On the evolution of polygyny: a theoretical examination of the polygyny threshold model

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The polygyny threshold model states that if costs incurred are less than the benefits gained from mating polygynously in terms of breeding-situation quality, then polygyny is favored and could evolve. We constructed mathematical models and computer simulations to evaluate this hypothesis. In the basic model, there is a single locus with two alleles, which regulates whether the female is receptive to polygyny. There are two breeding situations of differing quality on which males randomly assort. Females then select a mate based on the associated breeding situation and whether the male already has mates. This basic model is extended mathematically to include a cost for the initial female of a male with multiple mates and again to include gene expression in males. The computer simulations extend the basic model to multiple loci and alleles and to multiple breeding situations. The results presented here suggest that the polygyny threshold model is valid in a population genetic context: if the fitness of females that actually mate polygynously is greater than the fitness of monogamous females on poorer breeding situations, polygyny evolves. However, this approach reveals interesting dynamics not apparent from the verbal model. If the trait is expressed in males and females, then polygyny can evolve even if females mating polygynously have a lower fitness than females mating monogamously. In the multiple breeding-situations model, the polygyny allele increases to some equilibrium value above which it experiences no selection. Surprisingly, as the cost of polygyny increases, the equilibrium frequency of the polygyny allele also increases. The difference between this evolutionary model and the ideal free distribution is discussed. *Key words:* evolution, polyandry, polygamy, polgyny, polgyny threshold model. *[Behav Ecol 14:201–211 (2003)]*

A fter 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). 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 how polygyny evolved from monogamy in birds is the polygyny 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.

The polygyny threshold model is based on five assumptions. The first is that the two sexes invest differentially in ensuring progeny survival (Orians, 1969). The sex that invests more heavily incurs a greater loss from low fitness mating and thus will be more selective in the choice of mates. The second assumption is that there is a cost to polygyny (Davies, 1989). This cost results from having to share the territory, resources, and access to the mate with other individuals (Pribil, 2000). In many species, the initial mate is preferentially provided for (Searcy and Yasukawa, 1989; Slagsvold and Lifjeld, 1994); thus the cost is largely incurred by those that chose polygyny over monogamy. The third assumption is that reproductive success of mating pairs varies either because of differences in the territory or differences in parental ability (Orians, 1969). Using the terminology of Wittenberger (1976), we refer to this variability as the breeding-situation quality of the mating pair. The fourth assumption is that the choosy mate can differentiate between the breeding-situation quality and is

free to settle anywhere (Davies, 1989). The fifth assumption is that individuals optimize, over evolutionary time, their reproductive output.

Thus, the polygyny threshold model begins with the premise that one sex invests more heavily in ensuring progeny survival and is thus more selective in choosing mates. Because reproductive success varies among different breeding situations, when faced with an option to mate polygynously with a high breeding-situation quality or to mate monogamously with a low breeding-situation quality, individuals will optimize their fitness by selecting polygyny. Thus polygyny will evolve. Though this explanation is widely accepted and often cited in the literature and has considerable empirical support (see, e.g., Bensch, 1996; Ezaki, 1990; Petit, 1991; Pribil and Picman, 1996; Pribil and Searcy, 2001; 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). Examining this hypothesis within a population genetics context is important because mean fitness is not always maximized. Thus the most fit phenotype does not necessarily fix in a population; its fate depends on the dynamics of the genetic system. There is no guarantee that a polygyny allele will fix, even if it is associated with higher fitness as hypothesized under the polygyny threshold model. To begin addressing the theoretical feasibility of the polygyny threshold model, we developed models to examine whether the dynamics are such that a gene resulting in polygyny will spread through the population.

METHODS AND RESULTS

Mathematical model 1: basic model

The model we developed is predicated on the five assumptions outlined in the introduction. For simplicity, we assume there are two distinct types of breeding situations (T1 and

T2), either due to a difference in the males (e.g., males capable of using or not using some resource) or in the territories the males hold (e.g., presence or absence of some resource). We also assume that all other differences in breeding situation are distributed randomly among T1 and T2 and thus do not differ on average between T1 and T2. Females have a preference for T1, and this preference is beneficial; females breeding in T1 experience a higher fitness than females breeding in T2. We define (t) as the proportion of breeding situations that is composed of T2 and $(1 - t)$ as the proportion that is composed of T1, where the fitness in T1 is 1 and the fitness in T2 is $(1 - s)$, and $0 < s < 1$. Males are associated with T1 and T2 in proportion to the relative availability of T1 and T2 (i.e., in proportion to t and $1 - t$).

The receptivity of a female to polygyny is determined by one locus with two alleles. Females that possess the polygyny allele (phenotype A, allele A) always elect to breed in T1, even when this results in polygyny. These females are called "polygynous females." Females that do not possess this allele (phenotype a, allele a) always elect males without other mates. These females are called "monogamous females." The phenotype of heterozygous females is determined by whether receptivity to polygyny is dominant or recessive. While there are still T1 males available, monogamous females will select T1, but once there are no unmated T1 males left, monogamous females will select T2. We assume that both types of females are equally likely to obtain monogamous T1 mates. Thus, monogamous females, in effect, are distributed among T1 and T2 males in proportion to the frequency of females of phenotype a and the frequencies of T1 and T2. On the other hand, polygynous females are only found on T1. Initially we assume this trait is not expressed in males. Males of a certain genotype are not more likely to occupy T1.

Primary females are the first females mated to a male that later mates with other (secondary) females. There is a cost to polygyny, and initially we assume primary females do not incur this cost. This decrease in fitness is less than the decrease due to breeding in T2. Thus, the fitness for nonprimary females mating with polygynous males is $(1 - hs)$ where $0 < hs < s$. Thus, in this initial model, we assume that the male preferentially provides for the primary female and provides equally for all secondary females. Finally, we assume random pairing between males and females in terms of male genotype. Because males mate randomly according to genotype and are randomly assorted between T1 and T2, all males experience the same fitness regardless of genotype. In this initial model, all males equally prefer to mate polygynously, so there is no selection acting on males. Under these conditions, does the allele for polygyny increase in frequency and invade the population?

To answer this question, we define x, y, and z as the frequencies of the genotypes AA, Aa, and aa, respectively, and $p = x + \frac{1}{2}y$ is the frequency of A. A is recessive to a, where A is the frequency of the polygynous allele and a is the frequency of the monogamous allele. To mathematically describe how the frequency of the three genotypes changes over time, we sum the proportion of progeny produced by all possible mating pairs of each genotype, where the contribution of each mating pair is weighted by its fitness. For this model, there are three fitness classes of mating pairs: pairs with a primary female on T1 (fitness 1), pairs with a secondary female on T1 (fitness $1 - hs$), and pairs on T2 (fitness $1 - s$). Thus the fitness of each mating pair is found by summing these three fitness classes weighted by the proportion of mating pairs that experience this fitness class. So, using Table 1, the fitness associated with mating pairs involving a female of phenotype A is

$$f_A = 1(1 - t) + (1 - hs)t + (1 - s)0 = 1 - tsh \qquad (1)$$

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

$$f_a = 1(1 - t) + (1 - hs)0 + (1 - s)t = 1 - ts. \qquad (2)$$

As mentioned above, the recursion equations are derived by multiplying these fitnesses by the proportion of all gametes produced by all possible mating pairs. The proportion of all progeny produced by each mating pair of a given genotype is found by multiplying the frequency of the mating pair by the proportion of their progeny that is that genotype. Then these sums need to be normalized by summing across all progeny. Finally, the recursion equations, when A is recessive to a, are:

$$Fx' = 1[f_A]x^2 + \tfrac{1}{2}[f_A]xy + \tfrac{1}{2}[f_a]yx + \tfrac{1}{4}[f_a]y^2 \qquad (3)$$

$$Fy' = \tfrac{1}{2}[f_A]xy + 1[f_A]xz + \tfrac{1}{2}[f_a]yx + \tfrac{1}{2}[f_a]y^2 + \tfrac{1}{2}[f_a]yz$$
$$+ 1[f_a]zx + \tfrac{1}{2}[f_a]zy \qquad (4)$$

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

where F is the normalization factor and is equal to the sum of the right sides of Fx', Fy', and Fz'.

After substitution and simplification:

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

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

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

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

We are interested in the fate of the polygyny allele, allele A. The recursion equation for the frequency of allele A, p', is found by summing the frequency of AA individuals with $\frac{1}{2}$ frequency of Aa individuals (as only half the chromosomes are of type A). If the change in frequency from one generation to the next $(p' - p)$ is positive, then the frequency of A is increasing over time.

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

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

Results from the basic mathematical model

As seen from Equation 11, p monotonically increases in frequency until $p = 1$, and the allele that introduces polygyny 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 zp for the dominant case, rather than to xq as in the recessive case, but is otherwise identical.

Mathematical model 2: effects of primary females

The above rendition of the polygyny threshold model ignores the effects on primary females. Primary females might suffer a reduction in fitness and should then attempt to deter polygyny (Davies, 1989), and there is evidence for the aggression of primary females (see, e.g., Kempenaers, 1994; Sandall, 1998; Slagsvold and Lifjeld, 1994; Slagsvold et al., 1999). To capture this phenomenon the second model

Table 1

Mating table for the basic model when *A* (the polygynous allele) is recessive to *a* (the monogamous allele)

| Female × male | Fitness × proportion of mating type experiencing that fitness | | | Freq | Progeny | | |
| | T1 | | | | | | |
	Initially M	P	T2		AA	Aa	aa
$AA \times AA$	$1(1-t)$	$(1-hs)t$		xx	1	0	0
$AA \times Aa$	$1(1-t)$	$(1-hs)t$		xy	½	½	0
$AA \times aa$	$1(1-t)$	$(1-hs)t$		xz	0	1	0
$Aa \times AA$	$1(1-t)$		$(1-s)t$	yx	½	½	0
$Aa \times Aa$	$1(1-t)$		$(1-s)t$	yy	¼	½	¼
$Aa \times aa$	$1(1-t)$		$(1-s)t$	yz	0	½	½
$aa \times AA$	$1(1-t)$		$(1-s)t$	zx	0	1	0
$aa \times Aa$	$1(1-t)$		$(1-s)t$	zy	0	½	½
$aa \times aa$	$1(1-t)$		$(1-s)t$	zz	0	0	1

T1 is the preferred breeding situation and constitutes $1 - t$ of the mating pairs, s is the fitness decrement suffered by mating pairs of the unpreferred T2, and h is the amount of fitness reduction suffered by secondary females. M, monogamy; P, polygyny; freq, frequency.

assumes a reduction in fitness for primary females, as well as a reduction in the frequency of polygyny as a result of successful deterrence by the primary female. We define r as 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. The variable 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 polygynously on T1 and must find mates on T2. Thus, $0 \leq d \leq 1$, where if primary females are unsuccessful in deterring potential secondary females, then $d = 0$, and if primary females deter all potential secondary females, then $d = 1$. 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 $(1 - t) - g$, where g is the proportion of primary females among all females that chose an unmated male on T1, $0 < g < 1$, and g is a function of the frequency of the polygynous allele. Under these new conditions, does the allele introducing polygyny increase in frequency and invade the population?

Following the same methods as above but using Table 2, the fitness associated with mating pairs involving a female of phenotype A is:

$$f_A = 1[(1-t)(1-g)] + (1-rhs)(1-t)g$$
$$+ (1-hs)[t(1-d)] + (1-s)td \quad (12)$$
$$= 1 - rhsg(1-t) - tds(1-h) - ths, \quad (13)$$

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

$$f_a = 1[(1-t)(1-g)] + (1-rhs)(1-t)g + (1-s)t \quad (14)$$
$$= 1 - rhsg(1-t) - ts. \quad (15)$$

Finally, the recursion equations, when A is recessive to a, are:

$$Fx' = 1[f_A]x^2 + \tfrac{1}{2}[f_A]xy + \tfrac{1}{2}[f_a]yx + \tfrac{1}{4}[f_a]y^2 \quad (16)$$

$$Fy' = \tfrac{1}{2}[f_A]xy + 1[f_A]xz + \tfrac{1}{2}[f_a]yx + \tfrac{1}{2}[f_a]y^2$$
$$+ \tfrac{1}{2}[f_a]yz + 1[f_a]zx + \tfrac{1}{2}[f_a]zy \quad (17)$$

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

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

After substitution and simplification:

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

$$Fy' = 2(x + \tfrac{1}{2}y)(\tfrac{1}{2}y + z)$$
$$- 2(1-t)(rhsg)(x + \tfrac{1}{2}y)(\tfrac{1}{2}y + z)$$
$$- ts(x + \tfrac{1}{2}y)(\tfrac{1}{2}y + z)$$
$$- [tds(1-h) + ths - ts](\tfrac{1}{2}y + z)x \quad (20)$$

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

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

and

$$Fp' = (x + \tfrac{1}{2}y) - (1-t)(rhsg)(x + \tfrac{1}{2}y) - ts(x + \tfrac{1}{2}y)$$
$$- [tds(1-h) + ths - ts](x + \tfrac{1}{2}y)x$$
$$- \tfrac{1}{2}[tds(1-h) + ths - ts](\tfrac{1}{2}y + z)x \quad (23)$$

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

Results from mathematical model including effects on primary females

Thus, p monotonically increases in frequency until $p = 1$, and the allele that introduces polygyny becomes fixed in the population as long as the fitness of secondary females in T1 is greater than the fitness of females in T2 ($h < 1$) and the primary females are not completely successful in deterring all potential secondary females ($d \neq 1$). If $d = 1$—that is, the

Table 2
Mating table including the effects of primary female when *A* (the polygynous allele) is recessive to *a* (the monogamous allele)

| Female × male | Fitness × proportion experiencing that fitness | | | | | Progeny | | |
| | T1 | | | T2 | Freq | | | |
	M female	Primary female	Secondary female			AA	Aa	aa
$AA \times AA$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$	$(1-hs)t(1-d)$	$(1-s)td$	xx	1	0	0
$AA \times Aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$	$(1-hs)t(1-d)$	$(1-s)td$	xy	½	½	0
$AA \times aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$	$(1-hs)t(1-d)$	$(1-s)t$	xz	0	1	0
$Aa \times AA$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	yx	½	½	0
$Aa \times Aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	yy	¼	½	¼
$Aa \times aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	yz	0	½	½
$aa \times AA$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	zx	0	1	0
$aa \times Aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	zy	0	½	½
$aa \times aa$	$1[(1-t)(1-g)]$	$(1-rhs)(1-t)g$		$(1-s)t$	zz	0	0	1

T1 is the preferred breeding situation and constitutes $(1-t)$ of the mating pairs, s is the fitness decrement suffered by mating pairs of the unpreferred T2, and h is the amount of fitness reduction suffered by secondary females, r is the amount of fitness reduction suffered by primary females, d is the proportion of potential secondary females successfully deterred, and g is the proportion of primary females among all females that chose a unmated male of T1. M, monogamous; freq, frequency.

primary females are completely successful in deterring all of the secondary females- then there are no polygynous matings. If there are no polygynous matings, then there is no selection for the polygyny allele, and $F\Delta p = 0$. Note that if $d = 0$ (that is, the primary females are unsuccessful in deterring any of the secondary females), then the expression for Δp reduces to the initial model. The conditions under which p monotonically increases 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.

Note that the sign of Δp does not depend on r, 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 polygyny. Thus, even if primary females had a fitness of zero (i.e., $r = -1/hs$), polygyny would still invade, providing that the secondary females have a fitness advantage over monogamous females on the poorer breeding situation. 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 polygyny (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 polygyny; 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 polygyny. As in model 1, females that are phenotypically A all find mates on T1, either a male with no other mate (in which case the male is either phenotype) or a male with other mates (in which case the male is also of phenotype A). In this scenario, the frequencies of some mating types are no longer the product of the genotype frequencies because polygynous mating is no longer random; there is associative mating among those phenotypes that are receptive to polygyny (Falconer and Mackay, 1996; this has also been referred to a model of genetic correlation; see Halliday and Arnold, 1986). The mating table for those mates that are initially monogamous is identical to that in Tables 1 and 2. For the polygynous matings when *A* is recessive (Table 3), all *xt* females that are available for polygynous matings are mated to *AA* males. Thus the frequency of polygynous $AA \times AA$ mates is the proportion of *AA* females

available for polygyny, xt. For the polygynous matings when *A* is dominant, all *xt* females that are available for polygynous matings are mated to either *AA* or *Aa* males. Thus the frequency of polygynous $AA \times AA$ mates is the proportion of *AA* females available for polygyny, xt, times the proportion of all receptive males that are genotype *AA*, $x/(x+y)$.

Using Table 3, the recursion equations are again found by summing the proportion of progeny produced by all mating types, weighted by the fitness of the mating type:

$$Fx' = (1)[(1-t)x^2 + (1-hs)tx] + (½)[(1-t)xy]$$
$$+ (½)[(1-t) + (1-s)t]yx$$
$$+ (¼)[(1-t) + (1-s)t]y^2 \tag{25}$$

$$Fy' = (½)[(1-t)xy] + [1(1-t)xz] + (½)[(1-t) + (1-s)t]yx$$
$$+ (½)[(1-t) + (1-s)t]y^2 + (½)[(1-t) + (1-s)t]yz$$
$$+ (1)[(1-t) + (1-s)t]zx$$
$$+ (½)[(1-t) + (1-s)t]zy \tag{26}$$

$$Fz' = (¼)[(1-t) + (1-s)t]y^2 + (½)[(1-t) + (1-s)t]yz$$
$$+ (½)[(1-t) + (1-s)t]zy + 1[(1-t) + (1-s)t]z^2, \tag{27}$$

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

After substitution and simplification:

$$Fx' = (1-ts)(x+½y)^2 + (1-hs)tx - (1-s)(x+½y)tx \tag{28}$$

$$Fy' = 2(1-ts)(x+½y)(½y+z) - (1-s)(½y+z)tx \tag{29}$$

$$Fz' = (1-ts)(½y+z)^2 \tag{30}$$

$$F = (1-ts) + (1-hs)tx - (1-s)tx \tag{31}$$

and

$$Fp' = (1-ts)(x+½y) + (1-hs)tx - (1-s)tx$$
$$+ ½(1-s)(½y+z)tx \tag{32}$$

$$F\Delta p = t[(1-hs) - ½(1-s)](½y+z)$$
$$x > 0 \quad \text{if } [(1-hs) - ½(1-s)] > 0 \quad \text{or}$$
$$(1+s)/(2s) > h. \tag{33}$$

Table 3
Mating table if gene is also expressed in males when A (the polygynous allele) is recessive to a (the monogamous allele)

Female × male	Initially monogamous F × P[a]			Polygynous matings F × P[a]		Progeny		
	T1	T2	Freq[b]	T1	Freq[b]	AA	Aa	aa
$AA \times AA$	$1(1-t)$		xx	$(1-hs)t$	x	1	0	0
$AA \times Aa$	$1(1-t)$		xy			½	½	0
$AA \times aa$	$1(1-t)$		xz			0	1	0
$Aa \times AA$	$1(1-t)$	$(1-s)t$	yx			½	½	0
$Aa \times Aa$	$1(1-t)$	$(1-s)t$	yy			¼	½	¼
$Aa \times aa$	$1(1-t)$	$(1-s)t$	yz			0	½	½
$aa \times AA$	$1(1-t)$	$(1-s)t$	zx			0	1	0
$aa \times Aa$	$1(1-t)$	$(1-s)t$	zy			0	½	½
$aa \times aa$	$1(1-t)$	$(1-s)t$	zz			0	0	1

T1 is the preferred breeding situation and constitutes $(1-t)$ of the total range, s is the fitness decrement suffered by mating pairs of the unpreferred T2, and h is the amount of fitness reduction suffered by secondary females.

[a] Fitness times proportion experiencing that fitness.

[b] Frequency of mating type.

Results from mathematical model where gene is expressed in males also

Thus, if $(1 + s)/(2s) > h$, p monotonically increases in frequency until $p = 1$, and the allele that introduces polygyny becomes fixed in the population. Remember that s measures the fitness decrement to mating pairs on T2, the undesirable breeding situation, and that h measures the amount of fitness decrement for secondary females, where $(1 - hs)$ is the fitness of mating pairs involving a secondary female. With $0 < s < 1$, h can exceed 1, and the polygyny allele will still invade (Figure 1). That is, the fitness of the secondary female can be less than the fitness of the monogamous female on T2, 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 polygyny allele. However, in this third model, only males carrying the polygyny allele can have secondary females and thus have a selective advantage. Presumably, it is this selective advantage that compensates for the selective disadvantage of secondary females when $h > 1$. 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.

Note that in all of these mathematical models, we assume that there are enough males with the preferred breeding situation for all the potential secondary females. This assumption entails one of two conditions. The first is that males will take on an infinite number of females (and the cost to a secondary female is the same regardless of whether she is the second female or the nth female). Biologically this is implausible because the resources of the male are presumably finite. The second, more realistic, condition is that the number of males with the better breeding situation is large enough. In the basic model, "large enough" means that $(1 - t)n \geq mt$, where n is the number of secondary females each male will accept, and m is the frequency of polygynous 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 $(1 - t)n \geq mt(1 - d)$. In the model where the trait is expressed in both males and females, $(1 - t)n \geq t$. In the computer simulations we explore the outcome when the number of males on T1 is not large enough.

Simulation 1: basic simulation

To examine this model further, we wrote a computer simulation of the basic system which we then extend in two different ways. Note that all variables used in the various models and simulations are listed in Table 4. Results are shown from the basic model because these results serve as a benchmark for the results from the two extensions. This is especially important because the simulation differs from the 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 homozygotes.

In this first model there is 1 locus with 2 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 2 alleles. Half the males are assigned a breeding-situation quality of 1.0 and half a breeding-situation quality of 0.6, independent of their genotype. Unlike the mathematical models, heterozygotes are interme-
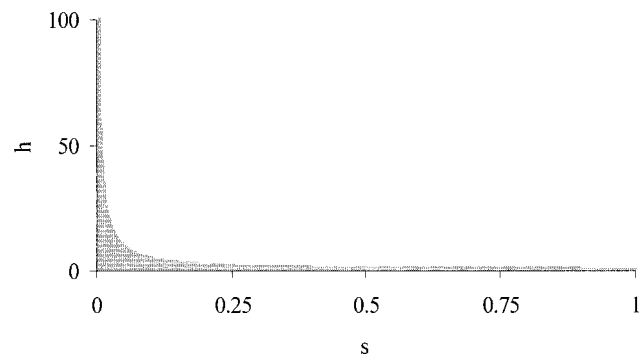

Figure 1
Plot of $(1 + s)/(2s) > h$ for the mathematical model in which the gene is expressed also in males, where s is the fitness decrement to mating on the less optimal breeding situation, and where hs is the fitness decrement to secondary females. If the above relationship holds, then the polygamy allele invades and fixes in the population.

Table 4
List and description of all variables used in the models

Variable	Model	Description
A	All	Polygynous allele
a	All	Monogamous allele
p	All	Frequency of Ap
x	Math	Frequency of AA individuals
y	Math	Frequency of Aa individuals
z	Math	Frequency of aa individuals
T1	All	Preferred type of breeding situation
T2	All	Unpreferred type of breeding situation
t	All	Proportion of the mating pairs that is T2
$(1 - t)$	All	Proportion of the mating pairs that is T1
s	Math	Selection decrement suffered by mating pairs of T2
$(1 - s)$	Math	Fitness of mating pairs of T2
h	Math	Amount of reduction in fitness for secondary females
$(1 - hs)$	Math	Fitness of mating pairs of T1 involving an already mated male
r	Math 2	Amount of reduction in fitness for primary females
$(1 - rhs)$	Math 2	Fitness of mating pairs of T1 involving a primary female
d	Math 2	Proportion of potential secondary females that are successfully deterred
$(1 - d)$	Math 2	Proportion of secondary females that are not deterred
g	Math 2	Proportion of primary females among all females that chose an unmated male of T1
$(1 - g)$	Math 2	Proportion of monogamous females among all females that chose an unmated male of T1
n	Math (end)	Number of secondary females each male will accept
m	Math (end)	Frequency of polygamous females
α	Appendix	Cost suffered by secondary females
Male's quality	Appendix	Breeding-situation quality associated with a male; also known as the male's fitness contribution

diate between the two homozygotes in phenotype and mate polygynously if possible with probability 50%. Females choose males one after another, but the order in which females choose is random. The fitness of the mating pair is the breeding-situation quality less the cost (0.9[breeding-situation quality]) if she mates polygynously or the breeding-situation 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, because by 1500 generations (and often much sooner) the system reaches mutation-selection balance. Averages are based on 500 iterations.

Results from basic simulation

Over time, the frequency of the polygynous allele rapidly increases to near fixation (Figure 2). It cannot 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
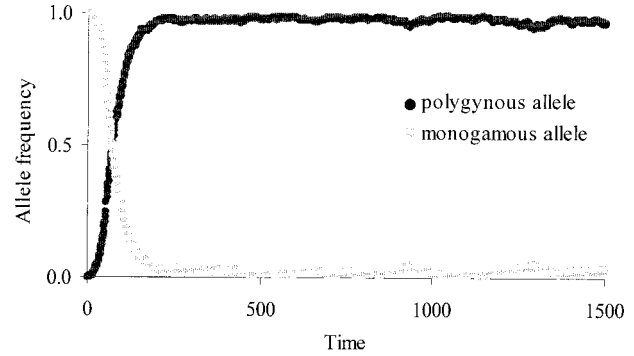

Figure 2
Plot of allele frequencies over time for the basic computer model of the polygyny threshold model.

fitness oscillates depending on the distribution of the few individuals on the two breeding situations (Figure 3). The average frequency of the polygynous allele is 0.969, the average fitnesses of the three genotypes (0, 1, 2) are 0.585, 0.711, and 0.742, respectively, and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous female) are 1.0, 0.9, 0.6, respectively. The less fit genotype and phenotypes are still present in the population at low frequencies due to mutation. If the cost of polygyny increases such that the fitness of polygynous matings is lower than that of monogamous matings on the poorer breeding situation, then no female mates polygynously, 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 breeding situation $(1 - t)$ is half or more. However, if the frequency is less than one-half, at high frequencies of the polygynous allele, there is a shortage of males with whom to mate polygynously, and some polygynous females will mate monogamously on the inferior breeding situation. In this case, the average fitness of the polygynous allele decreases over time. This does not affect the average fitness of the monogamous allele, which remains constant. Nevertheless, the fitness of the polygynous allele still exceeds that of the monogamous allele, and the polygynous allele will increase in frequency until the mutation-selection balance.

Simulation model 2: multiple loci and multiple alleles

Because the likelihood is small of having one locus with two alleles determining a complex behavior such as receptivity to polygyny, 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 because mean fitness is no longer necessarily maximized (Hartl and Clark, 1989). In this 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 for each of the two chromosomes, such that a single breakpoint is chosen with equal likelihood among all 10 loci. To assess the probability that a female will mate polygynously, the individual's genotype (the sum of both alleles across all loci) is divided by the maximum possible value (namely, $10 \times 3 \times 2$) to give a probability between 0 (all alleles that permit only monogamy) and 1 (all alleles that most strongly lead to polygyny).
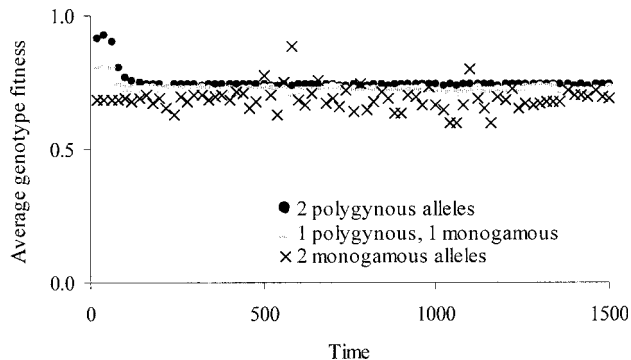
Figure 3
Plot of the average genotype fitnesses over time for the basic computer model of the polygyny threshold model. The points represent 20 generation averages because near equilibrium there are few individuals present that have two monogamous alleles. Also, because there are so few individuals present, the estimate of average genotype fitness of individuals with two monogamous alleles is variable.

Figure 4
Plot of the allele frequencies over time for the multiple alleles and loci model, in which there are 10 loci with 4 alleles each controlling the probability of mating polygynously. Each of the four alleles is associated with a likelihood of mating polygynously, and the alleles at different loci interact additively to give a phenotypic probability of mating polygynously.

Results from simulation of multiple loci and multiple alleles

Over time, the frequency of the polygynous alleles slowly increases, with the more polygynous alleles increasing faster (Figure 4). The increase in frequency is much slower because the individuals have a low probability of mating polygynously until the allele frequencies increase and the polygynous allele is prevalent at many loci (and thus individuals have a high probability of mating polygynously). 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 locus. 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, respectively, and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous female) are 1.0, 0.9, 0.6, respectively. The average fitness of the genotypes, for those present at final generation, is positively correlated with the genotype's probability of mating polygynously (Kendall's $\tau = 0.48$, $p < .001$, $n = 43$); thus individuals with a higher probability of mating polgynously have a higher fitness. The less fit genotype and phenotypes are still present in the population at low frequencies due to mutation.

Simulation model 3: multiple breeding-situations

The other extension is to multiple breeding situations, as having only two is overly simplistic. This third model is identical to the original, except every generation each male is randomly assigned the quality of his breeding situation using a number drawn from uniform (0,1). Thus, instead of having only two breeding situtations, there is an infinite number. If the female mates monogamously, she chooses the male with the best breeding situation that is not already mated. If the female mates polygynously, she chooses the male with the best breeding situation that has only one other mate, provided the breeding-situation quality less the cost is greater than the best breeding-situation 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 breeding-situation quality.

Results from multiple breeding situations model

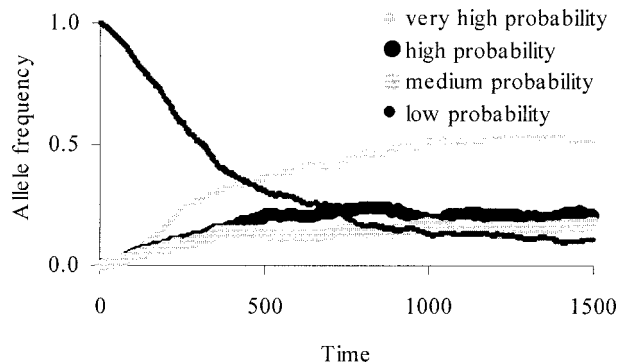Over time, the frequency of the polygynous allele rapidly increases to slightly above 0.5 (Figure 5). During this rapid increase, the fitness of the polygynous homozygote decreases, and the fitness of the monogamous homozygote increases (Figure 6). The average frequency of the polygynous allele is 0.569, the average fitnesses of the three genotypes (0, 1, 2) are 0.712, 0.713, 0.715, respectively, and the average fitnesses of the three phenotypes (primary female, secondary female, monogamous female) are 0.765, 0.688, 0.500, respectively. In this model, unlike the previous two, the polygyny allele reaches an internal equilibrium. As seen by the genotype fitnesses, there is no longer a selective difference; otherwise genotype frequencies would continue to change. There are, however, still differences in phenotype fitnesses. This is not surprising because phenotypes are not selected on; selection acts on differential fitnesses among alleles. The differential fitnesses are weighted averages of phenotype fitnesses. So, for instance, the fitness of the polygynous allele is the fitness average of secondary females, primary females that carry the polygynous allele, and monogamous females that carry the polygynous allele. This scenario is an example of why it is important to examine the dynamics of a system in its genetic context and not assume that selection will favor the phenotype with highest fitness.

If the cost increases to 0.5, then over the course of 500 iterations, the average frequency of the polygynous allele is 0.647, and the average fitnesses of the three genotypes are 0.580, 0.582, and 0.585, but the average fitness of the three phenotypes is 0.841, 0.420, and 0.500. Also with higher cost, the time during which the genotype fitnesses are changing is longer (Figure 7). Thus, in this model, unlike the previous two, the polygynous allele does not rise in frequency until mutation-selection balance, but it reaches a lower equilibrium value that is positively correlated with cost.

Why with multiple breeding situations does the polygyny allele reach an equilibrium far from mutation-selection balance? In the basic model, the average fitness of the polygynous allele is constant because all polygynous matings have the same fitness. This is not so for the multiple breeding-situations model. When rare, the average fitness of phenotypically polygynous females is high because genotypically polygynous females are so rare, these females mate polygynously only with the males on the best breeding situations. However, as their frequency increases, the females mate with a larger number of males, so the average fitness of polygynous females decreases. (Recall that males cannot mate with more than two females, so as the number of polygynous females
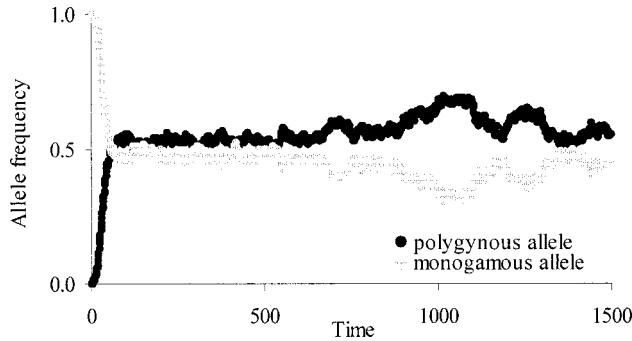
Figure 5
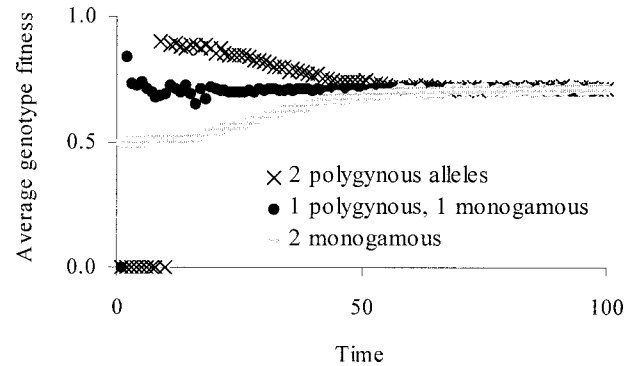Plot of the allele frequencies over time for the multiple breeding situations model.

Figure 6
Plot of the average genotype fitnesses over time for the multiple breeding situations model with a small cost to females mating polygynously.

increases, the number of males mating polygynously increases.)

In the basic model, the average fitness of monogamous females is also constant because all monogamous matings on the less optimal breeding-situations have the same fitness. Again, this is not so for the multiple breeding situations model. When frequent, the average fitness of monogamous females is near the average of the fitness distribution; because 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 fewer 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 polygynously.) Thus, in the multiple breeding situations model, unlike the basic model, the average fitness of the two alleles depends on their frequency. At some allele frequency these two fitnesses are equivalent, there is no further selection for (or against) polygyny, and an equilibrium is reached (see Appendix).

Why does this equilibrium allele frequency increase as the cost increases? As described above, the equilibrium is reached when the average fitness of individuals carrying monogamous alleles is equal to the average fitness of individuals carrying polygynous alleles. The fitness differential between polygynous females and monogamous females is due to polygynous females that actually mate polygynously. The average fitness of polygynous females that actually mate polygynously (i.e., average fitness of secondary females) depends on their frequency. At low frequency, these females are able to choose the best breeding situations, while as their frequency increases, these females are sampling more of the entire distribution, and consequently their average fitness decreases. However, the proportion of polygynous females that are secondary females depends on the cost: the higher the cost, the smaller proportion of polygynous females that will choose polygyny. Thus, with a higher cost, a higher frequency of polygynous alleles is required to achieve the same frequency of secondary females and thus the appropriate decrease in average fitness to achieve equilibrium. It is for this reason that the equilibrium allele frequency depends on the cost of polygynous matings, such that as the cost increases the equilibrium allele frequency of the polygynous allele increases (see Appendix).

DISCUSSION

The polygyny threshold model, as originally proposed by Orians (1969), states that if the costs incurred from polygyny

are less than the benefits gained from a polygynous relationship in terms of breeding-situation quality, then polygyny 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 the individual is receptive to polygyny. There are two breeding situations of differing quality on which males randomly assort. Females then select a male with whom to breed based on the associated breeding situation and whether the male already has mates. The computer simulations extend this model to multiple loci and alleles and to multiple breeding-situations. The results presented here suggest that the polygyny threshold model is valid in a population genetics context; in all cases in which the secondary females' fitness is greater than monogamous females' fitness in the poorer breeding situation, polygyny evolves.

The extension of the basic model to multiple breeding situations leads to interesting dynamics. There is an equilibrium allele frequency of the polygynous allele, such that below this frequency there is selection for polygyny, but above this frequency there is no selection either for or against polygyny. An equilibrium exists in this extension because the average fitness of two phenotypes depends inversely on the frequency of individuals exhibiting each phenotype. With higher frequency, individuals have increasingly more low-quality matings, and the average phenotype fitness decreases. At some frequency, the two phenotypes have equal average fitness and selection can continue no further; an equilibrium is reached. Because the fitness differential between monogamous and polygynous females is due to secondary females, this equilibrium depends on the frequency of secondary females reaching a certain threshold. However, the frequency of secondary females is in turn dependent on the cost, such that with higher cost, fewer polygynous females select polygyny. Consequently, this equilibrium allele frequency is a function of the cost of polygyny, where as the cost of polygyny increases, the equilibrium frequency of the polygynous allele increases. This relationship could be empirically tested by confirming that the difference in fitness for primary and secondary females is positively correlated with the prevalence of secondary females.

Also, there are cases in which the secondary females' fitness is less than monogamous females' fitness on the poorer breeding situation and polygyny 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

polygynous females. Presumably, polygyny can evolve despite the fitness cost to females because males gain a fitness advantage. If only males with the trait are receptive to polygyny, then only males with the gene attain the fitness advantage of having multiple mates. This outcome of a fitness loss in females being offset by a fitness gain in males is similar to that of another model of genetic correlation among mates that is used to explain multiple mating by females (Halliday and Arnold, 1984). Thus, one potential explanation of field measurements that indicates that the fitness of secondary females does not exceed the fitness of females monogamously mated (see examples listed in Slagsvold and Lifjeld, 1994) is that receptiveness to polygyny is in part a genetic trait expressed in both males and females. This possibility could be empirically tested by determining that only some males are receptive to secondary females. (However, failing to find differential receptiveness does not disaffirm this possibility if the polygyny allele is fixed in the population.)

This is not the only explanation. As seen in the results from the simulation of multiple breeding situations, when the cost of mating polygynously is high, the fitness of secondary females does not exceed the fitness of females monogamously mated, yet polygyny still evolves. With a high cost, only polygynous females faced with unmated males in very poor breeding situations will become secondary females, and thus secondary females have a low average fitness. In contrast, monogamous females mate with a wide range of males, and thus their average fitness is near the middle of the distribution. However, these phenotypically monogamous females are composed of a mixture of individuals carrying either the polygyny allele or the monogamy allele. The genotypically polygynous females are mating only with the males on the better breeding situations, whereas the genotypically monogamous females are mating also with the males on very poor breeding situations and thus have a lower average fitness. Thus, another potential explanation of field measurements (see examples listed in Slagsvold and Lifjeld, 1994) that indicate that the fitness of secondary females does not exceed the fitness of females monogamously mated is there is a large cost associated with polygyny. This possibility could be empirically tested by determining that the fitness difference between primary and secondary females is large.

Many authors use the ideal free distribution for modeling the process of finding mates (e.g., Cassini, 2000; Parker, 1978; Parker and Sutherland, 1986; Sutherland, 1996). Indeed, many of the assumptions of the polygyny threshold model are identical to the assumptions of the ideal free distribution (Fretwall and Lucas, 1970; Parker, 1970)—namely, that breeding situations differ in quality, that females are able to evaluate these differences, and that females act to optimize their reproductive success. However, the ideal free distribution makes additional assumptions. One additional assumption is that as males gain more mates, the fitness of all mates drops equally (i.e., that the resources of the male is distributed equally among all his mates; Kacelnik et al., 1992; Parker and Sutherland, 1986). However, there is evidence, as noted earlier, that at least for some species the male preferentially provides for the primary female as modeled in this study. Furthermore, if this assumption is included, then, as predicted by the ideal free distribution, all females have the same fitness, and there is no selective advantage for the polygyny allele. (This situation is described by mathematical model 2 with $r = 1$ and $h = 1$.) Without a selective advantage, the polygyny allele will not increase in frequency (except possibly by drift).

Second, the ideal free distribution requires that females are free to settle anywhere—that all females have equal access to the resource (Kacelnik et al., 1992). When placing the
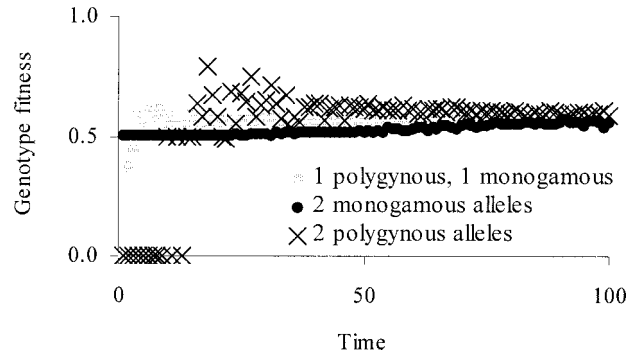

Figure 7
Plot of the average genotype fitnesses over time for the multiple breeding situations model with a high cost for females mating polygynously.

polygyny threshold model in terms of a genetic model, this assumption is violated by monogamous females. Monogamous females are free to settle only on territories in which there is no other female already present. To examine the evolution of a behavior (either genetic or learned), one has to assume that some individuals exhibit the novel trait and some individuals do not. Thus the females are not equal as assumed by the ideal free distribution. The original ideal free distribution is therefore useful for describing how individuals that are equivalent should arrange themselves on a resource to maximize fitness. However, it is not an evolutionary model, describing how some trait changes in frequency over time; especially it is not an adaptive model because this requires individuals that are not equivalent.

There have been multiple studies examining how the ideal free distribution changes when competitors are not equal. These studies examine competitors that differ in competitive ability (reviewed in Parker and Sutherland, 1986), in risk of predation (Grand and Dill, 1999), or in efficiency of resource utilization (Ruxton et al., 2001). None of these models fit the model presented here in which some females are capable of using a novel resource (already mated males) when the quality of the primary resource (unmated males) diminishes. Furthermore, most of these models still assume that as the number of competitors on a resource increases, the quality of the resource decreases proportionally.

The polygyny threshold model is discussed here in terms of males with multiple mates 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 polygyny in organisms other than birds, as well as the evolution of polyandry. For instance, if in some species the roles are reversed such that females have some characteristic that affects the quality of the breeding situation and males choose their mates, then the models presented here apply. Likewise, many of the conclusions reached here are also not restricted to either birds or polygyny. However, possible genotype to phenotype mappings for a genetic trait that predisposes individuals to polygyny when beneficial still need to be developed.

APPENDIX

This section develops the analytical proof that as the cost of polygyny increases, the equilibrium frequency of the polygyny allele increases for the multiple breeding situations model.
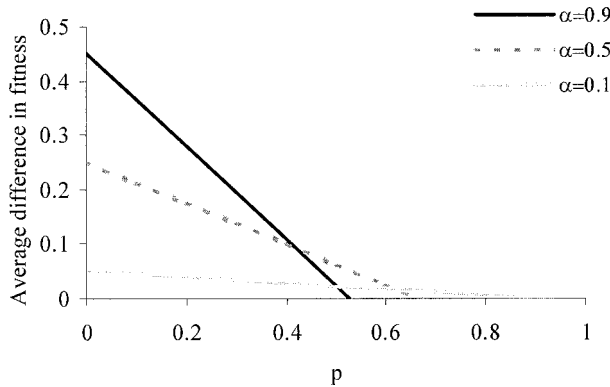
Figure 8
Plot of the average difference in fitness between monogamous females and polygynous females for the multiple breeding situations model. Average difference = $(½)(\alpha^2)(1 - p - p\alpha)$, where p is the frequency of the polygynous allele and α is the cost of polygynous matings (high α, small cost).

We assume an infinite population. A male's fitness contribution, due to the breeding-situation quality associated with him, is uniformly chosen from (0,1), and then the males are ordered from highest to lowest. Thus, the fitness contribution of a male with 80% of the population below him is 0.8, and the fitness contribution of a 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 polygynous females have the option of mating with a male who has one other mate. If females mate polygynously, then the pair suffers a reduction in fitness such that the male's fitness contribution is multiplied by some factor, α. Otherwise the fitness of the mating pair is the male's fitness contribution. Note that α is a measurement of the cost to polygyny, but it differs from h used in the mathematical models ($1 - hs$ = male's quality $\times$ α). We define the frequency of the polygyny allele as p, which is also the frequency of females mating polygynously: one-half of heterozygotes will mate polygynously as well as all homozygotes, so the frequency of polygynous females is $½(2pq) + 1(p^2) = p$ (heterozygotes and homozygotes at this point are found in Hardy-Weinberg equilibrium because there is no selection before mating). Under this process, we calculate the average fitness of monogamous females and the average fitness of polygynous females.

Initially all females mate monogamously regardless of genotype because initially the quality of males without mates exceeds that of males with another mate. This continues until these two fitnesses equilibrate (i.e., when the quality of the nth male = the quality of the first male $\times$ α = $1.0 \times \alpha$). During this period, the average fitness of polygynous and monogamous females is the same—namely, $(1 + \alpha)/2$, which is the average of the highest and lowest fitness. The proportion of polygynous 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 polygynous and monogamous females that are in the second group is $1 - (1 - \alpha) = \alpha$.

All polygynous females in this second group actually mate polygynously (assuming a "small" allele frequency of the polygynous allele; see below). The frequency of polygynous females mating polygynously is $p\alpha$, which is also the frequency of males with multiple mates. The fitness contribution of the last male with multiple mates is $(1 - p\alpha)$, since male quality

uniformly covers (0,1). The fitness contribution of the highest male that mates polygynously is the fitness contribution of the highest male, 1. Thus the average fitness of polygynous females mating polygynously is the average of these two fitnesses less the cost, $[1 + (1 - p\alpha)](\alpha)/2 = (2 - p\alpha)(\alpha)/2$. If $p\alpha$ males mate polygynously, 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 monogamously with the second group of monogamous females is α. Thus the average fitness of monogamous females in this second group is $(\alpha + p\alpha)/2 = (1 + p)(\alpha)/2$.

Putting it all together, the average fitness of polygynous females is the average fitness of the females that initially mate monogamously times the frequency of this group of females plus the average fitness of the females that mate polygynously times the frequency of this latter group of females, or $[(1 + \alpha)(1 - \alpha)/2] + [(2 - p\alpha)(\alpha)(\alpha)/2] = ½[1 + \alpha^2 - p\alpha^3]$. 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 $[(1 + \alpha)(1 - \alpha)/2] + [(1 + p)(\alpha)(\alpha)/2] = ½[1 + p\alpha^2]$. Even though monogamous females are mating monogamously the entire time, to calculate their average fitness, we need 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 because they are no longer competing with the polygynous females for the monogamous males.

Thus, the average fitness of both groups of females depends on α and on the frequency of the polygyny allele. As the allele frequency of polygynous females increases, the average fitness of polygynous females decreases, but the average fitness of monogamous females increases. The difference between the average fitness of monogamous and polygynous females is

$$½[1 + \alpha^2 - p\alpha^3] - ½[1 + p\alpha^2] = ½[\alpha^2 - p\alpha^2 - p\alpha^3]$$
$$= ½\alpha^2[1 - p - p\alpha]. \quad (A1)$$

As seen in Figure 8 (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 depends on the cost, such that as the cost decreases the equilibrium allele frequency decreases (remember as α increases, cost decreases). To solve for the relationship between allele frequency and cost, we set the above equation to zero and solve for p (Figure 9). This equilibrium is stable only from one direction. If the allele frequency of polygyny is less than this equilibrium value, then selection will favor polygyny. However, if the allele frequency of polygyny exceeds this equilibrium value, then there is no selection, only drift.

When the frequency of the polygyny allele exceeds this equilibrium value, not all polygynous females can mate polygynously; for some females there is not an already mated male whose fitness is higher than a single male. Instead of mating polygynously with an inferior male, as assumed by the math, these females will mate monogamously. Thus, the average fitness of monogamous females will never exceed that of polygynous females.
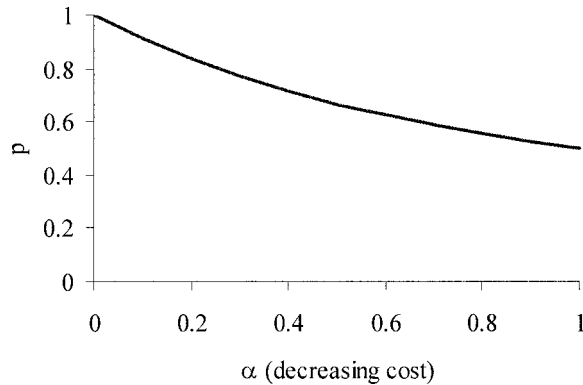
Figure 9

Plot of the relationship between cost of polygynous matings, α, and frequency of the polygynous allele, p, for the multiple breeding-situations model: namely, $p = 1/(1 + \alpha)$.

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