Coexistence of two polygynous mating strategies

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Abstract

We suggest a simple deterministic population model with sexual selection by male mating preference. Two mating strategies for males are distinguished by difference in the polygyny degree - the number of female mates per successful male. Strategy 1 is taken to be the initial male type and strategy 2 is viewed as a new male type entering the population. An important feature of the model is fitness dependence on population structure \( p := p_t \), which is the proportion of type 2 males in the current generation \( t \). Assumptions imposed on the relative fitnesses are based on a positive relationship between relatedness of mating parents and fitness. The analysis of a deterministic equation \( p_{t+1} = S(p_t) \) linking two consecutive frequencies of the new type leads to simple conditions ensuring the survival of the new type and the existence of a stable state.

1 Introduction

This paper is an attempt to address the following biological question posed by Dr William Amos from the Department of Zoology, University of Cambridge:

"Consider a closed population with two alternative mating systems: males compete with each other so that a small number get most matings, or they try to form monogamous pairs with females. The competitive strategy is good in the short-term because the winners father many offspring. But, there is a problem with inbreeding - over time the successful males become surrounded by their own daughters, with whom they cannot mate, and sons, who cannot mate with the increasing number of sisters they find. The monogamous strategy is poor in the short-term, but minimises the amount of inbreeding in the longer term. Question: under what circumstances this type of selection favours competitive/monogamous strategies? Are there stable points?"

In Section 2 we suggest a simple deterministic population model with two mating strategies for males. The two types of males differ by the polygyny degree - the number of female mates per successful male. Type 1 is taken to be the initial male type and type 2 is viewed

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as a new one entering the population. Assumptions imposed on the relative fitnesses are based on a positive relationship between relatedness of mating parents and fitness.

Section 3 contains the main results of the paper. We suggest simple conditions imposed on the degrees of polygyny and relative fitnesses that ensure the survival of the new type and the existence of an equilibrium population structure.

For another type of population model addressing a different question concerning sexual selection by polygyny degree the reader is referred to [2].

2 Model assumptions

Consider a large homogeneous population, where successful males mate and produce offspring with exactly $H_1$ females (it is assumed that each female chooses one mate, so that in the particular case of $H_1 = 1$ the mating is monogamous). Suppose a new type of males with different degree of polygyny $H_2$ enters the population. We call these two types of males type 1 and type 2 respectively, assuming that sons inherit father's type. To predict whether the new male line will survive we analyse the dynamics of the proportion $p := p_t$ of type 2 males in the current generation $t$, so that $p_0 = 0$, and if, for example, the new line takes over the population, then $p_t \to 1$ as $t \to \infty$. Next we present a set of simplifying assumptions leading to a deterministic population model fully described by the two degrees of polygyny and two monotone functions of $p$ quantifying inbreeding disadvantage due to polygyny. To distinguish between four possible types of mating we use a vector $(i,j)$ label, where $i$ is the type of female's father and $j$ is her partner's type.

Our model is set in the conventional framework of non-overlapping generations and equal sex ratio under the following specific assumptions:

- (RM1) random mating rule 1: the success rates for two types of males are equal,
- (RM2) random mating rule 2: females have no mating preferences,
- (AF) absolute fitnesses: the average numbers of children $f_{ij} := f_{ij}(p)$ in $(i,j)$-mating depend only on the current value of $p$ and satisfy $f_{11}(p) < f_{12}(p) \equiv f_{21}(p) > f_{22}(p)$,
- (RF1) relative fitness 1: function $F_1(p) := f_{11}/f_{12}$ is monotonically increasing and continuous over $0 \leq p \leq 1$,
- (RF2) relative fitness 2: function $F_2(p) := f_{22}/f_{21}$ is monotonically decreasing and continuous over $0 \leq p \leq 1$. 

2
Fitness

\[ \text{Relative Fitness} \]

\[
\begin{align*}
\text{Fitness} & \quad \text{Relative Fitness} \\
\text{low} & \quad f_{12}(p)/f_{21}(p) \equiv 1 \\
\text{high} & \quad F_2(p) := f_{22}/f_{12} \\
\end{align*}
\]

Figure 1

The last three assumptions (AF), (RF1), (RF2) concerning four fitness functions are based on a monotone relationship between relatedness of mating parents and fitness (see the left part of Figure 1) discussed in [1]. In our simple model we recognize four different degrees of parental relatedness corresponding to four mating type, which understandably results in the fitness rating given in (AF). The assumed equality of two mixed fitnesses is justified by a mating symmetry property, which follows from random mating rules (RM1) and (RM2). The monotonicity assumptions (RF1) and (RF2), graphically illustrated on the right part of Figure 1, reflect the fact that the larger is \( p \) the more related are the partners in a (1,1)-mating, and on the other hand, the less related become the partners in a (2,2)-mating.

3 Survival of the new type and stable equilibrium

Let us compare the offspring numbers \((w_1, w_2)\) of two successful males of types 1 and 2 respectively. Due to the equal sex ratio assumption the fraction of females born from type 2 males equals \( p \), and therefore

\[
\frac{w_1}{w_2} = \frac{H_1(pf_{21} + (1-p)f_{11})}{H_2(pf_{22} + (1-p)f_{12})} = \frac{H_1(p + (1-p)F_1(p))}{H_2(pF_2(p) + 1 - p)}
\]

given the current population structure \( p \). In particular, during the initial history of the new type the male reproduction rates relate as \( w_1 / w_2 = H_1F_1(0)/H_2 \). Thus, the condition of reproduction advantage of type 2 males for \( p \) close to 0 can be written as

\[
F_1(0) < H_2/H_1. \tag{1}
\]

If \( H_2 > H_1 \), then under the model assumptions (AF) and (RF1) condition (1) is satisfied automatically. In the case \( H_2 < H_1 \) condition (1) compensates the lower degree of polygyny of type 2 males by pressing down the fitness of the offspring to type \((1,1)\) matings relative to the mixed matings. (Note that the argument above does not use monotonicity of functions \( F_i(p) \).)

Under the model conditions two consecutive frequencies of type 2 males are linked by the relation \( p_{n+1} = S(p_n) \), where \( S(p) = pw_2/((1-p)w_1 + pw_2) \). It follows that the change in two consecutive frequencies of type 2 males

\[
S(p) - p = \frac{p(1-p)(w_2 - w_1)}{(1-p)w_1 + pw_2}
\]

3
will remain positive until \( w_2(p) > w_1(p) \). Putting \( a_1 := H_2 f_{12} - H_1 f_{11} \) and \( a_2 = H_1 f_{21} - H_2 f_{22} \) we can write \( w_2 - w_1 = (1 - p) a_1 - p w_2 \) and see that the incremental proportion \( p \) can be factorized as

\[
S(p) - p = \frac{a_1 + a_2}{(1 - p) w_1 + p w_2} p (1 - p) (F(p) - p),
\]

where

\[
F(p) := \frac{a_1}{a_1 + a_2} = \frac{H_2 - H_1 F_1(p)}{H_1 + H_2 - H_1 F_1(p) - H_2 F_2(p)}.
\]

According to (2) the equilibrium equation \( S(p) = p \) besides the trivial solutions \( p = 0 \) and \( p = 1 \) might have solutions in the range \((0, 1)\). Since under assumption \((AF)\) the sum \((a_1 + a_2)\) in the right hand side of (2) is strictly positive, to find such non-trivial equilibrium points we may turn to a more simple equation \( F(p) = p \).

Our analysis of the last equation hinges upon assumptions \((RF)\) and \((RF)\) implying that the fraction \( a_1(p) / a_2(p) \) increases with \( p \), which entails that function \( F(p) \) is monotonically increasing. Moreover, condition \((AF)\) implies that given (1), we have \( 0 < F(0) < 1 \). If we additionally assume that

\[
F_2(1) < H_1 / H_2,
\]

then \( 0 < F(1) < 1 \) and, due to monotonicity of \( F(p) \), equation \( F(p) = p \) must have at least one solution in the open interval \((0, 1)\). Condition (3) mirrors condition (1) leading to survival of the type 1 males when type 2 is assumed to be the initial type. In particular, (3) automatically holds if \( H_2 < H_1 \).

**Proposition 3.1** If conditions (1) and (3) hold, and \( p_0 = 0 \), then \( p_t \to \hat{p} \) as \( t \to \infty \), where \( \hat{p} \) is the minimal solution of the equation \( F(p) = p \) in the interval \((0, 1)\).

**Proposition 3.2** Let conditions (1) and (3) hold. If \( F(p) \) is either a concave or convex function, then the equation \( F(p) = p \) has a unique solution \( \hat{p} \) in the interval \((0, 1)\). For any initial value \( p_0 \) monotone convergence \( p_t \to \hat{p} \) as \( t \to \infty \) takes place with an exponential speed.

**Proof of Proposition 3.2**

It is easy to see that if \( F(p) \) monotonically increases with \( 0 < F(0) < F(1) < 1 \) and is either a concave or convex function, then the equation \( F(\hat{p}) = \hat{p} \) has a unique solution in the interval \((0, 1)\). Moreover, there exist constants \( 0 < c_1 < c_2 < 1 \) such that

\[
c_1 |p - \hat{p}| < |F(p) - \hat{p}| < c_2 |p - \hat{p}|, \quad 0 \leq p \leq 1.
\]

According to (2) we have

\[
\frac{S(p) - F(p)}{p - F(p)} = 1 - \frac{(a_1 + a_2) p (1 - p)}{(1 - p) w_1 + p w_2}
\]

which in turn implies

\[
\frac{S(p) - F(p)}{p - F(p)} = \frac{p H_2 f_{22} + (1 - p) H_1 f_{11}}{(1 - p) w_1 + p w_2}.
\]
The last two equalities show that
\[
    \frac{S(p) - F(p)}{p - F(p)} \in (c_3, c_4) \subset (0, 1)
\]
and therefore
\[
    \frac{p_{t+1} - F(p_t)}{p_t - F(p_t)} \in (c_3, c_4)
\]
implying
\[
    \frac{p_{t+1} - p_t}{F(p_t) - p_t} \in (1 - c_4, 1 - c_3).
\]
(5)

If \( p_t < \hat{p}_t \), then \( p_t < F(p_t) < \hat{p}_t \) and due to (5) and (4) we have
\[
    p_{t+1} - p_t > (1 - c_4)(F(p_t) - p_t) > c_1(1 - c_4)(\hat{p} - p_t).
\]
This implies that given \( 0 < p_0 < \hat{p} \)
\[
    0 < \hat{p} - p_{t+1} < c_5(\hat{p} - p_t) < (c_0)^t (\hat{p} - p_0), \quad c_5 := 1 - c_1(1 - c_4) \in (0, 1).
\]
Similarly, if \( \hat{p} < p_0 < 1 \), there is a constant \( c_6 \in (0, 1) \) such that \( 0 < p_t - \hat{p} < (c_0)^t (p_0 - \hat{p}) \) for all \( t \geq 1 \).

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References
