The interplay of sex ratio, male success and density-independent mortality affects population dynamics

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ABSTRACT

Environmental constraints can limit a population to a certain size, which is usually called the carrying capacity of a habitat. Besides to this 'external' factor, which is mainly determined by the limitation of resources, we investigate here another set of population-intrinsic factors that can limit a population size significantly below the maximum sustainable size. Firstly, density-independent mortality is a prominent factor in all organisms that show age-related and/or accidental death. Secondly, in sexually reproducing organisms the sex ratio and the success of pairing is important for finding reproductive partners. Using a simple model, we demonstrate how sex ratio, mating success and gender-specific mortality can strongly affect the speed of population growth and the maximum population size. In addition, we demonstrate that density-independent mortality, which is often neglected in population models, adds a very important feature to the system: it strongly enhances the negative influence of unbiased sex ratios and inefficient pairing to the maximum sustainable population size. A decrease of the maximum population size significantly affects a population's survival chance in inter-specific competition. Thus, we conclude that the inclusion of density-independent mortality is crucial, especially for models of species that reproduce sexually. We show that density-independent mortality, together with biased sex ratios, can significantly lower the abilities of a population to survive in conditions of strong inter-specific competition and due to the Allee effect. We emphasize that population models should incorporate the sex ratio, male success and density-independent mortality to make plausible predictions of the population dynamics in a gender-structured population. We show that the population size is limited by these intrinsic factors. This is of high ecological significance, because it means that there will always be resources available in any habitat that allows other species (e.g., invaders) to use these resources and settle successfully, if they are sufficiently adapted.

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1. Introduction

Early models of evolution tended to assume that organisms live and evolve in large panmictic populations and in homogeneous environments (Colegrave, 1997). In a hypothetical population of infinite size, a one-to-one sex ratio in the adult population was shown to be optimal, assuming random mating and Mendelian segregation (Fisher, 1930; Eshel and Feldman, 1982; Lessard, 1990). However, it became clear that populations are limited in space and resource availability. Thus, it can be expected that the population structure should have profound consequences for the evolution of organisms. The study of Williams (1966) asserted two predictions:

(1) male-biased sex ratios should evolve whenever the population density needs to be reduced; (2) female-biased sex ratios should evolve whenever the survival of the population is enhanced by an increased growth rate. He argued that there is no evidence that the sex ratio is changing in this way, because natural selection must not be acting to favor the group. However, Leigh (1983) demonstrated that group selection could effectively override individual-selection, but only under certain strict conditions of generation length, emigration and population size.

Population size is commonly linked directly to the carrying capacity of the habitat (Begon et al., 1996), although recent studies pointed out that populations possibly reside far away from any equilibrium. Thus, the observed population size does not necessarily reside close to a carrying capacity (Rohde, 2006). Williams (1966) provided a turning point from the early widespread concept of population level fitness (Wynne-Edwards, 1962) to the importance of individual level selection. The population size changes in course of the evolution via increasing the carrying capacity either

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by extending the resource availability in the habitat or by using the resources more efficiently.

Evolutionary theory has long relied on the hypothesis of the adult sex ratio (ASR) stability, but current studies (Le Galliard et al., 2005) demonstrate that ASR dynamics have profound consequences for individual behaviors, ultimately also affecting population dynamics. Population theory has remained strongly female-focused and the role of males in the population dynamics of animal species has been largely neglected (Mysterud et al., 2002). Engen et al. (2003) showed that fluctuations in sex ratios both in monogamous and polygamous systems add an important component to the demographic variances. However, sex ratios have some indirect effect as well. For example, it is well documented that the presence of males induces oestrus in females. In populations with both, skewed sex ratios and a young male age structures, calving of females is delayed and less synchronous (Mysterud et al., 2002). An explicit modeling of males and females is required to study the population dynamic consequences of these aspects. They cannot be successfully covered by "asexual" models that still prevail in theoretical studies of population dynamics (Berec and Boukal, 2004).

Among the many individual-based factors that were suggested as an explanation for the occurrence of biased sex ratios, local male competition was most commonly mentioned (Hamilton, 1967). In consequence, many studies were performed which focused on male mating success, but most models, that were used to interpret the observed population growth, did rely only on density-dependent parameters. However, individuals die in considerable extent due to density-independent reasons (e.g., age-related death). Such density-independent mortality rates were used in some classical ecological models like in predator-prey models (Lotka, 1925; Volterra, 1926) and also in some current models (e.g., Runge and Marra, 2005; Berec and Boukal, 2004; Berec et al., 2001). Slobodkin (1961) modified the basic Lotka–Volterra model by including a non-selective removal factor that was crucial to explain Gause's (1934) observations on competitive coexistence. However, most population models neglect the density-independent mortality (e.g., Ricker, 1954; see also the overview in Brännström and Sumpter, 2005). It is also known that male mortality rates are typically higher than those of females (Owen-Smith, 1993), even when males and females have a similar body size (Gaillard et al., 1993).

In this paper a mathematical model is constructed with consideration of all important factors mentioned above: sex ratio, male success and gender-specific density-independent mortality. Then we analyze how these factors affect population dynamics: For example, in case of sexual reproduction, we suggest that density-independent mortality intensifies the negative effects of sub-optimal adult sex ratios (ASRs) in a way that significantly lowers the abilities of a population to survive in conditions of strong inter-specific competition. Thus, we hypothesize that considering this mortality factor is important to understand sex ratio evolution and population dynamics of such species.

What is the effect of density-independent mortality on population growth when mortality and reproduction parameters are kept fixed? How does an optimal sex ratio change as a function of male mating success and of density-independent mortality? What is the predicted effect of gender-related mortality? Such dependencies may play a crucial role in species for which changing environmental conditions affect sex determination much more than other life-history characteristics (Charnov and Bull, 1977). We address these questions from an ecological perspective by investigating how ecology modulates selective pressure on the individual organism within a closed population with mixed genders.

2. Materials and methods

To investigate this problem set, we constructed a time-continuous model of the population dynamics of a sexually reproducing, iteroparous species. For mathematical tractability we chose a deterministic approach. Our aim was to show the major trends that are important in population biology. Our aim was not to build a specific model for a given species or explore the whole state-space of the parameter combination. The model was implemented in Maple and solved numerically using 4th order Runge–Kutta method.

2.1. The model formulation

We based our model on a classical logistic-growth model (Verhulst, 1838, 1845), assuming intra-specific competition limiting the population growth, as well as assuming overlapping generations and density-dependent growth and death (Eq. (1)).

$$\frac{dN}{dt} = R\left(1 - \frac{N(t)}{K}\right)N(t) \tag{1}$$

The parameter R represents the intrinsic (maximal) growth rate and the parameter K describes the carrying capacity of the habitat. This approach assumes either that $N(t)$ expresses only the female population and that males are available for fertilizing all eggs, or it assumes asexual reproduction.

In this paper, we treat different genders separately: $N_m(t)$ and $N_f(t)$ represent the current population of males and females at time t. Thus, the total population ($N(t)$) is given in Eq. (2).

$$N(t) = N_f(t) + N_m(t) \tag{2}$$

In turn we assume that every male fertilizes at most λ females and that every female mates with just one male. This is a strong simplification of the pair formation problems studied in detailed by Berec and Boukal (2004), however our goal was not studying different aspects of male success (mate search, mate choice, divorce behavior, etc.), but examine the compound effects of these parameters. Based on these assumptions, we calculate the number of successfully mated females ($F_m(t)$) as follows:

$$F_m(t) = \min\left(\begin{array}{c} N_f(t) \\ \lambda N_m(t) \end{array}\right) \tag{3}$$

Thus, the number of fertilized females has an upper bound of either $N_f(t)$ or $\lambda N_m(t)$. Based on this we substitute $N(t)$ by $F_m(t)$ in Eq. (1) to develop a new equation for population growth:

$$\frac{dN}{dt} = R\left(1 - \frac{N(t)}{K}\right)F_m(t) \tag{4}$$

In our model, the factor α expresses the birth sex ratio (BSR), which is the fraction of females in the offspring. The numbers of male and female offspring are calculated in separate cohorts as follows:

$$\frac{dN_f}{dt} = R\alpha\left(1 - \frac{N(t)}{K}\right)F_m(t) \tag{5}$$

$$\frac{dN_m}{dt} = R(1-\alpha)\left(1 - \frac{N(t)}{K}\right)F_m(t) \tag{6}$$

Classical models such as those that are derived from the Verhulst-equation are focused on density-dependent birth and death rates, mainly for the sake of simplicity and tractability (Begon et al., 1996). However, in real populations it is very common that death is highly independent on how close the current population ($N(t)$) has approached the carrying capacity K. A density-independent mortality (μ) reflects the summation of random (accidental) death events as well as age-related death.
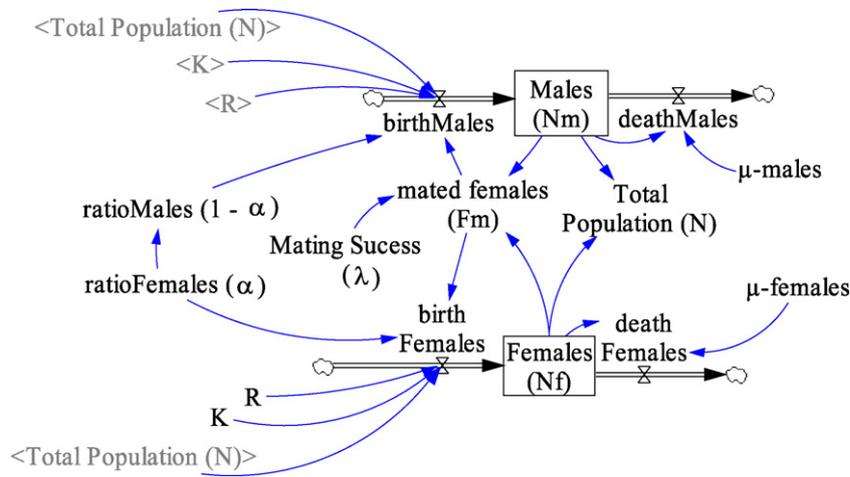
Fig. 1. Stock and flow diagram of the gender-specific population model. Stocks (boxes) represent compartments, in which material (individuals) reside. Flows (doubled arrows) indicate losses or gains of material (individuals) inside of these compartments (births and deaths). Other components (plain text) indicate auxiliary system variables and constants. Thin arrows indicate dependencies of components.

Using various values of μ for the two genders allows us to depict gender-specific mortality rates in our model. To include density-independent mortality we add a simple proportional death rate (μ_m and μ_f) to Eqs. (5) and (6), which leads us to our final model equations (Eqs. (7) and (8), see Fig. 1). Reproduction and mortality operate concurrently, that is, newborns do not die at the same time step and adults, that will die, have the full opportunity to reproduce at that step.

$$\frac{dN_f}{dt} = R\alpha \left(1 - \frac{N(t)}{K} \right) F_m(t) - \mu_f N_f(t) \tag{7}$$

$$\frac{dN_m}{dt} = R(1 - \alpha) \left(1 - \frac{N(t)}{K} \right) F_m(t) - \mu_m N_m(t) \tag{8}$$

From Eqs. (7) and (8) we calculate the equilibria of the population size by setting the rate of change (left hand side) to 0. This gives

$$N_{\text{total},f}^* = K \left(1 - \frac{\mu_f N_f(t)}{R\alpha F_m(t)} \right), \quad \text{and} \tag{9}$$

$$N_{\text{total},m}^* = K \left(1 - \frac{\mu_m N_m(t)}{R(1 - \alpha) F_m(t)} \right), \tag{10}$$

two equations showing total population sizes at which one of the two genders does not change anymore. The variable $N_{\text{total},f}^*$ represents the size of the total population at which female population does not change, and $N_{\text{total},m}^*$ represents the size of the total population at which the male population does not change. Eqs. (9) and (10) show clearly that the predicted total equilibria are both below K, as long as μ_f and μ_m are above 0. Note that all population variables have always to be positive. Thus, the model predicts that density-independent mortality of either gender keeps the population size below the carrying capacity of the environment. A fraction of resources, that is available in the habitat, is not exploited by the modeled population due to species-intrinsic limitations of growth. This effect of intrinsic population limitation by density-independent death and by sexual reproduction is of high significance in ecological considerations and has, to our knowledge, never been reported. How far populations are intrinsically limited below K depends on α and on $F_m(t)$, thus also on λ, as it is expressed in Eqs. (9) and (10).

We know that population sizes have to be non-negative and below K, thus, we conclude from Eq. (9) that

$$0 \leq \frac{\mu_f N_f(t)}{R\alpha F_m(t)} < 1. \tag{11}$$

We know from Eq. (3) that not more females are fertilized than present in the habitat at time t, thus $F_m(t) \leq N_f(t)$. Additionally we know that $F_m(t) \geq 1$ and $N_f(t) \geq 1$ to allow non-zero population equilibrium. Considering these facts in Eq. (11), we get $\mu_f < R\alpha$ for all population sizes that reach non-zero equilibrium. This means that the rate of female death has to be lower than the rate of female offspring production to allow non-zero populations. This is a plausible conclusion from a biological point of view.

For the male population, we conclude from Eq. (10) that a non-zero population equilibrium will be reached below K if

$$0 \leq \frac{\mu_m N_m(t)}{R(1 - \alpha) F_m(t)} < 1. \tag{12}$$

Eq. (3) shows that not more females are fertilized than the number of available males are able to mate with: $F_m(t) \leq \lambda N_m(t)$. Additionally, we know that $F_m(t) \geq 1$ and $N_m(t) \geq 1$ to allow non-zero population equilibria, because we need at least one male and one fertilized female to sustain a sexually reproducing population. From this, and assuming that females do not limit the population, we conclude from Eq. (11), that $\mu_m < R(1 - \alpha)\lambda$ for all population sizes that should reach a non-zero equilibrium. This means that rate of male mortality has to be below the rate of male production multiplied by the mating success rate.

By equating Eqs. (9) and (10), we search for the ratio of males to females at the point in time when both genders reached their equilibrium population size. This yields

$$\frac{N_f(t)}{N_m(t)} = \frac{\mu_m \alpha}{\mu_f(1 - \alpha)}, \tag{13}$$

showing that the ratio of females to males increases with decrease of μ_f and with increasing values of α. The final adult sex ratio (ASR) is independent from λ and R, thus also independent from $F_m(t)$.

Although the analysis of our focal model equations (Eqs. (7) and (8)) showed plausible and interesting results, it is not possible to calculate population sizes by analytically solving the equations. This is due to the fact that $F_m(t)$ is non-linear and a not continuously differentiable function of the female and of the male population, therefore we decided to solve Eqs. (7) and (8) using numeric methods. This analysis will show us how the combination of parameters μ_f, μ_m, λ and α affects the emergence of un-exploited resources in the habitat. We want to stress that our analytical finding, namely that not all resources are accessible for a sexually reproducing species, which is subject to density-independent death (e.g., age-related death), is of high ecological relevance. To demonstrate this,
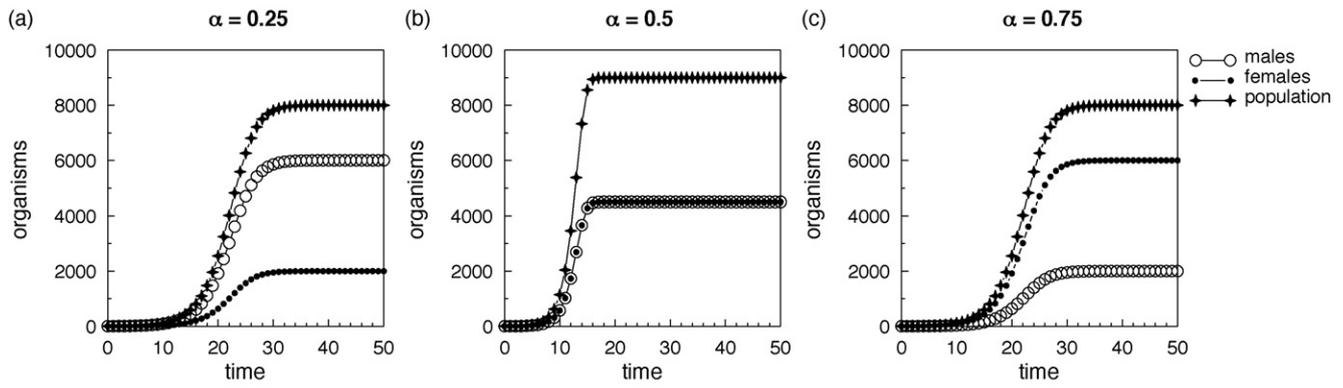
Fig. 2. The total population size depends on the value of α. For the male success $\lambda = 1$, the optimal α is 0.5, thus the middle graph depicts the highest possible population size with this value of α.

we present an extension of our model, which incorporates a scenario of two competing species with the properties mentioned above.

2.2. Simulation settings

If not stated differently, we used the following parameter set in our simulations: intrinsic growth rate: $R = 2$; sex ratio: $\alpha = 0.5$; carrying capacity: $K = 10,000$; mating success: $\lambda = 1$; mortality rates: $\mu_m = \mu_f = 0.1$. We started all our simulations presented here with one male and one female ($N_f(0) = N_m(0) = 1$) organism.

3. Results

Based on our mathematical model formulated in the previous section, we performed a variety of simulation experiments to analyze the effect of the key parameters on the final population sizes.

3.1. The effect of the birth sex ratio (α) on the population dynamics

In a first analysis, we assumed constant values of $\mu_m = \mu_f = 0.1$, $\lambda = 1$, and predicted the population dynamics for different values of α. Sub-optimal values of α (not enough males to fertilize all females or fewer females than males) resulted in a significantly decreased speed of growth and in a smaller population size at equilibrium (Fig. 2). All simulations predicted a final population significantly below the level of $K = 10,000$.

These results were clearly caused by the density-independent mortality, because whenever this mortality term was set to zero ($\mu_m = \mu_f = 0$), the population always reached the carrying capacity

($K = 10,000$), regardless of the value of α. However, the speed of population growth was still heavily affected by α, where $\alpha = 0.5$ produced the fastest population growth (Fig. 3).

3.2. The effect of the mortality rates on population growth

Varying the parameters μ_m and μ_f between 0 and 1 allowed us to explore how the density-independent mortality rates affect the dynamics of the population. Our simulations show that for all $\mu_m > 0$ and $\mu_f > 0$ the maximum population size at equilibrium was below K, that is, density-independent mortality drives populations towards an equilibrium. This equilibrium is below the maximum carrying capacity which is supported by the environment (compare Figs. 2 and 3). These results indicate that under the conditions tested, the given species cannot fully exploit all putative resources due to the intrinsic limitation of growth.

Different genders often have different mortality rates (Owen-Smith, 1993; Gaillard et al., 1993). Such gender-specific mortalities significantly influence population dynamics, and even lead to collapses of the populations in extreme conditions (Pettersson et al., 2004; Le Galliard et al., 2005). Our model is able to predict such extreme population dynamics when parameterized with different mortality rates for males and females. Our simulations showed (Fig. 4a and c) that these biased mortalities significantly affect the maximum population size. Gender-specific mortality rates decreased the total population size to $N(t) = 8500$ (compared to $N(t) = 9000$ in Fig. 2) although the average value of μ was the same (($\mu_m + \mu_f)/2 = 0.1$ for all cases).

The detrimental effect of gender-specific mortality rates is compensated by adjusting α. As we showed, a higher male mortality ($\mu_m = 0.15$) is compensated by a lowered value of α ($\alpha = 0.25$)
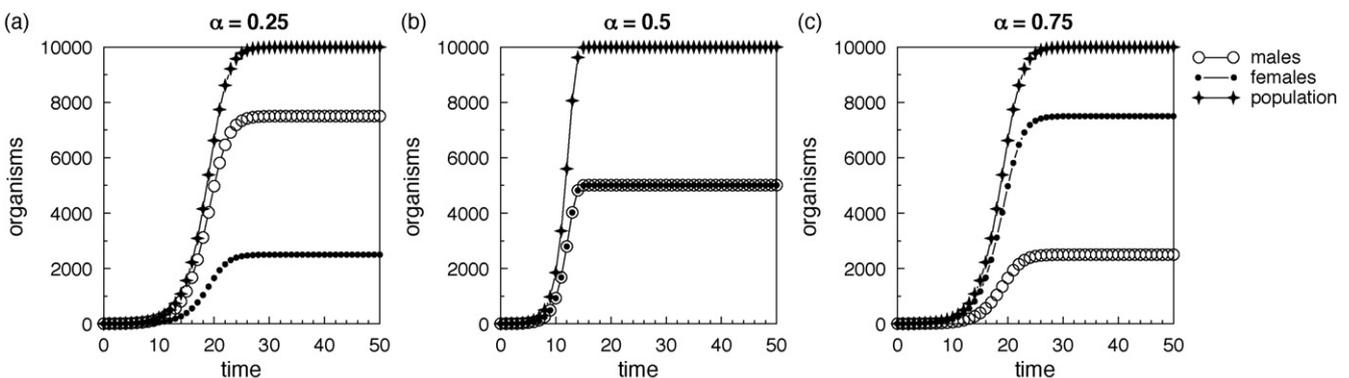
Fig. 3. Without density-independent mortality, the final population size was independent of α. Population size approached K in every case. Nevertheless, the speed of population growth was strongly affected by α. For $\lambda = 1$, the optimal value of α is 0.5.
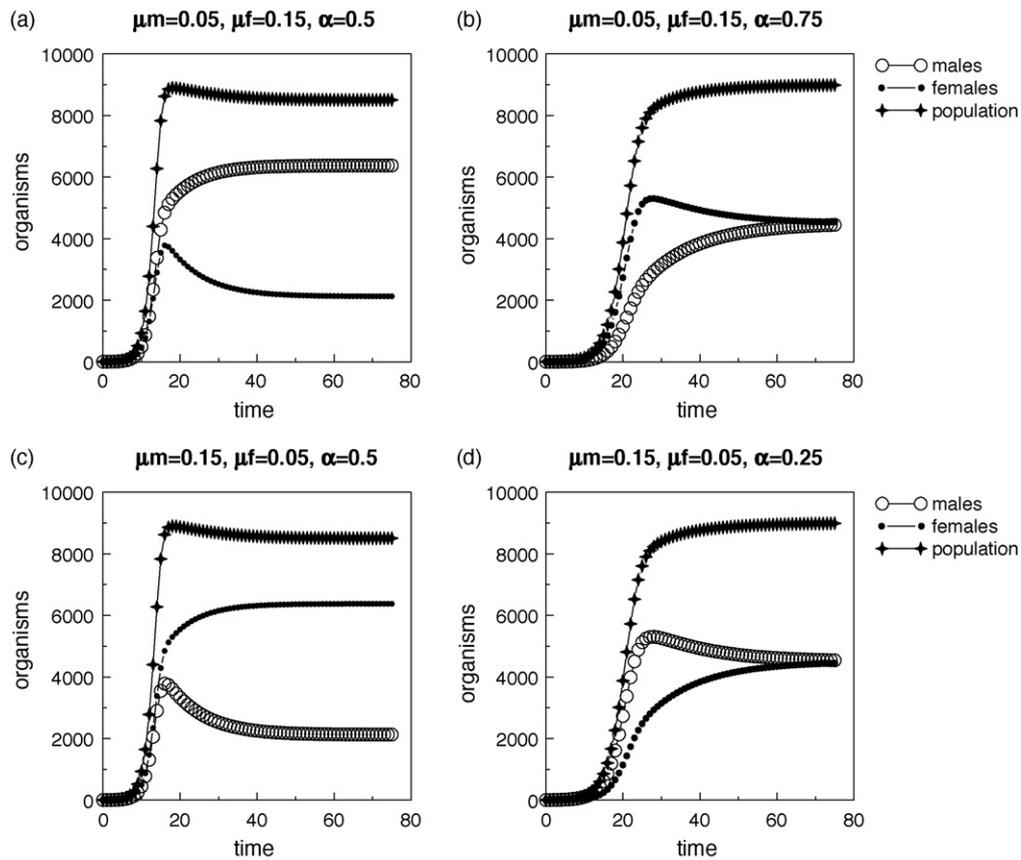
Fig. 4. The population dynamics emerged from different mortality rates of males and females. (a and c) An equal sex ratio at birth ($\alpha = 0.5$) leads to biased sex ratios of the adult population (ASR), if the mortality rates of the two genders differ. (b and d) This unequal ASR can be "balanced out" by a shift in α, which is the birth sex ratio (BSR).

(Fig. 4b) as well as the higher female mortality ($\mu_f = 0.15$) is compensated by an increased value of α ($\alpha = 0.75$) (Fig. 4d). Compensating the gender-specific mortality rates by adjusting the value of α led to the same final population size ($N(t) = 9000$) that was obtained before (Fig. 2).

3.3. How sex ratio (α) and male success (λ) affects population size

We generated 3 scenarios with different values of λ to investigate the effect of α and λ on the population size: $\lambda = 3$ indicates that each male was able to fertilize 3 females, $\lambda = 1$ indicates that each male was able to fertilize one female, and $\lambda = 0.33$ indicates that only every third male was able to mate successfully with a female. All analyses assumed density-independent mor-

tality of $\mu_m = \mu_f = 0.1$. Our results show that the population size never reached K in any of these scenarios. The higher λ was, the higher the optimal α had to be set to reach the highest population at equilibrium point (see Fig. 5).

3.4. Analyzing the interplay of our four focal parameters

The previous sections demonstrated the severe impacts of our four parameters (α, λ, μ_m, μ_f) on the population dynamics of a sexually reproducing species via examples. To analyze how these four parameters interact, we performed an exhaustive parameter sweep and investigated how combinations of values of these four parameters affect the population size. All simulation runs were started with one male and one female. At the end of each run ($t = 1000$), the total
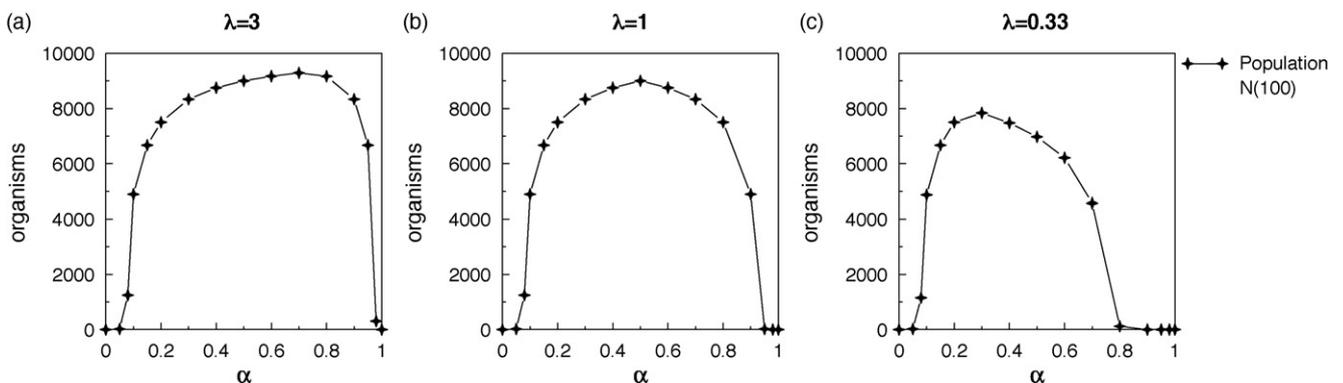
Fig. 5. Population levels reached at $t = 100$ as a function of λ and α. Higher values of λ allowed higher population levels. In the case of $\lambda = 1$ the 'optimal' α is 0.5. Low values of λ ($\lambda < 1$) led to smaller final populations and this effect could not be fully compensated by changing α.

(a)   α=0.5, λ=1   (b)   μ_f=μ_m=0.1

(c)   α=0.25, λ=1   (d)   α=0.75, λ=1
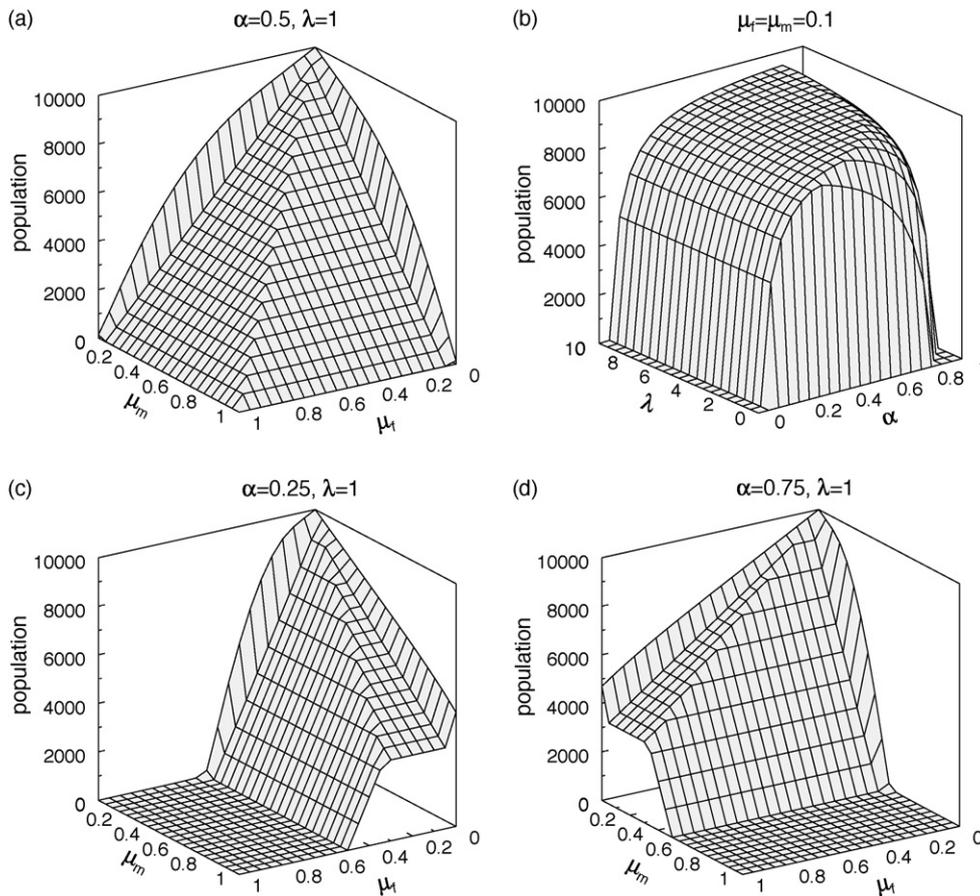
Fig. 6. The effect of sex ratio, male success and density-independent gender-related mortality on population size. (a) Unbiased sex ratio ($\alpha = 0.5$), standard male success ($\lambda = 1$) with variable density-independent mortalities were sampled. (b) Fixed density-independent mortalities, α and λ were sampled. (c) Male-biased sex ratio ($\alpha = 0.25$), standard male success ($\lambda = 1$), density-independent mortalities were sampled. (d) Female-biased sex ratio ($\alpha = 0.75$), standard male success ($\lambda = 1$), density-independent mortalities were sampled. Population size was measured after 1000 time steps.

population size was recorded. All simulation runs had reached the equilibrium population size at this point in time.

In case of unbiased sex ratio ($\alpha = 0.5$), the population size increased linearly with decreasing mortality rates (Fig. 6a). The highest population sizes were observed when the mortality rates were equal for both genders. Differences in mortality rates resulted in a decrease in the population size. The increase of male success (λ) increased the maximum population size (Fig. 6b). The sex ratio (α) that led to the highest population sizes got shifted towards bigger values of α as male success (λ) increased, that is, more females were born due to the increased male success. Fig. 6c and d shows the population sizes as a result of different density-independent mortalities. If the sex ratio was male-biased ($\alpha = 0.25$) and the mortality of females was high ($\mu_f > 0.5$, regardless of the level of μ_m), the population became extinct (Fig. 6c). In case of female-biased sex ratio ($\alpha = 0.25$), the population died out whenever μ_m was above 0.5 (Fig. 6d).

3.5. Implications of our findings

In order to demonstrate the implications of our findings described above, we constructed a classical two-species competition model following the assumption of linear decrease of growth due to inter-specific competition (Lotka, 1925; Volterra, 1926). For species 1, the variables and constants of our previous model are indexed by an additional index $i = 1$.

$$\frac{dN_{f,1}}{dt} = R_1 \alpha_1 \left(1 - \frac{N_1(t)}{K_1} - \frac{b_{12}N_2(t)}{K_1}\right) F_{m,1}(t) - \mu_{f,1}N_{f,1}(t) \qquad (14)$$

$$\frac{dN_{m,1}}{dt} = R_1(1 - \alpha_1) \left(1 - \frac{N_1(t)}{K_1} - \frac{b_{12}N_2(t)}{K_1}\right) F_{m,1}(t)$$
$$- \mu_{m,1}N_{m,1}(t) \qquad (15)$$

For the second species, the same kind of equations were used, just the parameters and constants were indexed by $i = 2$.

$$\frac{dN_{f,2}}{dt} = R_2 \alpha_2 \left(1 - \frac{N_2(t)}{K_2} - \frac{b_{21}N_1(t)}{K_2}\right) F_{m,2}(t) - \mu_{f,2}N_{f,2}(t) \qquad (16)$$

$$\frac{dN_{m,2}}{dt} = R_2(1 - \alpha_2) \left(1 - \frac{N_2(t)}{K_2} - \frac{b_{21}N_1(t)}{K_2}\right) F_{m,2}(t)$$
$$- \mu_{m,2}N_{m,2}(t) \qquad (17)$$

The number of fertilized females was modeled analogously to Eq. (3):

$$F_{m,i}(t) = \min \begin{pmatrix} N_{f,i}(t) \\ \lambda_i N_{m,i}(t) \end{pmatrix} \qquad (18)$$

The linkage between the two populations (i.e., the strength of inter-specific competition) depends on the two parameters b_{12} and b_{21}. Based on this model, we investigated four distinct scenarios of inter-specific competition. Two of these simulations showed the effects of sex bias (parameterized as a slightly sub-optimal value of α_2 compared to α_1, where the term "optimal" identifies those parameter ranges that are predicted to provide the biggest
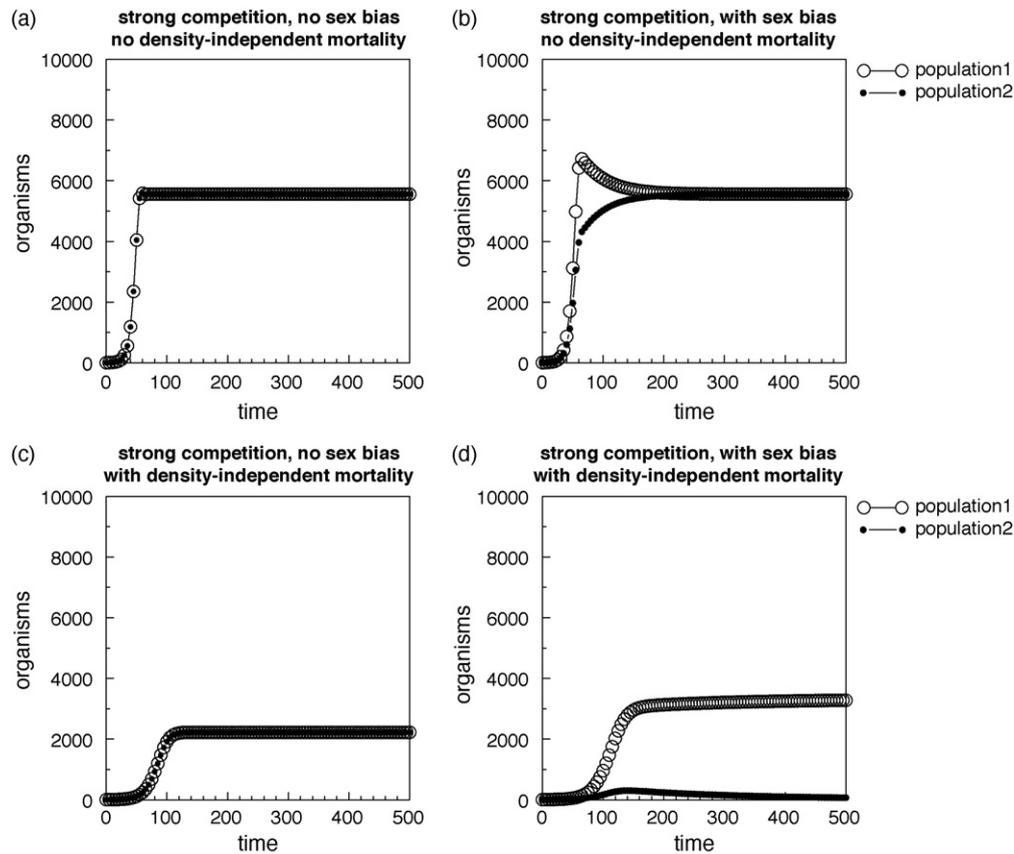
Fig. 7. Predicted population dynamics of two competing species with different values for sex ratio and density-independent mortality. Used parameter sets: (a) $\alpha_1 = 0.5$, $\alpha_2 = 0.5$, $\mu_{m,1} = y_{f,1} = \mu_{m,2} = \mu_{f,2} = 0$; (b) $\alpha_1 = 0.55$, $\alpha_2 = 0.6$, $\mu_{m,1} = y_{f,1} = \mu_{m,2} = \mu_{f,2} = 0$; (c) $\alpha_1 = 0.5$, $\alpha_2 = 0.5$, $\mu_{m,1} = y_{f,1} = \mu_{m,2} = \mu_{f,2} = 0.15$; (d) $\alpha_1 = 0.55$, $\alpha_2 = 0.6$, $\mu_{m,1} = y_{f,1} = \mu_{m,2} = \mu_{f,2} = 0.15$. With $\mu > 0$ and $\alpha \neq 0.5$. The population of the species with the less adapted sex ratio became extinct (d). The models, that discounted the existence of biased sex ratio and/or the density-independent mortality, predicted coexistence at identical population levels (a, b, c).

population size). The other two simulations showed the effect of density-independent mortality ($\mu_1 > 0$, $\mu_2 > 0$).

For all simulations the same parameterization of $N_{f,i}(0) = 1$, $N_{m,i}(0) = 1$, $\lambda_i = 1$, $R_i = 0.5$, $K_i = 10,000$ was used. We used values of $b_{12} = b_{21} = 0.8$ to express that our two populations have no perfect niche overlap. Each of the two-species has access to 20% of resources that are unavailable for the opponent species.

Without sex bias and without density-independent mortality (Fig. 7a), both populations were predicted to coexist at a stable equilibrium. By introducing density-independent mortality (Fig. 7c), the species were still able to coexist, but on a much lower equilibrium compared to the previous scenario. Still, the dynamics of both genders are symmetrical. Both species were predicted to reach the same final population size. With one species having a combination of male success and sex ratio which allows a higher maximum population size (Fig. 6b), the final population size depended strongly on the strength of the density-independent mortality. Without this mortality term (Fig. 7b, all μ values at 0), both species reached the same final population size as they would also reach without any sex bias (compare Fig. 7a and b). With biased sex ratio, the species with a sex ratio closer to 1:1 showed a faster population growth than the other species, what led to a short time advantage and to the emergence of an "overshoot pattern" before reaching the final equilibrium population size (see Fig. 7b, period of $50 < t < 150$). When the model also incorporated the density-independent mortality, the models predictions are fundamentally different from the previous three cases: one species with a sex ratio that allowed bigger population sizes and faster population growth, won the competition and the other species, which had just a slightly less adapted sex ratio, was predicted to go extinct (Fig. 7d).

4. Discussion

In this study we showed that there is a high interdependency among birth sex ratio (α), adult sex ratio (affected by gender-specific mortality rates) and male success (λ). All these factors affect the population size at equilibrium state. The Allee effect, that is population extinction at low density due to difficulties in partner pairing (Berec and Boukal, 2004; Engen et al., 2003; Allee et al., 1949), emerged automatically (internally) in this system when strongly biased sex ratios caused a lack of mating possibilities and consequently lead to extinction or very small population sizes. While it is known that the Allee effects strongly affect population dynamics (Dennis, 2002), we still lack quantitative understanding of the mechanisms involved (Fowler and Baker, 1991).

When density-independent mortality was implemented into the model, the population size was predicted to remain significantly below the carrying capacity (K). The distance between the actual equilibrium population size and K depends on both λ and α. Higher values of λ coupled with a less biased sex ratio (α closely around 0.5) decrease this difference while low male success and strongly biased sex ratio will increase the difference between the equilibrium population size and K. The bigger λ gets, the smaller are the growth limitations caused by deviations of α from 0.5. In the cases when λ gets very big (close to the level of K) and that α gets very big (close to 1), the predicted solutions of the gender-specific model presented here approach those of the Verhulst-equation (Eq. (1)), thus it converges towards a gender-less model, applicable for species that reproduce asexually.

We have shown that population models should incorporate sex ratio, male success and density-independent mortality (α, λ, μ_m,

μ_f, respectively) to make plausible predictions of the population dynamics in a gender-structured population, as these parameters severely influence the predicted size of populations (Fig. 6). Especially the inclusion of density-independent mortality restricts the final population size significantly below the value of *K*. The model predicts that a population that reproduces sexually and is affected by density-independent mortality (in addition to density-dependent mortality) will never be able to exploit all available resources in the environment. Interestingly, species-intrinsic limitations of growth (low mating success and sex ratio mismatch) keep the population size further away from *K*. This result is not predicted by models that exclude density-independent mortality from their base assumptions. In such models (as depicted in Fig. 3), the population always reaches *K* after some time, because the species-intrinsic factors decrease only the speed of growth but not the limit of growth.

Whenever the density-independent mortality was increased from zero to a larger value, a sudden decrease in the final population size is seen (Fig. 6a–c). By looking into the time dynamics of these simulation runs with just one μ-value at 0 (Fig. 6, dynamics not shown but only the final population sizes of these runs), an interesting phenomenon was observed. In each simulation run, the gender which was parameterized with non-zero μ, always became extinct after some time, because of the effect of intra-specific competition. Simultaneously, the gender with no density-independent mortality ($\mu = 0$) got fixed at the equilibrium level and the population consisted only of one single 'immortal' gender. This surviving gender resided on an equilibrium, because it was immortal (as its μ was set to 0), and because it was unable to reproduce because the other gender was missing. This shows clearly that a population model that tracks genders in separate variables has to include also age-related death as a crucial parameter, otherwise paradox predictions occur. These findings underline that our way of including the parameters μ_m and μ_f was very important to generate a reliable sexually resolved population model.

The prediction that population sizes are intrinsically confined below *K* has profound ecological importance. Classical competition models (Lotka, 1925; Volterra, 1926) predict that differences in the *K*-values of competing species have the highest importance in coexistence. In case of strong competition, usually the species with the highest *K* survives and the other species is predicted to go extinct. Thus all adaptations that will lead to an increase of the equilibrium population size towards *K* are considered to enhance the competitiveness of the individuals that belong to that population. By implementing a competition model based on our prior defined gender-specific model, we confirmed these assumptions.

Our results suggest that any sexually reproducing species, that shows age-related death, will be confined to a population size below *K* by population-intrinsic factors. Therefore, we assume that such a species will never be able to use all resources available in its habitat. This allows other (invading) species to access to these remaining resources. In turn, these free resources allow invading species to colonize the focal habitat and to use these resources for reproduction. If such an invading species has a high competing ability, it may out-compete the species that was present in the habitat before. Within such a process of biological invasion and succession, the existence of some unoccupied resources is fundamental.

It can be assumed that natural selection minimizes the intrinsic limitations of growth by decreasing density-independent mortality (μ_m, μ_f), by increasing male success (λ), and by adjusting the sex ratio (α), so that populations grow as closely as possible to the level that is supported by the environment. On the other hand, density-independent mortality is largely depending on factors that are difficult to adapt (e.g., age, fatal accidents).

We have refrained from inclusion of further details like population age, structure, and demographic stochastic factors. There is

no doubt, however, that population structure related to age, body size, etc. would result in more realistic and more detailed models. Incorporation of these factors and similar processes may shed further light on ecological and evolutionary implications of population dynamics.

5. Conclusion

Sex ratio, male success and density-independent mortality has a profound influence on a sexually reproducing species' population dynamics. Density-independent mortality (often neglected in population models), strongly enhances the negative influence of unbiased sex ratios and inefficient pairing to the maximum sustainable population size. A decrease of the maximum population size significantly affects a population's chance of survival in inter-specific competition, because there will always be resources available in any habitat that allow other species (e.g., invaders) to use these resources and open a possibility to settle successfully. Our study emphasizes that population models should incorporate a sex ratio, male success and density-independent mortality to make plausible predictions of the population dynamics in a gender-structured population.

References

Allee, W.C., Emerson, A.E., Park, O., Park, T., Schmidt, K.P., 1949. Principles of Animal Ecology. Saunders, Philadelphia, PA, USA, 837 pp.
Begon, M., Harper, J., Townsend, C., 1996. Ecology: Individuals, Populations and Communities. Blackwell Science, Oxford, 1068 pp.
Berec, L., Boukal, D.S., 2004. Implications of mate search, mate choice and divorce rate for population dynamics of sexually reproducing species. Oikos 104, 122–132.
Berec, L., Boukal, D.S., Berec, M., 2001. Linking the allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. Am. Nat. 157, 217–230.
Brännström, A., Sumpter, D.J.T., 2005. The role of competition and clustering in population dynamics. Proc. R. Soc. Lond. B 272, 2065–2072.
Charnov, E.L., Bull, J., 1977. When is sex environmentally determined? Nature (London) 266, 828–830.
Colegrave, N., 1997. Can a patchy population structure affect the evolution of competitive strategies? Evolution 51, 483–492.
Dennis, B., 2002. Allee effects in stochastic populations. Oikos 96, 389–401.
Engen, S., Lande, R., Sæther, B.-E., 2003. Demographic stochasticity and Allee effects in populations with two sexes. Ecology 84, 2378–2386.
Eshel, I., Feldman, M.W., 1982. On evolutionary genetic stability of the sex ratio. Theor. Popul. Biol. 21, 430–439.
Fisher, R.A., 1930. The Genetical Theory of Natural Selection. Oxford University Press, Oxford, 272 pp.
Fowler, C.W., Baker, J.D., 1991. A review of animal population dynamics at extremely reduced population levels. Report to the International Whaling Commission 41, 545–554.
Gaillard, J.-M., Delorme, D., Boutin, J.-M., Van Laere, G., Boisaubert, B., Pradel, R., 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. J. Anim. Ecol. 62, 778–791.
Gause, G.F., 1934. The Struggle for Existence. Williams and Wilkins, Baltimore, 163 pp. (republished in 1964 by Hafner, New York).
Hamilton, W.D., 1967. Extraordinary sex ratios. Science 156, 477–488.
Le Galliard, J.-F., Fitze, P.S., Ferriere, R., Clobert, J., 2005. Sex ratio bias, male aggression, and population collapse in lizards. Proc. Natl. Acad. Sci. U.S.A. 102, 18231–18236.
Leigh, E.G., 1983. When does the good of the group override the advantage of the individual? Proc. Natl. Acad. Sci. U.S.A. 80, 2985–2989.
Lessard, S., 1990. Évolution du rapport numérique des sexes et modèles dynamiques connexes. In: Lessard, S. (Ed.), Mathematical and Statistical Developments of Evolutionary Theory, NATO ASI Series C: Mathematical and Physical Sciences, vol. 299. Kluwer Academic Publishers, pp. 269–325.
Lotka, A.J., 1925. Elements of Physical Biology. Williams and Wilkins, Baltimore, 460 pp.

Mysterud, A., Coulson, T., Stenseth, N.C., 2002. The role of males in the dynamics of ungulate populations. J. Anim. Ecol. 71, 907–915.

Owen-Smith, N., 1993. Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. J. Anim. Ecol. 62, 428–440.

Pettersson, L.B., Ramnarine, I.W., Becher, S.A., Mahabir, R., Magurran, A.E., 2004. Sex ratio dynamics and fluctuating selection pressures in natural populations of the Trinidadian guppy, Poecilia reticulate. Behav. Ecol. Sociobiol. 55, 461–468.

Ricker, W.E., 1954. Stock and recruitment. J. Fish. Res. Board Canada 11, 559–623.

Rohde, K., 2006. Nonequilibrium Ecology. Cambridge University Press, Cambridge, 236 pp.

Runge, M.C., Marra, P.P., 2005. Modeling seasonal interactions in the population dynamics of migratory birds. In: Greenberg, R., Marra, P.P. (Eds.), Birds of Two Worlds: The Ecology and Evolution of Migration. Johns Hopkins University Press, pp. 375–389.

Slobodkin, L.B., 1961. Growth and Regulation of Animal Populations. Holt, Reinhart and Winston, New York, 184 pp.

Verhulst, P.-F., 1838. Notice sur la loi que la population suit dans son accroissement. Corréspondence mathématique et physique de l'observatoire de Bruxelles 10, 113–121.

Verhulst, P.-F., 1845. Recherches mathématiques sur la loi d'accroissement de la population. Nouveaux Memoires de l'Academie Royale des Sciences et Belles-Lettres de Bruxelles 18, 1–41.

Volterra, V., 1926. Fluctuations in the abundance of a species considered mathematically. Nature 118, 558–560.

Williams, G.C., 1966. Adaptation and Natural Selection. Princeton University Press, Princeton, 314 pp.

Wynne-Edwards, V.C., 1962. Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, Edinburgh and London, 653 pp.