STUDIA ECOLOGIAE ᴱᵀ BIOETHICAE

Population Consequences of Parent-Offspring Competition: An Individual-Based Model

Konsekwencje populacyjne konkurencji między rodzicami i potomstwem – model osobniczy

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Abstract: The article compares different versions of individual-based models of single population dynamics with overlapping generations with results of the model of population with non-overlapping generations. In all models, various versions of global competition for common resources and their unequal partitioning between competing individuals are analysed, i.e., when juveniles and adult individuals compete for the same resources, when juveniles and adult individuals use different resources, and a case called mother's care. The article analyses the relationship between individual variability and population persistence measured by the time of population extinction. Persistence of a population is increased by all forms of competition between individuals not weakened by any environmental factors (e.g. diversification of resources of competing individuals) or factors arising from evolutionary history of the species (e.g. mother's care) and related in an appropriate way to the mechanism shaping individual variability in the population. Any form of weakening competition leading to decreasing individual variability will adversely affect the persistence of the population. However, differences between versions of the model are not very big.

Keywords: individual-based model, non-overlapping generations, overlapping generations, individual variability, persistence, population extinction time

Streszczenie: Różne wersje modelu dynamiki pojedynczej populacji z zachodzącymi pokoleniami zostały porównane z modelem z niezachodzącymi pokoleniami. Badano różne wersje globalnej konkurencji o wspólne zasoby i ich nierównego podziału pomiędzy konkurującymi osobnikami: osobniki młodociane i dorosłe konkurują o te same zasoby, osobniki młodociane i dorosłe korzystają z różnych zasobów oraz pewną formę opieki matczynej. Analizowano zależność trwałości populacji mierzonej czasem, jaki upływa do jej wymarcia, od zmienności osobniczej. Trwałość populacji zwiększana jest przez wszystkie postaci konkurencji nie osłabionej przez jakiekolwiek czynniki środowiskowe (np. dywersyfikacja zasobów konkurujących osobników) lub wynikłe z ewolucyjnej historii gatunku (np. opieka matczyna) oraz w odpowiedni sposób powiązanej z mechanizmem powodującym powstawanie zmienności osobniczej w populacji. Wszystkie formy osłabienia konkurencji prowadzące do zmniejszenie zmienności osobniczej mają niekorzystny wpływ na trwałość populacji, chociaż różnice między modelami nie są duże.

Słowa kluczowe: model osobniczy, niezachodzące pokolenia, zachodzące pokolenia, zmienność osobnicza, trwałość, czas wymarcia populacji

Introduction

In theoretical ecology, there have long been established patterns of building models of population dynamics with an age structure (e. g. Ebenman and Persson 1988, Coulson and Godfrey 2007; Logofet and Ulanova 2017). These are mainly matrix models with constant parameters describing changes in the density within age classes. Parameters representing mortality and reproduction in age classes and describing survival at transitions between age classes are the average characteristics of individuals in these classes. The result is a description of exponential population growth. Of course, it is possible to modify this scheme and introduce density dependent parameters into the model, but it will still be a classic scheme for building population dynamics model.

This paper presents various versions of individual-based models of population dynamics with overlapping generations, which use the scheme of describing global competition between individuals for common resources and their unequal partitioning between competing individuals, which was previously used to describe the dynamics of a single population with non-overlapping generations (Uchmański 2000; Grimm and Uchmański 2002). Earlier models served analysing the impact of individual variability in the amount of resources acquired by competing individuals on the persistence of the population measured by the time of population extinction. Also now, individual variability will be the most important factor taken into account when analysing models with overlapping generations, where the network of interactions between individuals is more complex. The results of the model with non-overlapping generations will be compared with the results of the model in which individuals of different age classes compete for the same resources, and later with the results of the model in which individuals of different age classes use different resources, and with a model that can be interpreted as a description of some form of mother's care for offspring.

1. Non-Overlapping Generation

1.1. The Model

The model describes the population dynamics of animals with non-overlapping generations and the dynamics of resources available to them. The individuals represent a parthenogenetic species. The life-cycle of individuals starts at the beginning of the season. They grow over the season and reproduce at the end of the season, then they die. Juveniles overwinter and start growing at the beginning of the next season.

The growth rate of an individual is assessed as the difference between the rate of resource assimilation and the rate with which these assimilated resources are used for living costs. The rate of resource assimilation A and living costs as measured by the rate of respiration R are power functions of body weight w (Duncan and Klekowski 1975):

$$A = a_1 w^{b_1}, \qquad 1.1$$

$$R = a_2 w^{b_2}, \qquad 1.2$$

where a_1, a_2, b_1 and b_2 are parameters. This gives the following equation of individual growth (Majkowski and Uchmański 1980):

$$\frac{dw}{dt} = a_1 w^{b_1} - a_2 w^{b_2}. \qquad 1.3$$

The rate of consumption depends on the amount of resources available. The parameter a_1 for a single individual isolated from interactions with other individuals of the same species, as a function of the amount of resources V can be described by the equation proposed by Ivlev (1961):

$$a_1 = a_{1,max}(1 - e^{-sV}), \qquad 1.4$$

where $a_{1,max,}$ is the maximal value of parameter a_1 reached when $V = \infty$ and s is constant parameters describing the rate of reaching this maximal value.

However, if individuals live together, they may compete for resources. We assume that this is a global competition. Each individual competes with all other

individuals in the population by using common resources. This leads to unequal resource partitioning among competitors (Łomnicki 1988). If individuals often compete, then the individual who acquired more resources in the past, will also acquire more of them in the future. A good measure of the amount of resources acquired by an individual in the past, accounting also for the energy costs of resource acquisition, is its actual weight. For this reason, the rate of assimilation of an individual in the case of a group of globally competing individuals is described by Eq. (1.4) with additionally added dependence on the actual body weight of the individual according to the scheme below.

At each simulation step, individuals with the lowest weight w_{min} and the highest weight w_{max} are identified. The value of the parameter a_1 of resource assimilation by the lightest individual is described as

$$a_{min} = a_{1,max}(1 - e^{-s_{min}V}) \qquad 1.5$$

and that of the heaviest individual as

$$a_{max} = a_{1,max}(1 - e^{-s_{max}V}). \qquad 1.6$$

The parameter a_1 for individuals with intermediate weights are calculated by using interpolation between the values a_{min} for w_{min} and a_{max} for w_{max} (Fig. 1). The analysis of the positively skewed weight distributions of growing and at the same time competing individuals, shows that to obtain positively skewed weight distributions, a linear or convex function should be used for the interpolation (Uchmański 1985; Uchmański 1987; Uchmański and Dgebuadze 1990). The linear case has been chosen in the present model. When the number of individuals in population is equal to 1, assimilation was calculated in the following way: the value of parameter s equaled to half of the sum of s_{min} and s_{max}.

Between the values of constant parameters s_{min} and s_{max} of Eqs (1.5) and (1.6), there is an inequality

$$s_{min} \leq s_{max}. \qquad 1.7$$

When $s_{min} = s_{max}$, individuals in even-aged population are equal. Assimilation
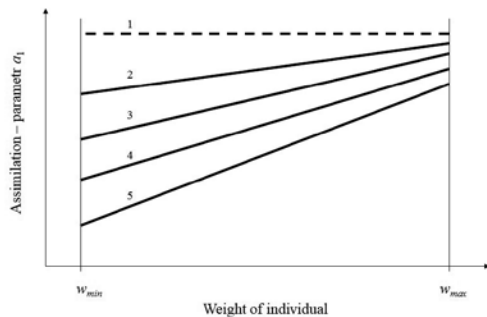
Figure 1. Non-overlapping generations. Resource partitioning among competing individuals in relation to the available amount of resources. The figure shows how the values of parameter a_1 were calculated for individuals that differ in actual body weight. The w_{min} and w_{max} represent the lowest and the highest body weights in the current population. Sections of straight lines represent linear approximations to calculate the value of parameter a_1 for individuals with body weights $w_{min} < w < w_{max}$ at various amounts of resources V. (1) – amount of resources $V = \infty$. The values of parameters a_1 are the same for all individuals in the population, and equal to the maximum value a_{max}. Successive lines (2, 3, 4 and 5) show the values of a_1 for decreasing amounts of resources V. It can be seen that when V is decreasing, differences between individuals in the amount of assimilated resources are increasing. But the decrease in the amount of resources V accounts for a much greater decline in assimilation for individuals with low body weights than for individuals with large weights.

of each individual depends in the same way on V. When $s_{min} < s_{max}$, individuals differ in the rate of assimilation. The degree of these differences increases with the increasing difference between s_{min} and s_{max} or decreasing V (Fig. 1). However, the differences disappear for $V = \infty$.

The greatest weight w_∞ at successive time steps of the simulation and at the end of growth w_∞^{end} has a hypothetical individual who is growing under conditions $V = \infty$:

$$\frac{dw_\infty}{dt} = a_{1,max}w_\infty^{b_1} - a_2 w_\infty^{b_2}. \qquad 1.8$$

The maximum final weight w_∞^{end} of an individual, asymptotically reached

when assimilation is equal to respiration, for the growth described by Eq. (1.8) is

$$w_\infty^{end} = \left(\frac{a_{1,max}}{a_2}\right)^{\frac{1}{b_2-b_1}}. \qquad 1.9$$

An individual growing under condition when $V < \infty$, after the end of growth will reach the weight $w_{end} < w_\infty^{end}$. The number of juveniles produced by an individual after the end of growth is proportional to the difference between its final weight and some threshold weight:

$$z = \begin{cases} round(c(w_{end} - w_{fak}w_\infty^{end}) \\ 0 \end{cases}$$

$$\begin{array}{c} for \quad w_{end} > w_{fak}w_\infty^{end} \\ for \quad w_{end} \le w_{fak}w_\infty^{end} \end{array}, \qquad 1.10$$

where c is the parameter describing the intensity of juvenile production, and w_{fak} ($0 < w_{fak} < 1$) says what part of the maximum end weight w_∞^{end} given by Eq. (1.9) is the threshold weight which allows the calculation of juvenile production by an individual. Individuals with body weights lower than or equal to the threshold weight die without producing progeny. The function rounds a real number to the nearest integer, as the number of juveniles can only be a natural number. The initial weights of juveniles of each individual are drawn from the normal distribution with a mean value $w_{o,mean}$ and variance $w_{o,variance}$, but only from the interval $[w_{o,min}, w_{o,max}]$.

The number of individuals in the population N_{t+1} at generation t +1 conforms to the following equation

$$N_{t+1} = \sum_{i=1}^{N_t} z_i, \qquad 1.11$$

where the summation is done over all N_t individuals present in the population at generation t. This was combined with the equation describing the resource dynamics:

$$\frac{dV}{dt} = -\sum_{i=1}^{N_t} A_i + g, \qquad 1.12$$

where V is the amount of resources, A_i is the resource assimilation by the i-th individual and g is the constant amount of resources added at each time step. The summation is the overall number of individuals present in the population. The resources not consumed by individuals in the population will linearly increase.

At the initial time instant, the population consisted of N_o individuals, and they had V_o available resources. Their initial weights are taken from the normal distribution with the properties noted above. The basic simulation step was to calculate the number of individuals in the population of successive generations. However, within each generation, the equations describing the growth of individuals and the resource equation were solved by using the Euler method in 80 smaller time steps. This number of smaller steps allowed a good enough fitting of the numerical solutions to the analytical solutions of the growth Eq. (1.8) for an individual with the maximum weight. The changes in the amount of resources were also calculated in smaller time steps. Weight increases at each smaller time step were calculated in the model with reference to the actual amount of resources available to individuals. After the end of growth, the number of juveniles for each individual was calculated and their initial weights were assessed. It was assumed that resources have continuous dynamics. The amount of resources available to the next generation was equal to the amount of resources at the end of the previous one, calculated with respect to their use and supplementation during that generation. This allowed for the same calculations at successive large time steps. The simulation was stopped when $N_{t+1} = 0$ or $V_{t+1} < 0$. Standard values of the parameters used in simulations are shown in Table 1.

1.2. Results

Population dynamics described by the model presented in this chapter are characterized by fluctuations in population size

Table 1. Standard values of the model parameters used in the simulation of population dynamics. For s_{min} and s_{max} the maximal range of their values is shown, as the results of simulations will be presented for different values of this parameter

	Parameter	Value
Growth equation parameters	$a_{1,max}$	0.11
-	a_2	0.03
-	b_1	0.7
-	b_2	0.9
Parameters of initial weight distribution	$w_{0,min}$	14
-	$w_{0,max}$	26
-	$w_{0,mean}$	20
-	$w_{0,variance}$	5
Parameters of resource partitioning function	s_{min}	$0.10 \times 10^{-6} - 0.55 \times 10^{-6}$
-	s_{max}	$0.60 \times 10^{-6} - 2.00 \times 10^{-6}$
Threshold for reproduction	w_{fak}	0.65
Progeny production	c	0.01
Initial number	N_0	10
Initial resources	V_0	6×10^6
Increase of resources	g	2×10^6

and resources, which sooner or later lead to the extinction of the population with the minimum number of individuals (Fig 2). Fig. 3 shows the mean from 100 simulations of extinction times of a single population for different ranges of values of the parameters s_{min} and s_{max}. Fig. 4 illustrates in more detail what the dynamics of population looks like for selected areas of values of the parameters s_{min} and s_{max}. The highest individual variability takes place in the upper left corner of the parameter space s_{min} and s_{max}. Here, the population number repeatedly goes through phases of increase and decrease without extinction on the time scale adopted in the simulations (1000 time steps). The smallest individual variation corresponds to the parameter values from the lower right corner of the parameter space s_{min} and s_{max}. Here, in turn, the population goes extinct most often after the first maximum and this happens after only a few time steps.

2. Overlapping Generations. No Competition Between Generations

2.1. The Model

Each individual lives for two seasons. In the first season it is a juvenile, in the second it is an adult. Let N_t^1 denote the number of juveniles in the generation t and N_t^2 the number of adults in the same generation. Assimilation and respiration in the juvenile and the adult are power functions of the individual's weight (see Eqs (1.1) and (1.2)). Assimilation depends on the amount of resources available in the environment according to the scheme described in Section 1.1. Juveniles use a different pool of resources than adults (V_1 and V_2 respectively). This means that the juvenile competes for resources with other juveniles, and the adult with other adults. There is no competition between adults and juveniles. In this version of the model, the same values of s_{min} and s_{max} parameters are used for both juveniles and adults. In each small time step, individuals with the smallest and largest weight in each age class are found separately for juveniles and adults. Further, according
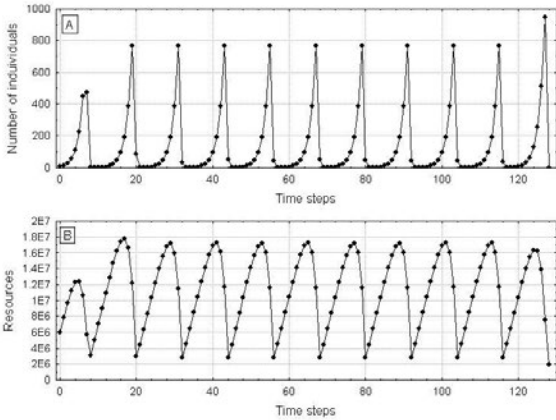
Figure 2. Non-overlapping generations. Example of typical dynamics of the population (A) and resources (B) used by individuals. Simulation results for $s_{min} = 1 \times 10^{-6}$ and $s_{max} = 4 \times 10^{-6}$. The other parameters had standard values (see Table 1)
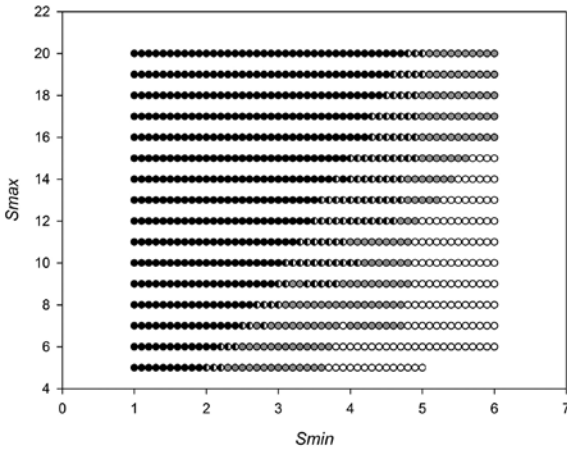

Figure 3. Non-overlapping generations. Parameter space s_{min} and s_{max} (the values on the axes should be multiplied by 10^{-7}). The average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Other parameters have standard values (Tab. 1). Simulations were run for a maximum of 1000 time steps. Empty circles – average extinction time less than 10 time steps. Grey circles – average extinction time greater than or equal to 10 time steps and less than 100 time steps. Half-filled circles – average extinction time greater than or equal to 100 time steps and less than 1000 time steps. Circles fully filled – extinction time greater than or equal to 1000 time steps
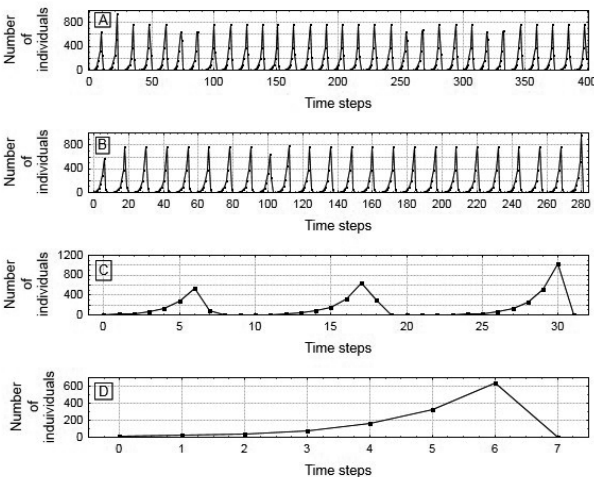

Figure 4. Non-overlapping generations. Types of population dynamics corresponding to the four different areas in the parameter space s_{min} and s_{max} from Fig. 3. A – extinction time greater than or equal to 1000 time steps – only the first 400 time steps are shown (fully filled circles). B – average extinction time greater than or equal to 100 time steps and less than 1000 time steps (half-filled circles). C – average extinction time greater than or equal to 10 time steps and less than 100 time steps (grey circles). D – average extinction time less than 10 time steps (empty circles). The other parameters have standard values (Tab. 1)
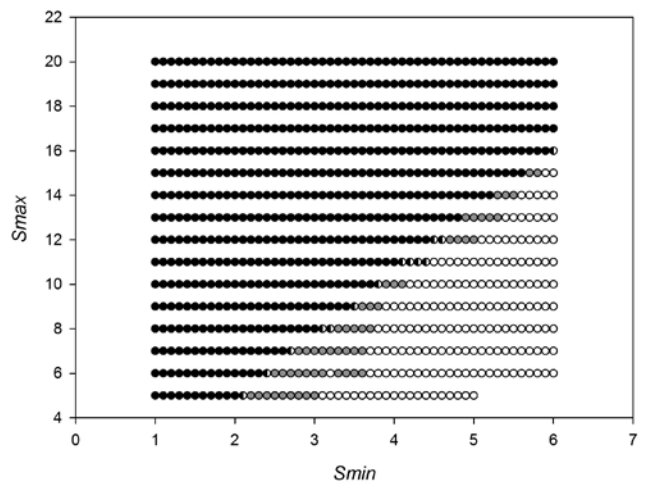
to the scheme described above (see Eqs (1.5) and (1.6)), the assimilation of each individual is determined. For the juvenile, the smallest and largest current juvenile weight in this small time step and the current resource value V_1 are used. For adults, the algorithm is analogous except that the smallest and largest current adult weight and the current V_2 resource value are used. Juveniles and adults can reproduce at the end of each generation as shown in Section 1.1 and using the same w_{fak} and $w_\infty{}^{end}$ values. After possible reproduction, the juvenile progresses to the adult category, continues to grow as an adult, and at the end of the second season makes a second attempt at reproduction. The adult, after second attempt at reproduction, dies at the end of the second season. Simulations were started with the following initial values: $N_0{}^1 = N_0$, $N_0{}^2 = 0$, $V_1 = V_0$ and $V_2 = V_0$. Resources V_2 and V_1 were renewed linearly with the same rate g. Standard parameter values see Tab. 1.
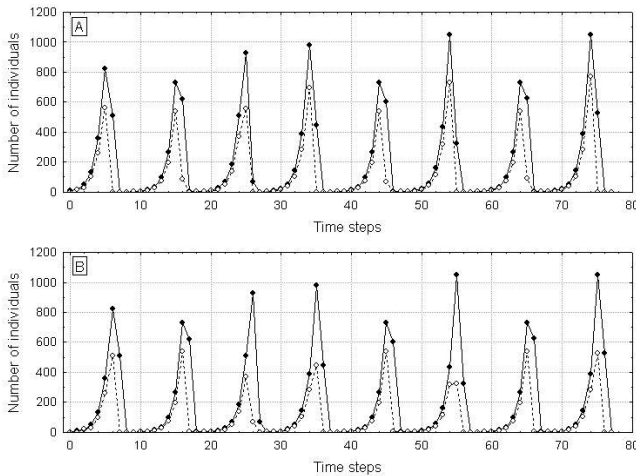
2.2. Results

Fig.5 shows the parameter space of s_{min} and s_{max}. As earlier it illustrates the mean of extinction times from 100 simulations of a single population dynamics for different ranges of values of the parameters s_{min} and s_{max}. Now, the condition for population extinction is that $N_t{}^1 = 0$ and simultaneously $N_t{}^2 = 0$. The remaining parameters had standard values (Tab. 1). Fig. 6 shows an example of the dynamics of the number of young and adults individuals in the population together with the number of offspring produced by them in successive time steps.

Figure 5. Overlapping generation. No competition between young and adult individuals. Parameter space s_{min} and s_{max} (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Other parameters have standard values (Tab. 1). Simulations were run for a maximum of 1000 time steps. Empty circles – average extinction time less than 10 time steps. Grey circles – average extinction time greater than or equal to 10 time steps and less than 100 time steps. Half-filled circles – average extinction time greater than or equal to 100 time steps and less than 1000 time steps. Circles fully filled – extinction time greater than or equal to 1000 time steps

Figure 6. Overlapping generation. No competition between young and adult individuals. Example of typical dynamics of the number of young (A) and adult (B) individuals in the population. Open circles – number of offspring produced by all individuals in each age category. Simulation results for s_{min} = 1x10^{-6} and $s_{max.}$ = 4x10^{-6}. The other parameters had standard values (see Table 1)

3. Overlapping Generations. Competition Between Generations

3.1. The Model

The only difference from the model without competition between generations, when adults and juveniles used different resources, is that now, when the competition between generations takes place, adults and juveniles use the same resources. Therefore, it is necessary to re-formulate the rule governing the partitioning of resources between competing individuals. In each small time step, the assimilation of competing individuals will be determined according to the rules described by Eqs (1.5) and (1.6) with the following modifications. A group of juveniles will be characterized by weights that will usually be lower than those of adults. However, it cannot be ruled out that the ranges of weight values in both age groups will overlap. We assume that the partitioning of resources as a result of competition is determined by interactions between adults. The presence of juveniles does not affect directly the assimilation of adults. Therefore, the assimilation of adults is determined as in the model without competition between generations. In each small time step, the smallest and largest adult weights are found, and the assimilation of adults with intermediate weights is calculated

according to Eqs (1.5) and (1.6). Adults, on the other hand, have an impact on the assimilation of juveniles. Their assimilation is calculated by extending the straight line to calculate the assimilation of adults to the left in the direction of juvenile weights. When calculating the assimilation of juveniles, the segment of this line between the points marked by the smallest and largest juvenile weight is used (Fig.7). In addition, the parameter b was introduced, which determines the strength of competition exerted on juveniles by adults. If $b = 1$, then the section determining the assimilation of juveniles lies on the extension of the line on which there is also a section used to calculate the assimilation of adults. If $b < 1$, then the segment determining the assimilation of juveniles is shifted downwards in parallel, proportionally to the value of parameter b (Fig. 7).

The scheme above describes how resources are partitioned when Nt^1 ¹ 0 and $Nt^2 > 1$. When $Nt^1 > 1$ and $Nt^2 = 0$ (this is the case, for example, in the beginning of the first generation) or when $Nt^1 > 1$ and $Nt^2 = 1$, then the assimilation of juveniles was calculated according to the same scheme as the one presented in the version of the model with non-overlapping generations: in the group of juveniles, the smallest and largest weight of an individual was searched. These values
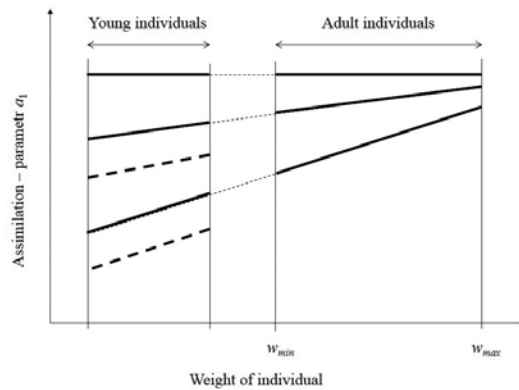
Figure 7. Overlapping generations. Competition between generations. Resource partitioning among competing individuals in relation to the available amount of resources. The figure shows how the values of parameter a_1 were calculated for individuals that differ in actual body weight in the category of young and adult individuals. The w_{min} and w_{max} represent the lowest and the highest body weights of adult individuals in the current population. These weights are used for calculation of resource partitioning between individuals according to Egs (1.5) and (1.6). Solid sections of straight lines represent linear approximations to calculate the value of parameter a_1 for: right part – adult individuals with body weights $w_{min} < w < w_{max}$, left part – young individuals for $b = 1.0$. The range covered by weight of young individuals is indicated on the x-axis, but these weights have no influence on assimilation of other individuals. Upper horizontal line shows equal resource partitioning for $V = \infty$. Two lower lines show unequal resource partitioning for two decreasing values of V. Dotted lines in the left part of the figure indicate resource partitioning among young individuals for $b < 1$

made it possible to determine the largest and smallest assimilation with fixed values of s_{min} and s_{max} parameters, and the assimilation of individuals with intermediate weights was determined on the basis of linear interpolation between these two points. When $N_t^2 = 1$, adult assimilation was calculated in the same way as in the previously presented models: the value of parameter s equaled half the sum of s_{min} and s_{max}. Later the procedure was followed as previously described.

3.2. Results

Parameter spaces of s_{min} and s_{max} for $b = 1.0$ and for $b = 0.75$ are shown in Fig. 8 and Fig. 10 respectively. They illustrate the mean extinction times from 100 simulations of a single population dynamics for different ranges of values of the parameters s_{min} and s_{max}. Fig. 9 for $b = 1.0$ and Fig. 11 for $b = 0.75$ show examples of the dynamics of the number of young and adults individuals in the population together with the number

of offspring produced by them in successive generations.

4. Overlapping Generations. Mother's Care

4.1. The model

As before, individuals live for two seasons. A juvenile grows in the first season. At the end of the first season, it reproduces. It also grows as an adult individual in season two but does not reproduce at the end of season two. The second season is devoted to caring for the offspring it produced at the end of the first season. All these activities are related to the assimilation of resources from the environment, for which the adult individual must compete with other individuals. Competition takes place only between adults. The partitioning of resources between adult competitors is described by the procedure known from the version of the model with non-overlapping generations. The weight of the lightest and heaviest adult individual in each
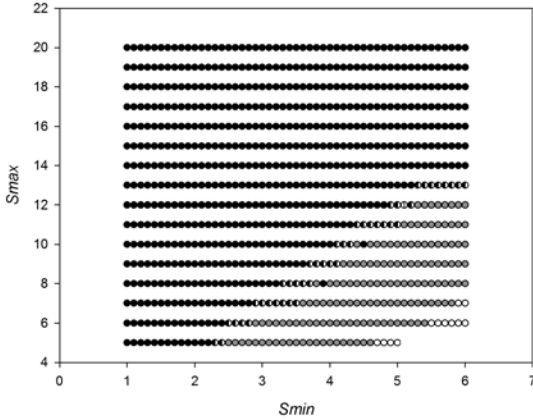
Figure 8. Overlapping generation. Competition between young and adult individuals. Parameter space s_{min} and s_{max} (the values on the axes should be multiplied by 10^{-7}). $\beta = 1.0$. Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Other parameters have standard values (Tab. 1). Simulations were run for a maximum of 1000 time steps. Empty circles – average extinction time less than 10 time steps. Grey circles – average extinction time greater than or equal to 10 time steps and less than 100 time steps. Half-filled circles – average extinction time greater than or equal to 100 time steps and less than 1000 time steps. Circles fully filled – extinction time greater than or equal to 1000 time steps. The other parameters had standard values (see Table 1)
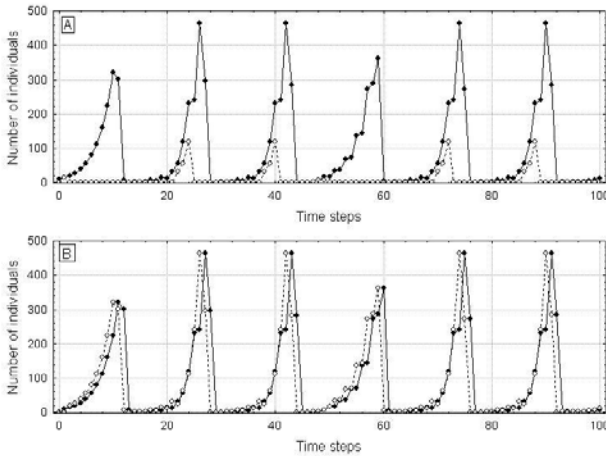

Figure 9. Overlapping generations. Competition between generations. Filled circles – example of typical dynamics of the number of young (A) and adult (B) individuals in the population for $\beta = 1.0$. Open circles – number of offspring produced by all individuals in each age category. Simulation results for $s_{min} = 1 \times 10^{-6}$ and $s_{max.} = 4 \times 10^{-6}$. The other parameters had standard values (see Table 1)
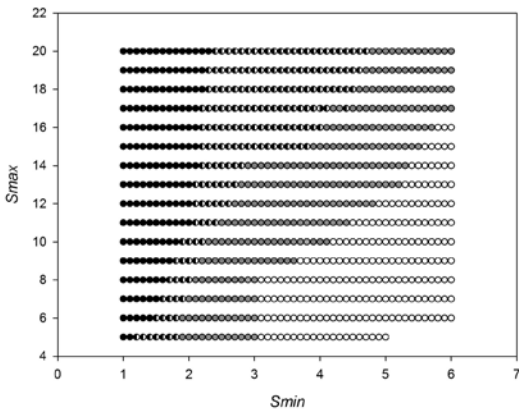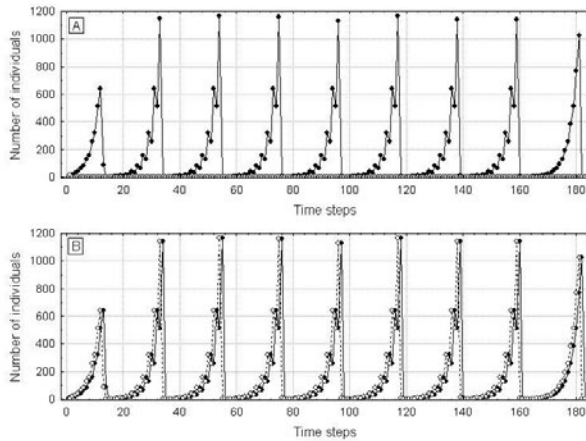

Figure 10. Overlapping generation. Competition between young and adult individuals. Parameter space s_{min} and s_{max} for $\beta = 0.75$ (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Other parameters have standard values (Tab. 1). Simulations were run for a maximum of 1000 time steps. Empty circles – average extinction time less than 10 time steps. Grey circles – average extinction time greater than or equal to 10 time steps and less than 100 time steps. Half-filled circles – average extinction time greater than or equal to 100 time steps and less than 1000 time steps. Circles fully filled – extinction time greater than or equal to 1000 time steps

Figure 11. Overlapping generations. Competition between generations. Filled circles – example of typical dynamics of the number of young (A) and adult (B) individuals in the population for β = 0.75 Open circles – number of offspring produced by all individuals in each age category. Simulation results for s_{min} = 1x10^{-6} and $s_{max.}$ = 4x10^{-6}. The other parameters had standard values (see Table 1)

small time step is determined. This allows the assimilation of the lightest and heaviest individual among adults to be calculated. The assimilation of adult with intermediate weight was calculated by linearly interpolating between these two values. Juveniles do not compete with other individuals. The mother's care for these individuals is expressed in the fact that the parameter a_1 in growth equations of her offspring is the same as its current value for the mother. If it so happened that the mother was missing, then a_1 in the growth equations of her offspring would be equal to 0. However, in the simulations whose results are shown in this paper the mortality of individuals was not observed.

Due to the assumption presented above, which says that a juvenile in the first season of life, whose mother is missing, has assimilation equal to zero, the initial conditions for the simulation of this model must be changed. They are as follows in this version of the model: $N_o{}^1$ = 0, $N_o{}^2 = N_o$, $V = V_o$. At the beginning of the first generation of the simulation, the weights of adults are selected from a normal distribution with a mean $w_{fak} w_\infty{}^{end}$ and variance equal to 100. These weights are used to calculate the number of offspring and their initial weights for each adult according to the previously described procedures. The offspring of all adults are included in the category

of juveniles and then the simulation in the first and subsequent large time steps proceeded as described above.

4.2. Results

Fig.12 shows the parameter space of s_{min} and s_{max}. As earlier it illustrates the mean of extinction times from 100 simulations of a single population dynamics for different ranges of values of the parameters s_{min} and $s_{max.}$

5. Discussion

The analysis of the dynamics of the populations whose models are discussed in this paper will be conducted at the level of distributions of different types of dynamics in the parameter space s_{max} and s_{min}. Due to the fact that the most characteristic event for the populations described by the models discussed in this paper is population extinction, this will be an analysis of the impact of the model assumptions on the time of population extinction.

In the model with non-overlapping generations, the relationship between individual variability and population persistence is relatively simple. Population dynamics is characterized by oscillations in number accompanied by corresponding oscillations in the amount of resources. When initially the population number is small and resources are sufficient, all individuals are
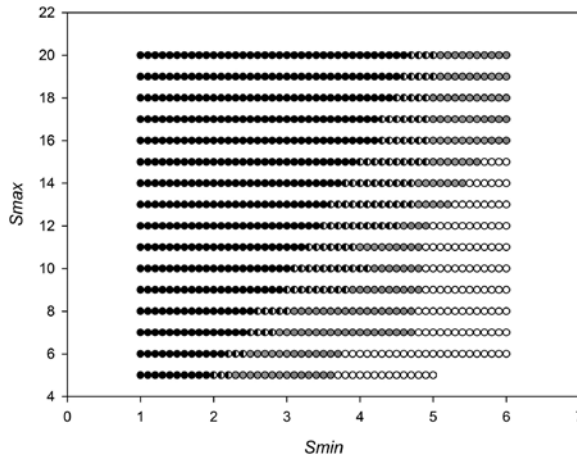
Figure 12. Overlapping generation. Mother's care. Parameter space s_{min} and s_{max}. Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max} (the values on the axes should be multiplied by 10^{-7}). Other parameters have standard values (Tab. 1). Simulations were run for a maximum of 1000 time steps. Empty circles – average extinction time less than 10 time steps. Grey circles – average extinction time greater than or equal to 10 time steps and less than 100 time steps. Half-filled circles – average extinction time greater than or equal to 100 time steps and less than 1000 time steps. Circles fully filled – extinction time greater than or equal to 1000 time steps

able to produce more than one offspring. The population is increasing. However, the increase in the number of individuals in the population causes systematic depletion of resources. This limits the number of offspring produced in each generation. In each generation, individuals in a population compete globally for resources, which are unequally partitioned between competing individuals. These variability between individuals increases as the amount of resources in the environment decreases. Thus, depletion of resources as population increases will not only reduce production of offspring by competing individuals, but also results in that not all individuals will be able to reproduce. As a consequence, as resources are depleted, population increases will become smaller, and after reaching a maximum, the population will begin to decline. In the minimum number, individual variability becomes a very important factor allowing the population to survive the crisis associated with the scarcity of resources in the environment. If individual variability is large enough, there is a high probability

that there will be at least one individual in the population capable of reproducing in these conditions. At the same time small number of individuals causes little exploitation of resources, which results in their slow increase. As a result, the population starts growing again and the cycle repeats itself. However, if the minimum number population does not contain at least one individual capable of reproduction, and this can happen more easily when individual variability is low, the population goes extinct. If individual variability is very low, this can happen even after the first population maximum. When individual variability is greater, the population goes through many cycles of growth and decline. However, sooner or later, at one of the minima, it turns out that there is no individual capable of reproduction and the population goes extinct. The time of extinction of a population depends on individual variability: the greater it is, the greater the time of extinction of the population.

What is important for longer population extinction time is not only the degree

of individual variability measured by the difference between s_{max} and s_{min}, but also the values of s_{max} and s_{min}. In the case of the values of the parameters s_{max} and s_{min} coming from the upper left corner of the parameter space, we will have individuals with the largest possible variability of assimilation. At the same time, there will be individuals with the highest and lowest assimilation in the population. In the lower right corner, we will have the population with the least variability in assimilation, but this will be achieved by the greatest possible reduction in the assimilation of individuals with the greatest assimilation. In turn, in the other two corners of the parameter space, there will be cases where the population is less variable in terms of assimilation than in the case of the upper left corner, although more than in the case of the lower right corner. In the upper right corner, there will be a population with individuals with high assimilations, while in the lower left corner the population of individuals with the smallest assimilations.

The fact that the cases with the largest population extinction times are concentrated in the upper left corner of the parameter space proves that for a long population extinction time, the presence of the entire spectrum of individuals with the largest and smallest assimilation in the population is needed. In the phase of resource decline, the latter will die childless. It is for this reason that the population will decrease, but at the same time it will weaken the exploitation of resources. Individuals from the first category, in turn, have a chance to produce offspring even with a minimum of resources, which will allow the population to enter the next phase of increase.

It is also important that the scheme of resource partitioning between competing individuals described in this paper, which is justified by positively skewed distributions of individual weights in even-aged populations (Uchmański 1985), causes that the number of individuals with the highest assimilation is small compared

to the number of individuals with the lowest assimilation. It is on these few individuals with the greatest assimilation that the mechanism ensuring the persistence of the population is based. Cases with the greatest population extinction times do not cluster around the upper right corner of the parameter space, where we will find populations with individuals with the greatest assimilation. Here, even individuals with the smallest assimilations are characterized by the highest possible s_{min} value. However, due to the relatively low variability and predominance of individuals with high assimilation in the population, which results in heavy resource exploitation, the population extinction time is shorter. This would be even more evident if we extended the range of s_{min} values towards larger values. We would see the same effect if we extended the range of s_{max} values to even smaller values in the lower left corner of the parameter space. Here, one could observe the extinction of the population eve in the first step of the simulation.

Some of the previous arguments explaining population dynamics with non-overlapping generations can also be applied to populations with overlapping generations, but the interactions between young and old individuals introduce new elements to the analysis. In general, a glance at the distribution of different types of dynamics in the parameter space s_{max} and s_{min} for different versions of the model with overlapping generations shows that they are not very different from the model with non-overlapping generations, although of course there are clear differences in the distribution of different types of dynamics. In each case, however, the population persistence gradient is preserved in the direction connecting the lower right and upper left corners of the parameter space. This means that in all versions of the model, an increase in individual variability in the amounts of resources obtained leads to an increase in the persistence of the population measured by the length of time that elapses until the extinction of the population.

The parameters space s_{max} and s_{min} in the case of the model with overlapping generations and with young and old individuals using the same resources, i.e. with global competition between all individuals of the population for common resources, also between young and old individuals, indicates a clear increase in the area occupied by cases characterized by long extinction times compared to the model with non-overlapping generations. This applies to the situation $b = 1.0$, when assimilation of juveniles in the presence of adults is not additionally reduced. The reason for this is as follows. In the case of the model with non-overlapping generations, the condition for population extinction is the absence in a certain generation of at least one individual capable of producing at least one offspring with current resources. In the case of a model with overlapping generations, three conditions must be met. Consider two generations: current and previous. If a population is to become extinct in the current generation, then, first, there must be no reproducing adults in that generation. Secondly, there cannot be any reproducing adult in the previous generation, and thirdly, there cannot be any reproducing juvenile in the previous generation. As can be seen from the simulation results, in the case of a population with overlapping generations, these three conditions are more difficult to meet simultaneously than one condition in the case of a population with non-overlapping generations. This is despite the fact that joint exploitation of the same resources by juveniles and adults may mean much more intensive depletion of them.

On the other hand, if it so happens that the current generation does not have a reproducing adult, then the population can survive in effect of the reproduction of the juveniles or adults of the previous generation. If there is no reproducing adult in the previous generation, the population can survive by reproducing juveniles in the previous generation or by transforming juveniles from the previous generation into adults in the current generation. If, on the other hand, there is no reproducing juvenile in the previous generation, then the population can survive by reproducing adults in the previous generation or, as before, by transforming juveniles from the previous generation into adults in the current generation. If there are no reproducing juveniles and adults in the previous generation, the population can survive by transforming the juveniles of the previous generation into adults of the current generation. If there are no reproducing adults in the current and previous generations, the population can survive by reproducing juveniles in the previous generation. Finally, if there are no reproducing adults in the current generation and no reproducing juveniles in the previous generation, then the population can survive by reproducing the previous generation's adults. All these conditions for population persistence will be weakened if the transformation of juveniles of the previous generation into adults of the current generation is not 100% efficient. Thus, it can be assumed that all ecological mechanisms that weaken this transformation, for example, increased juvenile-to-adult mortality, can significantly shorten the time of population extinction.

Increasing competitive pressure on juveniles from adults by reducing the value of parameter b has a negative impact on the persistence of the population. The area filled with cases with the longest population extinction times shrinks significantly for $b < 1$. A proportional reduction in assimilation of all juveniles weakens their growth and, consequently, also adversely affects the growth of adult individuals, reducing the production of offspring in both age groups. This is clearly seen in the fact that for $b < 1$, juveniles do not produce offspring after the end of growth, which means that they have not reached the appropriate weight. Production of offspring takes place only in adults.

The paper analyses two versions of the model with overlapping generation, in which competition between adults and juveniles is

deliberately eliminated or its effects reduced: a model with different resources used by juveniles and adults, and a model with the so-called mother's care. In both cases, the negative impact of these assumptions on population persistence was observed. In the parameter spaces s_{max} and s_{min}, the areas occupied by the longest population extinction times have shrunk significantly. The reason for this is the reduction of individual variability in the amount of resources acquired by individuals. However, in each of these models it happens differently. Separation of juvenile and adult resources eliminates competition between juveniles and adults. This does not significantly affect the adults, because in the case of shared resources, the presence of juveniles does not affect the distribution of resources between adults, it only reduces the amount of resources in the environment. However, it has a big impact on young individuals. Releasing from the competitive influence of adults by beneficially changing the way resources are partitioned and increasing the pool of resources available to juveniles causes them to grow better. This is manifested, for example, by the fact that after this stage of growth they produce offspring, which happens rarely or never in the case of juveniles using the same resources as adults. The increase in the number of offspring has a negative impact on the persistence of the population. In the case of a model with non-overlapping generations, increasing the value of the parameter c leads, especially for medium and low individual variability, to a decrease in the extinction time of the population (see analysis presented in Uchmański 2000; Grimm and Uchmański 2002). This is due to the increased exploitation of resources by more individuals. Separating juvenile and adult resources primarily means reduction in the variability within the category of juveniles, which in the next step of the simulation leads to reduced variability of adults. And this, as we already know, lowers the chance of a population surviving the crisis that occurs when

resources are at a minimum. In the case of the model with the so-called mother's care, assigning the same value of parameter a_1 to juveniles as their mother causes that variability among juveniles is not the result of the conditions in which they live, but it repeats the variability of adults. It can also be treated as a decrease in individual variability in the population, and in a way that is unfavourable for the persistence of the population, because it breaks the relationship between the variability of individuals and their living conditions.

Conclusions

Individual natural selection promotes such characteristics of an individual, called adaptations, that increase its reproductive success. It is the direct and immediate reproductive success of an individual – the number of offspring produced by it that survive to adulthood (Cooper 1984; Stearns and Hoekstra 2005). This is a pattern of thinking that holds true in evolutionary biology. From this perspective, mother's care, or the separation of resources of juveniles and adults, appears to promote the reproductive success of an individual. If, in some situation, such adaptations become fixed in the population, the models discussed in this paper show that this has an adverse effect on the persistence of the population. This can be regarded as the ecological costs of these adaptations, which are inevitable. Persistence of the population will be supported by all forms of competition between individuals not weakened by any environmental factors (e.g. diversification of resources of competing individuals) or factors arising from evolutionary history of the species (e.g. mother's care) and related in an appropriate way to the mechanism shaping individual variability in the population. Any form of weakening competition leading to decreasing individual variability will adversely affect the persistence of the population. At the same time, one must realize that such a way of regulating the population, in which individual variability is involved, entails

a demographic cost, which is not visible when looking at the number of living individuals in the population. In the models considered in this paper, mortality resulting for instance from poor growth of an individual was equal to zero (other causes of mortality were also not taken into account), so only childless death of individuals can be written down on the cost side.

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