On the Evolution of Polygamy: A Theoretical Examination of the Polygamy Threshold Model

Susan Ptak
Michael Lachmann

SFI WORKING PAPER: 2001-01-001

SFI Working Papers contain accounts of scientific work of the author(s) and do not necessarily represent the views of the Santa Fe Institute. We accept papers intended for publication in peer-reviewed journals or proceedings volumes, but not papers that have already appeared in print. Except for papers by our external faculty, papers must be based on work done at SFI, inspired by an invited visit to or collaboration at SFI, or funded by an SFI grant.

©NOTICE: This working paper is included by permission of the contributing author(s) as a means to ensure timely distribution of the scholarly and technical work on a non-commercial basis. Copyright and all rights therein are maintained by the author(s). It is understood that all persons copying this information will adhere to the terms and constraints invoked by each author's copyright. These works may be reposted only with the explicit permission of the copyright holder.

www.santafe.edu
On the evolution of polygamy: a theoretical examination of the polygamy threshold model

Running title: theoretical examination of polygamy threshold model

Susan E. Ptak

Corresponding author

Dept. of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, CA 94305

650-723-4952 (phone)

650-725-0180 (fax)

susan@charles.stanford.edu (email)

Michael Lachmann

Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501
The polygamy threshold model states that if costs incurred are less than the benefits gained from a polygamous relationship in terms of male or habitat quality, then polygamy is favored and could evolve. Here we construct mathematical models and computer simulations to evaluate this hypothesis theoretically.

In the basic model, there is a single locus with two alleles, where this locus regulates whether or not the female is receptive to polygamy. There are two habitats of differing quality for which females vie, and on which males randomly assort themselves. This basic model is extended mathematically to include cost to the initial female of a polygamously mated male and again to include gene expression in males. The computer simulations extend the basic model to multiple loci and alleles, and to multiple habitats. The results presented here suggest that the polygamy threshold model is valid in a population genetic context -- in all cases in which the fitness of females that actually mated polygamously is greater than the fitness of monogamous females on poorer habitats, polygamy evolved. However, using this approach revealed interesting dynamics not apparent from the original verbal model. If the trait is expressed in males and females, then polygamy can evolve even if females mating polygamously have a lower fitness than females mating monogamously. In the multiple habitat model, the polygamy allele increases to some equilibrium value above which it experiences no selection. Surprisingly, as the cost to polygamy increases, the equilibrium value of the polygamy allele also increases.

Key Words: polygamy, polygyny, polyandry, polygamy threshold model, evolution, theory
After monogamy, the next most frequent mating system in birds is polygyny, which occurs when one male forms long breeding associations with several females to rear offspring (Wittenberger, 1979). Polyandry, the mating of one female to multiple males is, in birds, quite rare. Monogamy is considered to have arisen early in avian evolution, whereas polygyny is considered to be a derived state that arose independently several times (Wesolowski, 1994). One hypothesis for the evolution of polygyny in birds is the polygamy threshold model (Orians, 1969). Briefly, this model states that polygyny should evolve when females experience greater reproductive success by mating with an already mated male, rather than an unmated one. Though this explanation is widely accepted and often cited in the literature, and despite the considerable empirical support (see e.g. Bensch, 1996; Ezaki, 1990; Petit, 1991; Pribil and Picman, 1996; Slagsvold and Lifjeld, 1994), there have been almost no theoretical examinations of this hypothesis within a population genetics context (see Ranta and Kaitala, 1999 for a game theory approach).

The polygamy threshold model is based upon five assumptions. The first assumption is that the two sexes invest differentially in reproduction (Orians, 1969). The sex that invests more heavily in reproduction incurs a greater loss from low fitness mating and thus will be more selective in the choice of mates. The sex that does not invest as heavily is therefore more likely to mate multiply, since its cost is less. The polygamy threshold model provides the conditions under which the sex that is least receptive to polygamy might favor polygamy, assuming that the other sex will also favor polygamy under these conditions. Usually it is assumed that female birds invest more heavily in reproduction, in that eggs are more costly to produce than sperm, since eggs contain large amounts of stored energy (Orians, 1969). Also, since fertilization is internal, females have a lag time between pregnancies (Wittenberger, 1979). Thus, the polygamy threshold model provides conditions under which female birds might favor polygamy, assuming that when these conditions hold, males should also favor polygamy.

The second assumption is that there is a cost to polygamy (Davies, 1989). This cost results from having to share resources and access to the mate with other individuals. In birds, the male can provide assistance in building the nest, in incubating the eggs, in defending the female and offspring from predators, and in providing food for the female and offspring (Trivers, 1972). A decrease in assistance, then,
potentially can have a substantial effect. Furthermore, in many species, polygynous males preferentially provide for their primary female (the female that arrived first) (Searcy and Yasukawa, 1989). Thus the cost is largely incurred by the later arriving females (those that actually select polygamy over monogamy).

The third assumption is that reproductive success of mating pairs varies (Orians, 1969). This variability can arise because of differences in the breeding habitat. For birds, the habitat where a parent elects to raise young can vary with respect to predation rates, nutrient resources, weather conditions, etc. that affect reproductive success. This variability arises also because of differences in parental ability. How capable and willing a parent is to defend and help rear the young also affects reproductive success. Finally, this variability arises because of differences in the genetic contribution of the parents. How genetically fit a parent is affects how genetically fit its offspring are.

The fourth assumption is that the choosy mate can differentiate between potential mates and/or breeding habitats, and is free to settle anywhere (Davies, 1989). There exists fairly strong evidence that differentiation between mates can and does occur in birds (Kirkpatrick, 1987). However, few experiments test the capability of individuals to sample different habitats and differentiate between them (Davies, 1989) though there is indirect evidence for preferred habitats (see e.g. Bensch and Hasselquist, 1991; Petit, 1991). Also, there is evidence to suggest that individuals may not be free to settle wherever they choose. If the primary female of polygynous males also suffers a reduction in assistance and resources, then it would benefit her to prevent the settlement of another female (Davies, 1989). There is evidence for the aggression of primary females (see e.g. Bensch and Hasselquist, 1992; Slagsvold and Lifjeld, 1994; Yasukawa and Searcy, 1982), suggesting limited access by other females to already mated males.

The fifth assumption is that individuals optimize, over evolutionary time, their reproductive output. Thus, the more selective sex, in this case female, favors monogamy since it maximizes access to the resources and assistance of her mate. The female also favors that mate and/or breeding habitat that maximizes her reproductive success. However, these two optimalities may conflict if an already mated male holds the better habitat. If a female gains more from mating with an already mated male than from mating with an unmated male, and if the female acts to optimize her reproductive success, then polygamy arises.
This difference between the benefits of monogamy and the benefits to mating with an already mated male is what Orians (1969) termed the polygamy threshold.

As a result of these five assumptions, the polygamy threshold model states that since females invest more heavily in reproduction, they are more selective in choosing mates. Since the reproductive success varies among males or on different habitats, when faced with an option to mate polygamously with a high fitness male or on a high fitness habitat or to mate monogamously with a low fitness male or on a low fitness habitat, females will optimize their fitness by selecting polygamy. Thus polygamy will evolve. More explicitly, the first female selects the male/habitat of the highest quality, the second female selects the male/habitat with the second highest quality, and so forth. Eventually, though, for the nth female, the most advantageous choice is an already mated male (the one mated to the first female) rather than an unmated male. The difference to the choosing female between the advantages of the polygamous situation over the monogamous situation is called the polygamy threshold. Thus the nth female selects the first male and introduces polygamy into this population. The (n+1) female then compares the quality of the first or second male (as a polygamous mate) to the quality of unmated males (as a monogamous mate) and again selects whichever mate optimizes her options. This process continues through all remaining females. This explanation for polygamy, however, does not specify any mechanism for the emergence of a trait predisposing females to polygamy when it is beneficial, nor does it examine whether such a trait could then proliferate and spread through the population. As an attempt to begin addressing the theoretical feasibility of the polygamy threshold model, we construct mathematical models and computer simulations of a diploid population that captures this verbal hypothesis.

METHODS: THE MODEL

Assume there are two habitats in which breeding may occur (T1 and T2), and females have a preference for one habitat (T1). Further assume that this preference is beneficial; females breeding in T1 experience a higher fitness than females breeding in the other habitat. Let t be the proportion of the entire breeding range that is comprised of the second habitat and let (1-t) be the proportion that is comprised of
the first habitat, where the fitness in T1 is 1 and the fitness in T2 is (1-s), and 0 < s < 1. Assume that males randomly assort among the two habitats in proportion to the relative availability of the habitat (i.e. in proportion to t and 1-t).

Assume that the receptivity to polygamy is determined by one locus with two alleles. Females that possess the polygamy allele (phenotype A, allele A) always elect to breed in T1, even when this results in polygamy. Females that do not possess this allele (phenotype a, allele a) always elect monogamy and while there are still males available in T1, these females will select T1, but once there are no unmated males left in habitat one, these females will select T2. Assume that both types of females are equally likely to obtain monogamous mates in T1. Thus, females of phenotype a, in effect, are distributed among the two habitats in proportion to their frequency in the population and the proportions of the habitats in the range. On the other hand, females of phenotype A are only found on T1. This trait is not expressed in males. The phenotype of heterozygous females is determined by whether receptivity to polygamy is dominant or recessive.

Primary females are the first females mated to a male that later mates with other (secondary) females. Assume there is a cost to polygamy and initially assume primary females do not incur this cost. Also let this decrease in fitness be less than the decrease due to breeding in habitat two. Thus, the fitness for non-primary females mating with polygamous males is (1-hs) where 0 < hs < s. Finally, assume random pairing between males and females in terms of male genotype. Since males mate randomly according to genotype and are randomly assorted between the two habitats, all males experience the same fitness regardless of genotype. In this initial model, all males equally prefer to mate polygamously so there is no selection acting on males. Under these conditions, does the allele for polygamy increase in frequency and invade the population?

RESULTS

Mathematical Model 1: Basic model
Let $x$, $y$, and $z$ be the frequencies of the genotypes AA, Aa, and aa respectively in the present generation, with $p = x + \frac{1}{2}y = 1-q$ the frequency of A.

(Table 1 here)

Using Table 1, the fitness associated with mating pairs involving a female of phenotype A is:

$$f_A = 1^* (1-t) + (1-hs)^* t = 1 - tsh \quad (1)$$

and the fitness associated with mating pairs involving a female of phenotype a is:

$$f_a = 1^* (1-t) + (1-s)^* t = 1 - ts \quad (2)$$

and the recursion equations:

$$Fx' = 1[f_a]x^2 + \frac{1}{2}[f_a]yx + \frac{1}{2}[f_a]y^2 \quad (3)$$

$$Fy' = \frac{1}{2}[f_a]xy + 1[f_a]xz + \frac{1}{2}[f_a]y^2 + \frac{1}{2}[f_a]yz + 1[f_a]zx + \frac{1}{2}[f_a]zy \quad (4)$$

$$Fz' = \frac{1}{4}[f_a]y^2 + \frac{1}{2}[f_a]yz + \frac{1}{2}[f_a]zy + 1[f_a]z^2 \quad (5)$$

where $F$ is the sum of the right sides of $Fx'$, $Fy'$, and $Fz'$.

After substitution and simplification

$$Fx' = (x + \frac{1}{2}y)^2(1-st) + st(1-h)x(x + \frac{1}{2}y) \quad (6)$$

$$Fy' = 2(x + \frac{1}{2}y)(\frac{1}{2}y + z)(1-st) + st(1-h)x(\frac{1}{2}y + z) \quad (7)$$

$$Fz' = (\frac{1}{2}y + z)^2(1-st) \quad (8)$$

$$F = (1-st) + st(1-h)x \quad (9)$$

and

$$Fp' = Fx' + \frac{1}{2}Fy' = (x + \frac{1}{2}y)(1-st) + st(1-h)x(\frac{1}{2}y + z) \quad (10)$$

$$F\Delta p = Fp' - Fp = \frac{1}{2} st(1-h)x(\frac{1}{2}y + z) > 0 \text{ if } (h < 1) \quad (11)$$

Thus, $p$ monotonically increases in frequency until $p = 1$ and the allele that introduces polygamy becomes fixed in the population as long as the fitness of secondary females on T1 is greater than the fitness of females on T2 ($h < 1$). The conditions under which $p$ monotonically increases are the same for the dominant case; $F\Delta p$ is proportional to $z_p$ for the dominant case, rather than to $x_q$ as in the recessive case, but is otherwise identical.
**Mathematical Model 2: Effects of primary females**

The above rendition of the polygamous threshold model ignores the effects on primary females. As mentioned earlier, primary females might suffer a reduction in fitness and should then attempt to deter polygamy. To capture this phenomenon the second model assumes a reduction in fitness for primary females, as well as a reduction in the frequency of polygamy as a result of successful deterrence by the primary female. Assume \( r \) measures the reduction in fitness for primary females, such that \((1-rhs)\) is the fitness of primary females. If \( r = 0 \) then primary females have the same fitness as monogamous females on T1 (the first model), and if \( r = 1 \) then primary females have the same fitness as secondary females. Assume \( d \) measures the amount of successful deterrence by the primary females, where \( d \) is the proportion of potential secondary females that are successfully deterred from mating polygamously on T1 and thus find mates on T2. Thus, \( 0 \leq d \leq 1 \). In this rendition of the model, primary females must be mathematically differentiated from monogamous females on T1. Together the proportion of primary females and monogamous females on T1 is still \((1-t)\). Thus, the proportion of monogamous females on T1 is \((1-t) - \text{proportion of primary females}\).

Let us call the proportion of all females on T1 that are primary, \( g \), where \( 0 < g < 1 \) and \( g \) is a function of the frequency of the polygamous allele. Under these new conditions, does the allele introducing polygamy increase in frequency and invade the population?

(Table 2 here)

Using Table 2, the fitness associated with mating pairs involving a female of phenotype \( A \) is:

\[
f_A = 1^* [(1-t)(1-g)] + (1-rhs)(1-t)g + (1-hs)^* t(1-d) + (1-s)^* td
\]

\[
= 1 - rhsg(1-t) - tds(1-h) - ths
\]

and the fitness associated with mating pairs involving a female of phenotype \( a \) is:

\[
f_a = 1^* [(1-t)(1-g)] + (1-rhs)(1-t)g + (1-s)t
\]

\[
= 1 - rhsg(1-t) - ts
\]

and the recursion equations are:

\[
F_x' = 1[f_A]x^2 + ½[f_A]yx + ½[f_a]yx + ¼[f_a]y^2
\]
\[ Fy' = \frac{1}{2}[f_A]xy + 1[f_A]xz + \frac{1}{2}[f_a]yx + \frac{1}{2}[f_a]y^2 + \frac{1}{2}[f_a]yz + 1[f_a]zx + \frac{1}{2}[f_a]zy \quad (17) \]

\[ Fz' = \frac{1}{4}[f_a]y^2 + \frac{1}{2}[f_a]yz + \frac{1}{2}[f_a]zy + 1[f_a]z^2 \quad (18) \]

where \( F \) is the sum of the right sides of \( Fx' \), \( Fy' \), and \( Fz' \).

After substitution and simplification:

\[ Fx' = (x + \frac{1}{2}y)^2 - (1-t)(rhsg)(x + \frac{1}{2}y)^2 - \frac{1}{2}[tds(1-h) - ths]y(x + \frac{1}{2}y) \quad (19) \]

\[ Fy' = 2(x + \frac{1}{2}y)(\frac{1}{2}y + z) - 2(1-t)(rhsg)(x + \frac{1}{2}y)(\frac{1}{2}y + z) - ts(x + \frac{1}{2}y)(\frac{1}{2}y + z) \]

\[ - [tds(1-h) + ths - ts]x(\frac{1}{2}y + z) \quad (20) \]

\[ Fz' = (\frac{1}{2}y + z)^2 - (1-t)(rhsg)(\frac{1}{2}y + z)^2 - ts(\frac{1}{2}y + z)^2 \quad (21) \]

\[ F = 1 - (1-t)(rhsg) - ts - [tds(1-h) + ths - ts]x \quad (22) \]

and

\[ Fp' = (x + \frac{1}{2}y) - (1-t)(rhsg)(x + \frac{1}{2}y) - ts(x + \frac{1}{2}y) - [tds(1-h) + ths - ts]x(x + \frac{1}{2}y) \]

\[ - \frac{1}{2}[tds(1-h) + ths - ts]x(\frac{1}{2}y + z) \quad (23) \]

\[ \Delta p = \frac{1}{2} ts[(1-h)(1-d)]x(\frac{1}{2}y + z) > 0 \text{ if } (h < 1 \text{ and } d \neq 1) \quad (24) \]

Thus, \( p \) monotonically increases in frequency until \( p = 1 \) and the allele that introduces polygamy becomes fixed in the population as long as the fitness of secondary females on T1 is greater than the fitness of females on T2 (\( h < 1 \)) and the primary females are not completely successful in deterring all potential secondary females (\( d \neq 1 \)). (Recall that by definition \( 0 \leq d \leq 1 \), since \( d \) is the proportion of potential secondary females that are deterred.) If \( d = 1 \), that is, the primary females are completely successful in deterring all of the secondary females, then there are no polygamous matings. If there are no polygamous matings, then there is no selection for the polygamy allele and \( \Delta p = 0 \). Note that if \( d = 0 \), that is, the primary females are unsuccessful in deterring any of the secondary females, then the expression for \( \Delta p \) reduces to the initial model. The conditions under which \( p \) monotonically increases are the same for the dominant case; \( \Delta p \) is proportional to \( zp \) for the dominant case, rather than to \( xq \) as in the recessive case, but is otherwise identical.

Note that the sign of \( \Delta p \) does not depend on the severity of the cost to primary females, since this cost...
is shared equally among females of all three genotypes. Only if this cost is distributed unequally among the three genotypes could selective pressures exist against polygamy. Thus, even if primary females had a fitness of zero (i.e. $r = -1/hs$), polygamy would still invade, providing that the secondary females have a fitness advantage over monogamous females on the poorer habitat. However, if the reduction in fitness of the primary female exceeds the gain in fitness the male receives from later matings, then the male may not favor polygamy (Trivers 1972). The model presented here gives males no choice.

**Mathematical Model 3: Gene is expressed also in males**

The above two models assume that males are always receptive to polygamy; the gene is not expressed in males. In the model below, this assumption is dropped; only males (and females) with the $A$ phenotype are receptive to polygamy. In this scenario, the frequencies of some mating types are no longer the product of the genotype frequencies since polygamous mating is no longer random – there is associative mating among those phenotypes that are receptive to polygamy. The mating table for those mates that are initially monogamous is identical to that in table 1 and 2. For the polygamous matings when $A$ is recessive (Table 3), all $xt$ females that are available for polygamous matings are mated to AA males. Thus the frequency of polygamous AA x AA mates is the proportion of AA females available for polygamy, $xt$. For the polygamous matings when $A$ is dominant, all $xt$ females that are available for polygamous matings are mated to either AA or Aa males. Thus the frequency of polygamous AA x AA mates is the proportion of AA females available for polygamy, $xt$, times the proportion of all receptive males that are genotype AA, $x/(x+y)$.

Using Table 3, the recursion equations are:

$$F_x' = (1)[(1-t)x^2 + (1-hs)tx] + (\frac{1}{2})[(1-t)xy] + (\frac{1}{2})[(1-t) + (1-s)t]yx + (\frac{1}{4})[(1-t) + (1-s)t]y^2$$  

(25)

$$F_y' = (\frac{1}{2})[(1-t)xy] + (1-t)zx + (\frac{1}{2})[(1-t) + (1-s)t]yx + (\frac{1}{2})[(1-t) + (1-s)t]y^2 + (\frac{1}{2})[(1-t) + (1-s)t]zy$$  

(26)

$$F_z' = (\frac{1}{4})[(1-t) + (1-s)t]y^2 + (\frac{1}{2})[(1-t) + (1-s)t]yz + (\frac{1}{2})[(1-t) + (1-s)t]zy + (1-t)(1-t)z^2$$  

(27)

where $F$ is the sum of the right sides of $F_x'$, $F_y'$, and $F_z'$.
After substitution and simplification:

\[ F_x' = (1-ts)(x + \frac{1}{2}y)^2 + (1-hs)tx - x(x + \frac{1}{2}y)(1-s)t \] (28)

\[ F_y' = 2(1-ts)(x + \frac{1}{2}y)(\frac{1}{2}y + z) - x(\frac{1}{2}y + z)(1-s)t \] (29)

\[ F_z' = (1-ts)(\frac{1}{2}y + z)^2 \] (30)

\[ F = (1-ts) + (1-hs)tx - (1-s)tx \] (31)

and

\[ Fp' = (1-ts)(x + \frac{1}{2}y) + (1-hs)tx - x(1-s)t + \frac{1}{2}x(\frac{1}{2}y + z)(1-s)t \] (32)

\[ F\Delta p = tx(\frac{1}{2}y + z)((1-hs) - \frac{1}{2}(1-s)) > 0 \text{ if } [(1-hs) - \frac{1}{2}(1-s)] > 0 \text{ or } (1+s)/(2s) > h \] (33)

Thus, if \((1+s)/(2s) > h\), \(p\) monotonically increases in frequency until \(p = 1\) and the allele that introduces polygamy becomes fixed in the population. For \(s < 1\), \(h\) can exceed one and the polygamy allele will still invade (Figure 1). Thus, the fitness of the secondary female can be less than the fitness of the monogamous female \((h > 1)\) and the polygamy allele will still invade. In the first two models, males of all genotypes have secondary females, so there is no selective advantage to males carrying the polygamy allele. However, in this third model, only males carrying the polygamy allele can have secondary females and thus have a selective advantage. Presumably, it is this selective advantage that compensates when secondary females have a lower fitness than monogamous females on the poorer of the two habitats. The conditions under which \(p\) increases monotonically are the same for the dominant case; \(F\Delta p\) is proportional to \(zp\) for the dominant case, rather than to \(xq\) as in the recessive case, but is otherwise identical.

(Figure 1 here)

Note, that in all of these mathematical models, we assume that there are enough males on the better habitat for all the polygamous females. This entails either assuming that males will take on an infinite number of females (and the cost to a polygamous female is the same regardless of whether she is the second female or the nth female) or that the number of males on the better habitat is large enough. In the basic model, "large enough" means that \((1-t)n \geq mx\), where \(n\) is the number of secondary females each male will
accept and m is the frequency of polygamous females (m = x if A is recessive to a and m = x+y if A is dominant to a). In the model that includes the effects on primary females, "large enough" means that (1-t)n ≥ mt(1-d). In the model where the trait is expressed in both males and females, (1-t)n ≥ t.

METHODS: SIMULATIONS

To examine this model further, we wrote a computer simulation of the basic system which we then extended in two different ways. Results are shown from the basic model since these results serve as a benchmark for the results from the two extensions. This is especially important since the basic simulation differs from the basic analytical model in several biologically interesting ways: a finite population is used, there is mutation between the two alleles, males are restricted to having at most two mates, and heterozygous females are intermediate between the two homozgyotes. Since the likelihood is small of having one locus with two alleles determining a complex behavior such as receptivity to polygamy, the first extension is to a model that involves multiple loci and multiple alleles. The model uses a simplistic extension in that the effects are additive, but even this case can give insight, since mean fitness is no longer necessarily maximized (Hartl and Clark, 1989). The second extension is to multiple habitats, since having only two is again overly simplistic. The second extension required further mathematical analysis to understand the results.

In the basic model, then, there is 1 locus with two alleles, and a constant population size of 3000 males and 3000 females. In the initial population, all individuals, at all loci, have the allele that permits only monogamy. There is reversible mutation, at rate 0.001 per locus, between the two alleles. Half the males are assigned a habitat quality of 1.0 and half a habitat quality of 0.6 independent of their genotype, depending upon which of the two habitats the male is on. Unlike the mathematical models, heterozygotes are intermediate between the two homozygotes in phenotype and will mate polygamously half the time. Females choose males one after another, but the order in which females choose is random. The fitness of the mating pair is the habitat quality less the cost (0.9 * habitat quality) if she mates polygamously or the habitat quality if she mates monogamously. Note that a single male can not have more than two mates. This
process is iterated for 1500 generations with statistics gathered at the final generation, since by 1500
generations (and often much sooner) the system reaches mutation-selection balance. Averages are based
upon 500 iterations.

In the second model, the number of loci is increased to 10 and the number of alleles at each locus to 4
(namely, 0, 1, 2, and 3). Recombination occurs, at rate 0.01 per chromosome, such that a single breakpoint is
chosen with equal likelihood between all 10 loci. To assess the probability that a female will mate
polygamously, the individual’s genotype (the sum of both alleles across all loci) is divided by the maximum
possible value (namely, 10 * 3 * 2) to give a probability between 0 (all alleles that permit only monogamy)
and 1 (all alleles that most strongly lead to polygamy).

The third version is identical to the original except each male is assigned a random number from
uniform(0,1) every generation that represents the quality of the male’s habitat (or equivalently, this number
could represent some aspect of male quality independent of genotype). If the female mates monogamously,
she chooses the male on the best habitat that is not already mated. If the female mates polygamously, she
chooses the male on the best habitat that has only one other mate provided the quality of the habitat less
the cost is greater than the best habitat quality for an unmated male. Otherwise she mates with the unmated
male. It is assumed that the females can distinguish among these minute differences in habitat quality.

RESULTS

Computer Model 1: Basic Model

Over time, the frequency of the polygamous allele rapidly increases to near fixation (Figure 2). It can
not fix due to mutation, instead it reaches a mutation-selection balance. During this rapid increase, the
fitnesses remain roughly constant, but once the monogamous allele becomes rare, its fitness oscillates
depending on the distribution of the few individuals on the two habitats (Figure 3). The average frequency
of the polygamous allele is 0.969, the average fitnesses of the three genotypes (0, 1, 2) are (0.585, 0.711,
0.742), and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous
female) are (1.0, 0.9, 0.6). If the cost of polygamy increases such that the fitness of polygamous matings is
lower than that of monogamous matings on the poorer habitat, then no female mates polygamously and the two allele frequencies become approximately equal due to the unbiased mutational pressure.

Unlike in the mathematical model, males can have a maximum of only two mates. This has no effect if the frequency of the optimal habitat (1-t) is half or more. However, if the frequency is less than a half, at high frequencies of the polygamous allele, there is a shortage of males with whom to mate polygamously and some polygamous females will mate monogamously on the inferior habitat. In this case, the average fitness of the polygamous allele decreases over time. This does not affect the average fitness of the monogamous allele, which remains constant. Nevertheless, the fitness of the polygamous allele still exceeds that of the monogamous allele, and the polygamous allele will increase in frequency until the mutation-selection balance.

(Figure 2 and 3 here)

**Computer Model 2: Multiple loci and multiple alleles**

Over time, the frequency of the polygamous alleles slowly increases, with the more polygamous alleles increasing faster (Figure 4). The increase in frequency is much slower, since the individuals have a low probability of mating polygamously until the allele frequencies increase and the polygamous allele is prevalent at many loci (and thus individuals have a high probability of mating polygamously). The frequencies of these alleles then seem to plateau at the levels shown in Figure 4, presumably reaching the mutation-selection balance for the four alleles at each loci. The average frequencies of the four alleles (0, 1, 2, 3) in the last 500 generations are (0.115, 0.147, 0.238, 0.500), and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous female) are (1.0, 0.9, 0.6). The average fitness of the genotypes, for those present at high frequencies, is positively correlated with the genotype’s probability of mating polygamously (Figure 5).

(Figure 4 and 5 here)

**Computer Model 3: Multiple habitats**
Over time, the frequency of the polygamous allele rapidly increases to slightly above 0.5 (Figure 6). During this rapid increase, the fitness of the polygamous homozygote decreases and the fitness of the monogamous homozygote increases (Figure 7). The average frequency of the polygamous allele is 0.569, the average frequencies of the three genotypes (0, 1, 2) are (0.712, 0.713, 0.715), and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous female) are (0.765, 0.688, 0.500). Interestingly, if the cost increases to 0.5, then over the course of 500 iterations, the average frequency of the polygamous allele is 0.647 and the average fitnesses of the three genotypes are (0.580, 0.582, 0.585) but the average fitness of the three phenotypes is (0.841, 0.420, 0.500). Also with higher cost, the time during which the genotype fitnesses are changing is longer (Figure 8).

(Figure 6, 7 and 8 here)

Initially all females mate monogamiy regardless of genotype; the males available for monogamous mating have a higher habitat quality than those available for polygamous less the cost. For the basic model, this continues until all males on the optimal habitat have one mate. For the multiple habitats model, this continues until the habitat quality of unmated males equals the maximum habitat quality less the cost. During this period there is no difference in fitness among the different genotypes. It is only during the second period, in which the genotypically polygamous females actually mate polygamously, that selection acts. In the basic model, the average fitness of the polygamous allele is constant, since all polygamous matings have the same fitness. This is not so for the multiple habitats model. When rare, the average fitness of phenotypically polygamous females is very high; since genotypically polygamous females are so rare, these females mate polygamously only with the males on the best habitats. However, as their frequency increases, the females mate with a larger number of males, so the average fitness of polygamous females decreases. (Recall that males can not mate with more than two females, so as the number of polygamous females increases, the number of males mating polygamously increases.) During this second period, monogamous females continue to mate with the less optimal males. In the basic model, the average fitness of these monogamous females is constant, since all monogamous matings on the less optimal habitats have the same fitness. Again, this is not so for the multiple habitats model. When frequent, the
average fitness of monogamous females is near the average of the fitness distribution; since the monogamous females are so frequent, they mate with most of the males and thus sample most of the fitness distribution. As their frequency decreases, these females are mating with a fewer number of males, so the average fitness of the monogamous allele increases. (More and more males at the bottom of the distribution are going unmated as more and more females mate polygamously). Thus in the multiple habitats model, unlike the basic model, the average fitness of the two alleles is dependent upon their frequency (Appendix).

At some allele frequency these two fitnesses are equivalent, and there is no further selection for (or against) polygamy. When polygamous females begin to mate polygamosly (at which point, the highest habitat quality associated with a male available for monogamous mating is equal to or just lower than the maximum habitat quality less the cost), the advantage of mating polygamosly is slight. Polygamous females come along and ratchet down the quality of the habitats available for polygamy while monogamous females come along and ratchet down the quality of the habitats available for monogamy. If the polygamy allele is frequent then the quality of the habitat available for polygamy is decreased as rapidly as the quality of the habitat available for monogamy and the advantage of mating polygamosly remains slight to nonexistent. However, the number of males that must be mated before the quality drops by a given unit differs between monogamous and polygamous matings (note the difference in the slope of the two graphs in Figure 9). The quality of habitats available for monogamous mating is uniformly distributed along (0,1). Thus, there are \((0.1)(3000)/(1-0) = 300\) habitats between 0.9 and 0.8 and likewise 300 habitats between 0.8 and 0.7 etc. The quality of habitats available for polygamous mating is uniformly distributed along \((0,1)*\text{cost} = (0, \text{cost})\), thus there are \((0.1)(3000)/(\text{cost}-0) = 300/\text{cost}\) habitats between 0.9 and 0.8 and likewise between 0.8 and 0.7 etc. For \(\text{cost} = 0.9\), this is 333 males and for \(\text{cost} = 0.5\) this is 600 males. Thus, with a higher cost, the habitat quality among potential polygamous males is not decreased as quickly and it requires a higher frequency of polygamous females to decrease the habitat quality among polygamous males as quickly as among monogamous males. Only when the quality is decreased at the same rate in both polygamous matings and monogamous matings does the selective advantage to mating polygamosly disappear. Thus, the equilibrium allele frequency is dependent upon the cost of polygamous matings, such that as the cost
increases the equilibrium allele frequency of the polygamous allele increases (Appendix).

(Figure 9 here)

DISCUSSION

The polygamy threshold model, as originally proposed by Orians (1949), states that if the costs incurred from polygamy are less than the benefits gained from a polygamous relationship in terms of male or habitat quality, then polygamy is favored and could evolve. Here we construct mathematical models and computer simulations to test this hypothesis theoretically. For the mathematical models there is a single locus with two alleles. This locus regulates whether or not the individual is receptive to polygamy. There are two habitats of differing quality that females vie for, on which males randomly assort themselves. The computer simulations extend this model to multiple loci and alleles, and to multiple habitats. The results presented here suggest that the polygamy threshold model is valid in a population genetics context – in all cases in which the secondary females’ fitness is greater than monogamous females’ fitness on the poorer habitats, polygamy evolved.

The extension of the basic model to multiple habitats leads to interesting dynamics. There is an equilibrium allele frequency of the polygamous allele, such that below this frequency there is selection for polygamy but above this frequency there is no selection either for or against polygamy. This equilibrium allele frequency is a function of the cost of polygamy, such that as the cost of polygamy increases, the equilibrium allele frequency of polygamous allele increases. Thus, under this model, although polygamy persists, it does not fix.

Also, there are cases in which the secondary females' fitness is less than monogamous females' fitness on the poorer habitat and polygamy can still evolve. This can occur if the trait is expressed not only in females but also in males, such that only males with the trait are receptive to polygamous females. Presumably, polygamy can evolve despite the fitness cost to females, since males gain a fitness advantage. If only males with the trait are receptive to polygamy, then only males with the gene attain the fitness advantage of having multiple mates. Thus, one potential explanation of field measurements that indicate that the fitness of females mating polygamously does not exceed the fitness of females mating
monogamously (see examples listed in Slagsvold and Lifjeld, 1994) is that receptiveness to polygamy is in part a genetic trait that is expressed in both males and females.

This is not the only explanation. As seen in the results from the multiple habitats computer model, when the cost of mating polygamously is high, the fitness of females mating polygamously does not exceed the fitness of females mating monogamously, yet polygamy still evolves. With a high cost, only females faced with monogamous mates on very poor habitats will mate polygamously and thus females that actually mate polygamously have a low average fitness. On the other hand, females mating monogamously mate with a wide range of males and thus their average fitness is near the middle of the distribution. However, among these females are genotypically polygamous and genotypically monogamous females. The genotypically polygamous females are mating only with the males on the better habitats, whereas the genotypically monogamous females are mating also with the males on very poor habitats and thus have a lower average fitness. Thus, another potential explanation of field measurements that indicate that the fitness of females mating polygamously does not exceed the fitness of females mating monogamously (see examples listed in Slagsvold and Lifjeld, 1994) is there is a large cost associated with polygamy.

The polygamy threshold model is discussed here in terms of polygyny (males with multiple males) and in the context of the vast literature on polygyny in birds. However, the assumptions of this model (detailed in the introduction) generally are not restricted to either birds or polygyny, and could be used more widely to model the occurrence of polygamy in organisms other than birds, as well as the evolution of polyandry. Likewise, many of the conclusions reached here are also not restricted to either birds or polygyny. However, a critical analysis of this hypothesis in terms of the ability for the trait to emerge is still needed.
We thank H. M. Pereira and M. W. Feldman for critical comments on the manuscript. SEP is supported by HHMI predoctoral fellowship and by NIH Grant GM28016 to M. W. Feldman.
REFERENCES


APPENDIX

Assume an infinite population. A male's contribution to fitness, due to male quality or quality of the male's territory, is uniformly chosen from (0,1) and then the males are ordered from highest to lowest. Thus, the fitness contribution of the male with 80% of the population below him, is 0.8 and the fitness contribution of the male with 20% of the population above him, is 1-0.2 = 0.8. Females come along one by one, and mate with the highest male available to them, where polygamous females have the option of mating with a male who has one other mate. If females mate polygamosously then the pair suffers a reduction in fitness such that the male's fitness contribution is multiplied by some factor, \( \alpha \). Otherwise the fitness of the mating pair is the male's quality. Note that \( \alpha \) is a measurement of the cost to polygamy, but differs from \( h \) used in mathematical models (1-hs = male's quality * \( \alpha \)). Let the frequency of the polygamy allele be \( p \), which is also the frequency of polygamous females: \( \frac{1}{2} \) of heterozygotes will mate polygamously as well as all homozygotes, so the frequency of polygamous females is \( \frac{1}{2}(2pq) + 1(p^2) = p \) (heterozygotes and homozygotes at this point are found in Hardy Weinberg equilibrium since there is no selection prior to mating). Under this process, let’s calculate the average fitness of monogamous females and the average fitness of polygamous females.

Initially all females mate monogamously regardless of genotype, since initially the fitness contribution of males without mates exceeds that of males with another mate. This continues until these two fitnesses equilibrate, i.e. when the fitness contribution of the \( n \)th male = fitness contribution of the first male * \( \alpha \) = 1.0 * \( \alpha \). During this period, the average fitness of polygamous and monogamous females is the same, namely \( (1 + \alpha)/2 \), which is the average of the highest and lowest fitness. The proportion of polygamous and monogamous females that are in this first group is equal to the range of fitness values covered, namely (1-\( \alpha \)). Thus, the proportion of polygamous and monogamous females that are in the second group is \( 1 - (1-\alpha) = \alpha \).

All polygamous females in this second group actually mate polygamously (assuming a "small" allele frequency of the polygamous allele, see below). The frequency of polygamous females mating polygamously is \( p\alpha \), which is also the frequency of males that mate polygamously. The fitness of the last
male that mates polygamosly is \((1 - p\alpha)\), since male fitness uniformly covers \((0,1)\). The fitness contribution of the highest male that mates polygamosly is the fitness contribution of the highest male, 1. Thus the average fitness of polygamous females mating polygamosly is the average of these two fitnesses less the cost, \((1 + (1 - p\alpha))(\alpha)/2 = (2 - p\alpha)(\alpha)/2\). \((34)\)

If \((p\alpha)\) males mate polygamosly, then the bottom \((p\alpha)\) males do not mate at all. The fitness contribution of the highest of these males is \((p\alpha)\). The fitness contribution of the highest male that mates monogamosly with the second group of monogamous females is \(\alpha\). Thus the average fitness of monogamous females in this second group is \((\alpha + p\alpha)/2 = (1 + p)(\alpha)/2\). \((35)\)

So, to put it all together, the average fitness of polygamous females is the average fitness of the females that initially mate monogamosly times the frequency of this group of females plus the average fitness of the females that mate polygamosly times the frequency of this latter group of females, or \([((1 + \alpha)(1-\alpha)/2) + [(2 - p\alpha)(\alpha)(\alpha)/2] = \frac{1}{2}[1 + \alpha^2 - p\alpha^3]\]. \((36)\)

The average fitness of monogamous females is the average fitness of the females in the first group times their frequency plus the average fitness of the females in the second group times their frequency, or \([((1+\alpha)(1-\alpha)/2) + [(1 + p)(\alpha)(\alpha)/2] = \frac{1}{2}[1 + p\alpha^2]\]. \((37)\). Even though monogamous females are mating monogamosly the entire time, to calculate their average fitness, one needs to break the females into these two groups. The females are not evenly distributed across the entire range of male fitnesses that they experience -- initially the monogamous females have access to every \(1/(1-p)\) male but then the monogamous females have access to every male since they are no longer competing with the polygamous females for the monogamous males.

Thus the average fitness of both groups of females depends upon \(\alpha\) and on the frequency of the polygamy allele. As the allele frequency of polygamous females increases, the average fitness of polygamous females decreases but the average fitness of monogamous females increases. The difference between the average fitness of monogamous and polygamous females is = \(\frac{1}{2}[1 + \alpha^2 - p\alpha^3] - \frac{1}{2}[1 + p\alpha^2] = \frac{1}{2}[\alpha^2 - p\alpha^2 - p\alpha^3] =\)
\[ \frac{1}{2} \alpha^2 [1 - p - \alpha p] \]  

(38)

As seen in graph A1 (a plot of this expression), as the allele frequency increases, the average difference in fitness decreases and at some point reaches zero. This equilibrium allele frequency is dependent on the cost, such that as the cost decreases the equilibrium allele frequency decreases (remember as \( \alpha \) increases, cost decreases). To solve for the relationship between allele frequency and cost, set the above equation to zero and solve for \( p \) (graph A2). This equilibrium is stable only from one direction. If the allele frequency of polygamy is less than this equilibrium value, then selection will favor polygamy. However, if the allele frequency of polygamy exceeds this equilibrium value, then there is no selection, only drift.

(Figure A1 and A2 here)

When the allele frequency exceeds this equilibrium value, not all polygamous females in the second group can mate polygamously -- for some females there is not an already mated male whose fitness is higher than a single male. Instead of mating polygamously with inferior male, as assumed by the math, these females will mate monogamously. Thus, the average fitness of monogamous females will never exceed that of polygamous females.
**Figure 1**

Plot of \(\frac{1+s}{2s} > h\) for the model in which gene is expressed also in males, where \(s\) is the fitness decrement to mating on the less optimal habitat and \(hs\) is the fitness decrement to polygamous females.

**Figure 2**

Plot of allele frequencies over time for the Basic Computer Model. The light plot is for the monogamous allele and the dark plot is for the polygamous allele.

**Figure 3**

Plot of the average genotype fitnesses over time for the Basic Computer Model. The plots darken for genotypes with a higher probability of mating polygamously.

**Figure 4**

Plot of the allele frequencies over time for the Multiple Alleles and Loci Model. The plots darken for alleles with a higher probability of mating polygamously.

**Figure 5**

Plot of the final average genotype fitnesses for the Multiple Loci and Alleles Model for those genotypes present at high enough frequencies to obtain a reasonable estimate of average fitness.

**Figure 6**

Plot of the allele frequencies over time for the Multiple Habitats Model. The light plot is for the monogamous allele and the dark plot is for the polygamous allele.

**Figure 7**

Plot of the average genotype fitnesses over time for the Multiple Habitats Model with a small cost to
females mating polygamously. The plots darken for genotypes with a higher probability of mating polygamously.

**Figure 8**
Plot of the average genotype fitnesses over time for the Multiple Habitats Model with a high cost for females mating polygamously. The plots darken for genotypes with a higher probability of mating polygamously.

**Figure 9**
Plot of the mating pair fitness for the Multiple Habitats Model as a function of which male the female mates with (males’ fitness contribution is ordered from lowest to highest) and whether she is a primary or secondary female. In the top Figure, cost = 0.9 and in the bottom Figure, cost = 0.5.

**Figure A1**
Plot of the average difference in fitness between monogamous females and polygamous females for the Multiple Habitats Model. Average difference = \((\frac{1}{2})(\alpha^2)(1-p-p\alpha)\), where \(p\) is the frequency of the polygamous allele and \(\alpha\) is the cost of polygamous matings (high \(\alpha\), small cost).

**Figure A2**
Plot of the relationship between cost, \(\alpha\), and allele frequency, \(p\) for the Multiple Habitats Model: \(p = \frac{1}{1+\alpha}\).
Table 1: Mating table for the basic model

<table>
<thead>
<tr>
<th>Mating Female x male</th>
<th>Initially</th>
<th>Polygamy</th>
<th>Frequency</th>
<th>Progeny</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Monogamy</td>
<td></td>
<td>in T1</td>
<td>in T2</td>
</tr>
<tr>
<td>AA x AA</td>
<td>1*(1-t)</td>
<td>(1-hs)*t</td>
<td>xx</td>
<td>1</td>
</tr>
<tr>
<td>AA x Aa</td>
<td>1*(1-t)</td>
<td>(1-hs)*t</td>
<td>xy</td>
<td>½</td>
</tr>
<tr>
<td>AA x aa</td>
<td>1*(1-t)</td>
<td>(1-hs)*t</td>
<td>xz</td>
<td>0</td>
</tr>
<tr>
<td>Aa x AA</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>yx</td>
<td>½</td>
</tr>
<tr>
<td>Aa x Aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>yz</td>
<td>0</td>
</tr>
<tr>
<td>Aa x aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zx</td>
<td>0</td>
</tr>
<tr>
<td>aa x AA</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zy</td>
<td>0</td>
</tr>
<tr>
<td>aa x Aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zz</td>
<td>0</td>
</tr>
</tbody>
</table>

Progeny:
- AA: 1
- Aa: 0
- aa: 0
Table 2: Mating table including the effects of primary female

<table>
<thead>
<tr>
<th>Mating Female x male</th>
<th>Monogamous Female</th>
<th>Primary Female</th>
<th>Secondary Female</th>
<th>Fitness * Proportion of mating type experiencing that fitness</th>
<th>Progeny</th>
<th>Frequency</th>
<th>AA</th>
<th>Aa</th>
<th>aa</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA x AA</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td>(1-hs)* t(1-d)</td>
<td>(1-s)* td</td>
<td>xx</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>AA x Aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td>(1-hs)* t(1-d)</td>
<td>(1-s)* td</td>
<td>xy</td>
<td>½</td>
<td>½</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>AA x aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td>(1-hs)* t(1-d)</td>
<td>(1-s)* td</td>
<td>xz</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Aa x AA</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>yx</td>
<td>½</td>
<td>½</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Aa x Aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>yy</td>
<td>¼</td>
<td>½</td>
<td>¼</td>
<td></td>
</tr>
<tr>
<td>Aa x aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>yz</td>
<td>0</td>
<td>½</td>
<td>½</td>
<td></td>
</tr>
<tr>
<td>aa x AA</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>zx</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>aa x Aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>zy</td>
<td>0</td>
<td>½</td>
<td>½</td>
<td></td>
</tr>
<tr>
<td>aa x aa</td>
<td>1* [(1-t)(1-g)]</td>
<td>(1-rhs)(1-t)g</td>
<td></td>
<td>(1-s)* t</td>
<td>zz</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Mating Female x male</td>
<td>Initially Monogamous Fitness * Proportion of mating type experiencing that fitness</td>
<td>Polygamous matings Fitness * Proportion of mating type experiencing that fitness</td>
<td>Progeny</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>----------------------</td>
<td>----------------------------------------------------------------------------------</td>
<td>-----------------------------------</td>
<td>--------</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>In T1</td>
<td>In T2</td>
<td>Freq of mating type in T1</td>
<td>(1-hs)*t</td>
<td>x</td>
<td>AA</td>
<td>Aa</td>
<td>aa</td>
<td></td>
</tr>
<tr>
<td>AA x AA</td>
<td>1*(1-t)</td>
<td>xx</td>
<td>(1-hs)*t</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AA x Aa</td>
<td>1*(1-t)</td>
<td>xy</td>
<td></td>
<td>½</td>
<td>½</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AA x aa</td>
<td>1*(1-t)</td>
<td>xz</td>
<td></td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aa x AA</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>yx</td>
<td>½</td>
<td>½</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aa x Aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>yy</td>
<td>⅛</td>
<td>⅝</td>
<td>⅛</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aa x aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>yz</td>
<td>0</td>
<td>⅝</td>
<td>⅝</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aa x AA</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zx</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aa x Aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zy</td>
<td>0</td>
<td>⅝</td>
<td>⅝</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>aa x aa</td>
<td>1*(1-t)</td>
<td>(1-s)*t</td>
<td>zz</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2

![Graph showing allele frequency over time.](image-url)
Figure 3

![Graph showing average genotype fitness over time.](image-url)
Figure 4
Figure 5

![Graph showing the relationship between Genotype and Average fitness. The x-axis represents Genotype ranging from 0 to 60, and the y-axis represents Average fitness ranging from 0.70 to 0.80. The graph shows a positive trend where fitness increases with genotype.]
Figure 6
Figure 7

Average genotype fitness vs. time.
Figure 8

![Graph showing the relationship between genotype fitness and time.](image-url)
Figure 9

Males’ fitness contribution ordered from highest to lowest

Fitness of mating

0th male 3000th male

Fitness for primary female
Fitness for secondary female

Males’ fitness contribution ordered from highest to lowest

Fitness of mating

0th male 3000th male

Fitness for primary female
Fitness for secondary female
Figure A1

![Graph showing average difference in fitness for different values of α.](image-url)
Figure A2

\[ p \] versus \( \alpha \) (decreasing cost)