave temperature. An optimal temperature is assumed to produce the longest deep torpor period and as temperature departs from this optimal the length of torpor bouts decreases. For any of these assumptions or formulations, more arousals lead to increased energy demand and consequently decrease survival and/or reproductive success. To give an idea of relative costs of torpor and arousals, the energetic cost of a day with an arousal at 2 ^{o}C is equivalent to approximately 53 days in deep torpor. It is clear that human disturbances that can cause extra arousals really put the individual at risk.

The results stated above agree with the conceptual and traditional idea that hibernators should benefit from minimizing winter energy requirements by maximizing torpor expression. However this idea might be too simplistic from the physiological viewpoint and the unclear triggers of periodic arousals. Another article by Humphries, Thomas et al. (2003) suggests an interesting optimality approach, by which trade-offs between the benefits of energy conservation and the physiological cost of metabolic depression can explain both why hibernators arouse periodically from torpor and why they should use energy available to minimize the depth and duration of their torpor bouts. The authors postulate the following hypothesis: "*…torpor expression by hibernating mammals reflects an optimization problem between costs and benefits of metabolic depression and that this trade-off is mediated by variation in energy available*." It would be interesting to view the timing of arousal as an optimization problem.

4.4 Summary of Results

4.4.1 Individual Dynamic

- The individual model captures the main patterns in the dynamic of lipid and structure components of the body as well as total mass. To be able to express the characteristic lipid cycle of a hibernator bat, the model had to include the process of synthesis of lipids from proteins and carbohydrates. This process was assumed to be negligible in previous related models for aquatic organisms.

4.4.2 Consistency with previous DEB estimates

- Even though methodologies differ, estimates for day and night roosting from previous studies (Burnett and August 1981; Kurta, Johnson et al. 1987) and the model presented here (see Figure 13) are consistent in that ranges obtained give a valid approximation to roosting expenditures. Day roosting expenditures from the literature range from 0.38 to 0.92 [$kJg^{-1}d^{-1}$] for pregnant and lactating females combined. The day roosting demand in the model varies daily with a minimum of 0.23[$kJg^{-1}d^{-1}$] and a maximum of 1.48 [$kJg^{-1}d^{-1}$]. Night roosting expenditures vary from 0.36 to 0.47[$kJg^{-1}d^{-1}$]. The model produces estimates that vary within 0.1 to 0.6 [$kJg^{-1}d^{-1}$]. The formulation of a thermoregulation function allows for testing of thermoregulation strategies that have been hypothesized.
- Estimates for energetic demand for flight vary significantly when different methodologies are used. Estimates using a classical allometric equation (Burnett and August 1981; Kurta,

Johnson et al. 1987) are approximately 3 times greater than the one predicted by the individual model using a biomechanical formulation.

- Flight efficiency is identified as a key parameter in determining flight energy demand because of its great effect on the flight cost estimate. This parameter has not been independently estimated for any species of bats. Videothermography could provide such estimates. It would be very valuable to have estimates of flight efficiency for species of different size and at different flight speeds.
- DEB estimates for hibernation from the individual model are consistent with a previous laboratory study (Thomas, Dorais et al. 1990).

4.4.3 Reproduction

- The model indicates that both pregnant and non-reproductive females need to use torpor at the beginning of the summer when insect availability is low to be able to meet their energetic demands.
- Without the discrete loss of mass due to parturition and the high cost of lactation, non-reproductive females gain more mass than expected; however, there is no data on solitary non-reproductive females to compare with. This suggests the model might be either underestimating their energy demand or overestimating the energy intake. These females might be subjected to lower temperatures than assumed in the model, which would increase thermoregulatory costs.
- In the model, non-reproductive females are likely to reproduce the following season because in general (depending on model parameters) they enter hibernation with sufficient reserves to survive the winter and to ovulate at the end of the period. This result agrees with the observation that in northern latitudes young females delay reproduction until their second year.
- Distinct patterns of sequences of reproductive and non-reproductive summers may occur for a single individual depending on its characteristics and environmental conditions (expressed as model parameters).
- For certain parameter values, the model simulations corroborate the hypothesis that postulates that species such as bats in which adult survival is higher than that of juveniles should forego reproduction when conditions are unfavorable to maximize fitness. A female that reproduces with a very low level of lipid dies at the beginning of pregnancy if energy demand during pregnancy is higher than the energy requirement of a non-pregnant individual. Under the same situation a female that does not ovulate would survive and would be likely to

successfully reproduce in the following year. When density dependence pressure is added, it is possible to have a female that when she reproduces under low lipid level produces an offspring that is not able to survive through the end of hibernation.

4.4.4 Thermoregulatory Strategies

- Model simulations support the concept that the use of torpor by lactating females is an energy saving strategy to afford good milk production and appropriate offspring development. Furthermore, the savings of using day torpor are sufficient to eliminate the need of going into torpor during the night when higher levels of milk synthesis and nursing would occur.
- Simulations with the individual model show that under the assumed decreasing insect density at the end of the active season, bats are forced to save energy by gradually spending more time conforming to ambient temperature until hibernation starts. However, the model also indicates that this strategy by itself may not be enough to account for the observed levels of fat stores obtained from field data (Kunz, Wrazen et al. 1998) or fat levels that would ensure successful hibernation (Humphries, Thomas et al. 2002).
- Changes in the mobilization rates of lipid and structure components during pre-hibernation offer might offer an additional mechanism to assure sufficient deposition of lipids to survive the winter and reproduce.

4.4.5 Young Training Period

- Juvenile bats that learn too “slowly” and start at a very inefficient foraging ability compared to adults die independently of availability of food supply.
- Juveniles that learn too “fast” and get big and fat quickly have higher maintenance and flight costs that they may not able to afford when food supply starts to decrease. This situation can cause the death of the juvenile at the end of hibernation.
- The limiting mechanism to mass accumulation in juveniles may result from the characteristics of the foraging learning process despite the food availability.

4.4.6 Diet Composition during Lactation

- Model simulations show a deficit in milk lipid content around peak lactation (supplied lipid is below required lipid). Simulations also show that for about 50% of the period the dietary lipid assimilated is below the required milk lipid. This indicates the need for synthesis of lipid from protein, which is an inefficient process when compared to using dietary lipids.
- A slight increase in diet lipid content, which would represent a switch in diet composition during lactation, can result in an adequate milk lipid supply.

- For the model parameters, a fat diet content of 7% or higher not only produces milk with the desired amount of lipid but also eliminates the need of lipid synthesis for milk lipid. This translates into a more efficient use of the energy sources.
- In order to test the hypothesis of a diet switch toward a more energetically rewarding diet with higher fat content and selective feeding in lactating insectivorous bats, more field experiments are needed. These should measure factors such as food consumption, diet composition in terms of insects and energetic content, insect availability, individual energetic demands, and milk composition.

4.4.7 Winter Survival

- Increasing lipid reserves allows winter survival hibernation at an increased range of temperatures around 2^{o}C (optimal hibernating temperature). However temperatures above 2^{o}C do not increase the hibernation cost as much as temperatures below 2^{o}C. Slight increases in lipid reserves allow survival under increasing maximum temperatures, indicating more flexibility of the species at the southern range or dealing with higher temperatures.
- Under variable temperature conditions, bats can survive days with temperatures lower that the predicted minimum for constant temperature if they are combined with warmer days. This gives more flexibility when determining the northern geographical range of the species based on minimum temperatures. Moreover, these results show the feasibility of hibernating in environments subject to fluctuating temperatures that are chosen by other temperate species of bats.

CHAPTER V
POPULATION MODEL DYNAMICS

Population dynamics is the study of how population numbers (and structure) change in time and space and the biological and environmental mechanisms that underline those changes. Population dynamics have been at the forefront of population ecology since the origins of the discipline and it has traditionally been the dominant branch of mathematical ecology. Mathematical models have been used and proven to be a powerful tool to understanding population dynamics.

Individuals are distinct units of a population and are the basis of population variation. Demographic processes of birth, growth, and death occur at the individual level, since these processes are functions of the individual characteristics. Thus, characteristics of the individuals ultimately determine the structure and, subsequently the dynamics, of the population. Having these considerations in mind, it seems natural to follow a reductionist approach to understanding population dynamics. Under this kind of approach the mechanistic basis for population ecology should be provided by the properties of entities one hierarchical level lower then populations, i.e., the individuals (Metz and Diekmann 1986). Foundations for individually based population models can be found in the reviews of Metz and Diekmann (1986), Huston, DeAngelis et al. (1988), DeAngelis and Rose (1992), and Kooijman (2000).

Recently, Bolnick, Svanback et al. (2003) emphasized the importance of individual specialization which reflects a diverse array of physiological, behavioral, and ecological mechanisms that can generate intra-population variation. Individual specialization has important ecological, evolutionary, and conservation implications. They remark about the need to develop models of population dynamics that incorporate individual variation and use the behavior of individuals to build descriptions of population dynamics.

Individual based population models are useful tools when physiological processes occurring at individual level are important in order to describe population dynamics. In population ecology, population survival can depend on reproductive success, which many times is governed by lipid physiology. The lipid component of an individual is also important in ecotoxicology applications, because it determines the susceptibility of the organism to hydrophobic chemicals (Hallam, Lassiter et al. 1990). Andrewartha and Birch (1954; 1984) stressed the need to understand the physiological ecology, particularly the energetics, of a species in order to assess the importance of abiotic factors such as climate or the environment in limiting distribution.

For example, there is a large collection of experimental evidence that indicates that the growth and development of individual *daphnids* have considerable influence on the dynamics of the population (McCauley and Murdoch 1987) and several physiologically structured population models have been used for this species (Hallam, Lassiter et al. 1990; Roos, McCauley et al. 1997). Structured populations models that take into account detailed mechanistic description of physiological processes have been developed mostly for aquatic organisms including fish (Krohn 2001), algae (Siopsis 2003), and daphnia (Hallam, Lassiter et al. 1990; Roos, McCauley et al. 1997).

5.1 Population Model Description

The energetic based individual model described and analyzed in previous chapters forms the core of the individual-based or structured population model described in this section. The population model tracks cohorts of individuals of the different ecotypes as they live, reproduce, and die. A main goal when developing the rules of the population model was to generate the population dynamics based on the individuals and not to introduce parameters at the population level such as population reproduction rate or population mortality rate. To my knowledge no population model has been developed and published to study bat population dynamics or fitted to population field data.

The code for the individual model solves numerically the system of equations for a single individual or a group (cohort) of identical individuals over a given period of time or until the individual dies or the cohort has zero individuals. The individual model code is structured in 3 nested loops, an outer loop that iterates time, inside a loop that goes over all ecotypes, and an inner loop that iterates over the cohorts within each ecotype. Given the appropriate initial conditions and parameter values the code simulates the dynamics of all individuals in the population. Three extra rules are added to fully represent the population model. These rules are related to the creation and management of new cohorts described below, age dependent mortality, and density dependence. The first two rules occur at the level of the inner loop (iteration over cohorts). After the “ecotypes’ loop” is completed for each time step, the total population size is calculated and the density factor is estimated (see description below). In the next time step the feeding rate of all ecotypes and cohorts is affected by this density factor.

5.1.1 Reproduction and new cohorts

All individuals in an ecotype have the same characteristics (see the definition in Section 5.1.4) as defined by individual parameters values. However, the individuals of the same ecotype

may have different ages and/or body composition. Within an ecotype, individuals are placed in cohorts. Cohorts are groups of individuals of the same age and theoretically are exactly the same body composition (lipid, structure, and water). But following cohorts under this definition for individuals that can live up to 15 years would lead to an enormous number of cohorts as reproduction takes place. Following the increasing number of cohorts would computationally be very costly and might turn to be eventually unmanageable. Several cohorts of the same age might have similar but distinct body composition and consequently would have to be treated separately. Hence, to control the number of cohorts, only 3 cohorts are created at each reproductive event every year for a given ecotype. Newborn pups from the existing cohorts are distributed among the 3 new cohorts in the same ecotype based on their lipid content at birth. Because equal sex ratio is assumed and the model is only for female bats, each reproducing adult cohort contributes with half its density to the corresponding new cohort. Then the body composition of the new cohort is initialized as a function of mother composition following the rules for pup body composition established in the individual model (see Section 2.4.5). During lactation period a tag is kept to indicate mother-daughter related cohorts in order to assess the processes affecting both cohorts. Also during lactation, each mother-cohort keeps the assigned number of its daughter cohort and each daughter-cohort keeps the assigned number of mother cohorts that contributed to it. Lactation and mortality processes use these relationships among cohorts. The milk intake of each daughter cohort is that generated by the corresponding mother in terms of its body condition and food intake (see rules in Section 2.4.6). In the case of several mothers contributing to one new cohort the milk generated by the first contributing mother is used. Note that if several mother cohorts contributed to the same new cohorts it is because they are very close in body composition and as a consequence their milk production will be almost equivalent. If a daughter cohort dies, the mother cohorts related to it change their physiological status from lactating to post-lactating. If an entire mother cohort or a proportion of it dies a corresponding proportion of its daughter cohort dies. In the case of the mother cohort dying, this cohort is erased from the list of cohorts contributing to the daughter cohort.

5.1.2 Mortality

Two kinds of mortality affecting individuals are assumed: “negative energy balance rule” and “age dependent mortality”. The “negative energy balance rule” was implemented in the individual component of the model. When the energy demand of an individual or cohort is greater than its energy available for a period longer than certain number of days the individual dies. In the individual model this period was set to 3 days, but this value could be modified to study its

effect on the population dynamics. Note that under this rule the entire cohort dies. Under favorable environmental conditions, this mortality factor mainly operates through reduction in resources caused by density dependence (see Section 5.1.3).

Under a favorable environment the "negative energy balance rule" mortality basically represents only "starvation" as the death cause. Individuals are subject to other natural causes of mortality that need to be accounted for in the population model. In this model all other factors related to natural mortality such as aging, and accidents (Humphrey and Cope 1976), i.e. not human-related, would be included in the "age dependent mortality".

For the "age dependent mortality" function two formulations are tested. First, the life span of the individuals is assumed to follow a normal distribution. This normal density function is used to calculate the probability of an individual dying between *d* and *d*+1 days of age. This probability is used as the proportion of individuals dying in each cohort because of age. Age dependent mortality is not assessed on pups or lactating juvenile cohorts because this would lead to a proportion of mother cohorts changing their status from lactating to post-lactating which would split the mother cohort in two each day. This is a reasonable assumption that will not influence the population dynamics and it simplifies the coding of the population model. Also because cohorts can survive almost forever with very low numbers of individuals when only age dependent mortality occurs, all cohorts are killed when they reach 15 years of age which is considered the maximum lifespan of the individuals. Second, the "age dependent mortality" is assumed to be the same constant for all ages. This kind of mortality is suggested by estimates on mortality provided by Humphrey and Cope (1976). Both sources of mortality are assessed daily.

5.1.3 Density Dependence

Density dependence is incorporated into the population model through competition for resources. A penalty function that decreases the feeding rate of individuals as total population size increases is introduced:

$$D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}, \text{ with } b > 0, d > 0, a \geq 1.$$

This penalty function or density factor takes values from $1-\frac{1}{a}$ to $1-\frac{1}{a+b}$. The function is plotted for different values of parameters a and d in Figure 25. As the total population *N*, goes to infinity $D(N) \to 1-\frac{1}{a}$. The function goes to zero only for $a = 1$. When $a > 1$ it might seem counter intuitive to have a positive asymptote, i.e. for large population sizes increasing *N* beyond certain value $D(N)$ remains "constant" and does not longer reduce the individuals' feeding rate.

However, when the function is applied, the range of values of population sizes is bounded and the population is reduced before facing a situation in which adding individuals has no effect on the feeding rate.

As described in Section 2.3 the feeding rate is given by $F(x)=\frac{Mx}{x+i}$ with maximum feeding rate M [g d^{-1}], and half saturation constant i [g $volume^{-1}$]. The resource available at a given time to a particular individual, x [g $volume^{-1}$], can be assumed to be diminished by the factor $D(N)$ due to increasing population. Hence the feeding rate takes the form $F(x)=\frac{MxD}{xD+i}$. This is the only way density dependence affects individuals in this model.

The resources are decreased equally to all members of the population as density increase, which has been defined as intraspecific *scramble* competition (Nicholson 1954). If the population density is high enough, it is likely that nobody captures sufficient resources to allow for reproduction. This leads to an overcompensatory response of the population to density dependence (Kot 2001). In general, the density dependence can be *compensatory* or *overcompensatory*. In the case of *compensatory* response, an increase in density leads to a reduction in per capita reproduction but does not reduce the recruitment of the entire population. In contrast, the response is *overcompensatory* when density dependence becomes so intense that recruitment for the entire population decreases with increasing density (Kot 2001).

The density dependence representation is also equivalent to $F(x)=\frac{Mx}{x+i/D}$, which can be interpreted as an increase in difficulty required to capture the resource because of high population numbers (e.g. an interference effect among too many bats foraging in the same area).

The decrease in the feeding rate caused by an increasing population leads to lower resource intake, which can put the individual under negative energy balance and leads to death because of the "negative energy balance" rule. Mortality due to reduced intake can occur within a few days of the reduction or later in time (e.g. at end of next hibernation) because the bat was not able to build sufficient reserves for future demanding times. It is also possible that lipid reserves were sufficient to survive but not to trigger ovulation in females; hence, this reduced intake during the summer may lead to a lower reproductive output in the next summer. Consequently, with the density factor incorporated as described, the population regulates itself first by lowering reproductive output and then increasing mortality due to insufficient resources.

5.1.4 Ecotypes Definition

From the list of most influential parameters identified through the individual model sensitivity analysis, 6 parameters were chosen to define ecotypes to form a heterogeneous population. Table 43 shows the parameters and corresponding values used to define each of the 243 ecotypes. Among the important parameters identified by the sensitivity analysis (see Section 3.1.4), I decided to chose the most influential and those that may vary more among individuals such as *maximum feeding rate*, *half saturation constant in feeding rate*, *minimum structure*, *maximum structure*. These parameters represent foraging ability and size, which are two important characteristics to structure the population. Finally, I chose *Euthermic body temperature* that may differ among species or populations in different regions and *water to structure ratio* whose variation may reflect different access to water among individuals.

Three values were assigned to each of the parameters, low, medium, and high. All the possible combinations define the ecotypes. Because *minimum structure*, *maximum structure* are related and both relate to the size of an individual, both are set to low or medium or high at the same time. Hence the ecotypes are really defined with the combinations of 5 parameters, each with three levels. This adds to 243 (3^5) ecotypes in the population.

The parameters are coded from 1 to 3, with 1 being the minimum and 3 the maximum, and following the order of parameters given in Table 43, a pattern based on 1, 2, and 3s like '111311 '(ecotype 162) will be used to refer to a certain combination of values.

5.2 Population Model Results

5.2.1 General Dynamics and Dominant Ecotype

The model developed here is sufficiently complicated to prohibit any analytical analysis and therefore its dynamics were explored only numerically. Simulations to study the behavior of the population model were performed starting with 243 ecotypes; each composed of 15 cohorts from ages 1 to 15 years. The initial conditions were the same for all ecotypes and cohorts. Simulations started at the beginning of hibernation period. The time to complete one simulation period varied significantly depending on the resulting dynamic. Because most of the ecotypes go extinct the simulation speeds up. Initial years took more time than years at the end of the simulation. A simulation in which the population persisted and only one ecotype dominates after a few years took roughly 1.5 CPU hours to complete running on a Solaris Intel Xeon 2.8 GHz, 1 GB Ram.

In order to better understand the dynamic the number of adults and juveniles (offspring from birth to beginning of 1st hibernation) were recorded separately as were reproductive 'adults' (older that 1 year) and reproductive 'yearlings' (adults born the previous season, less than 1 year). This allowed estimating and comparing survival rates for adults vs. juveniles, and reproductive rates for adults vs. yearlings. The survival rates were estimated annually from one summer to the next as $\frac{N_{t+1}}{N_t}$, $\frac{A_{t+1}}{A_t + Y_t}$, and $\frac{Y_{t+1}}{J_t}$, where N_t represents entire population, A_t are adults older than 1 years, Y_t are yearlings, and J_t are juveniles. The reproductive rates were also estimated annually at mid pregnancy for the entire population, adults and yearlings as the ratio of number of pregnant individuals in the corresponding group to the total number of individuals in the group. Then mean survival and mean reproductive rates were calculated by averaging the annual rates.

The results described in this section come from simulations performed using the two formulations proposed for "age dependent mortality" and different parameter values. In order to compare results and analyze the effects of the different sources of mortality on population dynamics I grouped the simulations in 4 sets. The specifications for each set are shown in Table 44. The first set of simulations was run under an "age dependent mortality" in which the probability of dying comes from the normal probability distribution of life span with parameters that yielded a very low mortality rate. Hence density dependence and "negative energy balance rule" have the biggest effect on regulating population size. The second set of simulations corresponds to the same kind of "age dependent mortality" function but with parameters that yield a higher age dependent mortality. The third set falls in between the first and second sets in terms of the values of age dependent mortality, also assuming a normal distribution for the individual life span. The forth set assumes a constant age dependent mortality.

Set 1: Low age dependent mortality

In this set of simulations, the general population dynamic is mainly determined by the density factor function $D(N)$, producing three possible dynamics:

- Population grows exponentially if density pressure is low
- Population shows an oscillatory dynamic that persist in time (Figure 26)
- Population oscillates and eventually crashes, i.e. the population suddenly goes extinction from high population numbers, if density pressure sufficiently high (Figure 27)

In most of the cases only one ecotype rapidly dominates the population. With a few exceptions ecotype 162 is the dominant. This is the expected dominant ecotype because of the

parameter combination defining it. Ecotype 162 has the highest maximum feeding rate, the lowest value for the half saturation constant, which increases feeding rate, and the minimum values for all the other parameters that contribute to lower the energy demand. Following the pattern notation described above, ecotype 162 is '111311'. The exceptions are ecotypes 189 ('111321'), 85 ('211222'), 218 ('111333'), 163 ('111312'). These ecotypes were dominant over a period of time and were the last ecotype to disappear in 3 simulations in which the population went to extinction.

During the phase of oscillatory dynamics (persistence or extinction cases) the following characteristics are observed:

- Year to year survival in adults oscillates over time taking values from 70% to 100 %. This results in a relative high adult average survival rate.
- Year to year survival in juveniles presents a different pattern. It alternates years in which 100% or close to 100% of the juveniles survives to the next summer with years in which nobody or close to 0% survive.
- The reproductive proportion of adults (adults older that 2 years) varies from 0 to 1 from year to year in different patterns. Depending on the parameters of $D(N)$ the average reproductive rate for adults varies from 70% to close to 100%.
- The proportion of yearlings (adults less than 2 years old) reproducing alternates in general between 100% and 0%. There are several years in which the yearlings do not reproduce.
- In the cases of extinction, the population crash occurs at the end of hibernation or at the beginning of the active season.

Another characteristic of the population dynamics is that only a few cohorts of the dominant ecotype form the population, both in persistence and extinction cases. The simulations were started with 15 cohorts per ecotype, of ages 1 to 15 years. After a period of time under the oscillatory dynamics, the population is formed by 3 to 6 cohorts of non-consecutive ages. This is probably a consequence of the patterns of reproduction and survival described above in which the entire juvenile population dies combined with years in which adults skip reproduction. This creates gaps in the distribution of ages of the population.

The exponential growth, persistence and extinction dynamics were explored by performing simulations across the 2 dimensional parameter space generated by the parameters a and d. Parameter b was set to 10^4. Simulation time was set to 60,000 days (~164 years) after several exploratory simulations for different times were performed. Figure 28 depicts the results for the different values chosen for a and d indicating the type of dynamic. The parameter a,

which sets the asymptotic value $\left(1-\frac{1}{a}\right)$ of the function $D(N)$, has the greatest effect on determining the fate of the population. Parameter d has an effect on the boundaries of the oscillatory dynamics. The greater d values are, the higher the minima and maxima of the population (Figure 26).

In order to find a threshold value to predict extinction or persistence of the population in relation to the dynamics of the individuals I studied the effect of $D(N)$ on a single individual of ecotype 162, which was, in most cases, either the persisting or the last ecotype to die. No age dependent mortality was applied to this individual. Because the age dependent mortality component in the population model is very low in this set of simulations I expected the dynamic of the individual to be directly related to the population dynamic. As described above, the effect of the density factor can be seen as a decrease in per capita availability of resource or as an increase of the half saturation constant in the feeding rate, which is an individual parameter. Following the latter interpretation I varied the half saturation constant, i, for ecotype 162 and simulated the individual dynamic. Note that as $D(N)$ decreases with increasing population size, $\frac{i}{D(N)}$ increases and consequently the feeding rate of the individual decreases. The following results were obtained:

1. If $D(N) \geq 0.71$ then the individual survives and reproduces every year.
2. If $0.68 < D(N) < 0.71$ then the individual survives; it does not reproduce every year or can even not reproduce anymore.
3. If $D(N) \leq 0.68$ then the individual dies at the end of hibernation.

These inequalities explain the results related to extinction and persistence obtained by simulations and depicted in Figure 28. Because $D(N) \geq 0.71$ for $a \geq 3.45$ and $D(N) \leq 0.68$ for $a \leq 3.125$, these values of a determine 3 regions in the parameters space for a and d. These regions correspond to '*extinction*' for $a \leq 3.125$, '*persistence*' for $a \geq 3.45$, and 'i*ntermediate*' for $3.125 < a < 3.45$ in which both fates are possible for a simulation time of 91,250 days (250 yrs). An individual subject to a constant $0.68 < D(N) < 0.71$ does not reproduce every year; hence, for population under a dynamic function $D(N)$ that can take values in that range at high population densities it is possible to go to extinction if a particular sequence to non-reproductive seasons combined with mortality occurs. When simulations in this region are run longer (200,000

days) all but one simulated population $(a = 3.25, d = 250)$ becomes extinct. The fate of the simulations with $a > 3.45$ did not change when running up to 500 yrs. For $a > 3.75$ exponential growth was observed. There was not found a strong positive correlation between the time to extinction and the value of the parameter a ($R^2 = 0.35$). The parameter d did not show any effect on the dynamics other than the maxima and minima, or average population sizes.

The cases in which a population oscillates over an extended period of time, e.g. sometime over 200 years, and then crashes are interesting because of the characteristics of the crash. It has been suggested that population crashes are more common in populations with high intrinsic growth rate, or high a responsiveness to environmental changes (Roughgarden 1975). It has been more recently shown (Ripa and Heino 1999) that populations with overcompensatory growth went to extinction from high densities, while populations with slower undercompensatory growth went to extinction from low densities. As described above, this population model represents overcompensatory growth and that translates to the tendency of the model to yield population crashes from high densities. However, the crash does not occur after the population reaches a certain threshold. Extinction can result at a peak in the population lower than a previous higher peak. This indicates that is not only a high population size that drives the population extinct but also the characteristics of its members. Individuals die in the population model because of energetic constraints when their energy available is less than the energy demand over a consecutive number of days (3 days is the baseline parameter value). This is directly related to the lipid and structure content of the individual. When the population is formed by several cohorts of one ecotype all individuals have the same defining characteristics; however, the current body condition of cohorts can vary. Even though the initial conditions for all cohorts are the same at the start of the simulation, as new cohorts are created at different years their body compositions differ. Consequently, individuals in some cohorts may reproduce on one year while others do not. The history of reproductive events of a female partially determines its body condition at the beginning of hibernation and throughout winter survival. During a high population peak, lipid reserves built during hibernation are decreased. Hence depending on each cohort body condition, the individuals may or may not survive hibernation. After a high population peak, all cohorts may die causing the crash at the end of hibernation or a few cohorts may survive and the population recovers. This shows a clear link between the population dynamics and the individuals' physiology. The health condition of the population, given by their amount of reserves (lipid and structure), may determine the fate of the population under density dependence pressure. Moreover, this health condition is a cumulative result of each individual's life history. The code

developed here that simulates the individual and population dynamic does not provide an output that allows detailed analysis of the individual dynamic of each cohort in a systematized manner. By manual inspection of some outputs it was possible to identify that the surviving cohorts after a high population peak and consequent severe population decrease, were those that did not reproduce in the previous active season and were consequently in better body condition to face hibernation. To my knowledge, effects like this have not been reported in bat populations.

Set 2: High age dependent mortality

The general dynamics observed in this set of simulations is the same as those observed in Set 1. However, there are some interesting differences. Extinctions occur as crashes as in the simulation in Set 1. The region of persistence is expanded. Since simulations for $2.5 < a \leq 3.25$ which result in extinction in Set 1, now persist for simulation time of 60,000 days (Figure 28). This suggests that a population with a higher age dependent mortality is less affected by a high-density dependence pressure and consequently lower "negative energy balance" mortality. Thus higher "age dependent mortality" helps the population to self regulate and prevent population crashes. This might be a consequence that age mortality reduces a portion of each cohort instead of eliminating complete cohorts as the "negative energy balance mortality" does. Many of the persistence cases show asymptotic oscillatory dynamics without sudden drops or increases in population size (Figure 29).

The results regarding patterns and rates of survival and reproduction are the same as those described for simulations in Set 1. There are years in which juveniles do not survive to reproduce. There are also years in which reproduction is foregone for all yearlings. Mean survival rates for juveniles are lower than average survival rates adults.

Set 3: Intermediate age dependent mortality

Simulations in this set were performed as an intermediate set between the two previous ones. As expected the results did not vary qualitatively from results obtained from simulations in Set 1 and 2. However the expansion of the persistence region along the parameter a axis is observed (Figure 28).

Set 4: Constant age dependent mortality

Given that no qualitative changes in dynamics were identified for different values of parameter d, the simulations in this set were performed only for $d = 100$ and $d = 300$. Then several combinations of values of parameter a and constant mortality η were used (Figure 30).

Extinctions occurred as rapid population decay at the beginning of the simulation and not as a population crash following a period of oscillatory dynamics as in the simulations from

previous sets. However gradual extinctions of non-persistent ecotypes are observed as the dominant ecotype emerges to dominate the population (Figure 31). This contrasts with simulations in Sets 1 to 3 where the extinctions of non-persistent ecotypes usually occurred as crashes. The simulations represented in Figure 30 indicate that populations would not recover for constant age dependent mortality values above 0.0015 (equivalent to 42% annual mortality) no matter the degree of density pressure (i.e. across all values of parameter a).

When the constant mortality η was not sufficiently large and density pressure was low ($a = 4$) the population grows exponentially.

An important difference is that persistence is possible even under a high level of density pressure ($a = 2.5$) for $\eta < 0.0015$. Also in the persistence cases, 7 to 14 cohorts from the persistent ecotype compose the population. In the previous sets, in general, no more than 7 cohorts formed an ecotype by the end of the simulation. This is a result of a constant mortality assessed across all cohorts and all ages. Another distinction is that in many cases less dominant ecotypes survive for longer periods of time. Moreover, in a few simulations the dominant ecotype was not ecotype 162 (111311'). Ecotype 191 ('111322') dominates in simulation ID#121 $(a = 2.5, d = 100, \eta = 0.00075)$, ecotype 222 ('211333') dominates in simulation ID#116 $(a = 2.5, d = 100, \eta = 0.001)$, 217 (111331) dominates in simulation ID#120 $(a = 2.5, d = 100, \eta = 0.0005)$. Even though these ecotypes are expected to be slightly less fit that ecotype 162, they still have the maximum possible value for the "maximum feeding rate" parameter, and have the smallest structural size (see Section 5.1.4 and Table 43). I do not have a definitive explanation for this result, however in this set of simulations the age dependent mortality operates uniformly across all cohorts and ecotypes without favoring the best and it is probably more important than "negative energy balance mortality" which definitely favors the fittest ecotype. In Sets 1 to 3, the effect of "negative energy balance mortality" is probably greater than the effect of "age dependent mortality" under density pressure.

The periodicity of the patterns of population dynamics observed for many of the simulations in each of the 4 sets is prominent (Figure 32), especially when constant age dependent mortality is assumed (Set 4). In order to better describe and summarize this aspect of the dynamics I calculated the Fast Fourier Transform (FFT) for the simulations in which the population persists and looked for patterns associated with the dominant frequencies. For each simulation the FFT was calculated only for the oscillatory part of the series of total annual

population size. Figure 38 shows the distribution of dominant periods (dominant frequency^{-1}) for simulations that yield persistence. Even though an intrinsic relation must exist between the period of the cycle in the population and its mortality and reproductive rates, the results do not show a clear pattern. There is no significant correlation between the period and parameter a, or the period and the average life span of the individual. Simulations whose dynamics look very periodic and without sudden large drops or peaks in population size have cycles from 2.6 to 10 years.

All the simulations were performed under a constant environment over time except for the seasonal changes in temperature and resources explained in Chapter 2. A fluctuating environment may cause significant changes in the dynamics generated by the population model. Effects of a changing environment could be studied under a stochastic formulation for the environmental parameters in the individual model.

5.2.2 Model Results and Field Data on Bat Populations

To my knowledge, there is no time series data on bat populations to study long-term population dynamics that would allow for validation studies of the model. But there are several field studies that have estimated population level parameters for *M. lucifugus* populations and have tried to explain mechanisms that may have produced such estimates. In this section I compare the general model results related to population reproductive and survival rates to field estimates and I produce simulations that provide more insight into regulatory mechanisms of a bat population.

Reproductive rates

The reproductive rate is defined as the proportion of females that reproduce in any breeding season. Barclay et al. (Barclay, Ulmer et al. 2004) reviewed reproductive rates of bat populations of different species of bats to test predictions based on life history theory. They found that temperate species have significantly lower and more variable reproductive rates than tropical species. In the Vespertilionidae family the reproductive rate varied significantly with latitude and body mass. Samples from higher latitudes had lower reproductive rates (latitude above 33^{o}: n=30; mean ± SE: 80.2+2%; latitude below 33^{o}: n=130; mean ± SE: 96.7+1.2%), and smaller species had lower rates. Moreover, samples from higher latitudes had significantly greater variation. For *Myotis lucifugus* the reproductive rate ranged from 27.5% to 100% at 49^{o}N in 4 different years (Fenton, van Zyll de Jong et al. 1980; Grindal, Collard et al. 1992; Barclay, Ulmer et al. 2004). Humphrey and Cope (1976) reported reproductive rates for *M. lucifugus* in Indiana and Kentucky ranging from 97 to 100%.

In most cases, the reproductive rate for temperate bats is assessed at the maternity colonies during the active season. Reynolds (1999) estimated reproductive rate as the proportion of reproductive females just at the maternity colony for *Myotis lucifugus* to be 93.8% across 5 years of study in New Hampshire. Due to the fact that non-reproductive females usually spend the active season at different smaller shelters this reproductive rate overestimates the population reproductive rate. Barclay, Ulmer et al. (2004) reports that for *Myotis lucifugus* the reproductive rate of females in random samples was significantly lower than that in the maternity roost samples. They conclude that caution should be taken when assessing reproductive rates from colonies and extrapolating to the entire population.

Through the population model developed here it is possible to estimate the population reproductive rate provided all females (reproductive and non-reproductive) are counted even though they may not be roosting at the same location. The results for all sets show great variation in the reproductive rate between adults (older than 2 years) and yearlings (adults less than 2 years old). For most of the cases, the adults' reproductive rate is higher than the yearlings' reproductive rate when compared over the oscillatory phase of the dynamics. When density pressure is high, all or most of the yearlings skip reproduction because they are not able to build lipid reserves sufficiently large to survive hibernation and reproduce in the following season. Even though these results come from reduced resource intake due to high population numbers, the same would occur under any other scenario that reduces insects in the previous active season such as decreased temperature.

Reynolds (1999) reports a reproductive rate of yearlings of 12.5%, (1 out of 8 recaptures). He also reported that half of the banded young that were recaptured as adults were not observed in the maternity colony as yearlings. This emphasizes that yearling *M. lucifugus* have a lower reproductive rate than adult females. He suggests that the lower reproductive rate in yearlings of *M. lucifugus* may reflect the fact that yearlings have lower levels of body fat than adults when they emerge from hibernation in spring and sexual maturity is more dependent on physiological constraints rather than age. The results from the individual based population model presented here support this hypothesis for most of the parameters combinations, especially for those that represent high-density pressure. For combinations of parameters that lead to extinction in Sets 1, 2 and 3, the model predicts years in which not only 100 % of yearlings skip reproduction but also 100% of adults forgo reproduction. In contrast, under lower density pressure, which leads to persistence, there is no year in which 100% of the adults forego reproduction in the simulations performed.

Survival rates

Humphrey and Cope (1976) calculated life tables for *M. lucifugus* as a result of a mark and recapture study of 17 years in Indiana and north-central Kentucky. Their estimates of survival are lower in the first year than those for consecutive years of study, which show constant rates. Their estimates for female annual mortality rates for 2nd and subsequent years range from 0.288 to 0.313. The estimates for males range from 0.256 to 0.452. Even though the constant rate pattern has been found for other mammals, they note the constant rate of survival might be an artifact of the smoothing procedure used and that needs verifications by studies in which recapture effort can be quantified. Their estimates of annual mortality for females translate to a daily mortality rate of approximately 0.001 and a life expectancy of 2.66 years calculated as $1/\ln(\text{annual survival})$. They indicate that their values are most probably underestimates of survival.

The model presented here shows a significantly lower average juvenile survival especially when density pressure is high and a complete new generation can die before reproduction. For simulations in Set 1 and $3 \le a \le 3.75$ the range of juvenile survival goes from 0.28 to 0.5 and the range of adult survival goes from 0.88 to 0.92. This comes directly from the individual dynamics and the fact that juveniles start hibernation with less energy reserves than adults. This lower energy reserve is exacerbated by decreased ingestion due to density dependence.

Regulatory Mechanisms of the Population

Humphrey and Cope's (1976) data on the sizes of undisturbed populations indicate that populations of little brown bats in Indiana and north central Kentucky are stable (at the time of their study). They propose that a density dependent factor is limiting the nursery population size by lowering survival given the fact that the populations show a high reproduction rate. However they did not identify this factor. They suggested that competition for food and/or roost space might explain why newly established populations became stable instead of continuing to grow.

The population model accounts for two sources of mortality, one representing the density dependence effect (under favorable environmental conditions) and one representing all other natural causes not related to energy deficit. The formulation provides a tool to study the effect of density dependence factors in relation to "age dependent mortality". The constant mortality rate of 0.001 estimated by Humphrey and Cope (1976) accounts for all natural causes of mortality including those related to density dependence. With the model it is possible analyze the population dynamics assuming a constant "age dependent mortality" less than or equal to 0.001 combined with various degrees of density pressure. Below I summarize the resulting dynamics

and population statistics for simulations that provide more insight on the regulatory mechanisms operating in the undisturbed populations studied.

- $a = 4, d = 100, \eta = 0.001$ (Set 4, ID #109) – Low density pressure

In this simulation the population persists as depicted in Figure 33. The statistics below are calculated for three clearly different phases of the population time series: the exponential phase (3 to 50 years), oscillatory phase 1 (50 to 110 years, population still growing), oscillatory phase 2 (110 to 164 years, ecotype 162 dominates). Average values are calculated considering total population size (all ecotypes aggregated).

Mean adult reproductive rate:

0.9831 (exponential phase), 0.9959 (oscillatory phase 1), 0.9984 (oscillatory phase 2)

Mean yearling reproductive rate:

0.9824 (exponential phase), 0.9086 (oscillatory phase 1), 0.8941 (oscillatory phase 2)

During the oscillatory phase 2 yearling cohorts completely forego reproduction in years following a high population peak (Figure 33). During the previous two phases, a complete yearling cohort never foregoes reproduction.

Mean adult annual survival:

0.6934 (exponential phase), 0.6924 (oscillatory phase 1), 0.6922 (oscillatory phase 2)

Mean juvenile annual survival:

0.6934 (exponential phase), 0.6934 (oscillatory phase 1), 0.6934(oscillatory phase 2)

There are no years in which a complete juvenile cohort dies

Total population mean annual survival:

0.6905 (exponential phase), 0.6927 (oscillatory phase 1), 0.6926(oscillatory phase 2)

These annual survival rate values are equivalent to a daily mortality rate of 0.001.

Annual survival rates are equivalent to those obtained from “age dependent mortality”. Only reproductive rates for yearlings are reduced during the oscillatory phases when density pressure is operating. This indicates that density dependence is not increasing mortality but rather it is decreasing reproductive rate of yearlings. Moreover the average yearlings’ reproductive rate is mainly reduced due to years in which the complete yearling cohort skips reproduction. In this application the population model shows explicitly how low density dependence may regulate the population by just lowering reproductive success of yearlings given constant age mortality.

- $a = 4, d = 100, \eta = 0.00075$ (Set 4, ID# 148) – Low density pressure

In this simulation the population persists (Figure 34). The statistics below are calculated for three different phases of the series: the exponential phase (3 to 20 years), oscillatory phase 1 (20 to 50 years, population still growing), oscillatory phase 2 (50 to 164 years). Average values are calculated considering total population size (all ecotypes aggregated).

Mean adult reproductive rate:

0.9883 (exponential phase), 0.8701 (oscillatory phase 1), 0.9855 (oscillatory phase 2)

Mean yearling reproductive rate:

0.9528 (exponential phase), 0.7040 (oscillatory phase 1), 0.8218 (oscillatory phase 2)

During the oscillatory phases 1 and 2 complete yearling cohorts forego reproduction in years following a of high population peak. During the exponential growth phase a complete yearling cohort never foregoes reproduction (Figure 35).

Mean adult annual survival:

0.7467 (exponential phase), 0.7533 (oscillatory phase 1), 0.7552 (oscillatory phase 2)

Mean juvenile annual survival:

0.7584 (exponential phase), 0.7387(oscillatory phase 1), 0.6109 (oscillatory phase 2)

There are 3 years during the oscillatory phase 2 in which the complete juvenile cohorts die (Figure 35).

Total population mean annual survival:

0.7499 (exponential phase), 0.7494 (oscillatory phase 1), 0.7125(oscillatory phase 2)

The annual survival rate for the oscillatory phase 2 is equivalent to a daily mortality rate of 0.0009.

This simulation could also match the data from Humphrey and Cope (1976), the reproductive rate of adults is very high and the mean annual survival approximate 0.001. Because the age dependent mortality, η, was set to 0.00075, the slight increase in the estimated daily mortality corresponds to density dependent mortality. After the exponential growth phase the population oscillates. Even though by the end of the simulation time ecotype 162 dominates, this particular set of parameters allows other ecotypes to reach significant numbers and remain in the population for a relative long time (Figure 34). In this scenario density dependence also regulates the population by lowering yearlings' reproductive rate. However juvenile survival is also decreased, and in 3 years the juvenile generation completely dies.

- $a = 2.5\ d = 100, \eta = 0.00075$ (Set 4, ID# 121) – High density pressure

  In this simulation the population persists (Figure 36). The statistics below are calculated for two different phases of the series: the exponential phase (3 to 40 years), and oscillatory phase

(40 to 164 years). Average values are calculated considering total population size (all ecotypes aggregated).

Mean adult reproductive rate:

0.9646 (exponential phase), 0.8279 (oscillatory phase)

Mean yearling reproductive rate:

0.5586 (exponential phase), 0.1588 (oscillatory phase)

During the oscillatory phase yearling cohorts completely forego reproduction during several opportunities. In some cases the yearlings skip reproduction for consecutive years (Figure 37).

Mean adult annual survival:

0.7488 (exponential phase), 0.7545(oscillatory phase)

Mean juvenile annual survival:

0.7584 (exponential phase), 0.7533(oscillatory phase 1)

There is 1 year during the oscillatory phase in which the juvenile cohorts completely die (Figure 37).

Total population mean annual survival:

0.7591 (exponential phase), 0.7557 (oscillatory phase)

The annual survival rate for the oscillatory phase is equivalent to a daily mortality rate of 0.0008.

In this simulation density dependence (set as high pressure) operates by drastically reducing the yearlings' reproductive rate and also by reducing adults' reproductive rate. However, it has no effect on the juvenile survival rate (except for one year in which the complete generation dies) or the adults' survival rate. The population under this higher density pressure oscillates at a much lower level (average population during oscillatory phase is 728 individuals for simulation ID#121) than the populations in the previous two cases (average populations during oscillatory phase 2 are 1,029 for simulation ID#109 and 1,281 for simulation ID#148).

The three simulations described above show how different mechanisms could operate to regulate population density producing relative the same total population survival rates and adult reproductive rates. The advantage of using a mathematical model to understand and propose regulatory mechanisms is well illustrated by this procedure. The density dependence operation that lowers reproductive rate in yearlings, suggests that observed low reproductive rates in yearlings may not only occur at high latitudes due to a short time availability of resources. Moreover, these results emphasize the importance of separately estimating juvenile and adult

survival and reproductive rates in order to understand or propose a regulatory effect in a particular population. In the case of bat populations estimating these rates might prove to be particularly challenging given the different roost locations for reproductive and non-reproductive females and the low recapture rates of juveniles.

5.3 Summary of Population Model Assumptions and Results

5.3.1 Population Model Assumptions

- Only the females in the population are modeled.
- The sex ratio at birth is 1:1.
- Reproductive events take place at individual level.
- The offspring belong to mother's ecotype.
- Mortality due to energy deficit occurs at the individual level.
- The density dependence formulation reduces individual resource intake and consequently may lead to death or to foregone reproduction of an individual.
- Individuals only interact at the population level through the density dependence effect.
- An age dependent mortality is assumed that accounts for nonhuman related and nonenergy deficit related causes of death.
- Environmental conditions are constant over time except for seasonal fluctuations in temperature and resources.
- Transitions through the life history of the individual occur at fixed calendar dates for all individuals in the population. Hence is better to consider the current model and parameterization to represent a population in one single spatial location.

5.3.2 Population Model Results

- The population dynamics are intrinsically related to individual dynamics.
- Under high-density pressure an oscillating population may crash (go to extinction after a high population peak).
- Population crashes are not only a result of high-density pressure but a consequence of body condition of individuals in the population at the time of the crash.
- Intermediate density dependence can regulate a persistent population, which oscillates around a mean value.
- If density pressure is not sufficiently high, then the population grows exponentially.

- A higher “age dependent mortality” stabilizes the system by expanding the persistence region (see Figure 28).
- Constant “age dependent mortality” allows persistence even under high-density pressure parameter combinations (see Figure 30).
- One ecotype (ecotype 162, ‘111311’in most of the cases) dominates the population. Ecotype 162 has the highest maximum feeding rate and the lowest value for the half saturation constant, which increases feeding rate, and the minimum values for all the other parameters that contribute to lower the energy demand.
- The dominant ecotypes have better ability to forage and lower energetic demands than most of the other ecotypes in the population.
- Survival rate of juveniles is, in general, lower than survival rate of adults.
- Reproductive rate of yearlings is usually lower than reproductive rate of adults.
- Density dependence may regulate population size by lowering yearlings’ reproductive rate without affecting survival rates (see Figure 33).
- Density dependence may regulate population density by lowering yearlings’ reproductive rate and juveniles’ survival (see Figure 34 and Figure 35).
- Density dependence may regulate population size by lowering the reproductive rate of yearlings and adults and without affecting their survival rates (see Figure 36 and Figure 37).

CHAPTER 6
FUTURE DIRECTIONS

The energetic based individual model was used both to test a number of different hypotheses related to the strategies used by hibernator bats to meet their energy demands and as the core of the population model. The population model was used to study the dynamics of the population resulting from individual processes. Some possible future directions derived from the work completed here are presented in this chapter.

Model Re-parameterization for another temperate-zone bat species

The individual model was parameterized for the little brown bat, *Myotis lucifugus*. By changing parameters and modifying processes, such as hibernation if the species of interest does not hibernate, the model could be use to study and simulate individual and population dynamics of other bat species. Because of existing data, interesting candidates to be modeled and parameterized in the future are the Mexican free-tailed bat, *Tadarida brasiliensis*, which plays an important role as a predator of the bollworm *Helicoverpa zea*, a corn and cotton consumer in Texas; and bat species whose populations have been declining in recent decades (e.g. Indiana bat, *Myotis sodalis*).

In the case of another hibernator species, the re-parameterization of the model would not only require a change in the parameters related to the species such as metabolic rates and morphological measurements. But it would also require an adjustment of the transition dates for the different life history events (e.g. end of hibernation, length of pregnancy, length of lactation, migration days). For migratory species that do not hibernate the adjustments would include a representation of the energetic demands in the location where the individuals spend the winter and current hibernation component in the model should be eliminated. It is also possible that the flight energetic component needs to be modified to take into account the effect of wind currents that aid during long migrations.

Modifications to the individual model

New components can be added to the individual model to be able to address other questions related to individual processes. For example, a water compartment could be explicitly modeled and the hypothesis related to water deficit to periodic arousals during hibernation could be tested. Calcium could be another component of interest as it has been proposed to be a constraint for reproduction (Barclay 1994).

The formulations for any of the processes occurring at the individual level could be modified depending on updated lab or field data and/or new applications of the model. Such

modifications may add detail or may simplify the details on some of the formulations. For example, it could be of interest to formulate the transitions between the different physiological categories (hibernation, pregnancy, lactation, etc) in a dynamic manner depending on the individual state variables and on environmental conditions (e.g. temperature). If these representations are included in the model then the timing and synchronization of events such as parturition, migration, beginning and end of hibernation could be studied.

Because of the reasons mentioned in the Model Limitations section (see 3.2), it would improve the model to reformulate the feeding rate representation to account for appetite regulation depending on the individual lipid reserves.

Modification of environmental conditions

It might be of interest to simulate scenarios representing different environmental conditions or changing conditions through time in different ways to those used in this model. For example, this model assumes a constant average diet composition. However there is evidence of significant changes in diet composition and energetic content throughout the summer for species like Mexican free-tailed bat (McCracken, personal communication). The results presented here suggest the importance of diet composition (lipid and protein) in relation to adequate milk production. Hence to study the effects of changes in diet on the individual dynamics might reveal interesting relationships between bats, their prey, and foraging behavior.

Development of an immuno-physiological model

A modification and new application of the individual model that might be pursued in the near future is the development of an immuno-physiological model for Brazilian free-tail bats at the individual and population level. The modeling approach will be partially based on the immune response model developed by Dimitrov (Dimitrov, Hallam et al. 2006; Dimitrov, Hallam et al. 2007) and the physiological model for bats proposed in this dissertation. A successful completion of this project will contribute to a better understanding of the dynamics of emerging viral infections in bats such as rabies, SARS, Ebola, etc. However the conceptualization might be applied to other mammalian species.

New Field and laboratory Experiments

In order to develop and parameterize the individual model and to compare the simulated population dynamics to natural populations, an extensive literature review was completed. This recompilation of information and data from several areas of bat research identified some gaps in the information. Conducting field and/or laboratory experiments in these areas would improve the

understanding of the mechanisms related to the dynamic energy budget of temperate zone bats and other hibernators in general.

To investigate the threshold level of lipid/leptin at the end of hibernation to ensure successful ovulation and reproduction would contribute greatly to the study of life history of the individuals, survival, reproduction, and population dynamics. The population dynamics simulated with the model are intrinsically related to the lipid dynamics and the history of reproductive events at the individual level. An estimation of this threshold would provide confidence in the predicted dynamics. Moreover, further investigation on the functional relationship between body lipid content with plasma leptin during different time of the life cycle/lipid cycle would provide a better understanding on the lipid cycle and information to formulate a feeding rate functional response related regulated by appetite, and lipid reserves. Any attempts to provide information to formulate a feeding rate functional response should also measure insect availability.

Assessment of the number of reproductive females through random sampling instead of sampling at maternity roost and assessment of juvenile survival / reproduction at end of hibernation would provide more reliable estimates of population level parameters.

Flight energetics compose an important proportion of the energy budget of individuals. And estimates from different models show the significant variation (see Section 4.2). In order to use a classical flight mechanical model, it is essential to estimate flight efficiency independently using video thermography techniques or some other methodology.

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APPENDIX A
TABLES

Table 1 - Parameters related to metabolism

Parameters related to metabolism					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
A_L	0.85	-	Assimilation efficiency of dietary lipids	The value corresponds to digestion efficiency and assumes 100% assimilation Several papers assumed 88%	(Barclay, Dolan et al. 1991)
A_P	0.80	-	Assimilation efficiency of dietary proteins and carbohydrates	The value corresponds to digestion efficiency and assumes 100% assimilation Several papers assumed 88%	(Barclay, Dolan et al. 1991)
M_L	Pup 2.00 Juvenile 2.00 Juvenile Pre-hibernation 0.25 Hibernation 1.00 Pregnant 4.00 Lactation 4.00 Post-lactation 4.00 Pre-hibernation 0.25	d^{-1}	Lipid mobilization rate		Created
M_S	Pup 1.80 Juvenile 3.00 Juvenile Pre-hibernation 5.00 Hibernation 0.40 Pregnant 1.40 Lactation 3.00 Post-lactation 1.80 Pre-hibernation 5.00	d^{-1}	Structure mobilization rate		Created

Table 2 - Parameters related to size and body composition

Parameters related to size and body composition of individual					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
ε	0.05	-	Protected lipid to protected structure ratio	From fish	Hint (Brett, Shelbourn et al. 1969)
α	0.7	-	Protected portion structural mass	From fish	Hint (Brett, Shelbourn et al. 1969)
ω	2.74	-	Ratio water to lean dry mass for weaned juveniles and adults	Average calculated from data	Fitted (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000)
ω_{pup}	3.48	-	Ratio water to lean dry mass maximum at birth	Water content relative to structural mass decreases as pup and lactating juvenile ends lactation	Hint (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000)
$m_{S\min}$	1.56	g	Minimum structure size		Hint (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000)
$m_{S\max}$	2.1	g	Maximum structure size of viable non pregnant individual		Hint (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000)
$m_{S\max P}$	2.4	g	Maximum structure size of viable pregnant individual		Hint (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000)
w	0.24	m	Volant juveniles and adults Wing span		(Norberg and Rayner 1987)

Table 3 - Parameters related to feeding

Parameters related to feeding					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
M	6.60	g d^{-1}	Maximum feeding rate		Hint (Kurta, Bell et al. 1989)
i	0.22	g $volume^{-1}$	Half saturation constant in functional response type 2		Created
φ	0.05	-	Initial percentage of adult maximum feeding rate for volant juveniles		Created
T	20.00	d	Training period	Same parameter as training period for flight	Hint (Buchler 1980; Racey and Swift 1985; Hamilton and Barclay 1998)

Table 4 - Parameters related to hibernation energetics

Parameters related to energy demand during hibernation					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
$T_{tor-\min}$	2	^{o}C	Lower ambient set point temperature	Same parameter as in roosting energy demand	(Hook 1951)
$TMR_{\min}$	0.03	ml O_2 $g^{-1}hr^{-1}$	Torpor metabolic rate at $T_{tor-\min}$	Same parameter as in roosting energy demand	(Hook 1951)
C_t	0.06	ml O_2 $g^{-1}hr^{-1}$ $^{o}C^{-1}$	Torpid thermal conductance coefficient		(Hook 1951)
T_{eu}	32	^{o}C	Bat body temperature at euthermic levels	Same parameter as in roosting energy demand	(Thomas, Dorais et al. 1990)
S	0.13	ml O_2 g^{-1} $^{o}C^{-1}$	Bat's tissues specific heat capacity		(Thomas, Dorais et al. 1990)
RMR	2.60	ml O_2 $g^{-1}hr^{-1}$	Euthermic resting metabolic rate	Same parameter as in roosting energy demand	(Fisher and University of Toronto. 1967)
C_{eu}	0.26	ml O_2 $g^{-1}hr^{-1}$ $^{o}C^{-1}$	Euthermic thermal conductance coefficient	Same parameter as in roosting energy demand	(Fisher and University of Toronto. 1967)
t_{eu}	0.13	-	Proportion of day spent euthermic	Euthermic for 3hs a day	(French 1985)
t_{ar}	0.03	-	Proportion of day spent arousing	Arousal takes 45 minutes	(Thomas, Dorais et al. 1990)
D_{tor}	16	d	Days between arousals		
Q_{10} Quadratic	-0.01	-	Quadratic coefficient in Q_{10} as function of temperature		Fitted (Hook 1951)
Q_{10} Linear	0.31	-	Linear coefficient in Q_{10} as function of temperature		
Q_{10} Independent	0.43	-	Independent coefficient in Q_{10} as function of temperature		

Table 5 - Parameters related to roosting energetics

Parameters related to energy demand during roosting					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
$T_{tor-\min}$	2	^{o}C	Lower ambient set point temperature	Same parameter as in roosting energy demand	(Hook 1951)
$TMR_{\min}$	0.03	ml O_2 $g^{-1}hr^{-1}$	Torpor metabolic rate at $T_{tor-\min}$	Same parameter as in roosting energy demand	(Hook 1951)
T_{eu}	32	^{o}C	Bat body temperature at euthermic levels		(Thomas, Dorais et al. 1990)
RMR	2.6	ml O_2 $g^{-1}hr^{-1}$	Euthermic resting metabolic rate	Same parameter as in roosting energy demand	(Fisher 1967)
MR_{pup}	2.38	KJ g^{-1} d^{-1}	Metabolic rate for pups	Estimated from data on growth assuming a given milk intake	Fitted (Reynolds and Kunz 2000)
C_{eu}	0.2638	ml O_2 $g^{-1}hr^{-1}$ $^{o}C^{-1}$	Euthermic thermal conductance coefficient	Same parameter as in roosting energy demand	(Fisher 1967)
D	16	hr	Number of daytime hours at roost	Temperature is T_{aD} during these hours	(Burnett and August 1981; Kurta, Johnson et al. 1987)
N	4	hr	Number of nighttime hours at roost	$24 - D -$ fligth hours Temperature is T_{aN} during these hours	(Burnett and August 1981; Kurta, Johnson et al. 1987; Henry, Thomas et al. 2002)
Q_{10}	2	-	Q_{10} Effect coefficient		Hint (Song, Kortner et al. 1995)
P_{regD}	Juvenile 0.95 Lactation 0.50 Post-lactation 095	-	Proportion of the D hours that the bat regulates its body temperature	The principal mechanism for energy conservation during lactation appears to be torpor (Wilde, Knight et al. 1999)	Created
P_{regN}	Juvenile 0.95 Lactation 1.00 Post-lactation 0.95	-	Proportion of the N hours that the bat regulates its body temperature		Created
$P_{regD\min}$	Pregnant 0.10 Post-lactation 0.10 Pre-Hibernating 0.00	-	Minimum proportion of the D hours that the bat regulates its body temperature	The value for post-lactating females corresponds for females that do not reproduce in a particular year	Created

Table 5, continued

Parameters related to energy demand during roosting					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
$P_{regN\,\min}$	Pregnant 0.10 Post-lactation 0.10 Pre-hibernating 0.00	-	Minimum proportion of the N hours that the bat regulates its body temperature		Created
$P_{regD\,\max}$	Pregnant 1.00 Pre-Hibernating 0.75	-	Maximum proportion of the D hours that the bat regulates its body temperature		Created
$P_{regN\,\max}$	Pregnant 1.00 Pre-Hibernating 0.70	-	Maximum proportion of the N hours that the bat regulates its body temperature		Created
$T_{postlact}$	60	d	Number of day over which a the proportion of the day regulating increases for a female that do not ovulate and goes to post-lactating category right after hibernation		Created

Table 6 - Parameters related to flight and foraging energetics

Parameters related to energy demand during flight					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
k	1.2	-	Induced drag factor	For birds	(Pennycuick 1989)
S_d	-	m^2	Wing disc area of the individual	See formula	(Pennycuick 1989)
C_{Db}	0.40	-	Drag coefficient of the body	For birds	(Pennycuick 1989; Norberg, Kunz et al. 1993)
$C_{D\ pro}$	0.02	-	Drag coefficient of the wings	For birds	(Norberg, Kunz et al. 1993)
S_b	-	m^2	Frontal projected area of the body	See formula	(Pennycuick 1989; Norberg, Kunz et al. 1993)
E_{FM}	0.15	-	Conversion efficiency	For birds	(Norberg, Kunz et al. 1993; Speakman and Thomas 2003)
C	1.1	-	Circulation and ventilation factor		(Norberg 1976)
V_{com}	3	$m\ s^{-1}$	Average forward flight speed during commuting to foraging area		Hint (De la Cueva Salcedo, Fenton et al. 1995)
V_{for}	4	$m\ s^{-1}$	Average forward flight speed during active foraging		
V_{mig}	5	$m\ s^{-1}$	Average forward flight speed during long distance migration		
t_{com}	0.5	$h\ d^{-1}$	Hours per day spent commuting to foraging grounds	Should add to 4 or 5 hours per day	(Burnett and August 1981; Kurta, Johnson et al. 1987; Henry, Thomas et al. 2002)
t_{for}	3	$h\ d^{-1}$	Hours per day spent in active foraging		
t_{mig}	1	$h\ d^{-1}$	Hours per day spent migrating during migration period		Created
ψ	0.5	-	Initial total hours per day spent flying for a Volant juvenile to $t_{com} + t_{for}$		Created
T	20	d	Length of training period starting at peak lactation	Same as training period for feeding	Hint (Buchler 1980; Racey and Swift 1985; Hamilton and Barclay 1998)

Table 7 - Parameters related to reproduction and lactation

Parameters related to reproduction and lactation					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
$m_{L\min}$	0.25	g	Minimum lipid to ovulate	The idea of a minimum lipid content to ovulate comes from (Frisch 2002)	Hint T.H. Kunz, personal communication
N	0.3	-	Total neonate mass to total mother mass ratio		(Burnett and Kunz 1982)
n_L	0.18	-	Neonate lipid content		(Fujita 1986)
n_P	0.03	-	Neonate protein and carbohydrate content		(Fujita 1986)
$v_{\min}$	1.57	g	Initial minimum volume of milk	Estimated from energy output estimates and energy density of milk	Hint (Kurta, Bell et al. 1989; Kunz, Oftedal et al. 1995)
$v_{\max}$	2.10	g	Maximum volume of milk at peak lactation	Estimated from energy output estimates and energy density of milk	Hint (Kurta, Bell et al. 1989; Kunz, Oftedal et al. 1995)
K_{L0}	0.11	-	Proportion of lipid in milk at beginning of lactation		(Kunz, Oftedal et al. 1995)
K_{LP}	0.19	-	Proportion of lipid in milk from peak lactation to end		(Kunz, Oftedal et al. 1995)
K_S	0.13	-	Proportion of protein and carbohydrates in milk	Protein: ~ 9% Carbohydrates: ~4%	(Kunz, Oftedal et al. 1995)

Table 8 - Parameters related to environmental and external variables

Parameters related to environmental o external variables					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
X_L	0.46	-	Proportion of lipids in diet		(Kurta, Bell et al. 1989)
X_P	20.00	-	Proportion of protein and carbohydrates in diet	Protein = 17.8% Carbohydrates= 2.2%	(Kurta, Bell et al. 1989)
T_a	2	^oC	Ambient temperature inside the cave at bat roosting location		(Humphries, Thomas et al. 2002)
T_{aD}	25	^oC	Daytime average ambient temperature inside the roost at bat location		Hint (Kurta, Johnson et al. 1987)
T_{aN}	17	^oC	Nighttime average ambient temperature inside the roost at bat location		Hint (Kurta, Johnson et al. 1987)
g	9.81	$m\ s^{-2}$	Acceleration of gravity		
ρ	1.21	$g\ m^{-3}$	Air density		
P	198	Julian Day	Peak day of distribution insects available Center of Cauchy distribution		Hint (Anthony and Kunz 1977)
s	6	-	Shape parameter in Cauchy distribution for insects available		Created
C	350	-	Constant multiplying Cauchy distribution for insects available		Created

Table 9 - Parameters related to conversion coefficients

Parameters related to external conversion coefficients					
Variable Name	**Value**	**Units**	**Description**	**Notes**	**Reference**
e	0.43	-	Conversion from protein and carbohydrates to lipid efficiency	Calculated from energy density in 1 g of protein and in 1 g of lipid	
e_L	39.41	KJ g^{-1}	Energy content of lipid		
e_P	16.75	KJ g^{-1}	Energy content of protein and carbohydrates		

Table 10 - Re-labeling of parameters for sensitivity analysis

	Parameter	Factor Name	Process related to
1	A_L	X1	Metabolism
2	A_P	X2	
3	M_L Pup	X3	
4	M_L Juvenile	X4	
5	M_L Juvenile Pre-hibernating	X5	
6	M_L Hibernating	X6	
7	M_L Pregnant	X7	
8	M_L Lactating	X8	
9	M_L Post-lactating	X9	
10	M_L Pre-hibernating	X10	
11	M_S Pup	X11	
12	M_S Juvenile	X12	
13	M_S Juvenile Pre-hibernating	X13	
14	M_S Hibernating	X14	
15	M_S Pregnant	X15	
16	M_S Lactating	X16	
17	M_S Post-lactating	X17	
18	M_S Pre-hibernating	X18	
19	ε	X19	Body size and body composition
20	α	X20	
21	ω_{pup}	X21	
22	ω	X22	
23	$m_{S\min}$	X23	
24	$m_{S\max}$	X24	
25	$m_{S\max P}$	X25	
26	w	X26	

Table 10, continued

	Parameter	Factor Name	Process related to
27	M	X27	Feeding
28	i	X28	
29	φ	X29	
30	T	X30	
31	$T_{tor-\min}$	X31	Thermoregulation during hibernation and summer roosting
32	$TMR_{\min}$	X32	
33	C_t	X33	
34	T_{eu}	X34	
35	S	X35	
36	RMR	X36	
37	C_{eu}	X37	
38	t_{eu}	X38	
39	t_{ar}	X39	
40	D_{tor}	X40	
41	Q_{10} Quadratic	X41	
42	Q_{10} Linear	X42	
43	Q_{10} Independent	X43	
44	MR_{pup}	X44	
45	D	X45	
46	Q_{10}	X46	
47	P_{regD} Juvenile	X47	
48	P_{regD} Lactating	X48	
49	P_{regD} Post-lactating	X49	
50	P_{regN} Juvenile	X50	
51*	P_{regN} Lactating	X51	
52	P_{regN} Post-lactating	X52	
53	$P_{regD\min}$ Pregnant	X53	
54	$P_{regD\min}$ Post-lactating	X54	
55	$P_{regD\max}$ Pre-hibernating	X55	

Table 10, continued

	Parameter	Factor Name	Process related to
56*	$P_{regD\max}$ Pregnant	X56	Thermoregulation during hibernation and summer roosting
57*	$P_{regN\max}$ Pregnant	X57	
58	$P_{regN\min}$ Pregnant	X58	
59	$P_{regN\min}$ Post-lactating	X59	
60	$P_{regN\max}$ Pre-hibernating	X60	
61	$T_{postlact}$	X61	
62	k	X62	Flight
63	C_{Db}	X63	
64	$C_{D\,pro}$	X64	
65	E_{FM}	X65	
66	C	X66	
67	V_{com}	X67	
68	V_{for}	X68	
69	V_{mig}	X69	
70	t_{com}	X70	
71	t_{for}	X71	
72	t_{mig}	X72	
73	ϕ	X73	
74	$m_{L\min}$	X74	Reproduction and lactation
75	N	X75	
76	n_L	X76	
77	n_P	X77	
78	$v_{\min}$	X78	
79	$v_{\max}$	X79	
80	K_{L0}	X80	
81	K_{LP}	X81	
82	K_P	X82	

Table 11 - Description of response variables for sensitivity analysis

Name of Response Variable	Description and comments
Lp bf Hib 1	Lipid mass [g] on the day before the 1st hibernation of individuals of the year starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage).
St bf Hib 1	Structural mass [g] on the day before the 1st hibernation of individuals of the year starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage).
Lp af Hib 1	Lipid mass [g] on the day that 1st hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage or 1st hibernation).
St af Hib 1	Structural mass [g] on the day that 1st hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage or 1st hibernation).
Lp bf Hib 2	Lipid mass [g] on the day before the 2nd hibernation starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult).
St bf Hib 2	Structural mass [g] on the day before the 2nd hibernation starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult).
Lp af Hib 2	Lipid mass [g] on the day that 2nd hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation).
St af Hib 2	Structural mass [g] on the day that 2nd hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation).
Lp bf Hib 3	Lipid mass [g] on the day before the 3rd hibernation starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation, or 2nd summer as an adult).
St bf Hib 3	Structural mass [g] on the day before the 3rd hibernation starts. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation, or 2nd summer as an adult).
Lp af Hib 3	Lipid mass [g] on the day that 3rd hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation, or 2nd summer as an adult, or 3rd hibernation).

Table 11, continued

Name of Response Variable	Description and comments
St af Hib 3	Structural mass [g] on the day that 3rd hibernation ends. Missing values for particular runs indicate that the individual characterized by that combination of parameters die before the day this measurement was recorded (individual did not survive Juvenile stage, or 1st hibernation, or 1st summer as an adult, or 2nd hibernation, or 2nd summer as an adult, or 3rd hibernation).
Survived Juvenile	This variable is defined in terms of the missing values for "Lp bf Hib 1". If the value is not missing the individual survived pup and juvenile stage and the variable takes the value of 1. If the value is missing the variable takes the value of 0.
Survived Hib 1	This variable is defined in terms of the missing values for "Lp af Hib 1" and "Survived Juvenile". Value of 1 indicates the individual survived its 1st hibernation given it had survived the juvenile period. Missing values correspond to individuals that did not survived the juvenile period.
Survived Adult	This variable is defined in terms of the missing values for "Lp bf Hib 2" and "Survived Hib 1". Value of 1 indicated the individual survived it 1st summer as an adult given it had survived its 1st hibernation. Missing values correspond to individuals that died at any time before the end of the 1st hibernation.
Survived Hib 2	This variable is defined in terms of the missing values for "Lp af Hib 2" and "Survived Adult". Value of 1 indicates the individual survived its 2nd hibernation given it had survived its first summer as an adult. Missing values correspond to individuals died at any time before the beginning of their 2nd hibernation.
Survived Adult 2	This variable is defined in terms of the missing values for "Lp bf Hib 3" and "Survived Hib 2". Value of 1 indicated the individual survived it 2nd summer as an adult given it had survived its 2nd hibernation. Missing values correspond to individuals that died at any time before the end of the 2nd hibernation.
Survived Hib 3	This variable is defined in terms of the missing values for "Lp af Hib 3" and "Survived Adult 2". Value of 1 indicates the individual survived its 3rd hibernation given it had survived its 2nd summer as an adult. Missing values correspond to individuals died at any time before the beginning of their 3rd hibernation.
Ovul Year 1	This variable is defined as a function of the "Lp af Hib 1". If lipid content is equal or greater than ovulation threshold the variable takes the value of 1. If the lipid content is less than the ovulation threshold the variable takes the value of 0. Missing value correspond to individuals that died before the end of their 1st hibernation.
Ovul Year 2	This variable is defined as a function of the "Lp af Hib 2". If lipid content is equal or greater than ovulation threshold the variable takes the value of 1. If the lipid content is less than the ovulation threshold the variable takes the value of 0. Missing value correspond to individuals that died before the end of their 2nd hibernation.
Ovul Year 3	This variable is defined as a function of the "Lp af Hib 3". If lipid content is equal or greater than ovulation threshold the variable takes the value of 1. If the lipid content is less than the ovulation threshold the variable takes the value of 0. Missing value correspond to individuals that died before the end of their 3rd hibernation.

Table 12 - Significant factors for survival

Survived Juvenile (161/256 ~ 63%)	**Survived Hib 1** Conditional to Juvenile survival (111/161 ~ 69%)
X20 – X34 – X22 – X47 – X27+ X44+ R^2 = 0.51 (logistic regression) Lack of fit: P= 0.61	X28 – X27 + X68 – X22 – X71 – X24 – X20 – X65 + R^2 = 0.55 (logistic regression) Lack of fit: P= 0.91

Table 13 - Significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X28 – X68 – X2 + X1 + X71– X65 + X34 – X22 – X36 – R^2=0.85 Residuals: acceptable	Stepwise regression untransformed X2 + X34 – X27 + X76 – X1 + X70 – X28 – X22 – X68 – X78 – X17 + R^2=0.72 Residuals: acceptable	Stepwise regression untransformed X2 + X27 + X34 – X76 – X1 + X28 – X68 – X22 – X71 – X36 – X65 + R^2=0.78 Residuals: acceptable
Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression X2 + X34 – X70 – X27 + X23 – X68 – X22 – X28 – X38 – X1 + X37 – R^2=0.66 Residuals: show pattern	Stepwise regression X34 – X76 – X2 + X22 – X70 – X1 + X38 – X45 + X27 + X17 + X44 – R^2=0.66 Residuals: acceptable	Stepwise regression X76 – X34 – X2 + X22 – X1 + X70 – X78 – X38 – X17 + X45 + R^2=0.64 Residuals: acceptable
Dif Lp bf af Hib 1	**Dif Lp bf af Hib 2**	**Dif Lp bf af Hib 3**
Stepwise regression X27 + X2 + X68 – X28 – X1 + X65 + X71 – X34 – R2=0.78 Residuals: acceptable	Stepwise regression X27 + X2 + X40 – X28 – X68 – X38 + X1 + X65 + X34 – X71 – R2=0.84 Residuals: acceptable	Stepwise regression X27 + X2 + X28 – X68 – X38 + X31 + X1 + X34 – X65 + X71 – R2=0.86 Residuals: acceptable

Table 14 - Significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X23 + X20 + X27 + X2 + X28 – X68 – X22 – X71 – R^2=0.80 Residuals: acceptable	Stepwise regression X20 + X24 + X23 + X2 + X27 + X17 – X65 + X30 – R^2=0.92 Residuals: acceptable	Stepwise regression X20 + X24 + X23 + X2 + X27 + R^2=0.89 Residuals: acceptable
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X27 + X34 – X2 + X68 – X22 – X28 – R2=0.74 Residuals: acceptable	Stepwise regression X20 + X24 + X27+ X2 + X34 – R2=0.85 Residuals: acceptable	Stepwise regression X20 + X24 + X2 + X27 + X34 – R2=0.86 Residuals: acceptable
Dif St bf af Hib 1	**Dif St bf af Hib 2**	**Dif St bf af Hib 3**
Stepwise regression X20 – X23 + X34 + X27 – X1 – X2 – X22 + X68 + R2=0.71 Residuals: acceptable	Stepwise regression X20 – X23 + X34 + X2 – X27 – X22 + R2=0.73 Residuals: acceptable	Stepwise regression X20 – X23 + X34 + X22 + X2 – X27 – R2=0.77 Residuals: acceptable

Table 15 - Description of environmental scenarios for sensitivity analysis

Scenario	Environmental Condition	Parameter Values
Baseline Scenario	Normal conditions	T_a = 2 ºC (temperature inside the cave at bat roosting location) T_{aD} =25 ºC (Daytime average temperature inside the roost at bat location) T_{aN} =17 ºC (Nigthtime average temperature inside the roost at bat location) X_L =0.046 (Proportion of lipids in diet) X_S =0.20 (Proportion of lipids in diet) P =198 (Peak day of distribution insects available, center of Cauchy distribution) C = 350 (Constant multiplying Cauchy distribution for insects available) s =6 (Shape parameter in Cauchy distribution for insects available)
Scenario 1	Warmer years (all seasons)	T_a = 3 ºC T_{aD} =27 ºC T_{aN} =19 ºC
Scenario 2	Colder years (all seasons)	T_a = 1 ºC T_{aD} =23 ºC T_{aN} =15 ºC
Scenario 3	Low insect availability	P =198 C = 300 s =5.75
Scenario 4	High insect availability	P =198 C = 400 s =6.25
Scenario 5	High energy density diet	X_L =0.04 X_S =0.21
Scenario 6	Low energy density diet	X_L =0.05 X_S =0.19

Table 16 - Scenario 1: significant factors for survival

Survived Juvenile (209/256 ~ 82%)	**Survived Hib 1** Conditional to Juvenile survival (153/209 ~ 73%)
X34 – X20 – X27+ **X30 –** X22 – R^2 = 0.57 (logistic regression) Lack of fit: P= 0.55 Only Significant in Baseline Scenario X47 – X44 + (at end of ranking)	X27 + X24 – X28 – X65 + X68 – X22 – **X1 +** **X34 –** X71 – X20 – R^2 = 0.61 (logistic regression) Lack of fit: P= 1.00 Only Significant in Baseline Scenario None

Parameters in plain font are significant under the baseline and new scenarios (however the rank order may have changed), parameters highlighted in bold indicate results that are significant only under the new scenario, parameters significant only under the baseline case are listed at the bottom of the tables, the sign beside a factor represents the sign of the relationship between the factor an the response variable.

Table 17 - Scenario 1: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X68 – X28 – X34 – X2 + X71– X1 + X22 – X65 + R^2=0.80 Residuals: acceptable Only Significant in Baseline Scenario: X36 – (at end of ranking)	Stepwise regression untransformed X34 – X27 + X2 + X22 – X68 – X28 – X1 + **X20 –** **X36 –** **X71 –** **X65 +** R^2=0.81 Residuals: acceptable Only Significant in Baseline Scenario: X76 – X70 – X78 – (at end of ranking) X17 + (at end of ranking)	Stepwise regression untransformed X34 – X27 + X2 + X1 + X68 – X22 – X28 – X71 – X36 – **X20** X65 + **X24** R^2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X76 –
Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression X27 + X34 – X22 – X2 + X68 – X23 – X28 – X1 + **X36 –** **X71 –** **X20 –** **X65 +** R^2=0.77 Residuals: show pattern Only Significant in Baseline Scenario: X70 – X38 – X37 – (at end of ranking)	Stepwise regression X34 – X27 + X22 – **X20 –** X2 + **X68** X1 + **X28 –** **X36 –** **X24 –** **X71 –** **X65 +** **X37 –** R^2=0.80 Residuals: acceptable Only Significant in Baseline Scenario: X76 – (top of the ranking) X70 – X38 – X45 + X17 + (at end of ranking) X44 – (at end of ranking)	Stepwise regression X34 – X22 – **X27 +** X2 + **X68 –** **X20 –** X1+ **X28 –** **X24 –** **X36 –** **X71 –** **X65 +** **X37 –** R^2=0.79 Residuals: acceptable Only Significant in Baseline Scenario: X76 – (top of the ranking) X70 – X78 – X38 – X17 + (at end of ranking) X45 + (at end of ranking)

Table 18 - Scenario 1: significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X23 + X20 + X27 + X2 + X28 – X68 – **X24 +** R^2=0.78 Residuals: acceptable Only Significant in Baseline Scenario: X22 – (at end of ranking) X71 – (at end of ranking)	Stepwise regression X20 + X24 + X23 + R^2=0.80 Residuals: acceptable Only Significant in Baseline Scenario: X2 + X27 + X17 – X65 + (at end of ranking) X30 – (at end of ranking)	Stepwise regression X20 + X24 + X23 + R^2=0.81 Residuals: acceptable Only Significant in Baseline Scenario: X2 + (at end of ranking) X27 + (at end of ranking)
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X27 + X34 – **X24+** X2 + X22 – X28 – X68 – R2=0.74 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X2 + X27+ R2=0.85 Residuals: acceptable Only Significant in Baseline Scenario: X34 – (at end of ranking)	Stepwise regression X20 + X24 + X27 + X2 + R2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: X34 – (at end of ranking)

Table 19 - Scenario 2: significant factors for survival

Survived Juvenile (92/256 ~ 36%)	**Survived Hib 1** Conditional to Juvenile survival (60/92 ~ 65%)
X20 – X34 – X47 – **X30 –** X22 – X27+	X27 + **X34 –** X28 – **X31 –** X65 + X68 – X20 – **X1 +**
R^2 = 0.50 (logistic regression) Lack of fit: P=0.29	R^2 = 0.66 (logistic regression) Lack of fit: P=
Only Significant in Baseline Scenario: X44+	Only Significant in Baseline Scenario: X22 – X71 – X24 –

Table 20 - Scenario 2: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X68 – X28 – X2 + X1 + X65 + X71– X34 – R^2=0.80 Residuals: acceptable Only Significant in Baseline Scenario: X22 – (at end of ranking) X36 – (at end of ranking)	Stepwise regression untransformed X2 + **X25+** **X30 –** X68 – **X45 +** **X44 –** **X71 –** **X29 +** **X21 –** **X65 +** R^2=0.76 Residuals: acceptable Only Significant in Baseline Scenario: X34 – X27 + X76 – X1 + X70 – X28 – X22 – X78 –(at end of ranking) X17 +(at end of ranking)	Stepwise regression untransformed **X25 +** X2 + X68 – **X78 –** **X58 +** **X12 –** **X32 –** X28 – **X72 +** **X29 +** **X45 +** R^2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X27 + X34 – X76 – X1 + X22 – X71 – X36 – (at end of ranking) X65 + (at end of ranking)

Table 20, continued

Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression untransformed X68 – X23 – X22 – X2 + **X73 +** X38 – X27 + **X69 –** X1 + **X76 –** **X66 –** R^2=0.76 Residuals: show pattern Only Significant in Baseline Scenario: X34 – X70 – X28 – X37 –	Stepwise regression untransformed **X25 +** X2 + X44 – **X21 –** **X68 –** **X16 –** **X13 –** **X18 –** **X82 +** R^2=0.76 Residuals: acceptable Only Significant in Baseline Scenario: X34 – X76 – X22 – X70 – X1 + X38 – X45 + X27 + X17 +	Stepwise regression untransformed X22 – **X52 +** **X68 –** **X51 +** **X10 +** X78 – **X71 –** **X36 –** X34 – **X13 –** R^2=0.82 Residuals: acceptable Only Significant in Baseline Scenario: X76 – X2 + X1 + X70 – X38 – X17 + X45 +

Table 21 - Scenario 2: significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X27 + X23 + X2 + X20 + X68 – X28 – X22 – X71 – **X65 +** **X24 +** R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X23 + X2 + X27 + **X18 –** **X41 +** R^2=0.95 Residuals: acceptable Only Significant in Baseline Scenario: X17 – X65 + X30 –	Stepwise regression X2 + X20 + X23 + X24 + X27 + R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: None
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X2 + **X25 +** X68 – **X44 –** **X24 +** **X18 –** R2=0.75 Residuals: acceptable Only Significant in Baseline Scenario: X27 + X34 – X22 – X28 –	Stepwise regression X20 + X2 + X24 + **X47 +** **X44 –** R2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X27+ X34 –	Stepwise regression X20 + X24 + X2 + **X25 +** **X18 –** R2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: X27 + X34 –

Table 22 - Scenario 3: significant factors for survival

Survived Juvenile (153/256 ~ 60%)	**Survived Hib 1** Conditional to Juvenile survival (40/153 ~ 26%)
X20 – X34 – X22 – X47 – **X36 –** **X50 –** X27+ R^2 = 0.54 (logistic regression) Lack of fit: P= 1.00 Only Significant in Baseline Scenario: X44+	No able to perform analysis due to number of runs (40 or less)

Table 23 - Scenario 3: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X68 – X28 – X2 + X1 + X71– X65 + X22 – X34 – **X20 –** X36 – R^2=0.88 Residuals: acceptable Only Significant in Baseline Scenario: None	No able to perform analysis due to number of runs (40 or less)	
Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Not able to perform analysis due to number of runs (40 or less)		

Table 24 - Scenario 3: significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X20 + X27 + X2 + X68 – X28 – **X65 +** X71 – X23 + X22 – R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: None	No able to perform analysis due to number of runs (33 or less)	
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Not able to perform analysis due to number of runs (40 or less)		

Table 25 - Scenario 4: significant factors for survival

Survived Juvenile (166/256 ~ 65%)	**Survived Hib 1** Conditional to Juvenile survival (152/166 ~ 92%)
X20 – X34 – X47 – X22 – X27+ R^2 = 0.51 (logistic regression) Lack of fit: P= 0.65 Only Significant in Baseline Scenario: X44+ (end of ranking)	Not able to fit model

Table 26 - Scenario 4: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X28 – X2 + X68 – X1 + X71– X65 + X34 – X22 – X36 – R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression untransformed X27 + X28 – X2 + X34 – X68 – X1 + X22 – **X71 –** **X65 +** **X36 –** **X20 –** **X24 –** R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: X76 – X70 – X78 – X17 +	Stepwise regression untransformed X27 + X2 + X28 – X34 – X68 – X1 + X71 – X22 – X36 – X65 + **X20 –** **X24 –** R^2=0.85 Residuals: acceptable Only Significant in Baseline Scenario: X76 –
Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression X27 + X28 – X2 + X68 – X34 – X22 – X23 – **X65 +** **X36 –** X1 + **X71 –** **X20 –** **X24 –** R^2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X70 – X38 – X37 – (at end of ranking)	Stepwise regression X27 + X34 – **X28 –** X2 + X22 – **X24 –** **X20 –** **X68 –** **X36 –** X1 + **X71 –** **X65 +** **X37 –** R^2=0.82 Residuals: acceptable Only Significant in Baseline Scenario: X76 – (at top of ranking) X70 – X38 – X45 + X17 + (at end of ranking) X44 – (at end of ranking)	Stepwise regression **X27 +** X34 – **X28 –** X2 + X22 – **X24 –** **X20 –** **X68 –** **X36 –** **X1 +** **X71 –** **X65 +** **X37 –** R^2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X76 – (at top of ranking) X70 – X78 – X38 – X17 + (at end of ranking) X45 (at end of ranking)

Table 27 - Scenario 4: significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X2 + X20 + X23 + **X24 +** X27 + R^2=0.85 Residuals: acceptable Only Significant in Baseline Scenario: X28 – X68 – X22 – X71 –	Stepwise regression X20 + X24 + X23 + X27 + X2 + R^2=0.89 Residuals: acceptable Only Significant in Baseline Scenario: X17 – X65 + X30 –	Stepwise regression X20 + X24 + X23 + X2 + X27 + R^2=0.88 Residuals: acceptable Only Significant in Baseline Scenario: None
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X27 + X34 – X22 – X28 – X2 + X68 – R2=0.73 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X27+ X2 + R2=0.77 Residuals: acceptable Only Significant in Baseline Scenario: X34 –	Stepwise regression X20 + X24 + X27 + X2 + R2=0.79 Residuals: acceptable Only Significant in Baseline Scenario: X34 –

Table 28 - Scenario 5: significant factors for survival

Survived Juvenile (132/256 ~ 52%)	**Survived Hib 1** (Conditional to Juvenile survival) (74/132 ~ 56%)
X20 – X22 – X34 – **X36 –** X47 – X68 –	X27 + X28 – X68 – **X34 –** **X31 –** X24 – X65 + **X2 +** X22 – X20 – **X36 –** **X1 +**
R^2 = 0.53 (logistic regression) Lack of fit: P=0.58	R^2 = 0.69 (logistic regression) Lack of fit: P=1.00
Only Significant in Baseline Scenario: X27+ X44+ (at end of ranking)	Only Significant in Baseline Scenario: X71 –

Table 29 - Scenario 5: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X68 – X28 – X2 + X65 + X71– X34 – X1 + X22 – X36 – R^2=0.86 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression untransformed X2 + X76 – **X45 +** **X62 –** X68 – X27 + **X32 –** X28 – **X44 –** **X21 –** **X65 +** **X49 –** R^2=0.66 Residuals: acceptable Only Significant in Baseline Scenario: X34 – X1 + X70 – X22 – X78 – X17 +	Stepwise regression untransformed X2 + **X25 +** **X78 –** X34 – X68 – X36 – **X51 +** **X5 –** R^2=0.66 Residuals: acceptable Only Significant in Baseline Scenario: X27 + X76 – X1 + X28 – X22 – X71 – X65 +

Table 29, continued

Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression X68 – X2 + **X44 –** **X47 +** **X21 –** X38 – **X78 –** **X73 +** **X36 –** **X50 +** **X4 –** X34 – **X76 –** X23 – R^2=0.67 Residuals: show pattern Only Significant in Baseline Scenario: X70 – X27 + X22 – X28 – X1 + X37 –	Stepwise regression X2 + **X25 +** X34 – **X78 –** X76 – **X68 –** **X20 –** **X36 –** **X47 +** **X41 +** **X37 –** **X21 –** R^2=0.71 Residuals: acceptable Only Significant in Baseline Scenario: X22 – X70 – X1 + X38 – X45 + X27 + X17 + X44 –	Stepwise regression **X25 +** X34 – X2 + X78 – **X36 –** **X68 –** **X51+** **X5 –** **X71 –** **X30 –** R^2=0.76 Residuals: acceptable Only Significant in Baseline Scenario: X76 – X22 – X1 + X70 – X38 – X17 + X45 +

Table 30 - Scenario 5: Significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X23 + X20 + X27 + X2 + X28 – X22 – **X65 +** X71 – X68 – **X24 +** R^2=0.85 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X23 + X27 + X2 + R^2=0.83 Residuals: acceptable Only Significant in Baseline Scenario: X17 – X65 + X30 –	Stepwise regression X20 + X24 + X23 + R^2=0.87 Residuals: acceptable Only Significant in Baseline Scenario: X2 + X27 +
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X2 + **X24 +** X34 – **X78 –** **X25 +** X68 – X27 + R2=0.72 Residuals: acceptable Only Significant in Baseline Scenario: X22 – X28 –	Stepwise regression X20 + X24 + X2 + X27+ X34 – **X40 +** **X22 –** **X76 –** R2=0.91 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + R2=0.79 Residuals: acceptable Only Significant in Baseline Scenario: X2 + X27 + X34 –

Table 31 - Scenario 6: significant factors for survival

Survived Juvenile (178/256 ~ 69%)	**Survived Hib 1** Conditional to Juvenile survival (140/178~79%)
X20 – X34 – X27+ **X30 –** X47 – X22 – X44 +	X28 – X24 – X27 + **X1 +** **X2 +** X68 – **X30 +** X22 – X65 + X20 – **X34 –**
R^2 = 0.56 (logistic regression) Lack of fit: P= 0.75	R^2 = 0.76 (logistic regression) Lack of fit: P= 1.00
Only Significant in Baseline Scenario: None	Only Significant in Baseline Scenario: X71 –

Table 32 - Scenario 6: significant factors for lipid content

Lp bf Hib 1	**Lp bf Hib 2**	**Lp bf Hib 3**
Stepwise regression untransformed X27 + X68 – X28 – X1 + X2 + X71– X22 – X34 – X65 + R^2=0.80 Residuals: acceptable Only Significant in Baseline Scenario: X36 – (at end of ranking)	Stepwise regression untransformed X27 + X34 – X2 + X68 – X1 + X22 – X28 – **X71 –** **X36 –** **X20 –** **X65 +** **X24 –** **X55 –** R^2=0.84 Residuals: acceptable Only Significant in Baseline Scenario: X76 – X70 – X78 – X17 +	Stepwise regression untransformed X27 + X34 – X2 + X68 – X1 + X28 – X22 – X71 – X36 – X65 + R^2=0.76 Residuals: acceptable Only Significant in Baseline Scenario: X76 –

Table 32, continued

Lp af Hib 1	**Lp af Hib 2**	**Lp af Hib 3**
Stepwise regression	Stepwise regression	Stepwise regression
X27 +	X34 –	**X27 +**
X34 –	X27 +	X34 –
X22 –	X22 –	X22 –
X68 –	**X68 –**	X2 +
X23 –	X2 +	**X68 –**
X28 –	X1 +	X1 +
X2 +	**X71 –**	**X28 –**
X1 +	**X36 –**	X38 –
X36 –	**X20 –**	**X71 –**
X20 –	**X28 –**	**X20 –**
X71 –	**X24 –**	**X36 –**
X65 +	**X37 –**	**X24 –**
X24 –	**X65 +**	**X37 –**
X37 –		**X65 +**
R^2=0.83	R^2=0.79	R^2=0.82
Residuals: show pattern	Residuals: acceptable	Residuals: acceptable
Only Significant in Baseline Scenario:	Only Significant in Baseline Scenario:	Only Significant in Baseline Scenario:
X70 –	X76 – (at top of ranking)	X76 – (at top of ranking)
X38 –	X70 –	X70 –
	X38 –	X78 –
	X45 +	X17 + (at end of ranking)
	X17 + (at end of ranking)	X45 + (at end of ranking)
	X44 – (at end of ranking)	

Table 33 - Scenario 6: significant factors for structure content

St bf Hib 1	**St bf Hib 2**	**St bf Hib 3**
Stepwise regression X23 + X20 + X27 + X2 + X28 – X68 – R^2=0.74 Residuals: acceptable Only Significant in Baseline Scenario: X22 – X71 –	Stepwise regression X20 + X24 + X23 + X27 + X2 + R^2=0.88 Residuals: acceptable Only Significant in Baseline Scenario: X17 – X65 + X30 –	Stepwise regression X20 + X24 + X23 + X2 + X27 + R^2=0.89 Residuals: acceptable Only Significant in Baseline Scenario: None
St af Hib 1	**St af Hib 2**	**St af Hib 3**
Stepwise regression X20 + X27 + X34 – X22 – X68 – X2 + X28 – **X65 +** **X71 –** **X1 +** R2=0.82 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X27+ X2 + X34 – R2=0.84 Residuals: acceptable Only Significant in Baseline Scenario: None	Stepwise regression X20 + X24 + X2 + X27 + X34 – R2=0.84 Residuals: acceptable Only Significant in Baseline Scenario: None

Table 34 - Field data on body composition and mass for *M. lucifugus*

Chronological information	**Assigned Julian Day**	**Total Body Weight (g)** $\overline{x} \pm SE$ **(*n; range*)**	**Lean Dry Mass (g)** $\overline{x} \pm SE$ **(*n; range*)**	**Lipid Dry Mass (g)** $\overline{x} \pm SE$ **(*n; range*)**	**Water (g)** $\overline{x} \pm SE$ **(*n; range*)**	**Comments**	**Reference**
Young - week 1 (7 days or less)	181		0.72 (16,NR)	0.21 (16,NR)	2.51 (16,NR)	Data collected from 16 June to 25 July S. Peterborough, New Hampshire	Reynolds and Kunz 2000
Young - week 2 (8 to 14 days)	188		1.17 (6, NR)	0.52 (6, NR)	4.01 (6, NR)		
Young - week 3 (15 to 21 days)	195		1.30 (5, NR)	0.51 (5, NR)	4.19 (5, NR)		
Young - week 4 (22 days or more)	202		1.56 (5, NR)	0.48 (5, NR)	4.36 (5, NR)		
Young Female – 14 August	209	6.7 ± 0.10 (11; 6.0-7.0)					Kunz, Wrazen and Burnett 1998
Young Female – 28 August	240	6.7 ± 0.11 (26; 5.4-8.0)					
Young Female – 17 September	260	6.4 ± 0.20 (12; 5.3-7.5)					
Young Female –17 September (at maternity site)	260	6.46 ± 0.42 (6; NR)	1.7 ± 0.05 (6; NR)	0.67 ± 0.14 (6; NR)		Differences were not statistically significant	
Young Female –17 September (at swarming site)	260	6.23 ± 0.52 (6; NR)	1.58 ± 0.04 (6; NR)	0.57 ± 0.06 (6; NR)			
Young Female – 1 October	274	7.8 ± 0.15 (11; 7.1-8.9)					
Young Female – 16 October	289	8.0 ± 0.35 (6; 7.1-8.9)					

NR: not reported

Table 34, continued

Chronological information	Assigned Julian Day	Total Body Weight (g) $\bar{x} \pm SE$ (n; range)	Lean Dry Mass (g) $\bar{x} \pm SE$ (n; range)	Lipid Dry Mass (g) $\bar{x} \pm SE$ (n; range)	Water (g) $\bar{x} \pm SE$ (n; range)	Comments	Reference
Adult - Early Pregnancy (captured from April to mid-June, fetus was not detectable by palpation)	140		2.07 (6, NR)	0.62 (6, NR)	6.02 (6, NR)	Data collected from 16 June to 25 July S. Peterborough, New Hampshire	Reynolds and Kunz 2000
Adult - Late Pregnancy (fetus was detectable by palpation)	171		2.29 (7, NR)	0.69 (7, NR)	6.69 (7, NR)		
Adult - Lactation	191		2.20 (12, NR)	0.61 (12, NR)	6.29 (12, NR)		
Adult – Post Lactation	213		2.07 (1, NR)	0.43 (1, NR)	5.6 (1, NR)		
Adult Female - 17 July	198	7.2 ± 0.1 (11; 6.8-7.8)					Kunz, Wrazen and Burnett 1998
Adult Female – 31 July	212	7.4 ± 0.08 (34; 6.8-8.5)					
Adult Female – 14 August	226	7.1 ± 0.07 (31; 6.1-8.0)					
Adult Female- 28 August	240	8.5 ± 0.25 (13; 7.3-10.2)					
Adult Female – 17 September	260	9.2 ± 0.18 (16; 7.8-10.4)					
Adult Female – 17 September (at maternity site)	260	7.45 ± 0.06 (6; NR)	2.01 ± 0.02 (6; NR)	0.52 ± 0.06 (6; NR)			
Adult Female – 17 September (at swarming site)	260	9.06 ± 0.40 (6; NR)	1.83 ± 0.05 (6; NR)	2.49 ± 0.40 (6; NR)			
Adult Female – 1 October	274	8.8 ± 0.19 (15; 7.5-10.4)					
Adult Female – 16 October	289	8.9 ± 0.38 (6; 7.5-10.3)					

Table 35 - DEB estimates from Anthony and Kunz 1977

	Pregnant	**Lactating**	**Juveniles**
Grams consumed per night (wet weight)	2.5 g	3.7 g	1.8 g
DEB (kJ $bat^{-1}d^{-1}$)	21.75 kJ d^{-1}	32.19 kJ d^{-1}	15.66 kJ d^{-1}
DEB (kJ $g^{-1}d^{-1}$)	**2.72 kJ $g^{-1}d^{-1}$**	**4.23 kJ $g^{-1}d^{-1}$**	**2.47 kJ $g^{-1}d^{-1}$**

Table 36 - DEB estimates from Burnet and August 1981

	Pregnant	
	Occupied Roost Temperature	Unoccupied roost Temperature
Day roosting **(15 hs)**	3.13 kJ $bat^{-1}day^{-1}$ **0.38 kJ $g^{-1}d^{-1}$**	7.35 kJ $bat^{-1}day^{-1}$ **0.89 kJ $g^{-1}d^{-1}$**
Night roosting (5 hs)	3.87 kJ $bat^{-1}day^{-1}$ **0.47 kJ $g^{-1}d^{-1}$**	3.87 kJ $bat^{-1}day^{-1}$ **0.47 kJ $g^{-1}d^{-1}$**
Flight (4hs)	18.98 kJ $bat^{-1}day^{-1}$ **2.30 kJ $g^{-1}d^{-1}$**	18.98 kJ $bat^{-1}day^{-1}$ **2.30 kJ $g^{-1}d^{-1}$**
DEB (kJ $bat^{-1}d^{-1}$)	25.98 kJ $bat^{-1}day^{-1}$	30.02 kJ $bat^{-1}day^{-1}$
DEB (kJ $g^{-1}d^{-1}$)	**3.15 kJ $g^{-1}d^{-1}$**	**3.64 kJ $g^{-1}d^{-1}$**

Table 37 - DEB estimates from Kurta et al. 1987

	Pregnant	**Lactating (peak)**
Day roosting **(15.57hs)**	7.67 kJ $bat^{-1}day^{-1}$ **0.92 kJ $g^{-1}d^{-1}$**	6.32 kJ $bat^{-1}day^{-1}$ **0.76 kJ $g^{-1}d^{-1}$**
Night roosting (4 hs)	2.97 kJ $bat^{-1}day^{-1}$ **0.36 kJ $g^{-1}d^{-1}$**	2.67 kJ $bat^{-1}day^{-1}$ **0.32 kJ $g^{-1}d^{-1}$**
Flight (4.43 hs)	21.22 kJ $bat^{-1}day^{-1}$ **2.54 kJ $g^{-1}d^{-1}$**	21.14 kJ $bat^{-1}day^{-1}$ **2.54 kJ $g^{-1}d^{-1}$**
Production (neonate or milk)	0.72 kJ $bat^{-1}day^{-1}$ **0.09 kJ $g^{-1}d^{-1}$**	18.98 kJ $bat^{-1}day^{-1}$ **2.29 kJ $g^{-1}d^{-1}$**
DEB (kJ $bat^{-1}d^{-1}$)	32.58 kJ $bat^{-1}day^{-1}$	49.11 kJ $bat^{-1}day^{-1}$
DEB (kJ $g^{-1}d^{-1}$)	**3.91 kJ $g^{-1}d^{-1}$**	**5.92 kJ $g^{-1}d^{-1}$**

Table 38 - DEB estimates from Kurta et al. 1989

	Pregnant (late)	**Lactating**
Maintenance energy per day (indicated by DWL)	33.2 kJ $bat^{-1}d^{-1}$ **3.68 kJ $g^{-1}d^{-1}$**	28.1 kJ $bat^{-1}d^{-1}$ **3.56 kJ $g^{-1}d^{-1}$**
Production (neonate or milk)	0.5 kJ $bat^{-1}day^{-1}$ (over last 30 days of pregnancy) **0.06 kJ $g^{-1}d^{-1}$**	13.2 kJ $bat^{-1}d^{-1}$ (26 days lactation period) **1.68 kJ $g^{-1}d^{-1}$**
Insects needed per day	6.7 g	5.5 g 1st day of lactation 9.9 g at peak lactation (18th day)
DEB (kJ $bat^{-1}d^{-1}$)	33.7 kJ $bat^{-1}day^{-1}$	41.3 kJ $bat^{-1}day^{-1}$
DEB (kJ $g^{-1}d^{-1}$)	**3.74 kJ $g^{-1}d^{-1}$**	**5.24 kJ $g^{-1}d^{-1}$**

Table 39 - DEB estimates from Thomas et al. 1990

	Day without arousal	**Day with arousal** 15 days during 193 days
Torpor 24 hs / ~ 20hs	0.0096 kJ g^{-1} Thomas et al 1990	0.008 kJ g^{-1} Thomas et al 1990
Warming phase 44.1±2.2 to warm from 5°C	-	0.0866 kJ g^{-1}
Cooling phase 65% of warming cost	-	0.0563 kJ g^{-1}
Homeothermic phase under estimated due to warming of metabolic chamber – 3hs	-	0.4969 kJ g^{-1}
DEB (kJ $g^{-1}d^{-1}$)	**0.0096 kJ g^{-1}**	**0.6478 kJ g^{-1}**

Table 40 - Summary of reviewed methodologies used to estimate DEB

Method used to:	**Previous estimates reviewed**	**Dynamic Individual Model Approach**
calculate total daily energy demand	1. Ingesta method 2. Time budget with adjustment for SDA and clustering 3. Time budget adjusting for activities other than resting 4. Time budget 5. Doubly labeled water 6. Time budget (hibernation)	Time budget method Day roosting: 15hs Night roosting: 5hs Flight: 4hs Hibernation Case: Time budget method, with metabolic rates estimated with model proposed by Humphries et al. 2002 See detailed formulations in sections 2.# and 2.#
estimate day/night roosting metabolic rates	1. NA, estimate gives total energy demand 2. Used roosting metabolism reported by Studier and O'Farrel 1976 at day and night temperatures 3. Used multiple regression to data on roosting metabolism reported by Studier and O'Farrel 1976 at recorded temperatures 4. Direct measure of oxygen consumption under simulated roost conditions 5. NA, measurement gives total energy demand excluding pregnancy and lactation costs 6. NA	Bats are assumed to regulate their temperature during some portion of day and night, and conform to ambient temperature the remaining portions. Metabolic rate is calculated as function of basal metabolic rate adjusted for ambient temperature and the thermoregulatory strategy (regulate vs. conform).
estimate energy required for flight	1. NA 2. Allometric Eqn. (Thomas 1975) 3. Allometric Eqn. (Thomas 1975) 4. Allometric Eqn. (Thomas 1975) 5. Assume time budget model, assume roosting terms equal to estimates in work #4, total demand was measured and solved for flight component. 6. NA	Mechanical model See detailed formulation in section #
estimate pregnancy costs	1. NA 2. NA 3. NA 4. Pierson and Kunz unpublished 5. Estimated from neonate energy equivalent 6. NA	Estimated from neonate energy equivalent (same as Kurta et al 1987). The cost is not included in the DEB. The mass of the neonate is subtracted as a discrete event at parturition.
estimate lactation costs	1. NA 2. NA 3. NA 4. Kunz 1987 5. Estimated from juvenile metabolic rates and milk composition 6. NA	Estimated from milk production and composition (some information obtained from Kurta et al 1987) The cost is not included in the DEB. The milk components are subtracted as mass losses from individual components.

Table 41 - Effect of lipid mobilization rate on pre-hibernation lipid deposition

Mobilization Rates				**Maximum Lipid Stores [g]**
Lipid, M_L Post-lactation	**Lipid, M_L Pre-hibernation**	**Structure, M_S Post-lactation**	**Structure, M_S Pre-hibernation**	
4	4	2	2	2.32 Survives winter Does not Reproduce
4	0.25	2	2	2.45 Survives winter Reproduces
4	0.09 <0.09 dies after migration	2	2	2.63 Survives winter Reproduces
4	0.25	2	5	2.8 Survives winter Reproduces

Note: All other parameters set at values specified in Tables 1 to 9

Table 42 - Effects of changes of parameters related to young training period

Simulation number	T **[d]**	φ **[.]**	ψ **[.]**	$m_{S\,\min}$ **[g]**	$m_{S\,\max}$ **[g]**	**First minimum or maximum lipid mass after peak lactation (p.l) [g] (age [d])**	**Lipid mass at beginning of hibernation [g]**	**Structure mass at beginning of hibernation [g]**	**Survive hibernation**
1	≤ 3	0.2	0.5	1.56	2.1	2.46 (36)	1.87	1.73	NO
2	4	0.2	0.5	1.56	2.1	2.34 (38)	1.94	1.71	YES
3	10	0.2	0.5	1.56	2.1	1.91 (42)	2.05	1.68	YES
4	15	0.2	0.5	1.56	2.1	0.48 (28)	2.07	1.68	YES
5	20	0.2	0.5	1.56	2.1	0.26 (30)	2.05	1.66	YES
6	25	0.2	0.5	1.56	2.1	0.17 (31)	2.05	1.65	YES
7	30	0.2	0.5	1.56	2.1	0.13 (31)	2.05	1.65	YES
8	≥ 31	0.2	0.5	1.56	2.1	0.12 (31) DIES	-	-	-
9	≤ 2	0.6	0.7	1.56	2.1	2.26 (39)	1.86	1.73	NO
10	10	0.6	0.7	1.56	2.1	2.57(35)	2.00	1.70	YES
11	25	0.6	0.7	1.56	2.1	1.4 (25)	1.99	1.68	YES
12	40	0.6	0.7	1.56	2.1	1.36 (25)	1.91	1.68	YES
13	≥ 60	0.6	0.7	1.56	2.1	1.35 (25)	1.73	1.68	NO
14	≤ 9	0.2	0.5	1.64	2.21	1.75 (41)	1.81	1.75	NO
15	25	0.2	0.5	1.64	2.21	0.15 (31)	1.86	1.72	YES
16	≥ 29	0.2	0.5	1.64	2.21	0.13 (31) DIES	-	-	-

Table 43 - Parameters defining ecotypes

Parameter	Low value	Medium value	High value
Ratio water to lean mass for weaned juveniles and adults $\omega = X_{22}$	2.60	2.74	2.88
Minimum and maximum structure size $m_{S\min} = X_{23}$ $m_{S\max} = X_{24}$	1.48 1.99	1.56 2.10	1.64 2.21
Maximum feeding rate $M = X_{27}$	6.27	6.6	6.93
Half saturation constant in functional response type 2 for feeding rate $i = X_{28}$	0.21	0.22	0.23
Euthermic body temperature $T_{eu} = X_{34}$	30.40	32.00	33.60

Table 44 - Specifications for the 4 sets of the population model simulations

Set 1	Set 2	Set 3	Set 4
Negative energy balance rule Individual dies if the number of days with $E_D > E_A$ is 3 **Density dependence function** $D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}$ $b = 10^4$ $2.5 \le a \le 4$ $100 \le d \le 600$ **Age dependent mortality** Life span $\sim N(\mu, \sigma)$ $\mu = 3650\ days\ (10\ yrs)$ $\sigma = 1095 days\ (3 yrs)$ The proportion dying at age x is $0 < f(x) < 0.00036$	**Negative energy balance rule** Individual dies if the number of days with $E_D > E_A$ is 3 **Density dependence function** $D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}$ $b = 10^4$ $2.5 \le a \le 4$ $100 \le d \le 600$ **Age dependent mortality** Life span $\sim N(\mu, \sigma)$ $\mu = 1095\ days\ (3\ yrs)$ $\sigma = 365\ days\ (1 yrs)$ The proportion dying at age x is $0 < f(x) < 0.001$	**Negative energy balance rule** Individual dies if the number of days with $E_D > E_A$ is 3 **Density dependence function** $D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}$ $b = 10^4$ $2.5 \le a \le 4$ $100 \le d \le 600$ **Age dependent mortality** Life span $\sim N(\mu, \sigma)$ $\mu = 2372.5\ days\ (6.5\ yrs)$ $\sigma = 730\ days\ (2 yrs)$ The proportion dying at age x is $0 < f(x) < 0.00056$	**Negative energy balance rule** Individual dies if the number of days with $E_D > E_A$ is 3 **Density dependence function** $D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}$ $b = 10^4$ $2.5 \le a \le 4$ $d = 100$ **Age dependent mortality** The proportion dying at age x is $f(x) = \eta$ $0.0005 \le \eta \le 0.003$

APPENDIX B
FIGURES

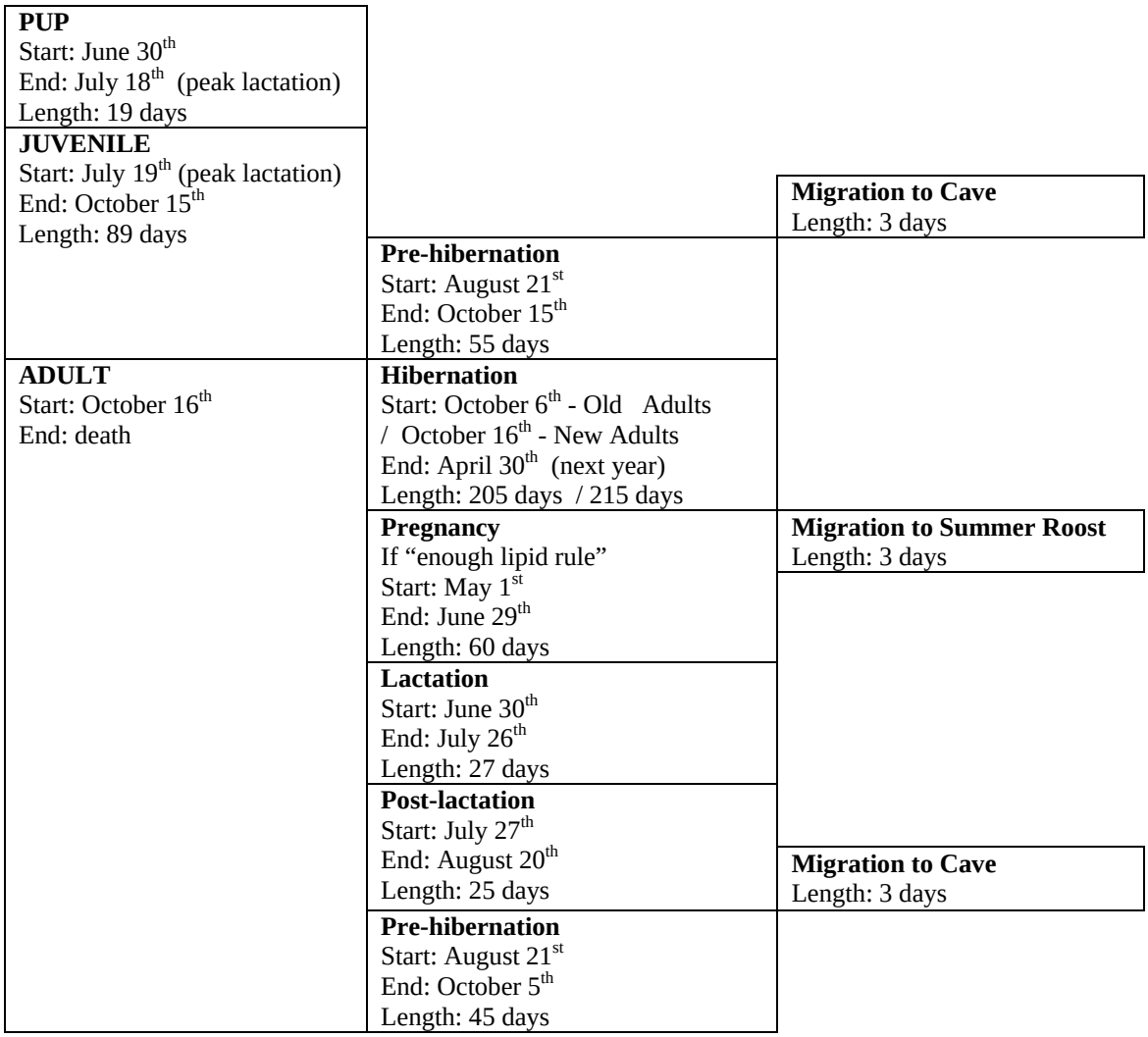


Figure 1 - Life history of female *M. lucifugus*

Assumed dates for transitions between stages for the individual model. Dates are mainly based on information provided by (Davis and Hitchcock 1965).

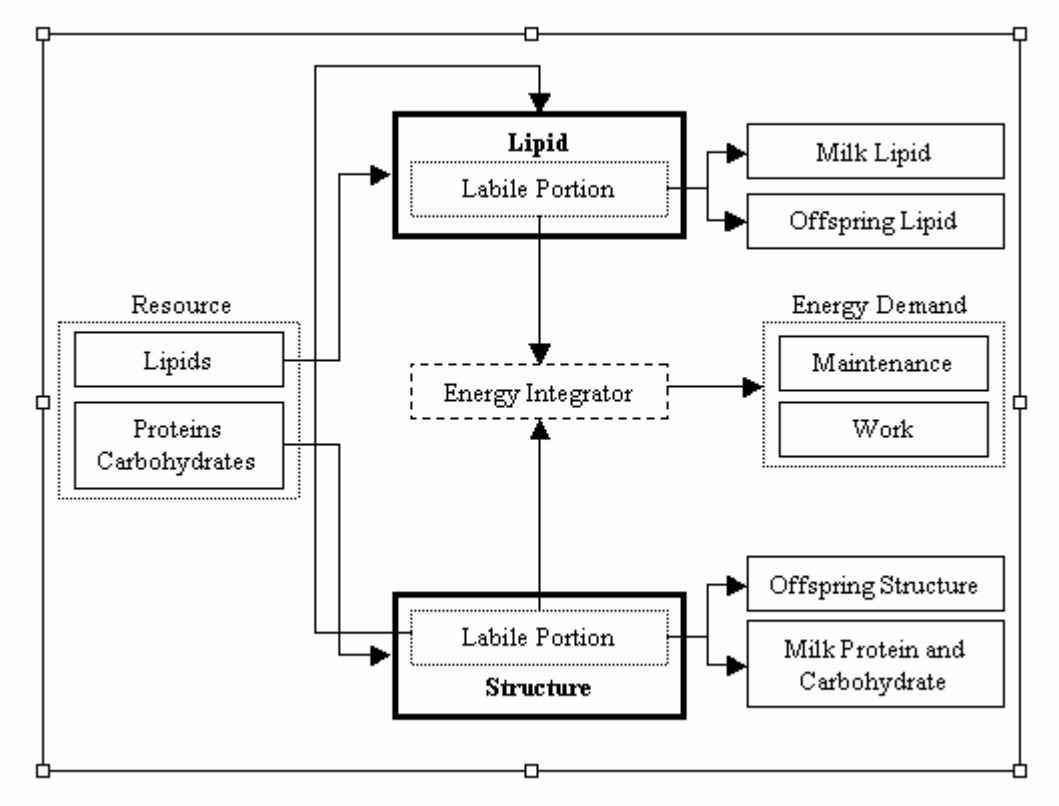


Figure 2 - Flow diagram for individual energetics

Conceptual flow diagram for individual model

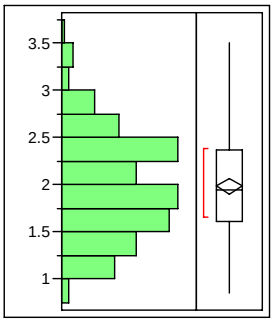
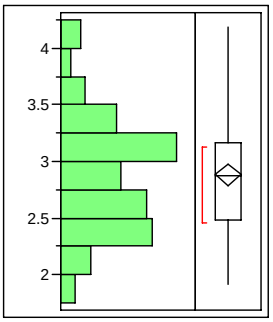
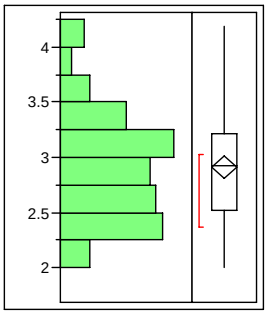
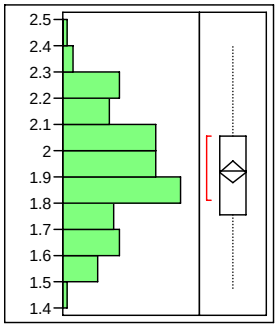
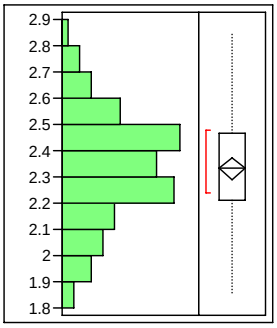
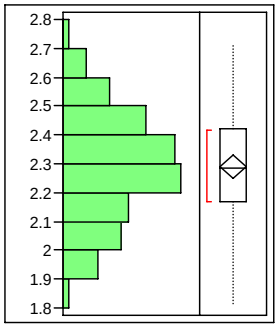
Lp bf Hib 1	Lp bf Hib 2	Lp bf Hib 3
		
Max value = 3.5g # of observations >3g = 6 N=161	Max value = 4.19g # of observations >3g = 43 N=101	Max value = 4.19g # of observations >3g = 39 N=94
Lp bf Hib 1-Lp af Hib 1	**Lp bf Hib 2-Lp af Hib 2**	**Lp bf Hib 3-Lp af Hib 3**
		

Figure 3 - Lipid content distributions

Distribution of individual lipid content (grams of dry mass) as a result of simulations with 256 parameter combinations used to perform the sensitivity analysis. The vertical axes represent grams of dry mass and the horizontal axes represent frequency (e.g. number of simulations producing a value in the specified range). The total number of observations, N, might be less than 256 because of simulations in which the bat dies before the time on which the mass of lipid is recorded. The top row shows the distribution of lipid content on the day that hibernation starts in the first 3 years a female bat. The bottom row shows the distribution of lipid spent during hibernation as the difference between the lipid content at the beginning and the lipid content at the end of hibernation.

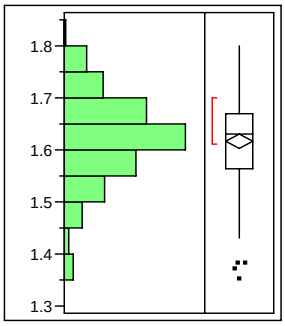
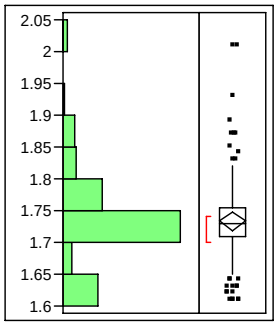
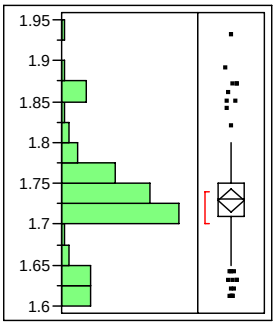
St bf Hib 1	St bf Hib 2	St bf Hib 3
		
Max value=1.80g Min value=1.35g N=165	Max value=2.01g Min value=1.61g N=101	Max value=1.93 g Min value=1.61g N=94

Figure 4 - Structure content distributions

Distribution of individual structure content (grams of dry mass) as a result of simulations with 256 parameter combinations used to perform sensitivity analysis. The vertical axes represent grams of dry mass and the horizontal axes represent frequency (e.g. number of simulations producing a value in the specified range). The total number of observations, N, might be less than 256 because of simulations in which the bat dies before the time on which the mass of lipid is recorded.

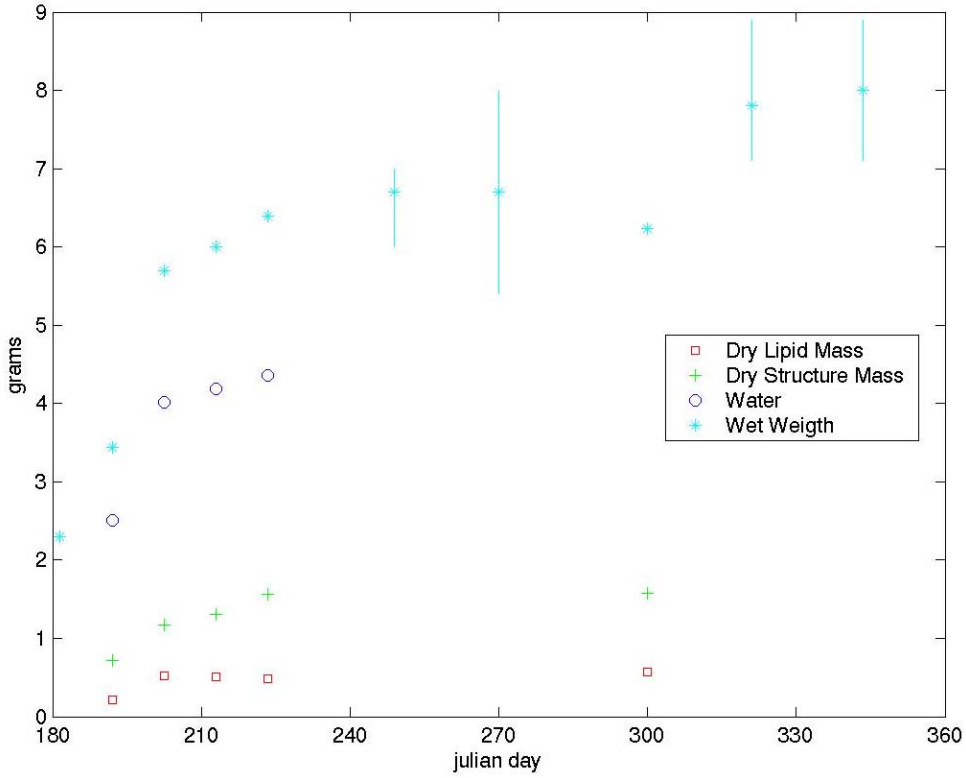


Figure 5 - Pseudo time series data for young *M. lucifugus*

Time series plot of data on body composition and body mass from field studies (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000). Actual data and dates of measure recording are presented in Table 34. Because the time coordinate was not always described in terms of calendar day the time location of the data points might be shifted and/or stretched along the horizontal axis. Note the data points do not correspond to a single individual tracked on time but to samples of individuals at different times. Vertical lines indicate range (e.g. minimum and maximum values) when reported.

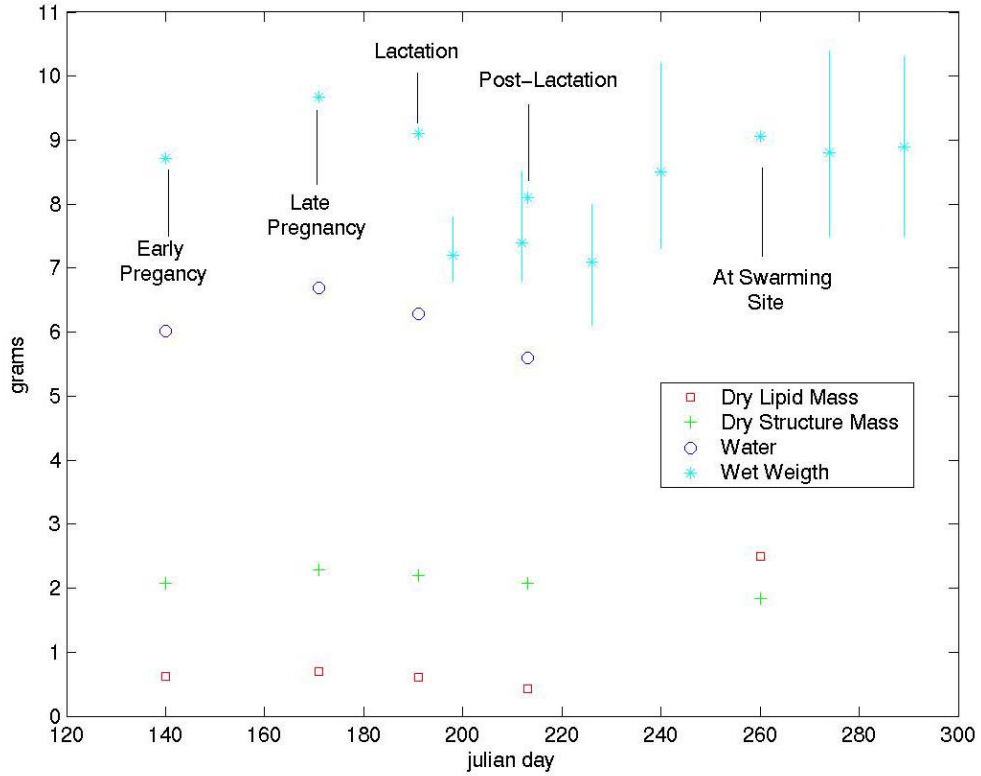


Figure 6 - Pseudo time series data for pregnant *M .lucifugus*

Time series plot of data on body composition and body mass from field studies (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000). Actual data and dates of measure recording are presented in Table 34. Because the time coordinate was not always described in terms of calendar day the time location of the data points might be shifted and/or stretched along the horizontal axis. Note the data points do not correspond to a single individual tracked on time but to samples of individuals at different times. Vertical lines indicate range (e.g. minimum and maximum values) when reported.

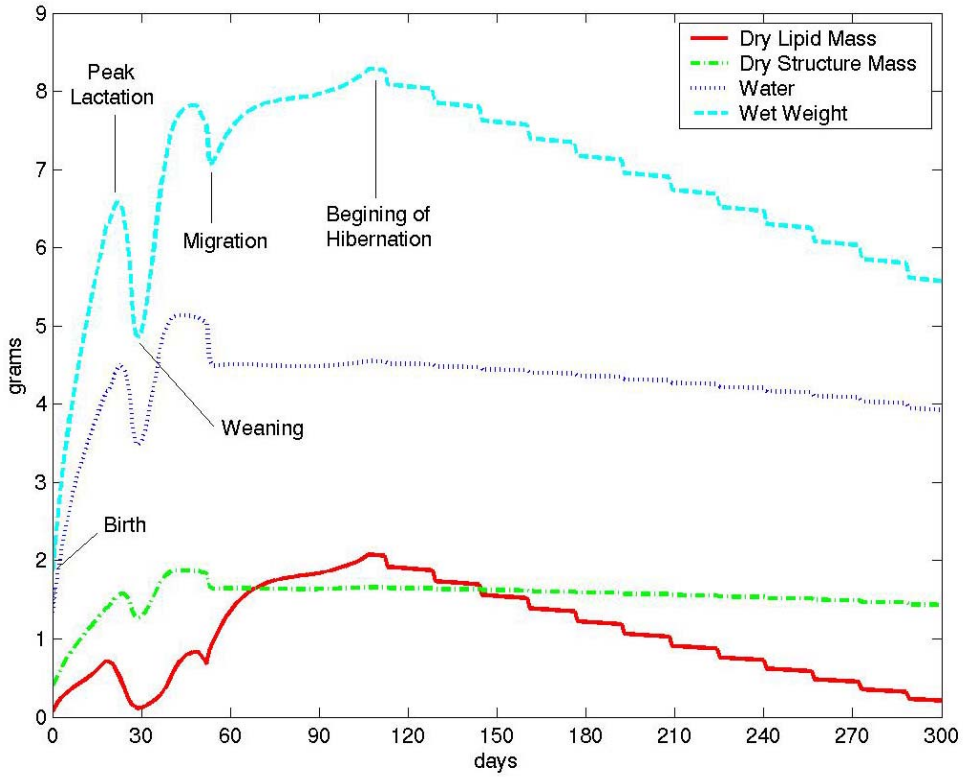


Figure 7 - Individual model dynamic for young

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. The parameter values for this simulation are those indicated in Table 1 to Table 9.

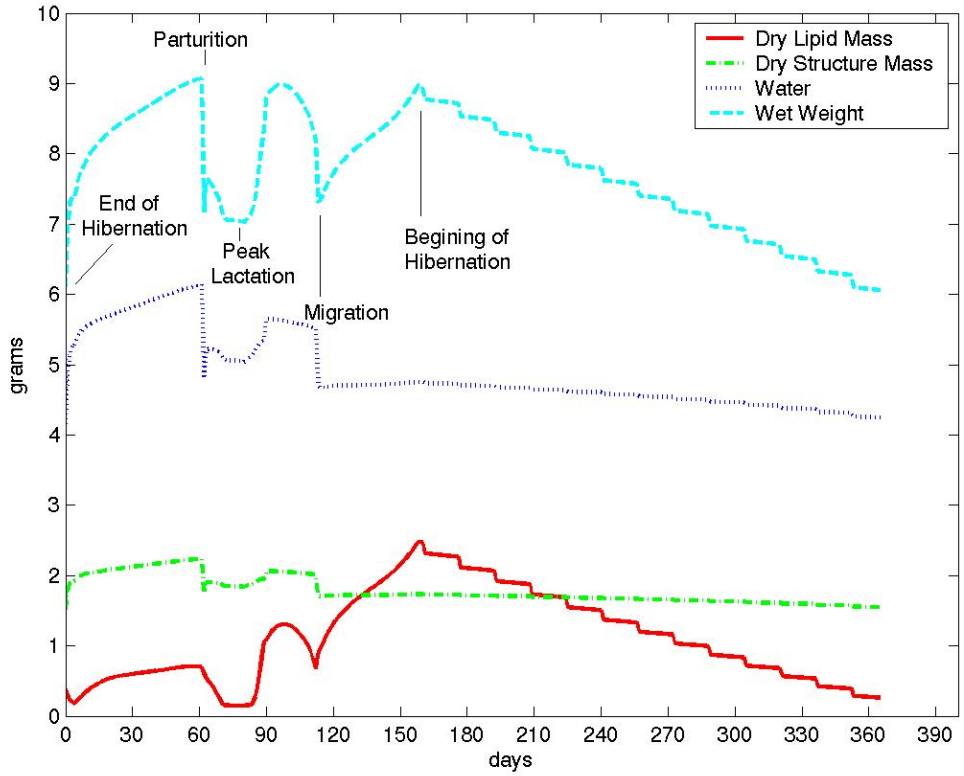


Figure 8 - Individual model dynamic for adult pregnant female

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate an adult female at the end of hibernation. The parameter values for this simulation are those indicated in Table 1 to Table 9.

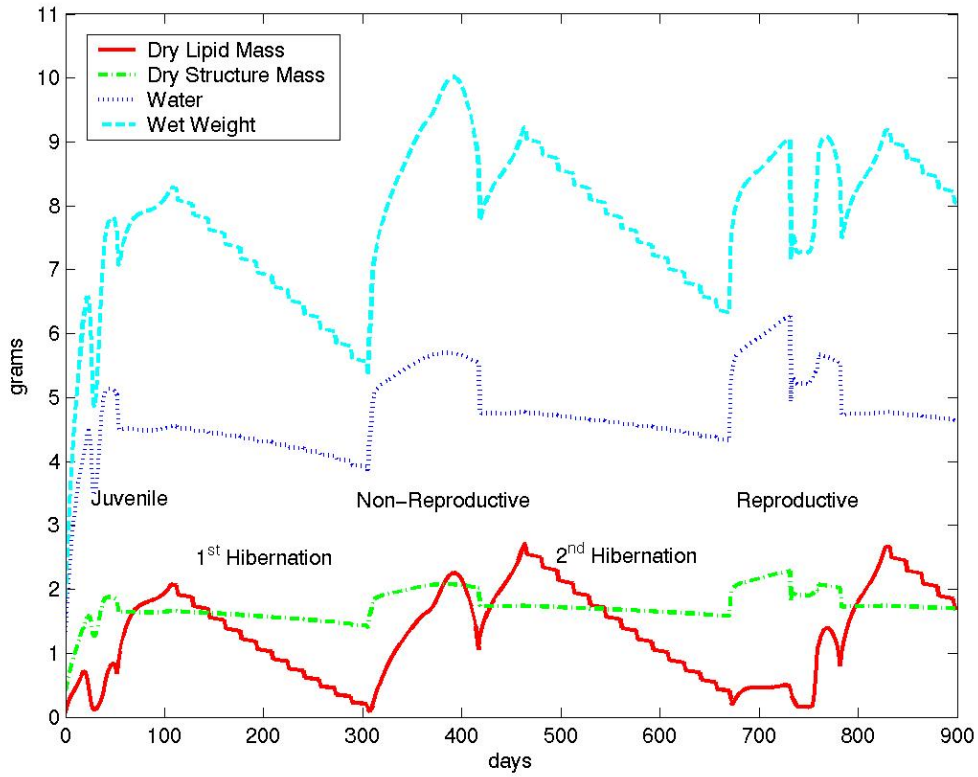


Figure 9 - Individual model dynamic for 1st year non-reproductive female

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. The parameter values for this simulation are those indicated in Table 1 to Table 9.

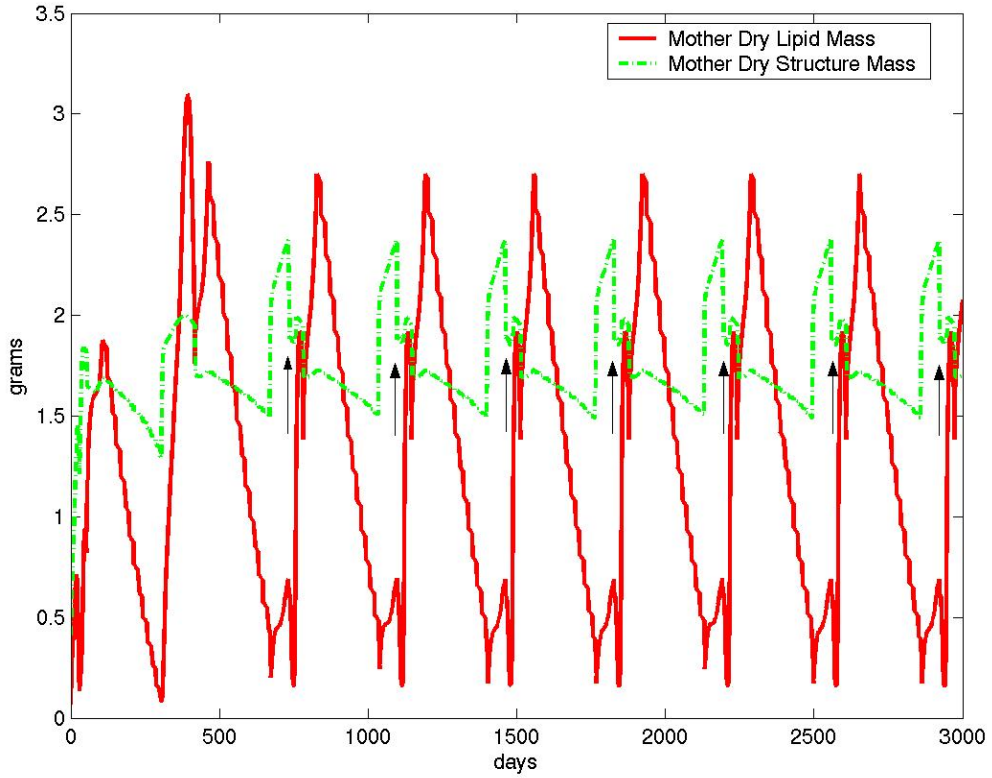


Figure 10 - Individual model dynamics for female reproducing every year after 2nd

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. The parameter values for this simulation are those indicated in Table 1 to Table 9.

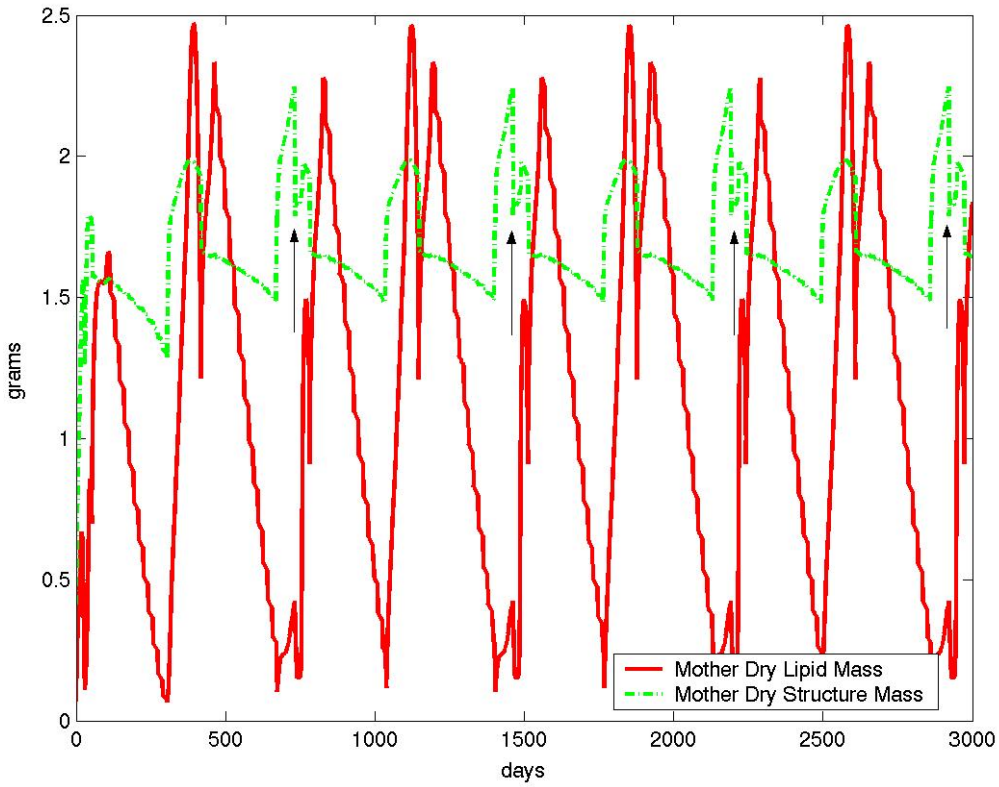


Figure 11 - Individual model dynamic for female reproducing every other year

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. This female reproduces every other year after its 1st reproduction in her 2nd year. The parameter values for this simulation are those indicated in Table 1 to Table 9, except for the following: $A_L = 0.82,\ A_P = 0.84,\ \omega = 2.6,\ m_{S\,\min} = 1.48,\ m_{S\,\max} = 1.99\ , M = 6.27,\ i = 0.23$

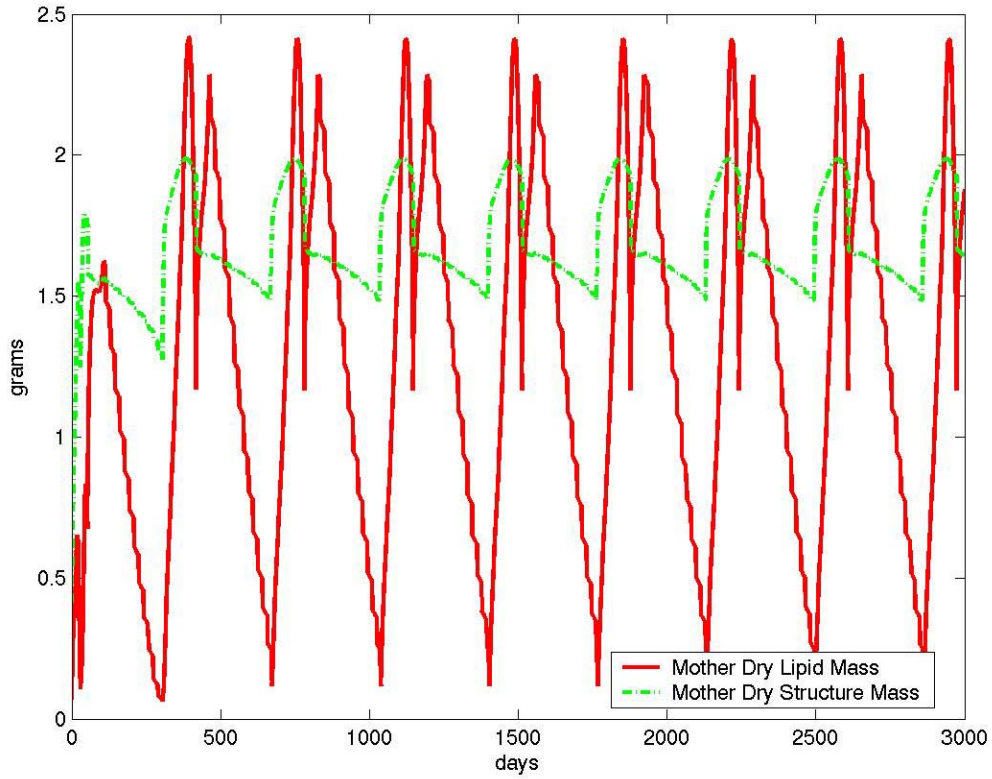


Figure 12 - Individual model dynamic for a female that never reproduces

Numerical solution of the individual model system of differential equations with initial conditions set to content of lipid, structure, and water appropriate for a newborn bat. This female never reproduces. The parameter values for this simulation are those indicated in Table 1 to Table 9, except for the following:

$A_L = 0.80,\ A_P = 0.84,\ \omega = 2.6,\ m_{S\min} = 1.48,\ m_{S\max} = 1.99\ ,M = 6.27,\ i = 0.23$

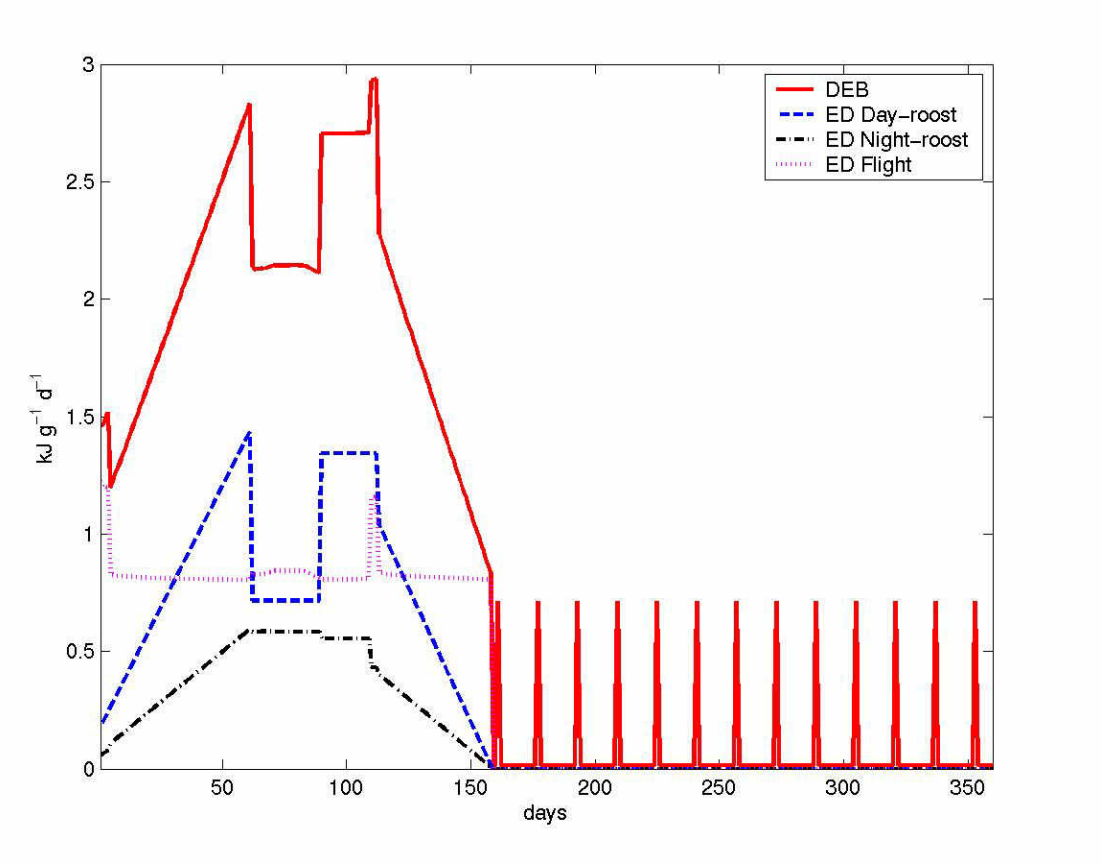


Figure 13 – Daily normalized DEB components estimates from individual model

Estimates of daily energy budget (DEB) components per unit time calculated with the individual model assuming the baseline set of parameters and constant environmental factors (Table 1 to Table 9). The total DEB (kJ $g^{-1}d^{-1}$) varies temporally as a result of time and physiological stage dependent thermoregulatory strategies (proportion of roosting time regulating vs. conforming). This simulation starts at the end of hibernation; the peak in energy demand for flight corresponds to the 3 days migration from hibernacula to summer roost.

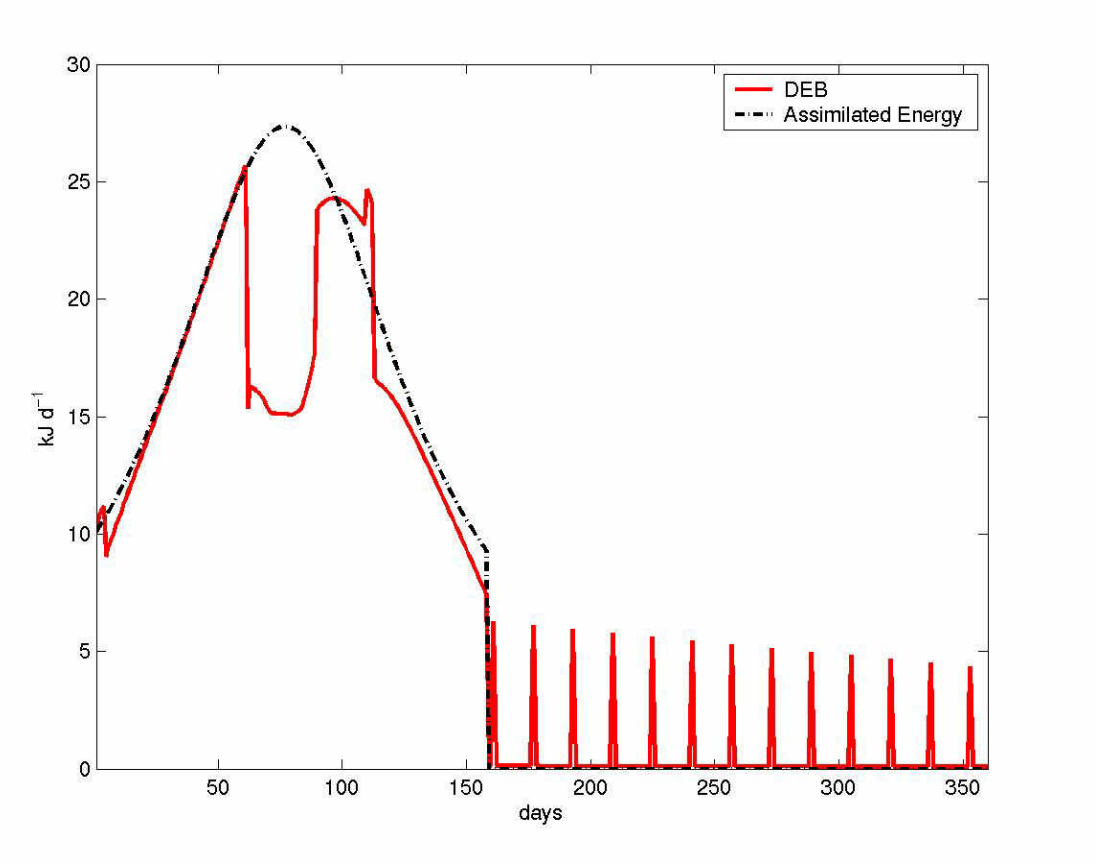


Figure 14 - Daily DEB per bat estimates from individual model

Estimates of total daily energy budget (DEB) per unit time calculated with the individual model assuming the baseline set of parameters and constant environmental factors (Table 1 to Table 9). The total DEB (kJd^{-1}) varies temporally as a function of physiological stage and individual's mass. This simulation starts at the end of hibernation. Assimilated energy is calculated in terms of daily ingestion rate and diet composition, and it is zero during hibernation. The individual gains mass when the "energy-assimilated" curve is above the DEB curve (e.g. pre-hibernation) except during lactation because the cost of lactation is not included in the DEB estimate.

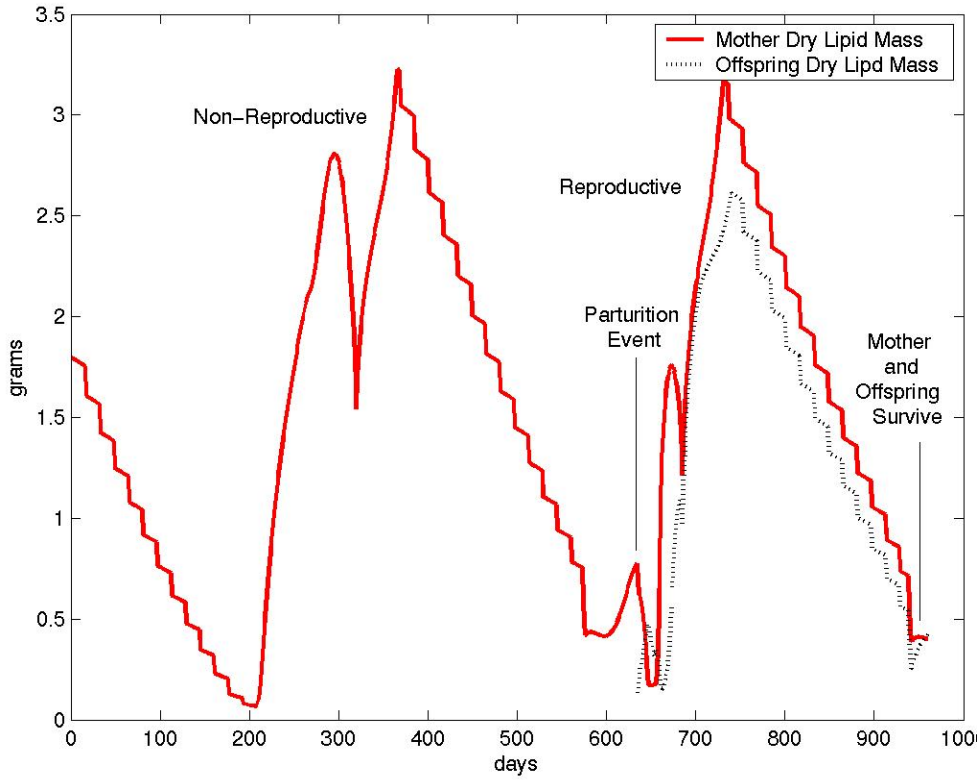


Figure 15 - Mother and offspring lipid dynamic for $m_{L\min} = 0.25g$

Numerical solution of the individual model system of differential equations for an adult female and her pup. In order to track the dynamics of her future pup, the individual model is run under the population model rules. However there is no effect of density dependence affecting individual female resource intake. Pup's initial body composition and milk intake depend on her mother's body components. Initial conditions are given for adult female at the beginning of hibernation. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for $M = 7.00$, $P_{regD\min}$preganant $= 0.23$.

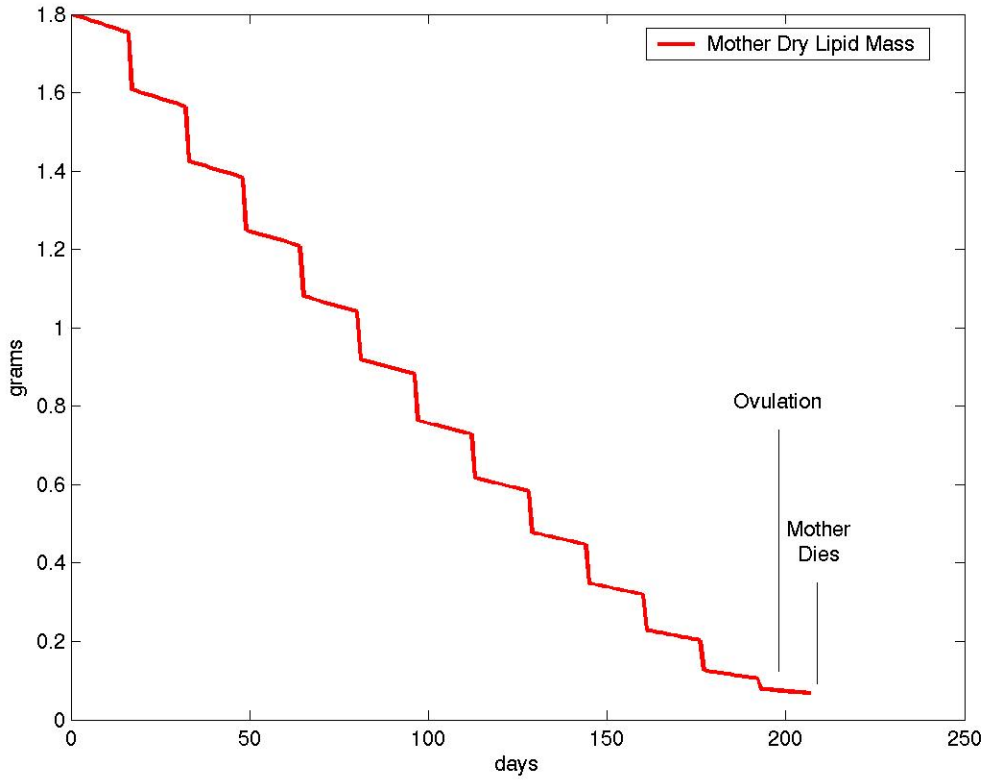


Figure 16 - Mother lipid dynamic for $m_{L\min} = 0.05g$

Numerical solution of the individual model system of differential equations for an adult female. In order to track the dynamics of her future pup, if corresponds, the individual model is run under the population model rules. However there is no effect of density dependence affecting individual female resource intake. Initial conditions are given for adult female at the beginning of hibernation. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for $M = 7.00$, $P_{regD\min}\text{pregnant} = 0.23$, $m_{L\min} = 0.05$.

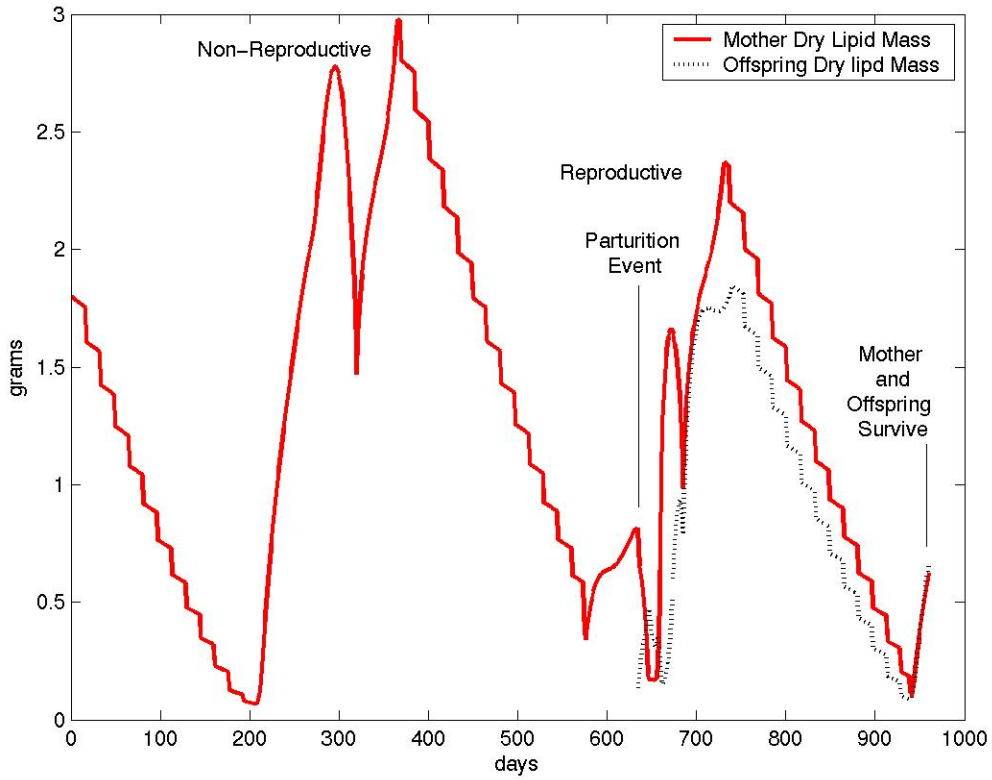


Figure 17 - Mother and offspring lipid dynamic for $m_{L\min} = 0.25g$ and density pressure

Numerical solution of the individual model system of differential equations for an adult female and her pup. In order to track the dynamics of her pup the individual model is run under the population model rules. In this simulation the effect of density dependence affects the individuals resource intake. Initial conditions are given for adult female at the beginning of hibernation. The parameters values for this simulation are those indicated in Table 1 to Table 9. The total population starts at 2000 individuals of the same ecotype and age. The parameters of the density factor (see Section 5.1.3) are $a = 5.5, b = 10^4, d = 300$.

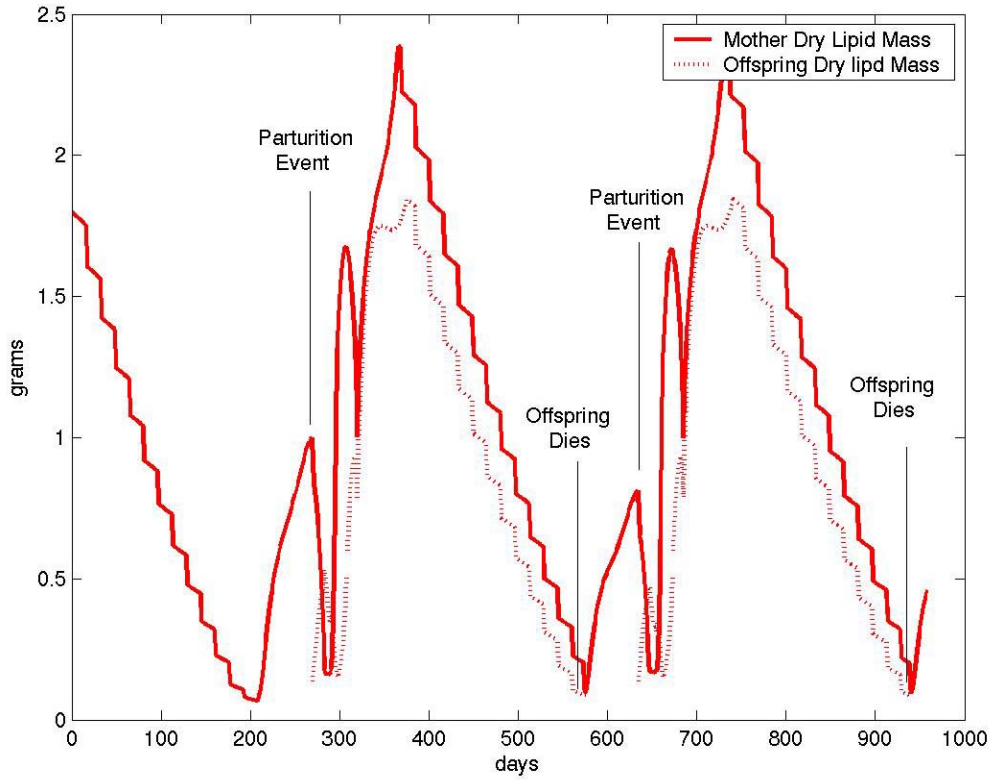


Figure 18 - Mother and offspring dynamic for $m_{L\min} = 0.05g$ and density pressure

Numerical solution of the individual model system of differential equations for an adult female and her pup. In order to track the dynamics of her pup the individual model is run under the population model rules. In this simulation the effect of density dependence affects the individuals resource intake. Initial conditions are given for the adult female at the beginning of hibernation. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for $m_{L\min} = 0.05g$. The total population starts at 2000 individuals of the same ecotype and age. The parameters of the density factor (see Section 5.1.3) are $a = 5.5, b = 10^4, d = 300$.

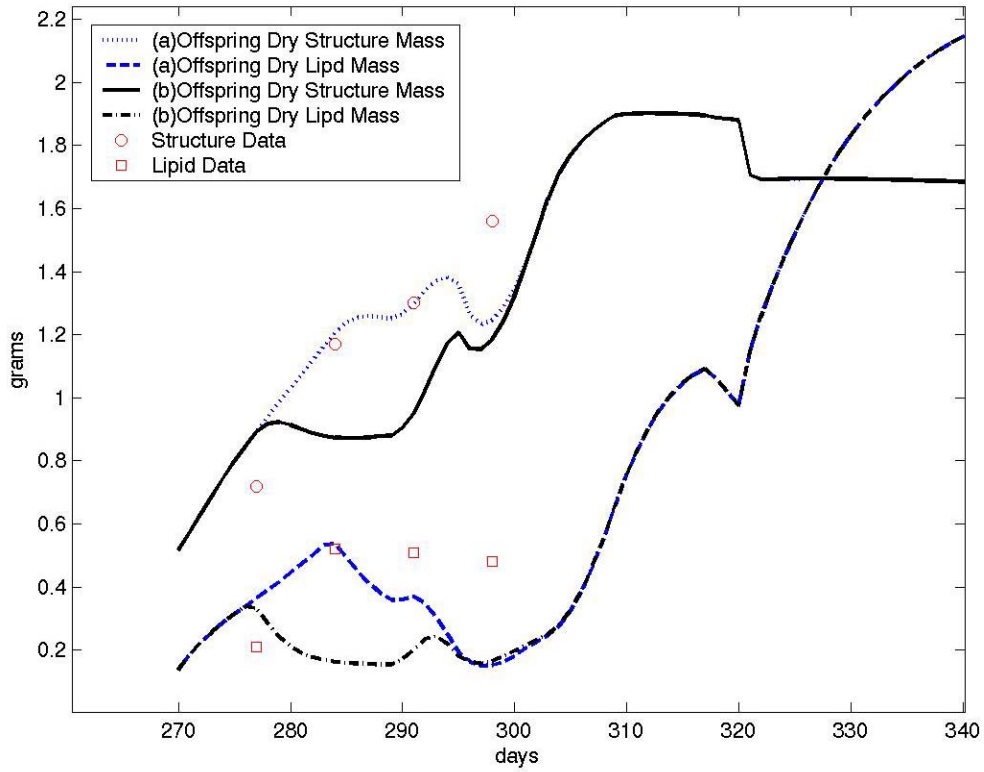


Figure 19 - Offspring lipid and structure dynamic and data

Numerical solutions of the individual model system of differential equations for a pup and juvenile individual, and published data on body composition (Kunz, Wrazen et al. 1998; Reynolds and Kunz 2000). In order to track the dynamics of this pup/juvenile in relation to her mother, the individual model is run under the population model rules. However there is no effect of density dependence affecting the individuals' resource intake. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for the "Proportion of day regulating temperature for lactating female (mother)":

(a) $P_{regD}\text{lactating} = 0.5$

(b) $P_{regD}\text{lactating} = 0.9$

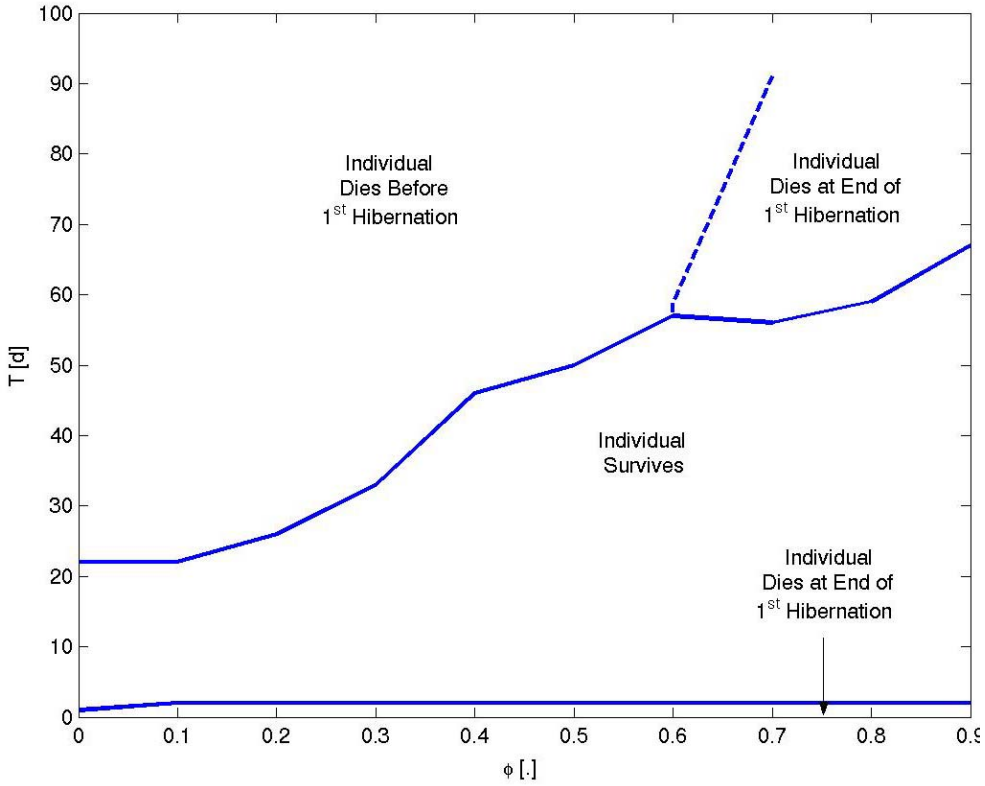


Figure 20 - Young training period

Fate of a pup/juvenile individual depending on two parameters involved in the "training period" formulation. The vertical axis corresponds to the length of the training period, T [d] and the horizontal axis corresponds to the initial percentage of adult maximum feeding rate, φ. For the simulations performed here the initial percentage of total adult's flight time, ψ was set to 0.5. All other parameters are those indicated in Table 1 to Table 9.

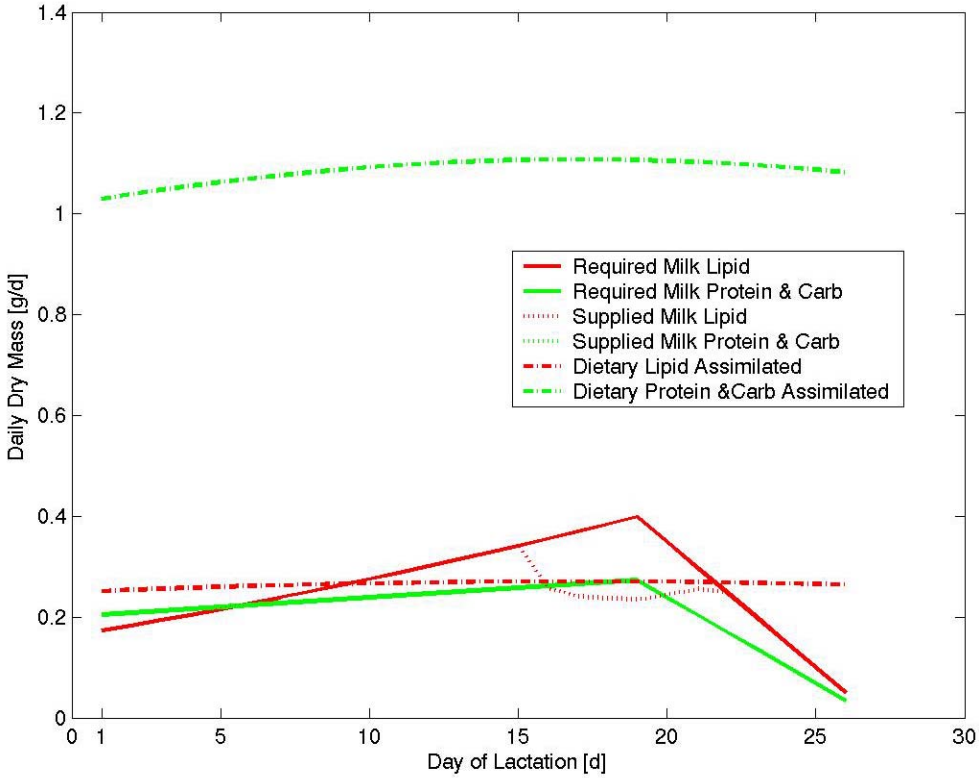


Figure 21 - Milk required, milk supplied, and dietary components for $X_L = 0.046$

Daily estimated “required milk lipid” and “required milk protein and carbohydrates” in solid lines, and “supplied milk lipid” and “supplied milk protein and carbohydrates” in dotted lines for a lactating female. Dotted lines are not visible when supplied amount overlaps with the required amount. Dietary lipid, protein and carbohydrate assimilated are also represented. The parameters values for this simulation are those indicated in Table 1 to Table 9.

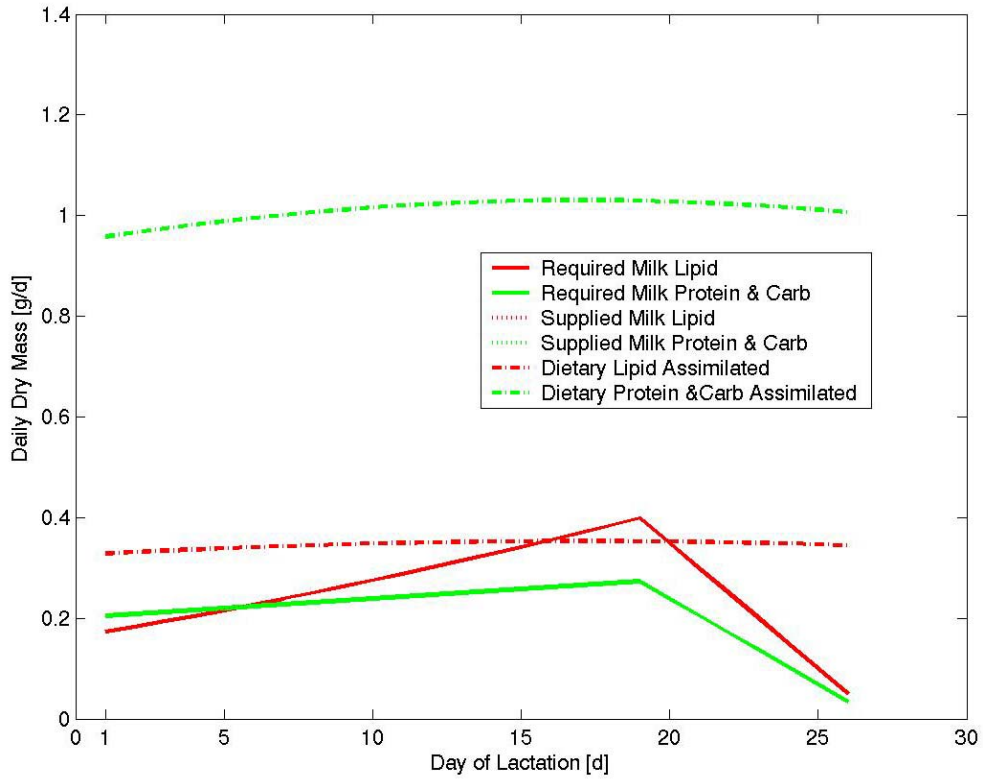


Figure 22 - Milk required, milk supplied, and dietary components for $X_L = 0.06$

Daily estimated "required milk lipid" and "required milk protein and carbohydrates" in solid lines, and "supplied milk lipid" and "supplied milk protein and carbohydrates" in dotted lines for a lactating female. Dotted lines are not visible when supplied amount overlaps with the required amount. Dietary lipid, protein and carbohydrate assimilated are also represented. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for those related to diet composition: $X_L = 0.06$, $X_P = 0.186$.

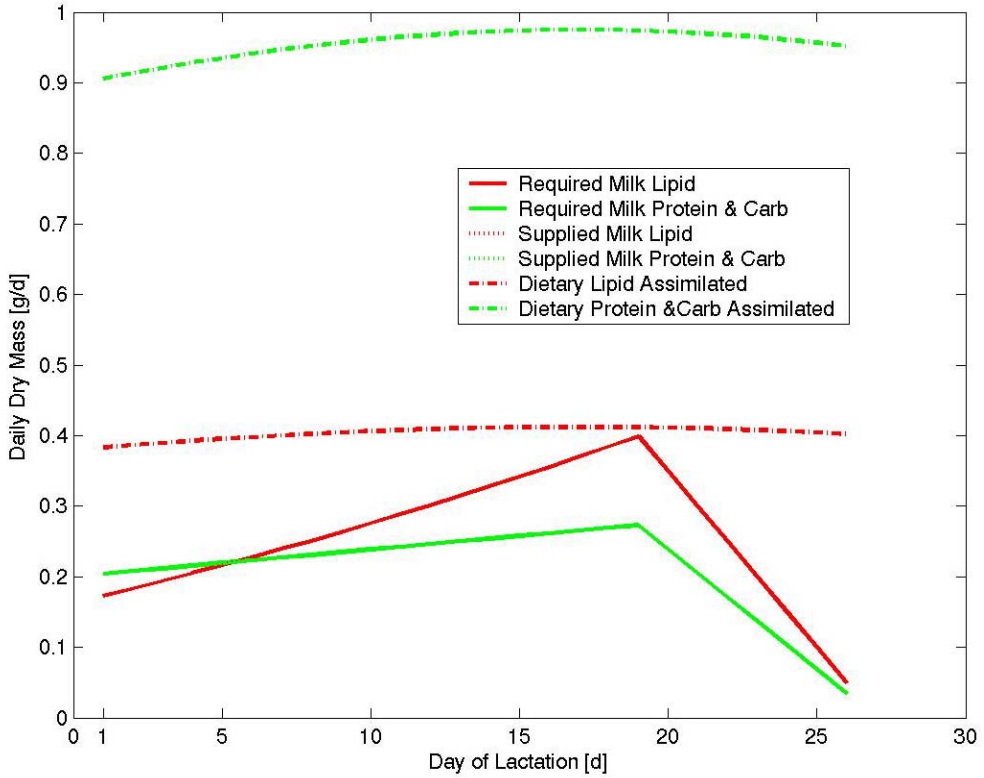


Figure 23 - Milk required, milk supplied, and dietary components for $X_L = 0.07$

Daily estimated "required milk lipid" and "required milk protein and carbohydrates" in solid lines, and "supplied milk lipid" and "supplied milk protein and carbohydrates" in dotted lines for a lactating female. Dotted lines are not visible when supplied amount overlaps with the required amount. Dietary lipid, protein and carbohydrate assimilated are also represented. The parameters values for this simulation are those indicated in Table 1 to Table 9 except for those related to diet composition: $X_L = 0.07$, $X_P = 0.176$.

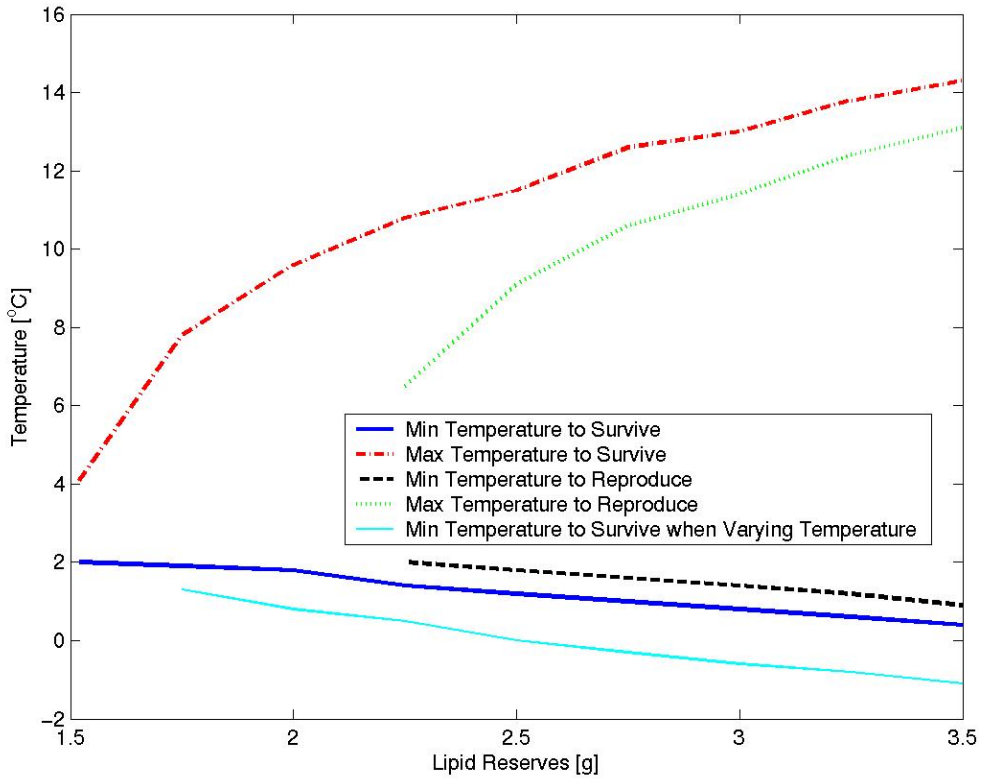


Figure 24 - Temperature ranges for successful hibernation

Constant maximum and minimum temperatures during entire hibernation period under which can bat survives or survive and reproduce with the lipid reserves given in the horizontal axis. If a temperature profile is assume the light blue line represents the minimum temperature in the profile. In these simulations winter ley se muength was assumed to be constant, 193 days, with a total of 12 arousals, one occurring every 16 days. All other parameters are those indicated in Table 1 to Table 9.

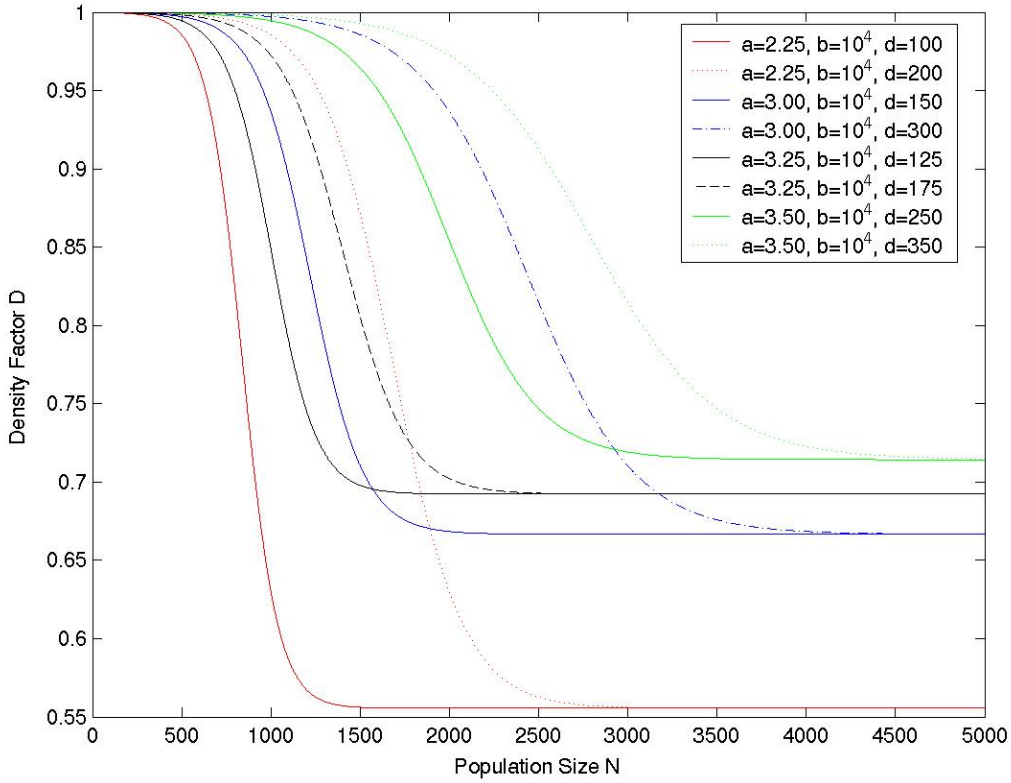
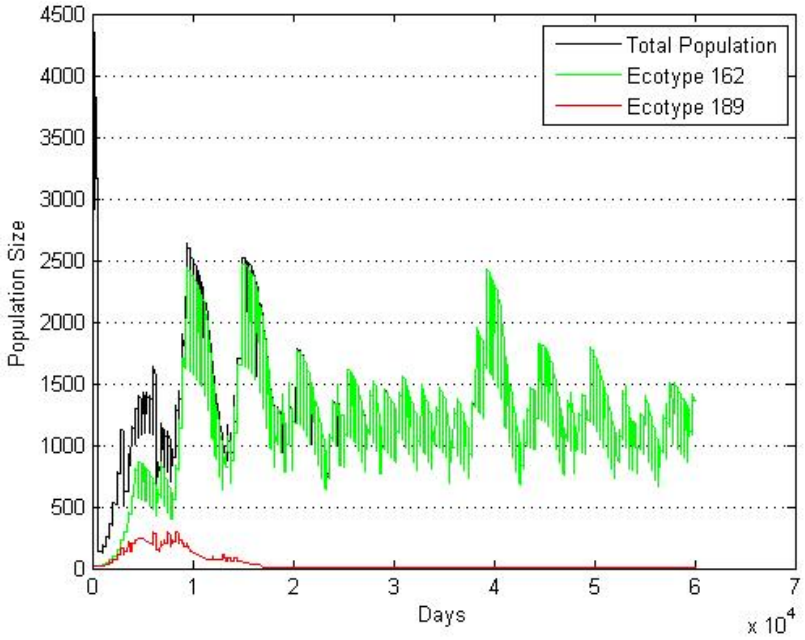


Figure 25 – Density factor function

The density factor or penalty function decreases the feeding rate of individuals as total population size increases and takes the following form:

$$D(N) = 1 - \frac{1}{a + b\exp\left(-\frac{N}{d}\right)}.$$

a)



b)

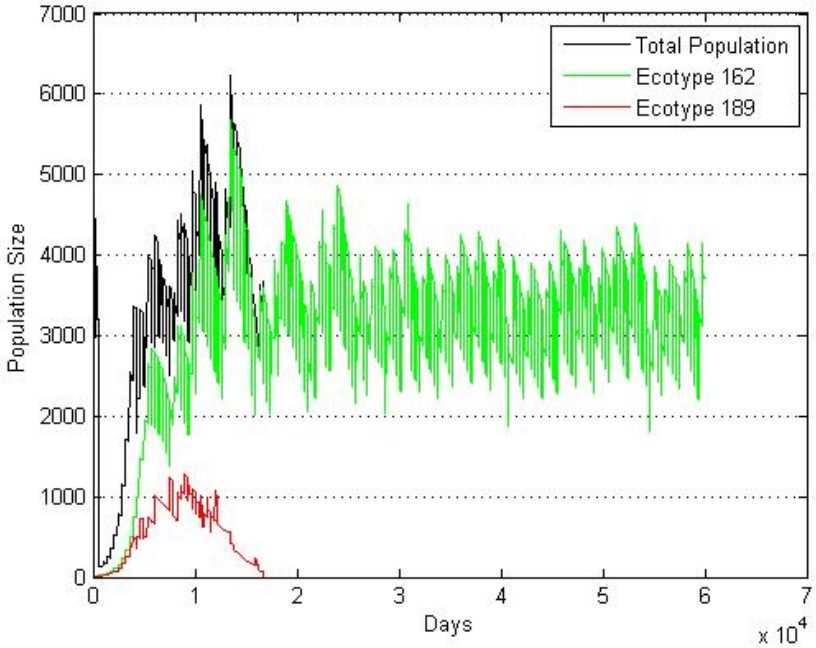


Figure 26 – Persistent population dynamics

a) Set 1, ID#32, $a = 3.75, d = 100$ b) Set 1, ID#35, $a = 3.75, d = 300$

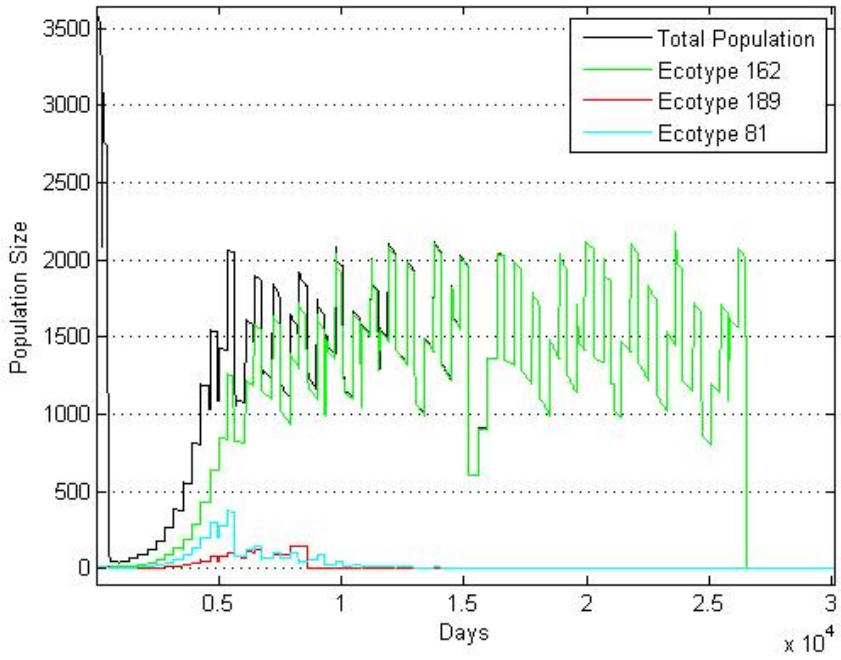
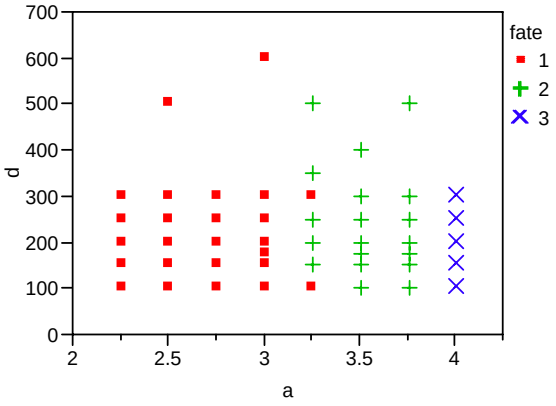


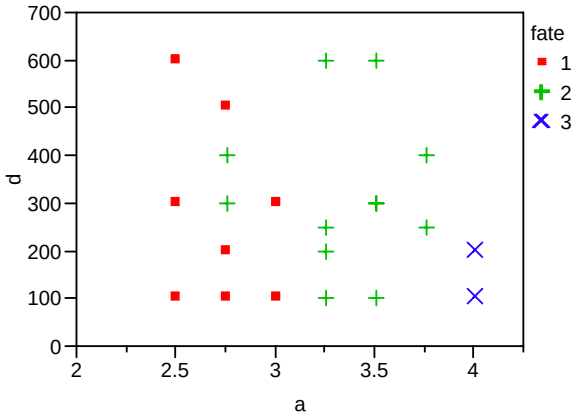
Figure 27 – Extinct population dynamics

Set 1, ID#25, $a = 3, d = 175$

a) Low age dependent mortality



b) Intermediate age dependent mortality



c) High age dependent mortality

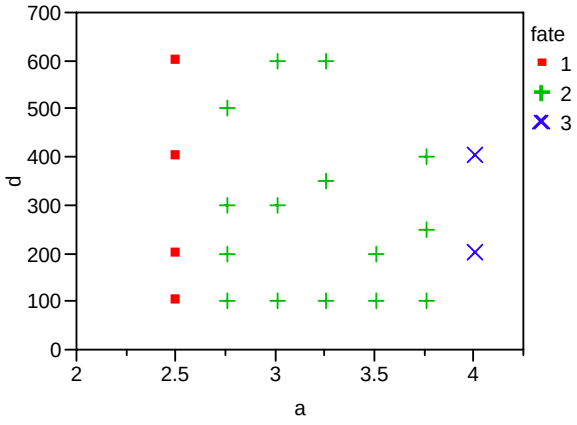
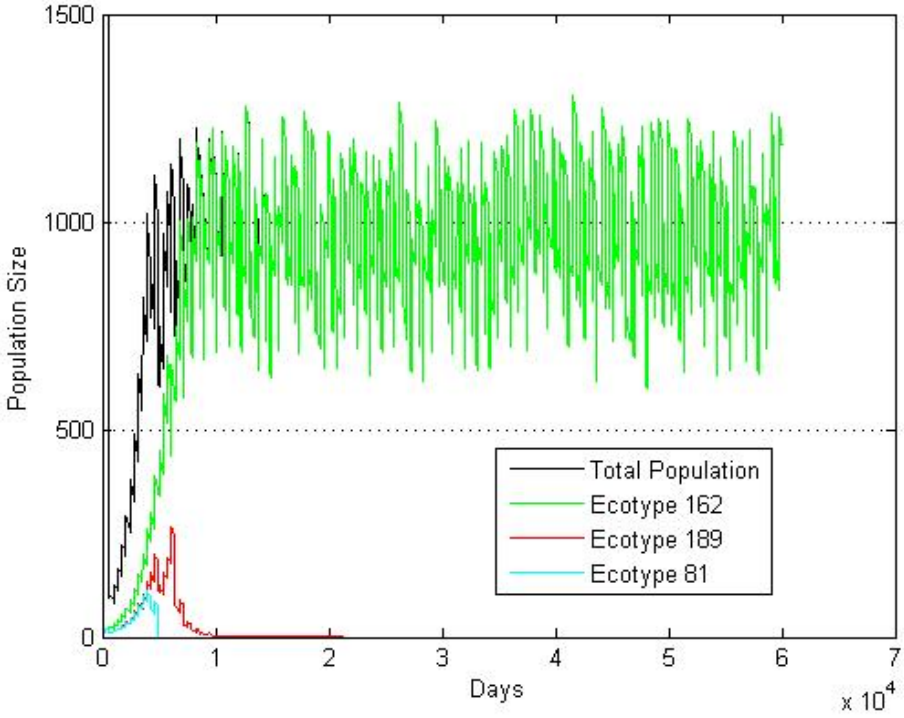


Figure 28 – Persistence and extinction regions in the parameter space $a \times d$

Fate 1 means extinction, 2 means persistence, and 3 means exponential growth. Figure a) corresponds to simulations in Set 1, b) in Set 3, and c) in Set 2.

a)



b)

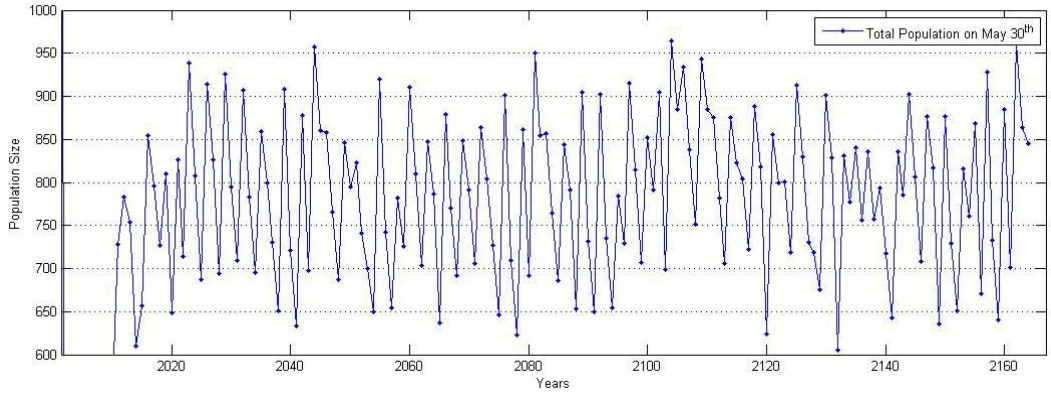
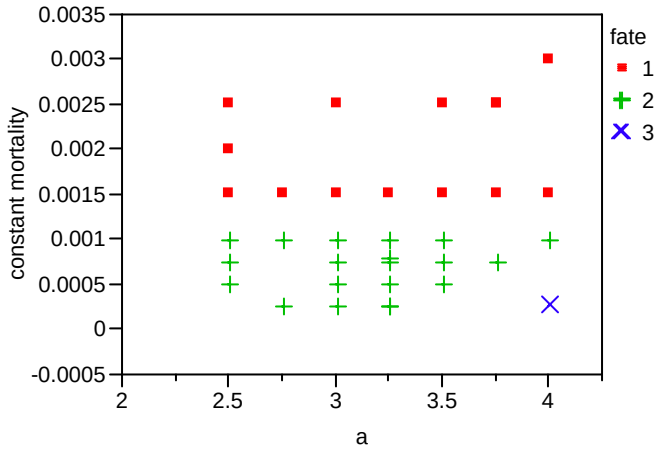


Figure 29 – Oscillatory dynamics

Set 2, ID#89, $a = 3.5$, $d = 100$

a)



b)

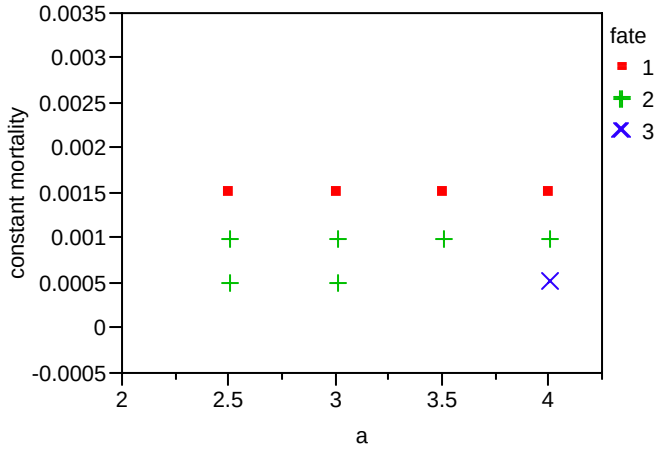


Figure 30 – Persistence and extinction regions in the parameter space $a \times \eta$

Fate 1 means extinction, 2 means persistence, and 3 means exponential growth. Figure a) corresponds to simulations in Set 4 with $d = 100$, b) in Set 4 with $d = 300$. Extinctions in Set 4 occur as a sharp decrease in population at the beginning of the simulation, and then the population does not recover.

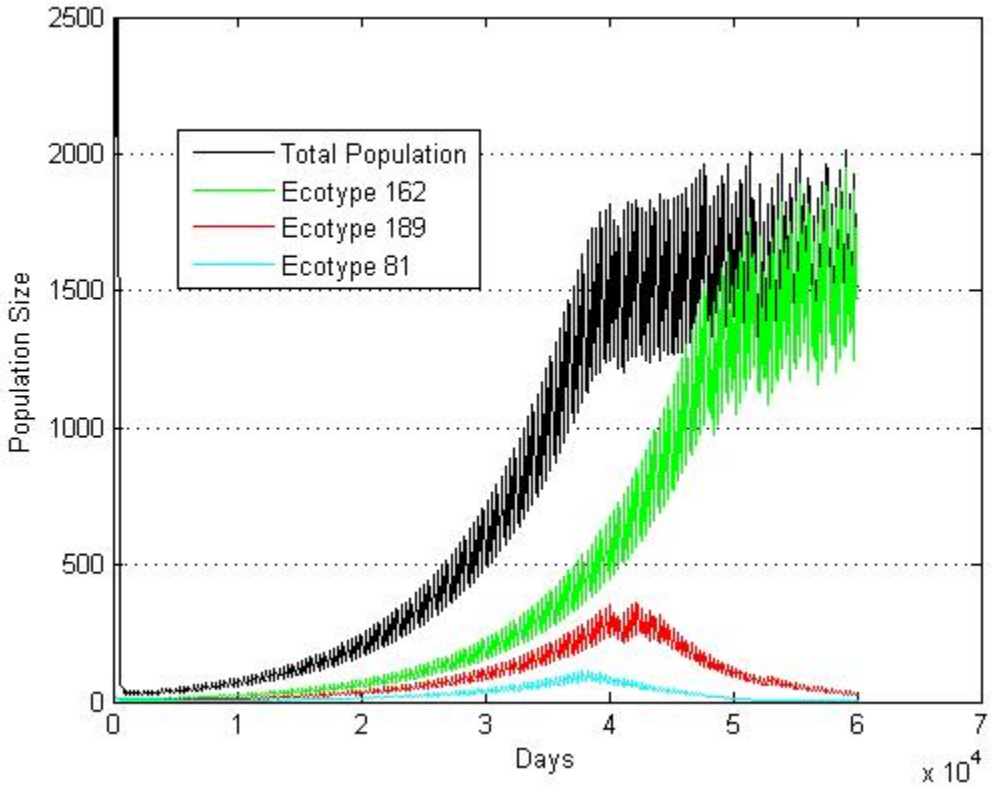
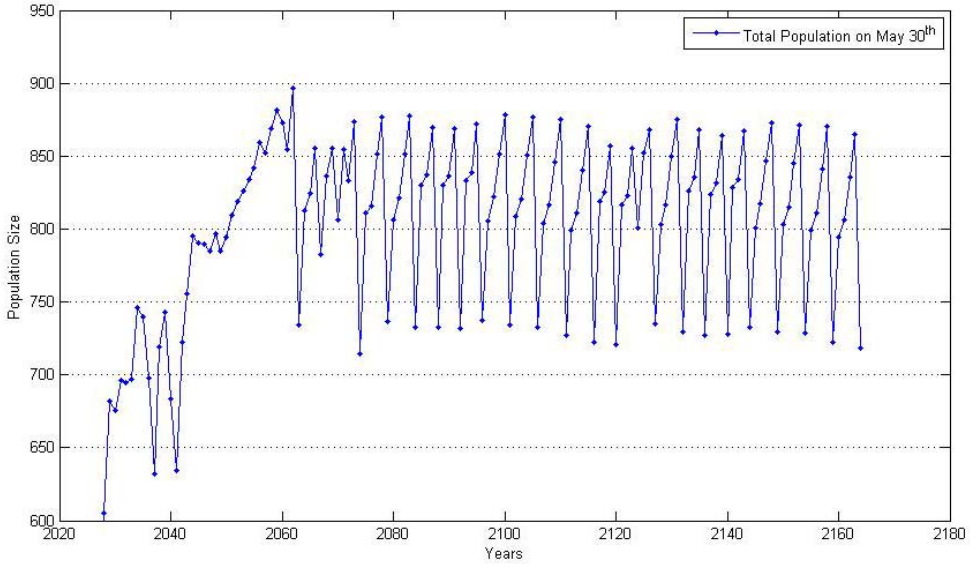


Figure 31 – Gradual extinctions of unsuccessful ecotypes

Set 4, ID#64 $a = 3.25, d = 100, \eta = 0.001$

a)



b)

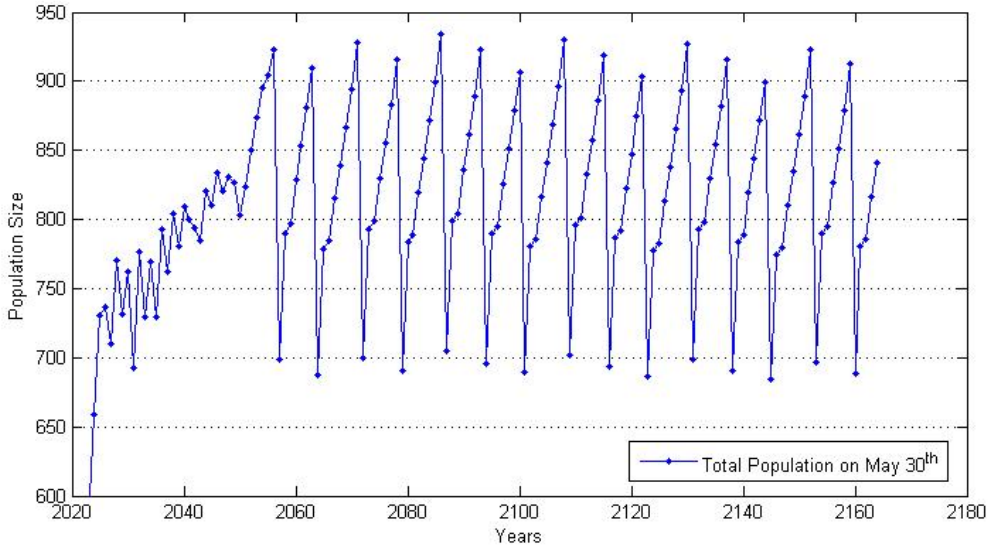


Figure 32 – Oscillatory patterns

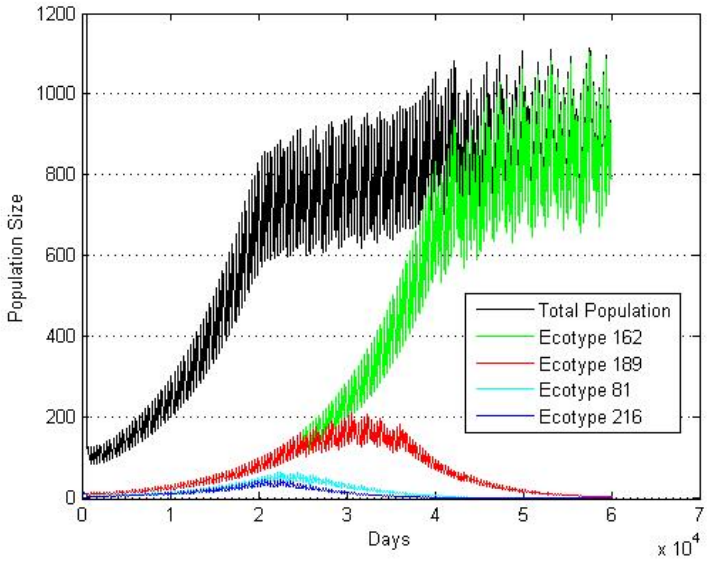
a) Set 4, ID# 124 $a = 3.25, d = 100, \eta = 0.00075$

   Dominant cycle=4.79

b) Set 4, ID# 99 $a = 3.50, d = 100, \eta = 0.00075$

   Dominant cycle = 7.5

a)



b)

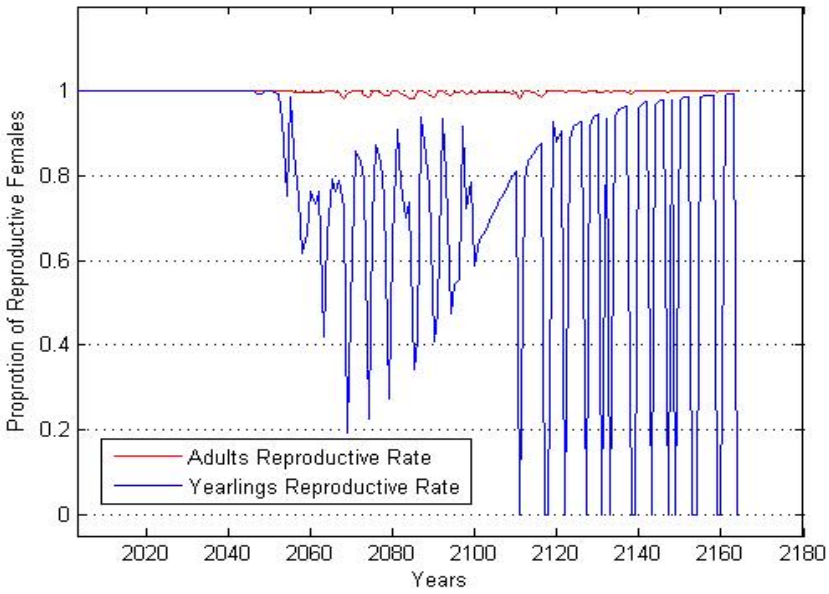
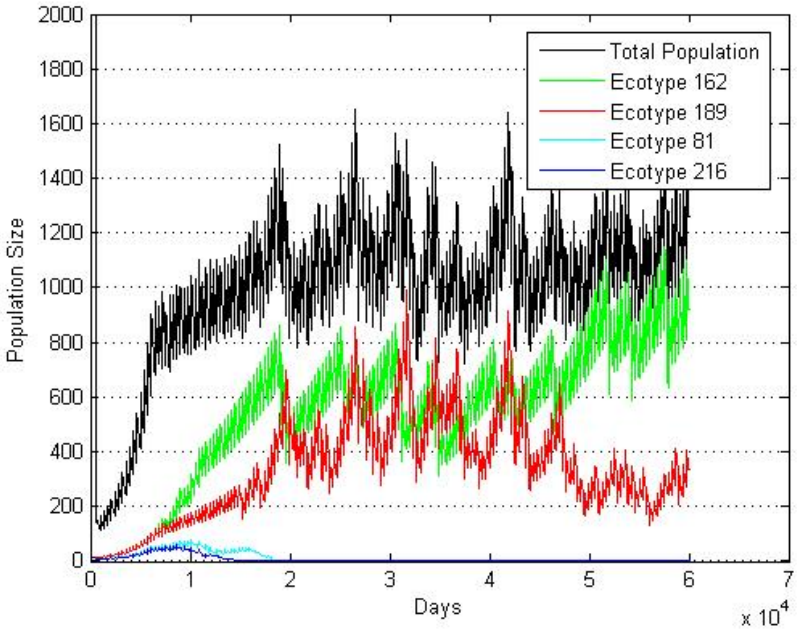


Figure 33 – Regulatory mechanism I

Set 4, ID#109, $a = 4.00, d = 100, \eta = 0.001$

a)



b)

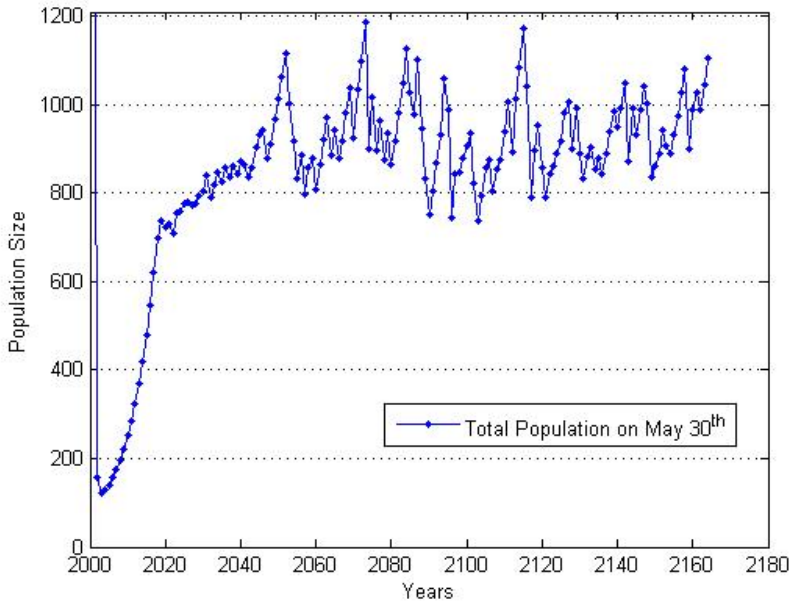
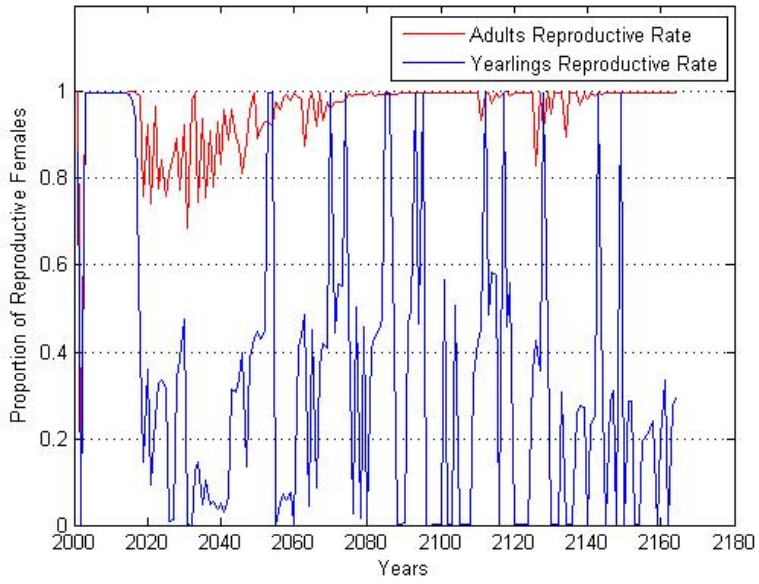


Figure 34 – Regulatory mechanism II (a)

Set 4, ID#148 $a = 4.00, d = 100, \eta = 0.00075$

a)



b)

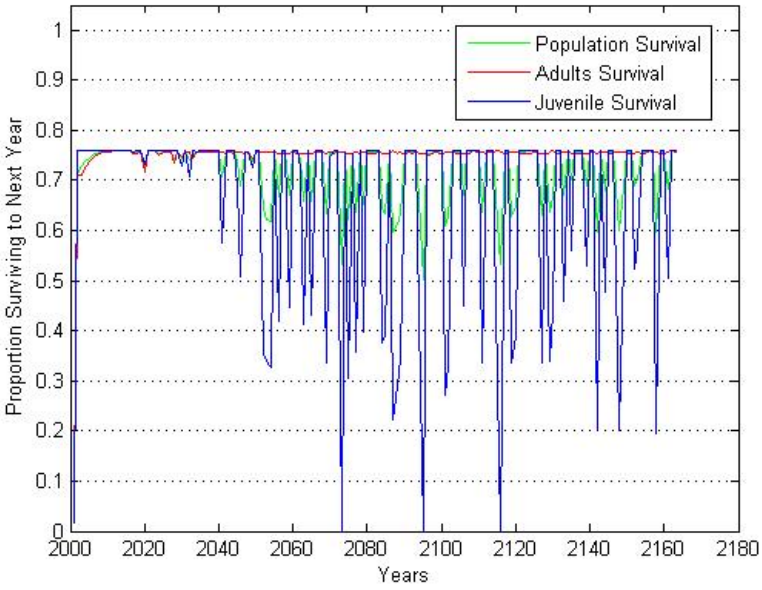


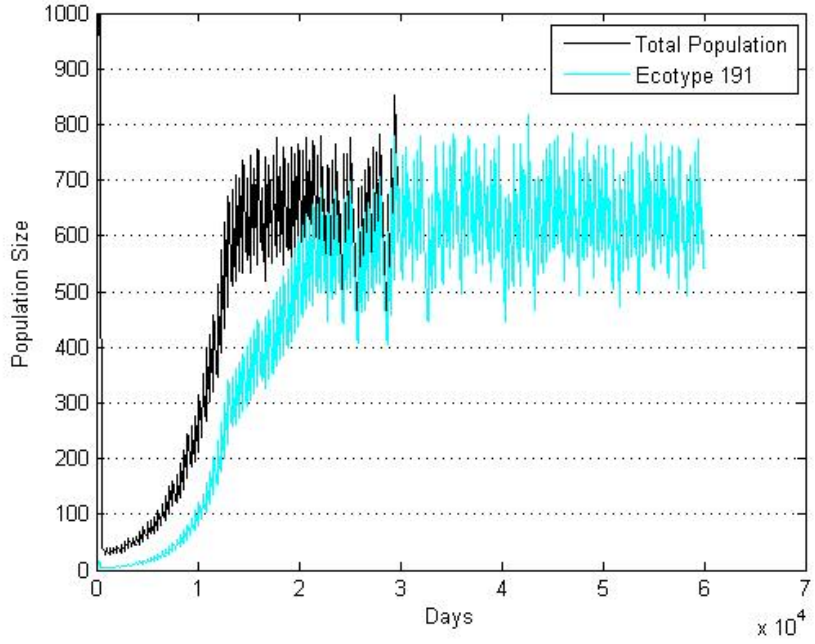
Figure 35 – Regulatory mechanism II (b)

Set 4, ID#148 $a = 4.00, d = 100, \eta = 0.00075$

a) Annual reproductive rate of adults and yearlings

b) Annual survival rate for entire population, adults and juveniles

a)



b)

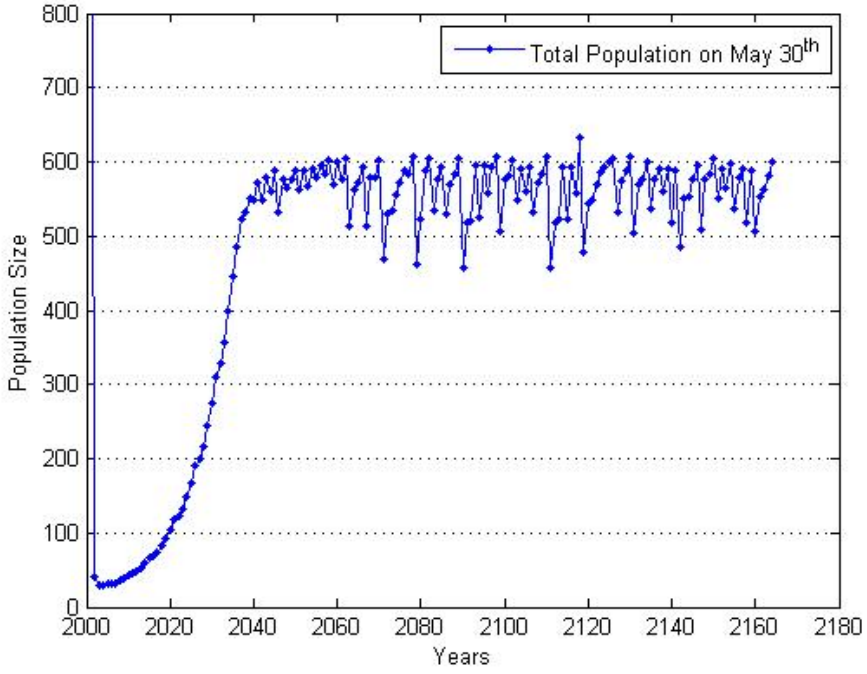
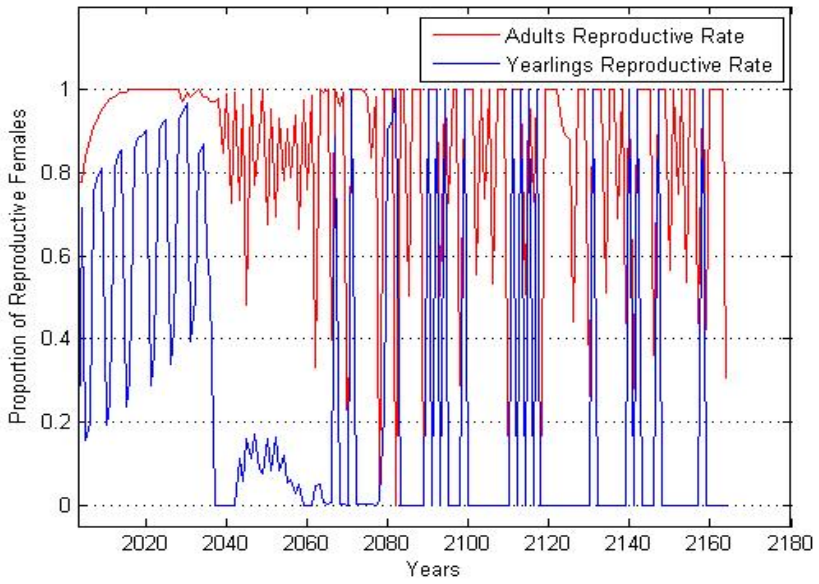


Figure 36 – Regulatory mechanism III (a)

Set4, ID#121, $a = 2.50, d = 100, \eta = 0.00075$

a)



b)

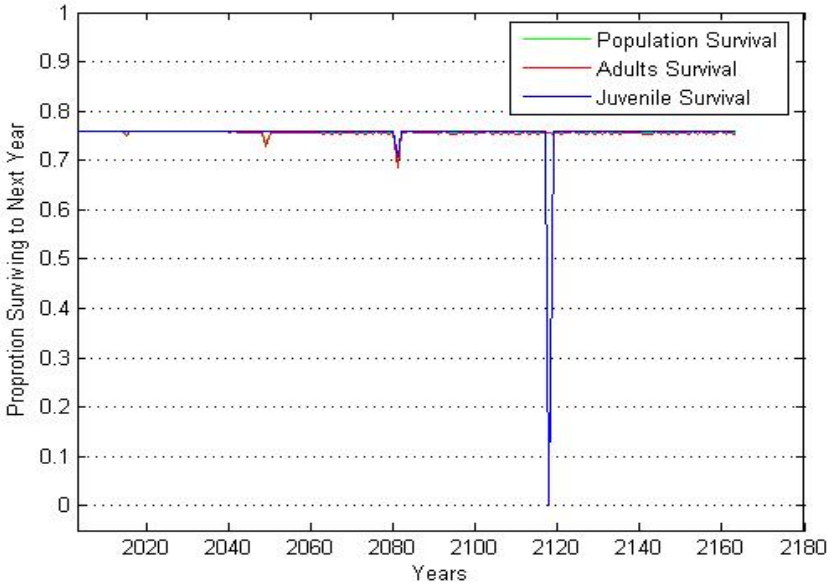


Figure 37 – Regulatory mechanism III (b)

Set4, ID#121, $a = 2.50, d = 100, \eta = 0.00075$

a) Annual reproductive rate of adults and yearlings

b) Annual survival rate for entire population, adults and juveniles

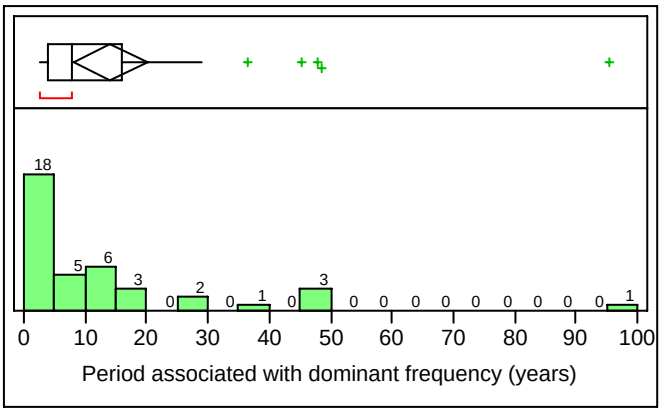


Figure 38 - Distribution of dominant periods

The numbers on the bars indicate number of simulations. The total number of simulations was 39. The median of the distribution is 7.66 years.

VITA

Paula Federico was born in Buenos Aires, Argentina on November 12, 1973. She received her B.A. degree from Universidad Nacional del Centro in Tandil, Argentina, 1998 with major in Mathematics. She then became a teaching and research assistant in the Department of Mathematics at Faculdad de Ciencias Exactas, Universidad Nacional del Centro. In August 2001, she began studying at University of Tennessee in Knoxville. She received a Graduate Certificate in Applied Statistical Strategies in 2006. In August 2007, she graduated with a Doctor of Philosophy degree in Ecology and Evolutionary Biology.