Mathematical model of bats’ subpopulations
development

Abstract The paper deals with the description of the mathematical model of bats’
subpopulations and fission-fusion societies development. The model is based on the
system of ordinary differential equations. Bats’ behaviour and their searching strategy
is presented on the basis of cavity roosting bats living in Białowieża Forest
located in Poland. Theoretical results are illustrated by a computer simulation and
its comparison with biological remarks.

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Key words and phrases: bats, population, differential equations, numerical simula-
tions.

1. Introduction We present the construction of the mathematical model
describing the growth of bats’ population. We consider a location of natural
roosts in the area and some natural bats’ abilities which determine searching
and populating tree cavities. Location of roosts and their capacity determine
the development of subpopulations and fission-fusion societies. We describe
the bats’ behaviour and their searching strategy on the basis of cavity roosting bats (Nyctalus noctula and Nyctalus leisleri) living in Białowieża Forest
located in Poland. Due to the difficulty of observing bats in the field, the
knowledge of their searching strategies is extremely poor and limited to ex-
periments conducted with artificial roosts such as bat boxes, or conducted
under laboratory conditions (see [3], [4], [5], [6]). Biological remarks concerning
bats’ behaviour, their natural skills and habits we adapted from [4] and
references therein. Bats are the only mammals capable to fly actively, pre-
dominantly leading nocturnal lifestyle. These animals, regardless of their age,
are looking for hiding places throughout their life. One colony of bats can
use up to a dozen hiding places within a year, changing them from time to
time, while transporting their juveniles. Some species of bats form breeding
colonies that spread to new places every few days. It allows to avoid parasites

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developing in hollows, as well as reduce the risk of predation. In winter bats form large colonies consisting of individuals of both sexes. Some species of bats also migrate at this time of year, breaking the state of hibernation. It happens during long-term thermal warming. Then, bats look for cooler hiding places, where a lower temperature allows to reduce all their vital functions and reduce fat tissue consumption. Therefore, constant migration is a hallmark of bats life. Bats use echolocation for orientation in space, as well as for detecting, identifying and localizing food or roosts. The detection range for an object does not exceed 90 m. Bats inhabit holes created by woodpeckers, cavities left by broken-off branches or spaces beneath bark. They usually select areas with a high density of trees suitable for roosting. Suitable roosts have to fulfil many conditions, such as offering protection from unfavourable weather and predators, or providing a suitable microclimate for temperature regulation. Roosts are especially important during the reproductive period, because their quality may influence the development of juveniles or breeding success. Bat social groups are often fission-fusion societies, which spread over multiple tree cavities, with the number of bats in each tree ranging from a few to several hundred individuals. Through grouping, they benefit from better protection from predators, increased movement efficiency, improved food discovery. Roosts are also recognised as “information centres”. Bats can transfer information about the presence of cavities to conspecifics either actively or passively, using acoustic calls or behaviours such as swarming. There are three alternative strategies for finding resources: selecting places or objects that offer the highest chance of success, memorising the resource distribution once discovered and obtaining information from conspecifics. Wherein the process of finding new tree cavities is as follows (see [4]): 1) the bat chooses the area to initiate the search for new cavities in the vicinity of known roosts; 2) it locates a potential roost tree; 3) the bat inspects the trunk surface to detect an entrance to the cavity; 4) it inspects and evaluates roost’s quality; 5) the information about the presence of a suitable new cavity is transferred to conspecifics through social calls that can be eavesdropped; 6) based on this information, the colony or part of the colony makes a decision on whether to use the cavity or not; 8) once detected, the cavity enters the pool of suitable and known cavities which can be reused in the future. Bats are long lived animals, thus they can gain benefits from learning and memory retention throughout their life. The memory of bats is specifically protected during hibernation. Bats’ longevity compensates their low fertility - the female usually gives birth to only one juvenile each year, while the twins or triplets are rare.

In the paper we propose the mathematical model describing the development of a bats’ colony and its division into subpopulations. In the model we consider the above biological remarks: the searching roosts strategy, limited detection range and spreading over many cavities. Our model is based on the system of ordinary differential equations. According to our knowledge there
are no other similar theoretical models describing the development of bats’ fission-fusion societies. We know only three papers [2], [4] and [7] concerning simulations of bat’s behaviour and its searching strategy. Paper [4] contains a computer simulation based on C++ programming language describing the cavity searching strategy for individuals in areas with different topography. The mathematical model proposed in [2] and [7] is based on the system of difference equations. It describes the behaviour and orbits of bats moving to a new roost.

In the next sections we introduce variables, coefficients and assumptions of the model. We illustrate theoretical results by computer simulations.

2. Variables, assumptions and construction of model

The model is based on the system of \( n \) ordinary differential equations, where \( n \in \mathbb{N} \) is the number of roosts in the considered area. \( x_i(t) \) denotes bats’ population size in \( i \)-th tree cavity, \( i = 1, \ldots, n \). In our model we used the following coefficients:

- \( k_0 \) the birth coefficient, common for the whole population of bats;
- \( c_i \) the capacity of \( i \)-tree cavity, for \( i = 1, \ldots, n \). Capacity of a roost means not only its volume, but also other conditions such as offering protection from unfavourable weather and predators, its location, suitable microclimate for temperature regulation, etc. \( c_i \) equals the maximum number of individuals which can live in \( i \)-th tree cavity;
- \( \xi_{ij} \) the distance between \( i \)-th and \( j \)-th tree cavity. It is clear that \( \xi_{ij} = \xi_{ji} \);
- \( a \) the maximum range of the detection in the bats’ roosts searching strategy.

There are the following functions considered in the model:

- \( k_i : [0, \infty) \to [-k_0, k_0] \), \( i = 1, \ldots, n \), the growth functions depend on a population size in \( i \)-th tree cavity, respectively; \( k_i(\tau) \) equals \( k_0 \) for arguments \( \tau < c_i - \eta \) and \( -k_0 \) for \( \tau > c_i + \eta \). Here \( \eta \) is sufficient small. The function \( k_i \) denotes growth and decline of a population in \( i \)-th cavity. It consists of proliferation, mortality and migration to the other tree roosts. In the case of a small population proliferation and mortality are the only causes of its development. As a population increases, individuals begin to migrate from \( i \)-th roost to others tree cavities. The migration starts at the moment when the population size has not yet reached the level of maximum capacity \( c_i \) of \( i \)-th tree roost, hence the coefficient \( \eta \) appears. Therefore we assume that the function \( k_i \) is continuous and decreasing in the interval \( (c_i - \eta, c_i + \eta) \).

- \( \varphi : (0, \infty) \to [0, 1] \) the function of the distance between two any tree cavities. \( \varphi \) is decreasing on the interval \( (0, a) \) and equals 0 outside this interval.
We assume that the bats’ colony living in \(i\)-th tree cavity uses the resources and capacity of this roost in the initial period of the development. When the capacity of \(i\)-th tree cavity becomes insufficient the individuals start to migrate. Suitable roosts located in the distance less than \(a\) are settled. In the model we consider bats’ sensory limitation (the coefficient \(a\)) and the roost searching strategy (only tree cavities with a surplus of resources are settled). The colony divides into subpopulations. The reproductive abilities of the migrating groups depend on the resources of the settled roosts and decrease as the populations increase. We get the following system of the equations

\[
 x'_i(t) = k_i(x_i(t))x_i(t) + \sum_{j=1,j\neq i}^{n} \varphi(\xi_{ij})(k_0 - k_j(x_j(t))) \cdot x_j(t) \tag{1}
\]

for \(i = 1, \ldots, n\). It should be noted, however, that the population in \(i\)-th roost cavity cannot increase unlimitedly, which could be observed in the above equation. Therefore, its right-hand side should be multiplied by the expression \(J\left(\frac{x_i(t)}{c_i}\right)\) where \(J(\tau)\) equals 1 for arguments \(\tau < 1 - \sigma\) and 0 for \(\tau > 1\). Here \(\sigma\) is sufficiently small. Such a definition of function \(J\) has the biological justification. It describes the "attractiveness" of a given \(i\)-th roost cavity, which decreases with the increase of the population of bats inhabiting it. Using the function \(J\) corresponds to the point 7) of the bats’ searching strategy of new cavities described in Introduction, i.e. a possible decision on the migration of some individuals of a colony and the continuation of further searches for the rest of a subpopulation remaining in the old habitat. We assume that \(J\) is differentiable on its domain. The equation in this case is the following

\[
 x'_i(t) = k_i(x_i(t))x_i(t) + \left[ \sum_{j=1,j\neq i}^{n} \varphi(\xi_{ij})(k_0 - k_j(x_j(t))) \cdot x_j(t) \right] \cdot J\left(\frac{x_i(t)}{c_i}\right). \tag{2}
\]

Let \(\gamma_i \in (c_i - \eta, c_i + \eta)\) be the only zero point of the function \(k_i\) for any \(i\). Here we will consider two cases when \(\gamma_i \geq c_i\) and \(\gamma_i < c_i\). For these two cases we will analyze a behaviour of the solutions. If \(\gamma_i \geq c_i\) then equation (2) is in the following form

\[
 x'_i(t) = k_i(x_i(t))x_i(t) \tag{3}
\]

for \(x_i \geq c_i\) (because of \(J\left(\frac{x_i(t)}{c_i}\right) = 0\)). The solution of this equation asymptotically converges to \(\gamma_i\). For \(x_i \leq c_i\) we have \(J\left(\frac{x_i(t)}{c_i}\right) = 1\) therefore the inequality

\[
 x'_i(t) \geq k_i(x_i(t))x_i(t) \tag{4}
\]

is fulfilled. Hence, the solution is the increasing function for \(x_i \leq \gamma_i\). After finite time it reaches the value \(c_i\). Above this value equation (3) applies and
we get the convergence to $\gamma_i$. Therefore, for the case $\gamma_i \geq c_i$ we get the convergence of the solutions to the value $\gamma_i$.

If $\gamma_i < c_i$ than for $x_i \geq c_i$ and $x_i \leq \gamma_i$ we get the convergence of the solutions to $\gamma_i$ according to the remarks from the first case. For $\gamma_i < x_i < c_i$ the values of the limits

$$
\lim_{t \to \infty} x_i(t) \in (\gamma_i, c_i)
$$

we can get solving the system

$$
k_i(x_i)x_i + \left[ \sum_{j=1,j\neq i}^{n} \varphi(\xi_{ij})(k_0 - k_j(x_j)) \cdot x_j \right] \cdot J \left( \frac{x_i}{c_i} \right) = 0,
$$

for $i = 1, \ldots, n$.

3. Computer simulations

Computer simulations are based on programm MAPLE 16. The choices of the functions used in the simulations are as follows

$$
k_i(x) = \begin{cases} 
  k_0 & \text{for } x \leq c_i - \tau \\
  \frac{k_0}{\tau}(c_i - x) & \text{for } c_i - \tau \leq x < c_i + \tau \\
  -k_0 & \text{for } x \geq c_i + \tau 
\end{cases},
$$

where $i = 1, \ldots, n$,

$$
\varphi(x) = \begin{cases} 
  1 - \frac{x}{a} & \text{for } x < a \\
  0 & \text{for } x \geq a 
\end{cases},
$$

$$
J(x) = \begin{cases} 
  1 & \text{for } x < \frac{7}{8} \\
  \frac{1}{2} + \frac{1}{2} \sin \left( -8\pi x + \frac{15}{2}\pi \right) & \text{for } \frac{7}{8} \leq x < 1 \\
  0 & \text{for } x \geq 1 
\end{cases}.
$$

3.1. Case A

We consider three roosts with the capacities $c_1 = 50$, $c_2 = 20$ and $c_3 = 10$. The distances between these tree cavities are the following $\xi_{12} = 5$, $\xi_{13} = 5$, $\xi_{23} = 9$. The chosen maximum range of the detection is $a = 90$. We fix $k_0 = 0.2$ and $\tau = 2$. In Figures 1–3 we present the graphs of the functions of the model. We choose the initial conditions in the model:

$$
x_1(0) = 0, \quad x_2(0) = 0, \quad x_3(0) = 5.
$$

Therefore, the only one of three tree cavities is inhabited. In Figure 4 we present numerical simulations.

We can see that bats’ colony living in the third tree cavity uses the resources of this roost in the initial period of the development. When the sources run out, then individuals start to migrate to the other tree cavities. Finally, the sizes of three bats’ subpopulations stabilize on the levels of the capacities of each tree roosts.

3.2. Case B

Three roosts with the capacities $c_1 = 50$, $c_2 = 20$ and $c_3 = 10$. The chosen maximum range of the detection is $a = 90$. The distances
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Figure 1: The graph of the function $\varphi$.

Figure 2: The graph of the function $J$.

Figure 3: The graphs of the functions $k_1$, $k_2$ and $k_3$.

Figure 4: Case A. Initial conditions: $x_1(0) = 0$, $x_2(0) = 0$, $x_3(0) = 5$.

Figure 5: Case B. Initial conditions: $x_1(0) = 5$, $x_2(0) = 0$, $x_3(0) = 0$.

between these tree cavities are the following $\xi_{12} = 2$, $\xi_{13} = 89$, $\xi_{23} = 88$. Therefore, the third roost is for the bats at the limit of their detection range. We fix $k_0 = 0.2$ and $\tau = 2$. The initial conditions in the model: $x_1(0) = 5$, $x_2(0) = 0$, $x_3(0) = 0$. Theoretical results are in Figure 5.

3.3. Case C We add the fourth tree cavity with $c_4 = 20$ to the case
B. The distances between tree cavities from the case B and the additional fourth roost are the following: \( \xi_{14} = 113, \xi_{24} = 107, \xi_{34} = 28 \). Therefore, the fourth roost is out bats’ detection range from first and second cavities. We can observe the migration to the fourth tree cavity only from the third roost - see Figure 6 (initial conditions \( x_1(0) = 5, x_2(0) = 0, x_3(0) = 0, x_4(0) = 0 \)).

![Figure 6: Case C. Initial conditions: \( x_1(0) = 5, x_2(0) = 0, x_3(0) = 0, x_4(0) = 0 \).](image1)

![Figure 7: Case D. Initial conditions: \( x_1(0) = 10, x_2(0) = 10, x_3(0) = 5 \).](image2)

3.4. **Case D** We consider case A with new initial conditions \( x_1(0) = 10, x_2(0) = 10, x_3(0) = 5 \), see Figure 7. All tree cavities are inhabited. We can see that each population growth is independent, with unnoticeable migration.

4. **Conclusions and remarks** The theoretical model quite well reflects the described natural bats’ abilities: constant migration, limited detection range, settling tree cavities with a surplus of resources, dividing into subpopulations. We can expand the model considering bats’ abilities to learning and eavesdropping social calls (see [1]). Memory can also play an important role in decision making processes: where and when to search for new cavities. The model with delays could reflect the ability to build “cognitive maps” for orientation in space (see [8]) and the possibility to return to the found roost even after the hibernation period. Under the current assumptions, we do not observe oscillations. The subpopulation sizes always converge to the values close to the capacities of the roosts. We suspect that oscillations of solutions would be possible under the assumption of variable habitat capacity. It has biological justification. Bats change habitats due to lack of space in the roost, lack of food in the nearby hunting area, to avoid parasites developing in tree cavities and reduce the risk of predation. At the same time, bats have memory skills about the distribution of habitats in the area and often return to
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roosts previously inhabited, and in which conditions may have improved. Introducing the variable capacity of the habitat is an idea for further work on the generalization of the model.

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Matematyczny model rozwoju subpopulacji nietoperzy.
Antoni Leon Dawidowicz i Anna Poskrobko

Streszczenie
Artykuł dotyczy opisu matematycznego modelu subpopulacji nietoperzy oraz rozwoju procesu zasiedlania nowych dziupli. Model oparty jest na systemie równań różniczkowych zwyczajnych. Zachowania nietoperzy i ich strategię poszukiwań przedstawiono na podstawie obserwacji nietoperzy zamieszkujących dziuple w Puszczy Białowieskiej. Wyniki teoretyczne ilustruje symulacja komputerowa i jej porównanie
z uwagami biologicznymi.

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