

BAT POPULATION DYNAMICS: MULTILEVEL MODEL BASED ON INDIVIDUALS' ENERGETICS

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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. We present a novel, multilevel theoretical approach that integrates information on bat biology collected at a lower level of organization, the individual with its physiological characteristics, into a modeling framework at a higher level, the population. Our individual component describes the growth of an individual female bat by modeling the dynamics of the main body compartments (lipids, proteins, and carbohydrates). A structured population model based on extended McKendrick-von Foerster partial differential equations integrates those individual dynamics and provides insight into possible regulatory mechanisms of population size as well as conditions of population survival and extinction. Though parameterized for a specific bat species, all modeling components can be modified to investigate other bats with similar life histories. A better understanding of population dynamics in bats can assist in the development of management techniques and conservation strategies, and to investigate stress effects. 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.

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1. Introduction. Individual-based population models are useful tools when physiological processes occurring at the level of the individual are important to describe population dynamics. Structured populations models that take into account detailed mechanistic description of physiological processes have been developed for aquatic organisms including fish [15], algae [30], and daphnia [10][3][22]. These models are motivated by a large collection of experimental evidence which indicates that the growth and development of individuals have considerable influence on the dynamics of the population [22]. They emphasize the roles of lipids, proteins, and carbohydrates in relation to the energetics of the individual. The lipid component is particularly important because it serves for energy storage and as regulator of metabolic functions. It also determines the susceptibility of the organisms to hydrophobic chemicals as shown in ecotoxicology applications [10] and other stressors. Andrewartha and Birch [1][2] stressed the need to understand the individual physiological processes, particularly the energetics, in order to assess the influence of abiotic factors such as climate changes or the environment on species distribution. In this paper we apply an individual-based population model to investigate the population dynamics of bats. Concerns for understanding the population dynamics of bats arise from their beneficial roles in many ecosystems as insect predators, seed dispersers, and pollinators [17]. Bats have been identified as the most likely reservoirs for various pathogens, such as rabies and other lyssaviruses, SARS-like coronaviruses [33], Hendra [11], Nipah [12] [25], Ebola [21] and Marburg [31] [32] viruses. This characteristic has motivated increased interest in their ecology, life history, and responses to disease stressors. As a result of new observational techniques, and analytical methods, there have been enormous advances in the study of bats during the past three decades [8][18]. However, little is known about their population dynamics. 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 [24]. Long-term data on birth and death rates and reliable population size estimates over time are essentially nonexistent, although they are fundamental for ecological studies and concerns for conservation, disease ecology, and pest control. We have developed an individual physiological model for bats [7] that describes the dynamics of lipids, proteins, and carbohydrates in terms of resource intake and energetic demands. As expected from animal's life history and confirmed by studies of body composition [19][27], the lipid profile of a female bat is dynamic over the life stages of the individual and plays an important role in population dynamics. The main objective of this work is to examine the implications of these dynamic fluctuations at the individual level on survival and reproduction at the population level. To our knowledge no previous population model has been developed to study bat population dynamics and interface with the available field data.

2. Modeling framework. The proposed integrative framework includes modeling components at individual and population levels and provides descriptive and predictive analysis of the dynamical growth, age structure, and reproductive activity of a colony of little brown bats (*Myotis lucifugus*).

2.1. Individual model. The individual model is built upon the life history characteristics of a hibernating female bat and energetics. It represents the individual by featuring two major compartments: "lipid" (fats) and "structure," and associates them with energetic flows (Fig. 1). Each compartment consists of a labile

and nonlabile portion. Protein and carbohydrate are aggregated in the “structure” compartment to maintain the model in a simple representation, but this union is sufficiently complex 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 [20]. Lipid synthesis from proteins and carbohydrates is a novelty that was not featured in previous models constructed under this framework [10][9].

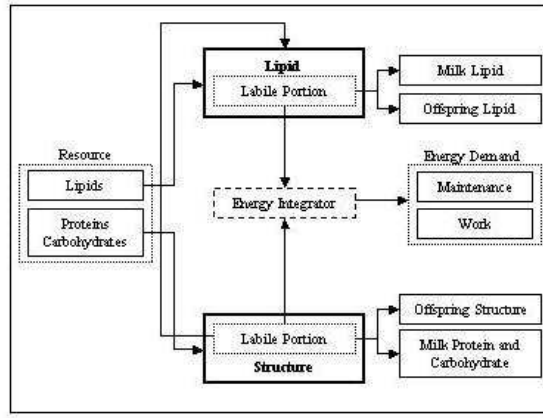


FIGURE 1. Conceptual flow diagram for the individual model

On a continuous time scale, the individual model of a female bat consists of two ordinary differential equations representing the rates of change of the mass of lipid, m_L , and the mass of structure, m_S . The mass of protected structure (nonlabile portion), m_{PS} [g], is assumed to be nondecreasing with age and is a constant proportion of mass of structure; i.e., $m_{PS} = \alpha m_S$. Nonlabile lipid is given by ϵm_{PS} [g] where ϵ is a dimensionless parameter that gives the ratio of non-labile lipid to nonlabile structure. Given these representations, the mass of labile lipid is given by $(m_L - \epsilon m_{PS})$ and the mass of labile structure by $(m_S - m_{PS})$. The rates of change of the mass of lipid and the mass of structure are determined by the differences in the inputs and outputs shown in the conceptual diagram and depend on the amount of the available energy (E_A) relative to the energetic demand (E_D) as follows:

If $E_D < E_A$:

$$\begin{aligned} \frac{dm_L}{dt} &= A_L X_L F - M_L (m_L - \epsilon m_{PS}) \frac{E_D}{E_A} + e S M_S (m_S - m_{PS}) (1 - \frac{E_D}{E_A}) = g_L \\ \frac{dm_S}{dt} &= A_S X_S F - M_S (m_S - m_{PS}) \frac{E_D}{E_A} - S M_S (m_S - m_{PS}) (1 - \frac{E_D}{E_A}) = g_S. \end{aligned} \quad (1)$$

If $E_D \geq E_A$:

$$\begin{aligned} \frac{dm_L}{dt} &= A_L X_L F - M_L (m_L - \epsilon m_{PS}) = g_L \\ \frac{dm_S}{dt} &= A_S X_S F - M_S (m_S - m_{PS}) = g_S. \end{aligned} \quad (2)$$

The available food resource, x , is a function of time that reaches a maximal peak in abundance in July. The proportions of lipid and structure (proteins and

carbohydrates) of the resource are denoted by X_L and X_S while A_L and A_S stand for the assimilation efficiencies of the lipid and structure. The feeding rate F is a Holling type II function of the resource x . The coefficients M_L and M_S measure the labile lipid and labile structure mobilization rates. The energy available E_A is given by $e_L M_L (m_L - \epsilon m_{PS}) + e_S M_S (m_S - m_{PS})$, where e_L and e_S are the energetic contents of one gram of lipid and structure respectively. The energy demand E_D is a function of the individual physiology, morphology, and temperature as an environmental variable/parameter. Its formulation changes during the various periods of the life history such as hibernation, migration, pregnancy, lactation, and prehibernation. The first positive terms in the equations (1) and (2) correspond to assimilated lipid and structure through feeding whereas the first negative terms represent the losses due to maintenance (basal metabolism and thermoregulation costs), activity (flight cost), and reproduction (allocation to neonate tissue and milk production). When the available energy exceeds the energetic demand additional terms in the equations (1) express the transfer of structure into lipids (lipid synthesis). The function $S = S(m_S)$ represents the fraction of the energy excess to be stored as lipid and 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. Two aspects of the individual model utilize its unique integration with the population model: individual's reproduction and mortality. In the individual model a female reproduces only if her lipid reserves at the end of hibernation are sufficient to promote ovulation. Each pregnant female produces one offspring at the beginning of the summer. Mortality is assessed at the individual level by the negative energy balance rule, which implies that if the energy demand remains greater than the available energy for a predefined period the individual dies. Further details of this model can be found in [7]. Body composition dynamics generated by the individual model are shown in Figure 2 for an adult female bat. In addition to the lipid and structure components, measured in grams of dry mass, the water portion of the individual and the total wet weight can be calculated. The water compartment is assumed to be a constant proportion of structure compartment. The wet weight of the individual is equal to the sum of the mass of each compartment (lipid, structure, and water).

2.2. Population model. The energetic-based individual model summarized above forms the core of the structured population model presented here. To study the dynamics of the population, the individual growth model is incorporated into a system of hyperbolic partial differential equations of extended McKendrick-von Foerster type:

$$\frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial a} + \frac{\partial(\rho g_L)}{\partial m_S} + \frac{\partial(\rho g_S)}{\partial m_S} = -\mu(\rho)\rho, \quad (3)$$

where the population density function, $\rho = \rho(t, a, m_L, m_S)$, is given in numbers at time t , per age a , per mass of lipid m_L , per mass of structure m_S , per volume of environment; and μ is the mortality rate. The growth rates of the lipid and structure components, represented by g_L and g_S , are calculated from the individual

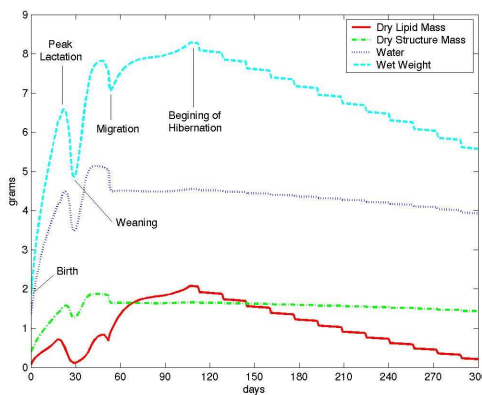


FIGURE 2. Numerical simulations of the dynamics of the individual model

model equations (1 and 2). The birth process is specified by a boundary condition:

$$\rho(t, 0, m_{L0}, m_{S0}) = \int_0^\infty \int_{m_{L0}}^\infty \int_{m_{S0}}^\infty \beta(t, a, m_{L0}, m_{S0}, m_L, m_S) \rho(t, a, m_L, m_S) dm_S dm_L da. \quad (4)$$

The birth function, β , represents the number of offspring with body composition corresponding to (m_{L0}, m_{S0}) given by females with body composition (m_L, m_S) . This function is formulated directly from the reproduction assessed at the individual level. It takes value 1 at the time of parturition for females with lipid mass m_L above the reproductive threshold level at the time of ovulation. Otherwise it equals 0. Because different types of mortality are assessed, details on the mortality rate will be given later. Variation among individuals within the population is implemented through different ecotypes, which are groups of individuals with the same defining characteristics, i.e., same individual model parameters. We introduce additional partial differential equations, one for each ecotype, and integrate them through growth and mortality mechanisms at the population level. From the list of all individual characteristics, those that represent foraging ability (*maximum feeding rate, half saturation constant in feeding rate*), size (*minimum structure, maximum structure*), and physiological characteristics (*euthermic body temperature, water to structure ratio*) were chosen to build the ecotypic structure of the population. They have been selected by their biological significance as determined through experimental data or by their influence on dynamical properties of the individual model, identified through sensitivity analysis. We consider a population structured of 243 ecotypes as each of the above parameters assumes one of three predefined levels (low, medium, and high).

We study the dynamics of the McKendrick-von Foerster system by the method of characteristics that reduces the partial differential equations to systems of ordinary differential equations along the characteristic curves. This allows us to follow groups of individuals (cohorts) of the same age and identical body compositions (lipid, structure, and water). Since solutions cannot be found explicitly we use numerical simulations to track these cohorts of individuals from different ecotypes as they live, reproduce, and die. Figure 3 shows population density by age aggregating over all ecotypes and cohorts of different body composition for each age. Note that the total

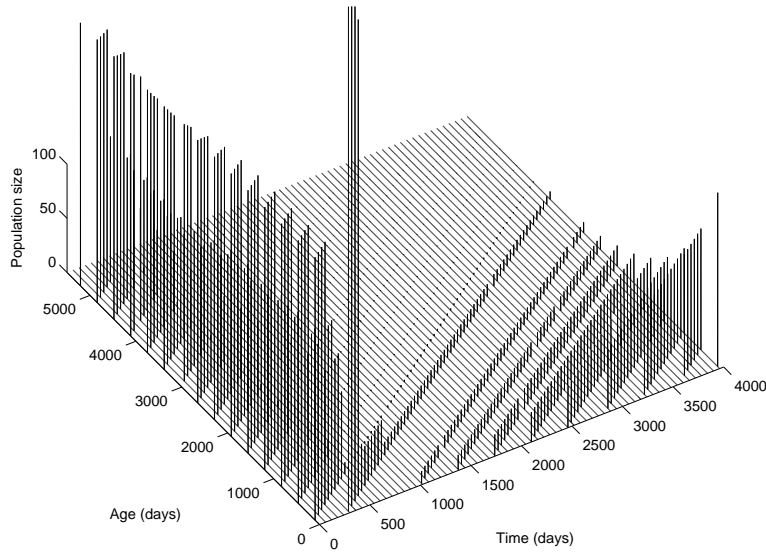


FIGURE 3. Age cohorts along the characteristic curves

population size, $N(t)$ is given by the integral of $\rho(t, a, m_L, m_S)$ over the variables a , m_L , and m_S at each time t and summed over all the existing ecotypes. A brief description of the specific mechanisms of cohorts' integration follows.

2.2.1. Reproductive mechanism. During the reproduction period cohorts of newborns arise with body compositions resulting as a function of mothers' compositions following the rules established in the individual model. Several cohorts of the same age might have similar but distinct body composition and consequently would have to be treated separately. This can potentially lead to an enormous number of cohorts after just several reproduction cycles increasing substantially the computational cost of the simulations. We establish a control on the number of cohorts by a modified birth mechanism that place all newborns from each ecotype in only 3 distinct cohorts based on the estimated lipid content at birth. The resulting groups of "small", "medium", and "large" pups combine the babies of maternal cohorts with similar body compositions. A system of tags is used to indicate mother-daughter relationships in order to assess lactation and mortality processes affecting both cohorts. The milk intake of each daughter cohort is generated by the corresponding mother in terms of its body condition and food intake. If a newborn cohort dies, the connected mothers change their physiological status from lactating to post-lactating. Conversely, if a part of maternal cohort dies during lactation a corresponding proportion of its daughter cohort dies.

2.2.2. Density-dependence mechanism. Competition for a common resource between individuals from a common habitat is an important factor that regulates the population size and prevents it from explosion. In standard predator-prey models it is introduced through additional terms in the functional response function to express the mutual interference between predators [4][16]. In most of the structured population models constructed under the energetic framework intraspecies competition is accounted through a mortality rate depending on the population density [10][9].

We utilize a novel approach to address that problem through density-dependent depression of the available resource x . A density factor $D(N)$ is introduced to decrease the individual feeding rate $F(x) = \frac{Mx}{x+i}$ as total population size N increases. The resource available for an individual bat at a given time diminishes by the density factor $D(N)$ and the individual's feeding rate takes the form $F(x) = \frac{MxD}{xD+i}$. An equivalent representation of the feeding rate $F(x) = \frac{Mx}{x+\frac{1}{D}}$ can be interpreted as an increase in difficulty required for capturing the resource due to the interference among bats foraging in the same area.

We consider the following class of functions to represent the density factor:

$$D(n) = 1 - \frac{1}{a + b \exp(\frac{-N}{D})}, \text{ with } b > 0, d > 0, a \geq 1. \quad (5)$$

The parameter a regulates the minimum portion of the resource that remains available to the bat while the parameter b is responsible to ensure a sufficient range for the density factor to operate as a regulator of the population size. The decrease in the resource is equal for all bats as the population density increases, which has been defined as intraspecific scramble competition [23]. The decrease in the feeding rate caused by an increasing population leads to lower resource intake, which affects the energy balance and causes death based on 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) if the bat could not build sufficient reserves to meet future energetic demands. 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. If the population growth is high enough, it is likely that no bat captures sufficient resources to allow for reproduction. This leads to an overcompensatory response of the population to density dependence [14].

2.2.3. Background mortality mechanism. The main mortality in the model is assessed at the individual level through the negative energy balance rule that controls the success of the individual to satisfy its energetic demands by energetic distribution of the available resources from food uptake and storage. However, bats are subject to other natural causes of mortality that need to be in the population model. All other factors related to natural mortality such as aging, accidents [13], and dispersal from the population, are handled by the background mortality mechanism. We implement and simulate two distinct formulations of that mechanism. First, we assume a uniform background mortality level for all ages. This scenario expresses the idea that the probability of accident and dispersal do not vary significantly between different age groups; i.e., it does not depend on the demographic profile of the colony. Its average cross-ecotypic level is determined by the estimates provided by [13]. In our second scenario the life expectancy of bats is assumed to follow a normal distribution with a mean value equal to one of three distinct levels corresponding to early, medium, and late mortality peaks. This scenario allows us to analyze the affect of age-dependent dispersal and mortality patterns on the population dynamics. The final component of our mortality mechanism is the “terminal age mortality” that kills the remaining bats in each cohort when they reach a predefined “maximum” age estimated from the available bat ecology data [17]. The background mortality at the population level and the negative energy balance mortality at the individual level are assessed daily.

3. Results. We use the multilevel model described in the previous section to investigate the expected population fluctuations in several scenarios with respect of the major modeling parameters. We concentrate our attention on the effects of the variations in background mortality and density factor function on the dynamics of the total population size as well as the ecotypic and age structure of the colony. We also analyze the annual survival and reproductive rates of bats recorded for three distinct groups: juveniles (offspring from birth to beginning of first hibernation), reproductive “yearlings” (adults born the previous season, less than one year), and reproductive “adults” (older than one year). The survival rates for the entire population, adults and juveniles are 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 stands for adults older than one year, Y_t are yearlings, and J_t are juveniles. The reproductive rates are also estimated annually at midpregnancy 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. A comparison between annual survival rates for adults vs. juveniles and annual reproductive rates for adults vs. yearlings allow us to understand their influence on the observed population dynamics. The complexity of the modeling setup does not allow systematic analytical work and therefore all dynamical patterns are explored numerically. All simulations to study the behavior of the population model start at the beginning of hibernation period with 243 ecotypes; each composed of fifteen equally distributed cohorts. An extensive set of computational runs helped us to identify three possible dynamical outcomes for such a heterogeneous colony: a) extinction of the population, b) oscillatory population dynamic that persists in time, and c) long-term stable exponential growth. We will concentrate in the description and analysis of the first two kinds of dynamics. We consider that the combinations of parameters that lead to exponential growth do not correspond to a realistic situation. The computational time needed to complete one simulation varies significantly depending on the resulting dynamics. Because most of the scenarios are characterized by a gradual reduction of the remaining ecotypes, the time to simulate every consecutive year decreases. An average simulation of a persistent population takes approximately 1.5 CPU hours to complete running on a Solaris Intel Xeon 2.8 GHz, 1 GB Ram. It is important to note that all the alternative scenarios are investigated under constant environmental conditions and predefined seasonal fluctuations in temperature and resource’s availability. Effects of environmental changes are left for future analysis under a stochastic formulation of the environmental parameters in the individual model.

3.1. Population dynamics with constant background mortality. Variations in the parameters a and d of the feeding factor function $D(N)$ as well as in the constant background mortality, η , are studied to understand how each of the observed dynamical outcomes occurs. Population extinctions are the result of a rapid population decay under the assumption of high background mortality ($\eta > 0.0015$ daily rate, equivalent to 42% annual mortality). At this level the background mortality governs the population dynamics because the reproductive gains are not enough to support of the colony. The degree of densitydependence does not influence the fate of the population. Conversely, a persistent population is observed when the background mortality η is low. In this case the colony can overcome its accidental losses and outgrow them through reproduction. When the density pressure is

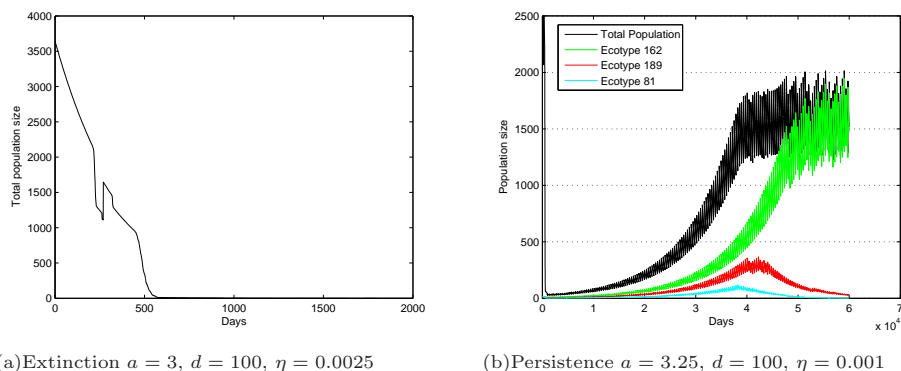


FIGURE 4. Population dynamics with constant background mortality

weak, the resource availability remains strong even for a large colonial size and it is enough to keep the individual bats healthy and reproductively active. As a result, the population grows exponentially.

The population shows oscillatory dynamics that persist in time for low and intermediate values of background constant mortality (see Fig. 4.b), even under strong density-dependent limitations in the resource. The simulations in this dynamical scenario support the standard “survival of the fittest” paradigm; i.e., lead to population dominated by a single ecotype. In most of the cases this ecotype is the one with ideal individual characteristics (Ecotype 162) including the highest maximum feeding rate, the lowest value for the feeding half-saturation constant, and the minimum values for all the other parameters that ensure the lowest energetic demand. However, in a few simulations the dominant ecotype is different from the ideal one. In these cases the lack of the individual fitness might be compensated by the communal ability to control population size in manageable ranges that prevent sharp decreases in the available resource and consequent starvation problems. The age structure of dominant ecotypes consists of seven to fourteen cohorts, which means that the environmental conditions provide stable resource levels for the adult individuals to grow and give birth almost every year.

In the cases of oscillatory dynamics we investigate the periodicity patterns in the population size (Fig. 5). To better describe and summarize this dynamical aspect, we calculate the fast Fourier transform (FFT) for the simulations in which the population persists and estimate the dominant frequencies. For each simulation the FFT is calculated only for the oscillatory part of the series of total annual population size. 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. We found no significant correlation between the period and parameter a , or the period and the average life span of the individual. However, simulations that express quasiperiodic dynamics without sudden drops in the population size show cycles from 2.6 to 10 years. This provides a possible explanation of the persistent changes in the size of some bat colonies that have been attributed to imperfect counting mechanisms.

3.2. Population dynamics with age-dependent background mortality. In this set of simulations the resulting dynamic was explored across the parameter

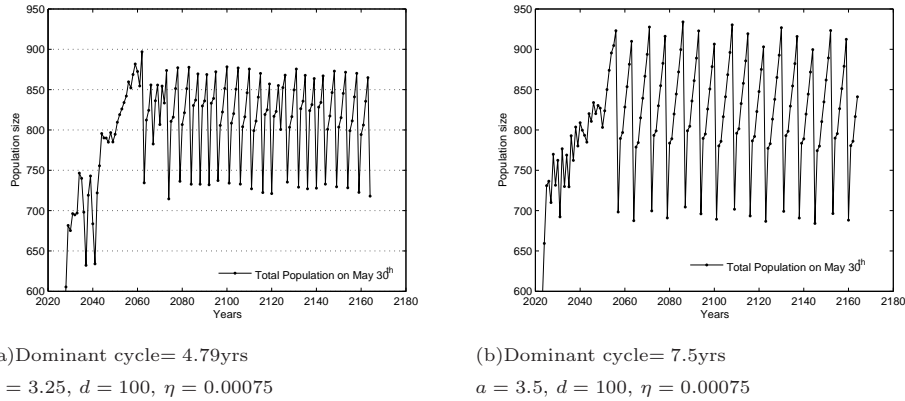


FIGURE 5. Oscillatory patterns in population dynamics

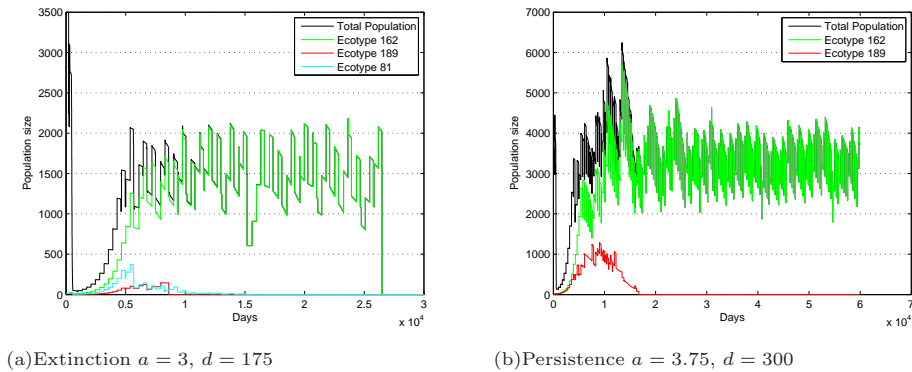


FIGURE 6. Population dynamics with age-dependent background mortality

space generated by parameters $a, b,$ and d in the density factor function $D(N)$ as well as the mean lifespan and standard deviation of the normal distribution associated with the age-dependent background mortality. We investigate what combinations of those parameters lead to each of the possible dynamics, namely a) population extinction, b) persistent oscillatory dynamics or c) stable exponential growth. Our analysis shows that the parameter a that regulates the maximum level of density-dependent reduction of the feeding rate has the greatest influence on the fate of the population while the parameter d affects the boundaries of the oscillatory dynamics. An increase in d causes an increase in the minima and maxima of the population. Parameter b did not produce any qualitative changes in the dynamics.

Colonial extinctions in this scenario are results of sudden crashes occurring when density pressure is sufficiently high (Fig. 6.a). Characteristically, the population experiences a period of oscillatory behavior that can persist more than two hundred years, followed by a total population collapse from high population numbers. Populations are specifically vulnerable to such an event at the end of a hibernation period or shortly after the beginning of the active season when the individuals' energy reserves are exhausted and food is still very scarce. That dynamical alternative is observed in populations with high intrinsic growth rates and attributed to a high

responsiveness to environmental changes [29]. Moreover, some recent studies [28] suggest 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 earlier, our population model represents overcompensatory growth, and that translates to the tendency of the model to yield population crashes from high densities. However, the crashes in the models simulations do not occur after the population reaches a certain threshold. A collapse can occur when the colony is at a local peak in size that is lower than previously recorded values. This indicates that high population size is not the only factor driving a population to extinction and confirms the role of the individual characteristics in that process. At the individual level, bats die because they cannot meet the energy demand directly related to their lipid and structure content. Consequently, the chances of surviving the hibernation period with enough energy resource are strictly individual. On the other hand, the feeding rate is accessed at population level and depends on the size of the colony. Therefore the level of the accumulated energy reserves for hibernation directly relates to the population density. During a population peak, the lack of appropriate reserves may lead to the death of some or all cohorts. Similarly, individuals' physiology influences the ability of the bats to reproduce. The history of reproductive events of a female bat partially determines its body condition at the beginning of hibernation and throughout winter survival. Not surprisingly, the cohorts that survive a population peak and consequent severe population decrease are those that did not reproduce in the previous active season and preserve higher lipid reserves to face hibernation. The scenario with persistent oscillatory population dynamics occurs at intermediate values of parameter a , and for all values of parameter d . The ranges of values of parameter a that lead to persistence vary with changes in the parameters associated with the life span distribution. When the life span distribution assumes a lower mean life span and lower standard deviation the region of persistence is expanded. For example simulations for $2.5 < a \leq 3.25$ which result in extinction for mean life span of 10 years and a standard deviation of three years, persist for simulation time of sixty thousand days a mean life span of three years and a standard deviation of one year. This suggests that a population with lower life expectancy is less affected by a high-density dependence pressure and consequently lower "negative energy balance" mortality. Thus, shorter life expectancy of individuals helps the population to self regulate and prevent population crashes. Population dynamics in this scenario expresses similar properties with regard to the "survival of the fittest" paradigm and the dominant ecotype characteristics. A distinctive dynamical difference is that the structure of the dominant ecotype consists of only 3 to 6 cohorts of nonconsecutive ages as a result of several consecutive years in which individuals do not reproduce. Exponential growth occurs for sufficiently low-density dependence pressure.

3.3. Annual survival and reproductive rates. Finally, we analyze the dynamics of the annual survival and reproductive rates and their role in determining the fate of the colony. In general and for both background mortality mechanisms, we observed that the year-to-year adult survival oscillates over time taking values from 70% to 100%, while the corresponding survival rates in juveniles express much stronger fluctuations ranging from 0% to 100% in consecutive years. Similarly, the average reproductive rate for adults varies from 70% to close to 100%, depending on the parameters of feeding factor. In comparison, the proportion of reproducing yearlings often alternates between 0% and 100% with periods of several years in

which the yearlings do not reproduce. In most cases, the reproductive rate for temperate bats is assessed at the maternity colonies during the active season. Reynolds [26] estimated reproductive rate as the proportion of reproductive females just at the maternity colony for *Myotis lucifugus* to be 93.8% across five years of study in New Hampshire. However, because nonreproductive females usually spend the active season at different smaller shelters this reproductive rate overestimates the population reproductive rate. Our analysis provides information on what age groups are reproducing and how each contributes to the population growth.

4. Discussion and conclusion. We have taken a classical approach with novel additions to integrate individuals' physiology and energetics to study population dynamics of a temperate zone hibernating bat species. However the application was not trivial. Most of the complexity of the model is "hidden" in the individual model component [7] which forms the core of the population model presented here. The population model not only tracks cohorts of individuals as they live, reproduce, and die but also represents interaction among them through mortality and density-dependent distribution mechanisms. The later adjusts the feeding rate of the individuals through a density factor function that depends on the total population size. Under this approach, high population density explicitly reduces food intake and, through the resulting physiological effects, reduces reproductive output and chances for winter survival. This direct interaction between individual physiology and population dynamics provides a biologically meaningful explanation for the effect of population density on individuals. In the cases where extinctions occur, lipids and the reproductive history of the individual are crucial factors. In persistent populations, density dependence pressure determines regulatory mechanisms, such as reducing yearling reproductive output, reducing adults' reproductive output, and reducing survival of young, adults, or both. These changes occur at different levels and combinations. The health of the population results from reserves of lipid and structure, and may determine the fate of the population under density dependence pressure. Moreover, this overall population health is a cumulative result of each individual's life history. To our knowledge, there are no published time series data on long-term population dynamics of bat populations that would allow for validation of the model. However, several field studies have estimated population level parameters for *M. lucifugus* populations and have tried to explain mechanisms that may have produced these parameter values. We are analyzing under our model framework the results provided by Humphrey and Cope [13], who calculated life tables for *M. lucifugus* as a result of a mark and recapture study of seventeen years in Indiana and north-central Kentucky. We expect to provide insight on regulatory mechanisms that operate within bat populations. Our model can provide separate estimates of reproductive rates for yearlings and adults. The results from our simulations show great variation in the reproductive rate of adults (older than two years) versus yearlings (adults less than two years old). For most of the cases, the adults' reproductive rate is higher than that of the yearlings' reproductive rate when compared over the oscillatory phase of the dynamics. Simulations for a given set of parameters representing low density pressure in which populations persist, show that 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. These simulations show explicitly how low density dependence may regulate the population by just lowering reproductive success of yearlings given constant background mortality. We expect to find other mechanisms that lead to persistent and stable population dynamics in relation to the field data available. A new application of the individual model will be pursued to develop an immunophysiological model for bats that will investigate the effects of the individuals physiology on its ability to fight viral infections. The modeling framework will consist of two separate but linked units, one modeling energy budgets based on physiological processes as presented in this paper and the other representing the dynamics of the components of the host immune system (T cells, B cells, and antibodies) involved in the defense against pathogens [5][6]. These units will be coupled through mechanisms of damage control and energetic cost estimation. This project will address the unique role of bats as reservoirs of different viral infections such as rabies and other lyssaviruses, SARS, Ebola, etc.

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