Evolutionary Ecology Research, 2002, **4**: 275–292

A genetic algorithm approach to study the evolution of female preference based on male age

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ABSTRACT

In many species, females prefer to mate with older males, possibly because older males are of higher genetic quality than younger males. However, the relationship between age and genetic quality may differ among populations depending on rates of age-dependent mortality. Therefore, we examined the evolution of female preference in populations with different age structures arising from differences in rates of age-dependent and age-independent mortality. To determine the shape of optimal female preference functions for males in each of 10 ages, we used a genetic algorithm approach. This approach allowed female preference for each male age to evolve independently. At moderate levels of mortality, females showed a bias in favour of the oldest males. At higher mortality rates, however, females showed the greatest preference for intermediate age males and, at very low mortality rates, females showed little bias overall. We also examined whether costs of choice influenced equilibrium preference functions. As opportunity costs increased, females were less likely to discriminate against young males and age structure became less important in determining preference function. Our results demonstrate that demographic patterns and costs of choice can influence female preference for young versus old males. In addition, the existence of female preference can alter the underlying demographic structure in a population.

Keywords: age effects, genetic algorithm, mate choice, senescence, sexual selection.

INTRODUCTION

Some researchers have argued that viability selection will lead to older males of higher genetic quality than younger males and that, at least in species in which males provide only sperm to females, females should prefer to mate with older males (Trivers, 1972; Manning, 1985; Kirkpatrick, 1987; Andersson, 1994). In some species, females do prefer to mate with older males (Zuk, 1988; Simmons and Zuk, 1992; Simmons, 1995; peacocks: Manning, 1989; pheasants: Grahn and von Schantz, 1994).

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Recent theoretical studies of female preference for males of particular ages have led to contradictory conclusions. In a simulation model, Kokko and Lindström (1996) contrasted two different mate-preference functions, one in which females preferred older males and one in which there was no age bias. They found that a strong female preference for older mates was likely to evolve under a variety of environmental conditions, given a sufficiently high genomic mutation rate.

By contrast, in a quantitative genetic model of mate choice, Hansen and Price (1995) showed how genes with antagonistic pleiotropic effects could result in young to intermediate-age males of higher genetic quality than older males. According to this model, if females chose mates based on genetic quality alone, they would prefer younger rather than older males. Empirical evidence from studies of a few species supports the suggestion that younger males can be of higher genetic quality, on average, than older males. For example, in collared flycatchers (*Ficedula albicollis*), the offspring of females that mated with younger males had higher lifetime reproductive success than offspring of females that mated with older males (Alatalo *et al.*, 1986). Similarly, in *Drosophila melanogaster*, male age negatively affected larval survival and mating ability of sons (Price and Hansen, 1998). In the sandfly *Lutzomyia longipalpis*, eggs of females mated to older males had lower hatching success than those of females mated to young and intermediate-age males (Jones *et al.*, 2000).

In line with Hansen and Price's analytical work, in a recent simulation model based on Kokko and Lindström's (1996) study, Beck and Powell (2000) showed that, just as females with a bias in favour of older males outperformed females with no age preference (as Kokko and Lindström had shown), there were also conditions in which females with a bias in favour of *younger* males also had higher fitness than females with no preference.

Thus, both Hansen and Price (1995) and Beck and Powell (2000) provide examples where females should not prefer to mate with older males. Empirical evidence to the contrary might be due to positive correlations between male age and values of sexually selected traits (Hansen and Price, 1995). In this light, it may be premature to conclude that female mate choice for older males evolved due to 'good genes' sexual selection (Andersson, 1994).

Although previous theoretical studies of female preference based on male age (Hansen and Price, 1995; Kokko and Lindström, 1996; Beck and Powell, 2000) have provided important first steps in understanding the evolution of female preference for older males, their conclusions are somewhat limited by the underlying assumptions of these models. For example, Hansen and Price (1995) assumed a genetic trade-off between early- and late-life fitness components, but evidence for such trade-offs is equivocal (Curtsinger *et al.*, 1995). Furthermore, if individuals vary in quality due to environmental variation or G × E interactions, we might expect to find positive correlations between early-age and late-age fitness traits in nature (van Noordwijk and de Jong, 1986; Kokko, 1998), rather than the trade-off postulated by Hansen and Price (1995).

In studies by Kokko and Lindström (1996) and Beck and Powell (2000), the authors assumed fixed mating preference functions. In reality, females may exhibit any degree of preference (from 100% rejection to 100% acceptance) for males of a particular age. Therefore, finding an 'optimal' preference function in this context may be extremely difficult.

A final assumption in many models has been that demographic structure does not play a role in the evolution of mate preference. When Beck and Powell (2000) considered the effect of demography in their model, they found that female preference for young and intermediate-age males could evolve when juvenile survival was low and adult survival was high, because mean viability did not differ among males of different ages.

Here we present a model that we have developed that allows us to relax these many simplifying assumptions. We have sought an approach that allows us not simply to compare two preference functions against each other, but rather to find an optimal preference function from among an extremely large number of possible functions, while simultaneously considering the effects of age structure, senescence and costs of choice.

Given the vast size of the possible search space, one powerful tool for finding optimal solutions is provided by the genetic algorithm, which uses the mechanics of natural selection to find optimal solutions (Goldberg, 1989). In a typical genetic algorithm, a computer program is written that simulates virtual 'chromosomes', which are subject to mutation, genetic recombination, Mendelian inheritance and selection. The aim of the genetic algorithm approach is to identify a global optimum for a complex function. In the case of this study, our aim was to identify the optimal solution to the problem of whether females should mate preferentially with males of a particular age. Thus, the genetic algorithm was used to find that preference function which maximized female fitness.

Our model differs from previous models for the evolution of female preference based on male age in three fundamental ways. First, and most importantly, by using a genetic algorithm approach, we allowed the strength of female preferences for males of particular ages to evolve. We did not determine *a priori* which preference strategy would be optimal. The success of a particular preference strategy was determined solely by the persistence of alleles that favour or disfavour mating with males in each of several age classes.

Second, unlike Hansen and Price (1995), we did not assume a trade-off between early- and late-life fitness components. In our model, while mortality rates increased exponentially with age, individuals differed genetically with respect to an age-independent mortality parameter that acted in a constant fashion throughout life. This variation in intrinsic mortality led to individuals that varied in quality, which was maintained by mutation–selection balance. In addition, unlike age-based indicator models of female preference for older males (e.g. Kokko, 1997, 1998), in which life-history trade-offs are important, in our model age may be an indicator of good genes but need not be, because we did not assume trade-offs between age-specific fitness components. Furthermore, because the relationship between age and genetic quality may depend on age-specific mortality rate in a population and we varied age-specific mortality rate in our model, age may not be an indicator of genetic quality in our model.

Third, survivorship in our model was determined by intrinsic mortality rates. In the simulation models of Kokko and Lindström (1996) and Beck and Powell (2000), survivorship was determined by viability traits that influenced extrinsic mortality. Individual survival was determined by comparing values of viability-related traits to optimal values in a particular environment. As a result, survival was determined in part by factors extrinsic to individuals in the population. In contrast, in the current model, survival was determined solely by a genotype- and age-dependent mortality function.

The structure of our model allowed us to address four specific aims. Our primary aim was to determine the shape of the optimal preference function for female preference based on male age. Because the results of Beck and Powell (2000) suggest that age-specific mortality may affect the evolution of female preference, the second goal of the study was to examine the effects of age structure on optimal preference functions.

Previous studies have indicated that the evolution of female preference may be altered or may not occur at all if there are even slight costs associated with choice (Pomiankowski, 1987; Kokko and Lindström, 1996; Beck and Powell, 2000). Costs associated with female choice can take many forms (see table 1 in Reynolds and Gross, 1990). Real (1990) suggests that there are two basic types of costs of choice: (1) direct costs, such as increased risk of predation and increased energy expenditure; and (2) opportunity costs, such as the loss of mating status. Direct costs have been documented in some taxa (e.g. frogs: Grafe, 1997; butterflies: Wickman and Jansson, 1997; fish: Reynolds and Côté, 1995). However, in other taxa, such as lek-breeding birds, direct costs are low and opportunity costs are more important (Gibson and Bachman, 1992; Rintamäki *et al.*, 1995). Therefore, the third aim of the study was to incorporate costs of choice into our model in such a way that we could examine the interaction between demographic structure and the effects of costs of choice on the evolution of mate preference. In the simulations presented here, we examined the effects of varying levels of opportunity costs on the evolution of female preference functions.

Finally, the causal relationship between mate preference and demographic structure can go in both directions. As a result, the fourth aim of our study was to examine the effects of preference on demography by determining the effect of female preference on mortality rates.

The results we present here demonstrate the general power of a genetic algorithm approach to study the evolution of age-specific mate preference. We show that females can, indeed, evolve a preference for older males, but that the specific pattern of preference depends on the underlying age structure of the population. Such preferences are quite sensitive to costs of choice. And, finally, we demonstrate that the causal relationship between mate preference and demographic structure can go in both directions. Although age structure influences the extent to which females discriminate among age classes, the existence of age-specific mate preference can act as a selective force, reducing overall mortality rates in a population.

METHODS

Model initiation and random mating

To examine the evolution of female preference based on male age, we use a closed-population, object-oriented simulation model of a haploid species incorporating a genetic algorithm. The state of each haploid individual is defined by 20 loci. Ten loci define the preference function and 10 loci define the mortality function. Both males and females possess all 20 loci, although the preference loci are not expressed in males. In addition, we also keep track of the age of each individual. To minimize the effects of genetic drift on the evolution of a preference function, we use a large population of 10,000 individuals and maintain a 50 : 50 sex ratio in the entire population.

For each simulation, each individual is assigned initial values for each of the 10 preference loci by choosing random numbers from a uniform distribution ($0 \leq n \leq 1$). Thus, for any age of male, the initial population preference among females will have an expected mean of 1/2 and an expected variance of 1/12 (Fraser, 1976). Individual mortality rates are determined by a combination of genotype-independent mortality function (see equations 1 and 2) and 10 mortality loci that can differ among individuals. Each of the 10 mortality loci ($m_1 \ldots m_{10}$) are randomly assigned one of two alleles, with a value of −1 or 1 (at initiation, the sum of the mortality loci, $M = \Sigma m_i$, has expected mean 0 and variance 10). The mechanics of mate choice and mortality are described in greater detail in the sections below.

We begin each simulation with all individuals at age 1. To establish an initial population with males of all ages, we start the simulation with 10 cycles, or generations, of random mating. After this initiation process, each subsequent cycle includes four components: (1) mate choice, (2) reproduction and mutation with Mendelian inheritance, (3) adult age-specific, density-independent mortality and (4) juvenile, density-dependent mortality.

Mate choice

The population consists of individuals of ages 1 through 10. The *j*th female in the population has mate preference loci $a_{1,j}$, $a_{2,j}$, . . . , $a_{10,j}$, where $0 \le a_{i,j} \le 1$ and $a_{i,j}$ determines the degree of preference by female *j* for a male of age *i*. In each cycle, each female randomly selects a male from the population. Females are able to determine the male's age with complete accuracy. Although in natural populations females may choose males based on secondary sexual traits, we were interested in whether male age was an indicator of good genes and not whether secondary sexual traits of males are indicators of male age, which is assumed to be an indicator of good genes. When a female *j* encounters a male of age *i*, the probability that she will mate with that male is equal to $a_{i,j}$. For example, if a female with $a_7 = 0.35$ encounters a 7-year-old male, there is a 35% chance that she will mate with that male. If the female rejects a particular male (with probability $1 - a_i$), another male is chosen at random from the pool of all males and presented to the female. Females mate with only one male per cycle. We examine the evolution of age-specific preference both with and without the cost of choice. In the no-cost model, females that have not chosen a male after a fixed number of attempts are assigned a random male. In the costly preference model, a female that has not chosen a male loses the opportunity to mate until the next cycle. To increase the cost of choice, we simply reduce the maximum number of males that a female is allowed to sample before she loses the opportunity to mate in that cycle. Whereas females mate at most once per age (or cycle), males can mate more than once per cycle.

Reproduction, inheritance and mutation

Once a female has mated, she produces exactly four sons and four daughters. For a given offspring, each mate preference locus and each mortality locus is inherited from either the father or mother with equal probability and is unlinked to any other locus.

Each of the 20 genes inherited by each offspring has a 1% chance of experiencing a mutation. If a mutation occurs at a mate preference locus, the value of that locus is altered by a value φ_i, where φ_i is drawn from a uniform random distribution with $-0.02 \le \varphi_i \le 0.02$ ($\mu_\varphi = 0$, $\sigma^2_\varphi = [0.04^2/12]$), with the constraint that $0 \le a_i \le 1$ after mutation. We describe mutations at mortality loci below.

Adult mortality

After each female has produced eight offspring, we impose mortality on the population according to a genotype- and age-dependent mortality function. Extensive studies of mortality in both laboratory and natural populations (e.g. Promislow, 1991; Tatar and Carey, 1995; Promislow *et al.*, 1996; Ricklefs, 1998) have established that mortality rates are often well described by the Gompertz trajectory

$$\mu_x = A\mathrm{e}^{Bx} \tag{1a}$$

or

$$\ln \mu_x = \ln(A) + Bx \tag{1b}$$

(Gompertz, 1825), where μ_x is the intrinsic rate of mortality at age x, A is the age-independent rate of mortality and B is the age-dependent rate of increase in mortality. In our model, 10 independent loci (m_1 to m_{10}), each with a value of −1 or +1, contributed to the intrinsic rate of mortality, according to the equation

$$\ln \mu_x = \left(c_1 + c_2 \sum_{k=1}^{10} m_k \right) + Bx \tag{2}$$

where c_1, c_2 and B are constant across all individuals in the population. The probability of an individual surviving is given by $\mathrm{e}^{-\mu_x}$, where the value of μ_x is determined from equation (2) given the age of that individual (x) and the sum of its m loci. The model in equation (2) implies that variation in Σm results in individuals that vary with respect to the age-independent mortality rate ($\ln(A)$) (see Fig. 1b), but not with respect to the rate of senescence, B. At the beginning of each simulation, mortality among individuals will be log-normally distributed (Promislow and Tatar, 1998), with mean of the log of mortality rate of $c_1 + Bx$ for individuals of age x and maximum variance $10 \cdot (c_2)^2$. Variance will decline at later ages due to selective death of individuals with relatively high values of M.

To determine the effect of overall age structure on the evolution of the mate preference function, we ran simulations under a variety of different demographic regimes (see Fig. 2). These included: (i) three different rates of senescence ($B = 0.1$, 0.3 and 0.5) with constant values of $c_1 = -2.0$, $c_2 = 0.2$; (ii) three different rates of age-independent mortality rate ($c_1 = -3.0$, −1.0 and −0.1) under no senescence ($B = 0$); and (iii) three different rates of senescence with values of c_1 adjusted such that life expectancy was equal to 5 years in all cases. The first two approaches allowed us to test for the effects of age distribution on optimal mate preference, whereas the third approach allowed us to test for the effects of rates of senescence on preference, independent of life expectancy.

As with the preference loci, each of the 10 m loci is inherited with equal probability from either the mother or father and experiences a mutation with probability 0.01. Because individuals with higher intrinsic rates of mortality are more likely to die than those with lower rates, as a cohort ages selection will reduce the frequency of positive m alleles in that cohort. To avoid a constant increase in viability during the life of the simulation, we imposed biased mutation on each of the m loci, such that only mutations from $m_k = -1$ to $m_k = 1$ can occur. The balance between biased mutation and selection ensures that there is always genetic variation for mortality rate in the population (Fig. 1).

After imposing adult mortality on age classes 1–10, individuals in each age cohort advance to the next age. All individuals that survive past age 10 are culled.

Juvenile mortality

Each generation, 40,000 juvenile offspring (age $x = 0$) are created by the mating and reproduction procedure. After adult mortality occurs, we impose genotype-dependent mortality on the juvenile cohort. In what constitutes density-dependent mortality, we then sample

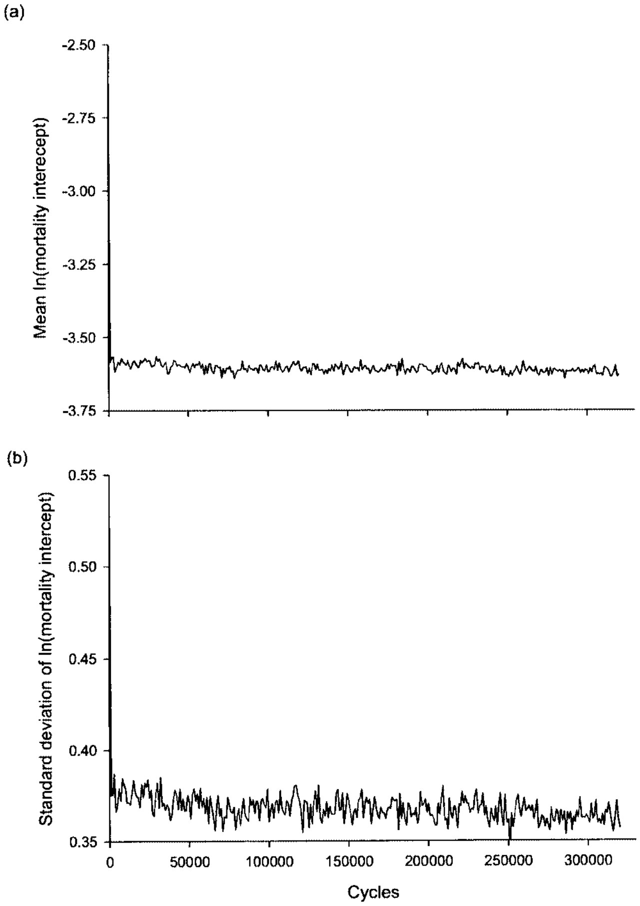

Fig. 1. Variation among males in intrinsic mortality rate was maintained by a balance between selection on the total value of the mortality intercept loci (M – see equation 2 and text) and mutation probability of 0.01 for each mortality locus. (a) A plot of log(mortality intercept) over time shows that the mean mortality intercept in the population stabilized within a few tens of generations (shown here for $c_1 = -2$, $c_2 = 0.2$ and $B = 0.1$). (b) Similarly, for the same set of parameters, the variation in mortality intercept (equations 1 and 2) among males was fairly constant over time.

sufficient males and females at random from the surviving offspring to reconstitute the age 1 cohort, such that once again there are exactly 5000 males and 5000 females in the population. The population is then complete and a new cycle of mate choice, reproduction and mortality is initiated.

Costs of female preference

As we noted above, simulations are run both with and without costs of choice. To incorporate opportunity costs, we set an upper limit to the number of males that a female could sample per cycle. If a female does not choose a male before reaching that upper limit, the

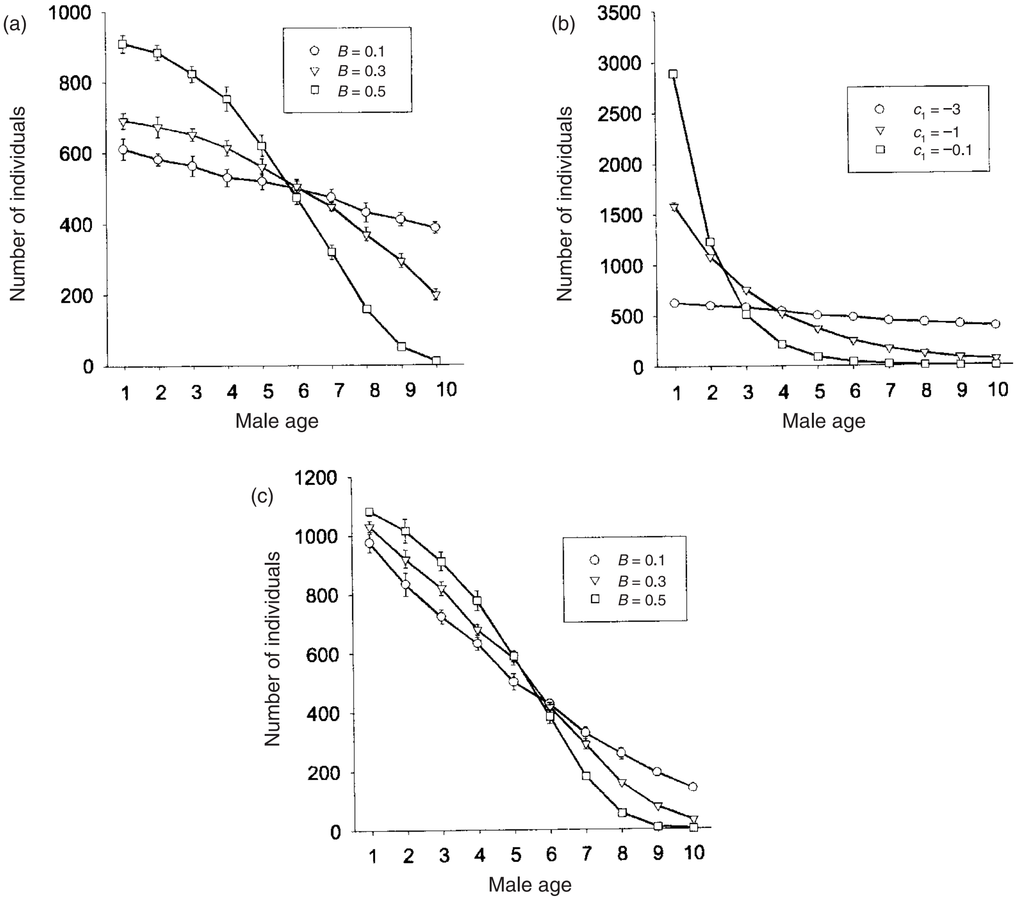

Fig. 2. Population age structure under different demographic regimes. Numbers of individuals represent the mean ± 1 standard error among eight replicate simulations after 320,000 cycles. (a) Effect of rate of senescence with constant age-independent mortality parameters ($c_1 = -2.0$ and $c_2 = 0.2$). (b) Effect of age-independent mortality rate in the absence of senescence ($B = 0$), for $c_2 = 0.04$ and $c_1 = -3$, -1 or -0.1. (c) Effect of changes in both age-independent (c_1, c_2) and age-dependent (B) parameters with mean life expectancy held constant at 5.

female does not reproduce during that cycle. The female may remain in the population and potentially reproduce during the following cycle. In the 'no cost' simulations, a female is paired with the tenth randomly selected male if she rejects all previous males she encounters. To simulate a small opportunity cost, we set the maximum number of males that a female could sample at 10. To simulate a higher opportunity cost, we set the upper limit at five males.

We also examined whether there was an effect of age structure on the evolution of female preference if there was a cost associated with female preference. We determined the effect of costs for the three different population age structures derived using three different rates of senescence ($B = 0.1$, 0.3 and 0.5) with constant values of $c_1 = -2.0$, $c_2 = 0.2$.

Analysis of simulations

For each set of parameters, the simulation was run for 320,000 cycles on a Silicon Graphics Origin 2000 Series computer, with each simulation being repeated 30 times. From these replicate simulations, we were able to determine the mean and standard error of the female preference for each age (i.e. $\bar{a}_1$ through $\bar{a}_{10}$).

We used the data from these replicate simulations to test for significant effects of selection on age-specific mate preference. At the onset of each simulation, the mean female preference value was 0.5 ($\sigma^2 = 1/12$) at each locus. After the simulation was complete, if two standard errors from the mean female preference for a particular male age did not include 0.5, we concluded that there was significant selection on female preference for ($a_i > 0.5$) or against ($a_i < 0.5$) males of that age.

In addition to the effect of age structure on female preference, we were interested in how female preference affected life-history traits. Therefore, we also determined whether the presence of female preference led to a significant change in overall mortality rates. To do this, we used a two-way analysis of variance to examine the effects of female preference, rate of senescence and the interaction between the two factors on the mean intercept of the mortality rate model for males.

RESULTS

Equilibrium female preference functions

In our genetic algorithm model for the evolution of female preference, females consistently evolved a mating bias against younger males and in favour of males of intermediate or older ages (Fig. 3). This basic result demonstrates that the genetic algorithm provides a powerful approach to study the evolution of mate preference when there are a large number of possible classes that a female might prefer.

In addition, we also found that the specific preference function depended on the intrinsic, age-specific mortality rates in the population and on the opportunity cost of choice. Details of these results follow.

Effects of age structure on female preference

No cost of choice

We examined preference functions for three different rates of senescence ($B = 0.1$, 0.3 and 0.5). Variation in rate of senescence gave rise to different population age structures (Fig. 2a). In each case, females showed a bias against younger males and in favour of older males (Fig. 3a). The greater the rate of senescence, the greater the distinction that females made between young and old males, although at the highest rate of senescence, females showed the greatest preference for males of age 6, and there was no evidence of selection in either direction on preference for the oldest males (age 10). Furthermore, at very high rates of senescence, females showed a dramatic shift from a strong bias against age 5 males ($\bar{a}_5 = 0.0951$) to a strong preference for age 7 males ($\bar{a}_7 = 0.911$).

In the absence of senescence ($B = 0$), age structure still had a significant effect on female preference (Fig. 3b). At very low rates of mortality ($c_1 = -3$), females showed only a very weak bias against males younger than 5 and in favour of males older than 6. As mortality

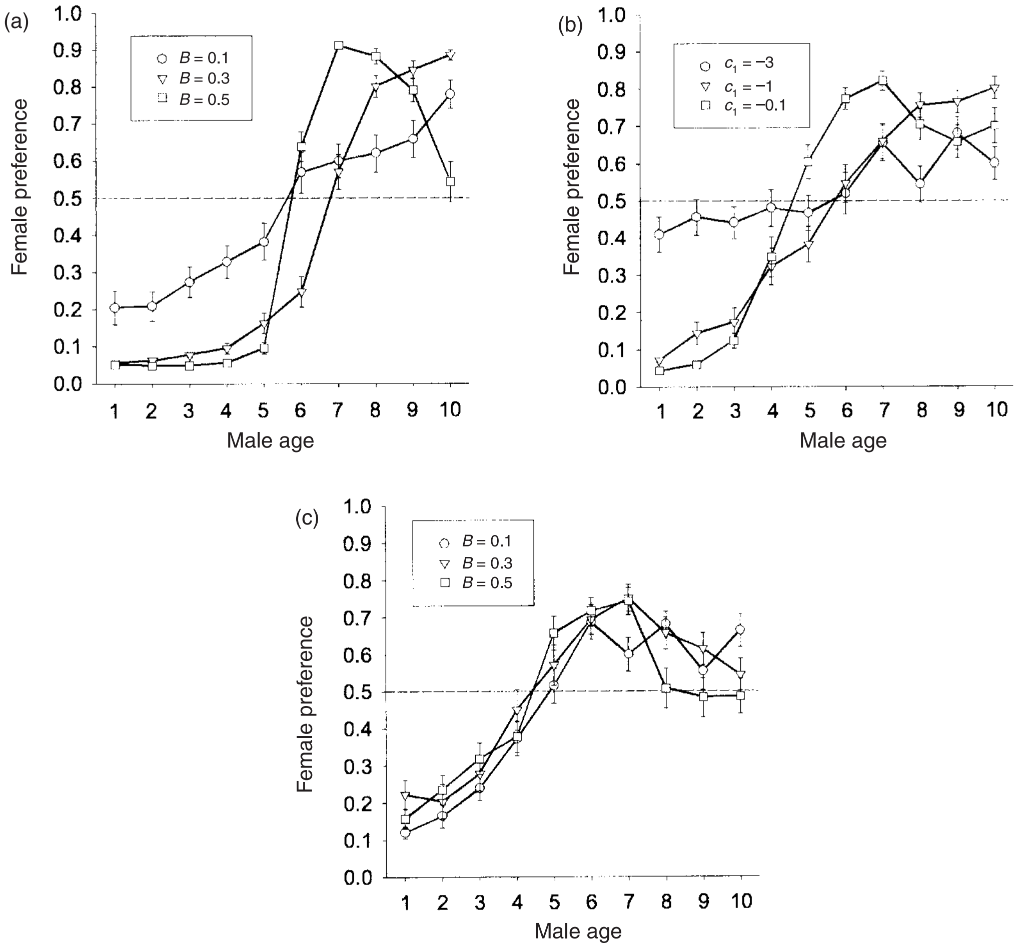

Fig. 3. Female preference based on male age. Values are based on means from 30 replicate simulations of 320,000 cycles, with error bars representing ±1 standard error. The dashed line is the expected female preference function if the evolution of female preference were determined solely by drift. (a) Effect of rate of senescence. (b) Effect of different rates of constant, age-independent mortality, in the absence of senescence. (c) Effect of rate of senescence, given a constant initial life expectancy of age 5 for all populations.

increased, so did the female bias against mating with younger males and in favour of mating with older males (Fig. 3b).

Age structure, rather than rate of senescence, appears to be the important determining factor in female preference. When populations differed in their rate of senescence, but had similar age distributions (see Fig. 2c), there were only slight differences in female preference over a five-fold range of senescence rate, from $B = 0.1$ to $B = 0.5$ (Fig. 3c). For the parameters analysed, females showed a gradual, although steady, increase in preference from age 1 to age 7 males. At very high rates of senescence, few males were still alive after age 7 (Fig. 2c), and females were unlikely to evolve any preference for these older males.

Costs of choice

When opportunity costs were included in the model, age structure was less important in determining female preference (Fig. 4). For low opportunity costs, when females could sample a maximum of 10 males, females still exhibited a preference for the oldest males when mortality rates were low or intermediate and a preference for intermediate-age males when mortality rates were high (Fig. 4a). Interestingly, females showed a preference ($\bar{a}_i > 0.5$) for a greater range of age classes compared within the no cost simulations. When opportunity costs were high (a maximum of five males could be sampled), females generally exhibited no preference based on male age as a result of high female preference for males of all ages (Fig. 4b). However, with a high opportunity cost, we found a decrease in female preference for the oldest age classes when mortality rate was high (Fig. 4b).

Effects of female preference on mortality rate

Our results demonstrate that age structure can play a critical role in shaping the force of natural selection on female preference for males of specific ages, especially when costs associated with female choice are low or absent. However, the causal arrow can move not only from demography to mate preference, but also in the other direction. In the absence of costs, we found that the presence of female age-specific mate preference affected the underlying demographic structure of the population. Female preference for older males significantly reduced average mortality rate in the population (Fig. 5, Table 1). The effect of female preference on reducing mortality rate was most pronounced in populations with the highest mortality rate (Table 1). In the absence of female mate preference, demographic selection alone can lead to older males that have higher than average genetically determined viability. In the presence of female preference, however, the mean intercept of the mortality

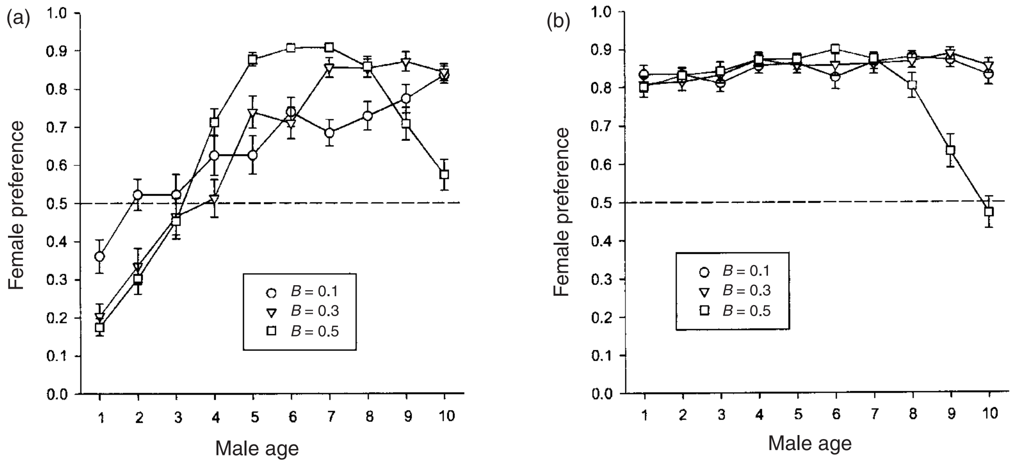

Fig. 4. Effect of opportunity cost on female preference based on male age. Values are based on means from 30 replicate simulations of 320,000 cycles, with error bars representing ±1 standard error. The dashed line is the expected female preference function if the evolution of female preference were determined solely by drift. (a) Low costs, maximum of 10 males sampled. (b) High costs, maximum of five males sampled.

rate across all males was significantly lower (i.e. age-specific survivorship was higher) than the mean intercept in the same population if females mated at random (Fig. 5). Thus, sexual selection acts to decrease intrinsic mortality rates *at all ages* as a result of female preference for older males.

DISCUSSION

Optimal female preference functions

We found that, under a wide range of demographic conditions, females will evolve a preference function such that they discriminate against younger males and prefer to mate with older males. This preference for older males appears to be due to the fact that older males, by virtue of their having survived to old age, tend to be those with better than average viability genes (Fig. 6). A female who mates with an older male will, on average, pass on relatively good viability genes to her offspring. Our results are consistent with empirical studies that have found that females prefer to mate with older males, even in the absence of paternal care (e.g. Zuk, 1988; Manning, 1989; Simmons and Zuk, 1992; Grahn and von Schantz, 1994; Simmons, 1995).

These results are also in line with those of previous theoretical studies (Kokko and Lindström, 1996; Beck and Powell, 2000), which found that pre-assigned preference functions that are biased in favour of older males will outcompete a 'no preference' function under certain conditions. However, with our genetic algorithm model, we have identified the optimal preference function that will evolve under specific demographic scenarios. By using

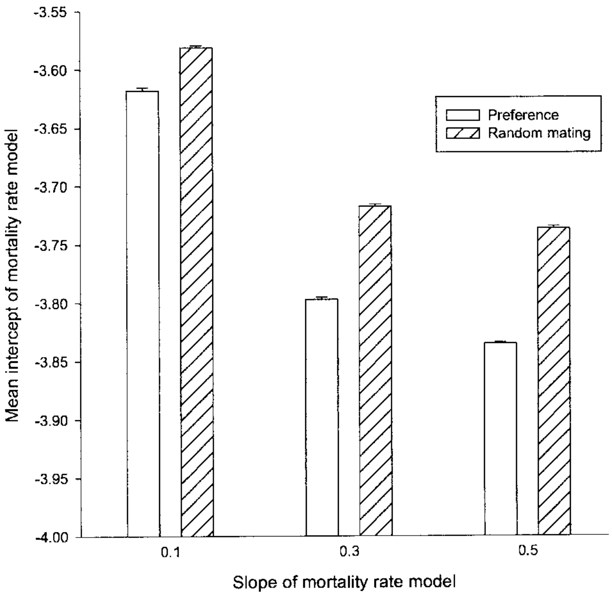

Fig. 5. Effect of female preference for older males on the intercept of the intrinsic mortality rate model, given constant values of c_1 and c_2, but differing slopes of the mortality rate model (B). See Table 1 for results of analysis of variance.

Table 1. Effect of female preference and rate of senescence on mean intercept of the mortality function

Source	d.f.	F-value	P-value
Rate of senescence	2	4803.8	0.0001
Female preference	1	1852.9	0.0001
Senescence × preference	2	120.5	0.0001
Residual	174		

Note: Rate of senescence was determined by the slope (B) of the mortality rate model (see equation 2). The female preference effect is the comparison between populations in which females mate at random and populations in which females exhibit preferences based on male age.

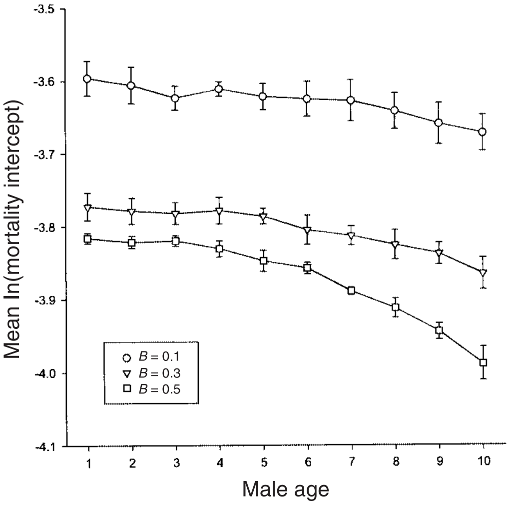

Fig. 6. Effect of male age on the mean of the intercept ($c_1 + c_2M$).

a genetic algorithm approach, we were able to identify not only an increase in preference for males as they age, but also a subsequent decline in preference for very old males in populations with high mortality rates.

Before running these simulations, we had not anticipated that very old males would lose their attractiveness. However, this result is easily understood in terms of classical theories of senescence. Fisher (1930), Haldane (1941) and Medawar (1946) pointed out that genes expressed very late in life would experience little if any selection. Few individuals would survive to those late ages, and those who did would probably have already passed the mutation on to subsequent generations. Similarly, in our simulated populations, at very high mortality rates, the probability of surviving to age 9 or 10 was vanishingly small. If a female never encountered a male that old, then there would never be an opportunity for selection to act on those loci that influence mate preference for very old males. Any selective force acting on late-age preference loci would therefore be overwhelmed by mutation and drift.

Few empirical studies have found a decrease in female preference for old males relative to intermediate-age males (Jones *et al.*, 2000). However, Jones *et al.* (2000) suggest that the full range of male ages may not have been considered in previous studies, especially if the oldest males in a population are rare. Furthermore, if the oldest males are lumped with intermediate-age males, any female preference against the oldest males may be obscured.

Effects of age structure on female preference

Females showed a preference for intermediate-age males when mortality rates were very high. However, in general, bias in favour of older males and against younger males increased as mortality rates increased. This result expands on findings of a previous study (Beck and Powell, 2000). Beck and Powell (2000) found that an age-specific increase in mortality (low juvenile mortality, high adult mortality) favoured female preference for older males. In contrast, if mortality rates declined with age (high juvenile mortality, low adult mortality), preference for young and intermediate-age males evolved.

In the current study, at very low mortality rates, females showed little discrimination due to the low intensity of selection on viability genes. Not surprisingly, high mortality led to an age-related decline in mean intrinsic mortality rate (Fig. 6). By choosing an older male, a female will pass better than average viability genes to her offspring. But when mortality rates are very low, variation within a single age cohort of males may be greater than that between age classes, and there will be little to distinguish between young and old males.

We tried to determine whether the effect of demographic parameters on female preference was due to changes in the age-independent mortality parameter (A in equation 1) or the rate of senescence (B in equation 1). It appears that the optimal preference function was most responsive to the change in age distribution caused by overall mortality levels, independent of whether these changes were due to shifts in age-independent or age-dependent mortality.

Although there is an effect of age structure on female preference in the absence of costs of choice, the importance of age structure is reduced when there is a cost for choice. Similar to the results of previous models of the evolution of female preference (e.g. Pomiankowski, 1987; Kokko and Lindström, 1996), we found that costs associated with female preference can reduce the strength of female preference for particular males and, as a result, the effect of age structure on female preference. In our model, costs led to a decrease in bias against younger males and a concomitant increase in the range of preferred male age classes (Fig. 4). Similarly, in Trinidadian guppies (*Poecilia reticulata*), females from high predation populations exhibit no preference based on colour pattern, whereas females from low predation populations prefer males with more orange coloration (Houde, 1988). When costs were high, we found in general that female preference would be consistent for all male age classes and, therefore, mating would be random with respect to male age (Fig. 4b). Because older males are of higher quality than younger males, females are sacrificing the possibility of mating with higher quality males in order to ensure that they reproduce in a given year. This finding conflicts with the conclusion of Pomiankowski (1987) that female choice will evolve even if it is costly, as long as female preference is based on male traits correlated with viability.

Effect of mate preference on life-history evolution

Few models have explored the way in which life-history strategies can influence behaviour and vice versa, despite the obvious importance of these interactions (e.g. Partridge and

Endler, 1987; Promislow, 1996; Svensson and Sheldon, 1998). Our results suggest the possibility for extensive causal interactions between behaviour and life-history strategies in both directions. As we have already discussed, in our models higher mortality rates gave rise to stronger selection on viability genes and thus favoured female preference for older males. But at the same time, female preference itself acted as a strong selective force, leading to lower overall mortality rates in the population (Fig. 5). This effect was most pronounced at relatively high rates of mortality. While equilibrium age-specific mortality rates were reached by a balance between mutation and selection, the forces of selection were themselves a balance of viability selection exerted by intrinsic mortality probabilities and male fertility selection imposed by female mate preference. Female preference can thus change patterns of mortality, which, in turn, will affect selective forces on female preference. Although this model is not designed to explore these interactions in detail, there is clearly the possibility for interesting, non-linear dynamics in this system, as previous models of two-sex demographic systems have already demonstrated (Caswell and Weeks, 1986).

Given the interaction between these behavioural and demographic factors, age-specific mate preference could be a causal factor leading to the evolution of lower rates of senescence. Female preference for older males could lead to the evolution of lower rates of senescence in two ways. First, if females prefer to mate with older males, there will be stronger selection for males to survive beyond a certain age. This, in turn, could lead to selection to reduce the frequency of late-acting deleterious mutations (Medawar, 1952) and so reduce the rate of senescence. Second, some models of senescence and recent data suggest that rates of senescence will decrease in populations with low baseline mortality rates (Williams, 1957; Ricklefs, 1998; but see Abrams, 1993). Given our finding that female preference leads to a reduction in the age-independent mortality parameters, this could, in turn, lead to reduced rates of senescence. To test this explicitly, future models should incorporate a modifier allele that allows rates of senescence to evolve over the course of the simulation. Based on our theoretical result, one might expect that rates of senescence should be lower in those species with greater opportunity for mate choice, *ceteris paribus*.

Some empirical evidence supports the claim that social interactions can affect selection on senescence. For example, in a study of sexual dimorphism in passerines, Promislow *et al.* (1992) suggested that sexually selected traits were more likely to evolve when mortality rates were low (see also McLain, 1991; Winemiller, 1992). In addition, in a study of life span in different species of ants, Keller and Genoud (1997) showed that queens of eusocial species lived much longer than their non-eusocial sister taxa.

Future analysis

We used a novel, genetic algorithm approach to explore the conditions under which female preference for older males could evolve. In doing so, we have seen that the causal interactions between behaviour and life-history evolution can be varied and complex, even in a model that is conceptually quite simple. The present model proved to be of excellent heuristic value but, as with all models, future genetic algorithm models of mate preference could increase their biological reality by relaxing some of the simplifying assumptions built into the present model. These modifications might include variation in choosiness among females of different ages, age-specific variation in mutation rates (Crow, 1997), and a reduction in recombination rates of preference and viability genes to allow for the possibility of runaway sexual selection. Finally, to fully examine the effect of mate preference on the evolution of senescence, future models should incorporate modifier loci that allow the actual rate of senescence to evolve over the course of the simulation.

ACKNOWLEDGEMENTS

We thank Alan Ferrenberg for his help in optimizing and parallelizing our model, which allowed us to complete this project more quickly. Computer time was provided by the Research Computing Resource at the University of Georgia. Hanna Kokko, Ben Sheldon and Peter Taylor provided valuable comments on previous drafts of the manuscript. This work was supported in part by a National Institute on Aging grant AG14027 to D. Promislow.

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