

Evolution of female mate choice based on male age: Are older males better mates?

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ABSTRACT

Many empirical studies suggest that females often prefer to mate with older males. It is generally assumed that females prefer older males because older males are of higher genetic quality. We used a viability-based simulation model to determine whether female preference for older mates is more likely to evolve than female preference for younger mates when males provide only sperm to females. The results of our simulations suggest that female preference for young and intermediate age mates is more likely to evolve than a strong preference for older mates, and that female preference based on male age will not evolve if there is a cost associated with the preference. Therefore, based on the results of our model, female preferences for older mates cannot be explained by 'good genes' models of sexual selection. A comparison of our results with those of a previously published model suggest that whether female preference for older males can be explained by 'good genes' models of sexual selection depends on age-specific survival probabilities. When juvenile survival is high and adult survival is low, older males have higher mean viability than younger males. As a result, female preference for older males will evolve. In contrast, when juvenile survival is low and adult survival is high, mean viability does not differ among males of different ages. Therefore, female preference for older males is unlikely to evolve. The importance of age-specific survival rates in determining the importance of a 'good genes' process suggests that future studies of sexual selection should consider potential effects of life-history variation.

Keywords: age effects, age-specific survival, female mate choice, genetic algorithm, genetic quality, good genes, life-history evolution, sexual selection.

INTRODUCTION

It is widely held that females should prefer to mate with older males in species in which males provide only sperm to females, because viability selection leads to older males of higher genotypic quality than younger males (Trivers, 1972; Manning, 1985; Kirkpatrick, 1987; Andersson, 1994). Several empirical studies have suggested that females do indeed

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prefer to mate with older males (e.g. Zuk, 1988; Manning, 1989; Simmons and Zuk, 1992; Grahn and von Schantz, 1994; Simmons, 1995). Furthermore, using a simulation model, Kokko and Lindström (1996) showed that a strong female preference for older mates is likely to evolve under a variety of environmental conditions, given a sufficiently high genomic mutation probability.

Although the idea that females prefer to mate with older males because of the higher genetic quality of older males is intuitively appealing, such age-based preferences may have evolved for other reasons. Hansen and Price (1995) argued that young to intermediate age males have the highest breeding values for fitness, and thus are of higher genetic quality than older males. Therefore, if females choose mates based on genetic quality alone, females should prefer younger rather than older males. Some empirical evidence supports the contention that younger males are of higher genotypic quality than older males. 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). If female preference for older males is not due to the higher genetic quality of older males, females may exhibit preferences for older males solely due to positive correlations between male age and values of sexually selected traits (Hansen and Price, 1995). Consequently, empirical evidence for female preference for older males does not necessarily support the idea that female mate choice for older mates evolved due to 'good genes'.

The different conclusions reached by Hansen and Price (1995) and Kokko and Lindström (1996) may be a result of the different approaches they used to model female preference based on male age. Hansen and Price (1995) assumed a trade-off between early- and late-life fitness components. In contrast, Kokko and Lindström (1996) assumed that such trade-offs may not exist and that individuals may differ in genetic quality, leading to increased survival and fecundity of higher-quality individuals at all ages. Although it is probable that individual males in a population differ in genetic quality, Kokko and Lindström (1996) examined only the evolution of female preference for older males and did not test whether female preference for young or intermediate age males could evolve. Therefore, it is not clear that the results of Kokko and Lindström rule out the conclusions of Hansen and Price.

To examine whether female preference for young and intermediate age males could evolve when males differ in genetic quality, we used a simulation model similar to that used by Kokko and Lindström (1996) (Table 1). We varied the strength of female preferences for particular age classes and examined how likely female preference was to become fixed in a population initially composed of randomly mating females and females that exhibited a preference based on male age.

METHODS

Our model was based on that of Kokko and Lindström (1996), but differed in several fundamental ways (Table 1). Both approaches are biologically based. A comparison of the results of the two models suggests which components of the model, and therefore what characteristics of a species biology, may be important in determining the evolution of female preference for older males (see Discussion). Here we detail the basic structure of our model.

Table 1. Differences in structure of models used to explore female mate choice based on male age

Component	Kokko and Lindström (1996)	Current model
Population size	50 males, 50 females	60 males, 60 females
Number of age classes	3	3
Initial age structure	all 1 year old	evenly distributed among age classes
Survival	proportional to viability	<i>n</i> best viabilities
Maximum age	none	5 years old
Individual female preference	probabilistic based on preference probabilities	fixed for a particular male age class
Individual female choice	based on preference probabilities and number of males in each age class	fixed for a particular male age class if males in that age class are present

To determine if there was an advantage to female preference based on male age, we created a population in which half the individuals were choosy (i.e. exhibited a preference) and the other half were non-choosy (i.e. mated at random) and examined whether choosiness became fixed under different conditions. For each set of simulations, we used a population of 60 males and 60 females. At the beginning of each simulation, each individual was randomly assigned values for 10 viability-related traits from a normal distribution with a mean of zero and a standard deviation of one. The traits represent polygenic and broadly defined viability traits. For example, one trait could represent ‘the strategy to avoid desiccation’, and therefore would include such factors as behavioural decisions and physiological mechanisms (Kokko and Lindström, 1996). Also at the beginning of each simulation, half of the males and females were assigned at random to be choosy and half to be non-choosy. In addition, individuals were assigned at random to one of three initial ages (1, 2 and 3 years old) and age classes such that there were an equal number of males and females of each age at the beginning of each simulation. The age classes were defined as follows: age class one had 1-year-olds, age class two had 2-year-olds and age class three had 3- to 5-year-olds. Unlike Kokko and Lindström (1996), we set a maximum age for individuals in the population; all 5-year-olds were removed from the population in the following year.

For each set of preference parameters, we followed the proportion of choosy individuals in the population for 1000 generations or until choosiness was fixed or lost in the population. We ran 100 replicates of each set of preference parameters. In each generation, choosy females were assigned an age-class preference based on the preference probabilities for the particular set of simulations. Females chose males either at random from all age classes or at random from their preferred age class, depending on whether a female was non-choosy or choosy, respectively. Individual males could mate with more than one female, but individual females with only one male, in a given generation. Each mating produced two male and two female offspring. Therefore, there were no direct effects of female mate choice on female fitness. Each offspring inherited viability trait values and the value for the choosiness gene with equal probability from either its mother or father. As a result, the model was essentially haploid. Values for each trait were inherited independently of the others; therefore, there was no linkage between traits.

Although we are interested in diploid organisms, the results of our model are not compromised by the simplifying assumption of haploidy. As stated above, the viability traits were polygenic and described by a normal distribution. Such a normal distribution will result if the effects of the genes are additive and the effects of the alleles at each locus are also additive. Because the change in allele frequencies over time are identical for a haploid model and a diploid model in which alleles are additive (Crow and Kimura, 1970), then the results of the model should not be affected by the assumption of haploidy. As for the preference gene, if we had modelled it as diploid rather than haploid, we would have had to assume arbitrarily that either the choosy or non-choosy allele was dominant. However, no matter which allele was dominant, if choosy individuals had higher fitness than non-choosy individuals, non-choosiness would be lost from the population. The only effect that assuming haploidy would have on the choosiness gene is to increase the speed with which the frequency of alleles would change. Given the number of generations for which we ran our simulation, assuming haploidy would not affect the outcome of the model.

During each generation, viability trait values inherited by offspring from their parents mutated with probability q , where $(1 - q)^n = 1 - Q$, and Q is the probability that at least one mutation occurred in the entire genome and n is the number of traits (in this case, $n = 10$) (Kokko and Lindström, 1996). Because the viability traits were polygenic, mutations were modelled such that trait values before and after mutation were not independent. If a trait of an individual mutated in a particular generation, its value was changed by an amount randomly chosen from a normal distribution with a mean of zero and standard deviation of one (Kokko and Lindström, 1996). Because mutations were chosen from a normal distribution of mean zero and standard deviation of one, most mutations will result in little change in trait values, as might be expected if only a few of the genes that determine a trait's value mutate. However, by selecting the mutation from a normal distribution, there is the possibility of rare mutations that lead to large changes in a trait's value. Such changes might occur if most of the genes that determine a trait's value mutate.

At the end of each generation, the population of parents and offspring was reduced to the initial population size of 60 males and 60 females; individuals with the highest viabilities based on values of viability traits survived to the next generation. Viabilities were calculated in the same way as in Kokko and Lindström (1996). Overall viability, V , was calculated as

$$V = \prod_{i=1}^n V_i = \prod_{i=1}^n \exp(-w_i(T_i - T_i^*)^2)$$

where T_i was the value of viability trait i , T_i^* was the optimal value of viability trait i and w_i was the relative importance of trait T_i to viability. In some sets of simulations, as a result of being choosy, the viability of choosy females was reduced by a factor C , such that

$$V = (1 - C) \prod_{i=1}^n V_i$$

After viability selection, the next generation was begun by assigning choosy females age-class preferences.

Optimal trait values were determined as randomly chosen values from a normal distribution with a mean of zero and standard deviation of one. Weights were randomly assigned from a uniform distribution such that the sum of the weights was one. Both optimal values and weights were set at the beginning of each of the 100 replicates and were held constant for all generations of that replicate. The results of Kokko and Lindström (1996) suggest that

the manner in which optimal values and weights are determined does not greatly affect the outcome of simulations.

To examine whether female preference for young and intermediate age males could evolve when males differ in genetic quality, we varied the strength of female preferences for particular age classes. We ran the following sets of female preferences for particular age classes, represented as probabilities that females would mate with a male of a particular age class and listed in order of increasing age classes: (1) strong preference for older males (0, 0.17, 0.83), (2) equal preference for intermediate age and older males (0, 0.5, 0.5), (3) strong preference for younger males (0.83, 0.17, 0), (4) equal preference for intermediate age and younger males (0.5, 0.5, 0), (5) equal preference for all three age classes (0.3333, 0.3333, 0.3333), and (6) strong preference for intermediate age class with equal preference for the other two age classes (0.2, 0.6, 0.2). All of Kokko and Lindström's simulations used a strong preference for older males (i.e. preference set 1). We examined the probability of fixation of choosiness for genomic mutation probabilities (Q) between zero and one at one-tenth intervals for each set of female preferences. All simulations were run with no cost for choosiness and a 2% decrease in viability for choosy females. In addition, we re-ran preference set 4 with costs of 0.5% and 1% to examine whether choosiness was likely to evolve given slight viability costs of choosiness. We used preference set 4 because choosiness was most likely to become fixed for this preference set, given no cost for being choosy; therefore, if choosiness were to be fixed even with a viability cost, we would expect it to occur with this preference set.

To determine whether female preference based on male age was likely to evolve for a given preference set and genomic mutation probability, we used chi-square tests to compare the proportion of simulations for which choosiness was fixed with the null hypothesis of 0.5 at which random mating and female preference were equally likely.

RESULTS

Female preference for older males was unlikely to become fixed in the population in most cases. When choosy females exhibited a strong preference for older males, random mating by females was more likely to become fixed than choosiness (Fig. 1a). At 6 of 11 genomic mutation probabilities, choosiness was fixed less often than expected by chance. In all other cases, the proportion of simulations for which choosiness was fixed was not significantly different from 0.5. In contrast, when choosy females showed an equal preference for intermediate age and older males, choosiness was fixed more often than expected at four lower genomic mutation probabilities and less often than expected at the lowest and second highest mutation probabilities (Fig. 1a).

Female mate choice based on male age was most likely to become fixed in the population when choosy females exhibited preferences for younger and intermediate age males. When choosy females had an equal preference for intermediate age and younger males, choosiness was fixed more often than expected at 7 of 11 genomic mutation probabilities. Choosiness was more likely to evolve when mutation probabilities were intermediate; at the lowest and at the higher mutation probabilities, the proportion of times random mating and choosiness were fixed did not differ significantly (Fig. 1b). We found a similar pattern when choosy females showed a strong preference for younger males (Fig. 1b) and when they exhibited a strong preference for the intermediate age class with equal preference for the other two age classes (Fig. 1c). When choosy females had an equal preference for all three age classes,

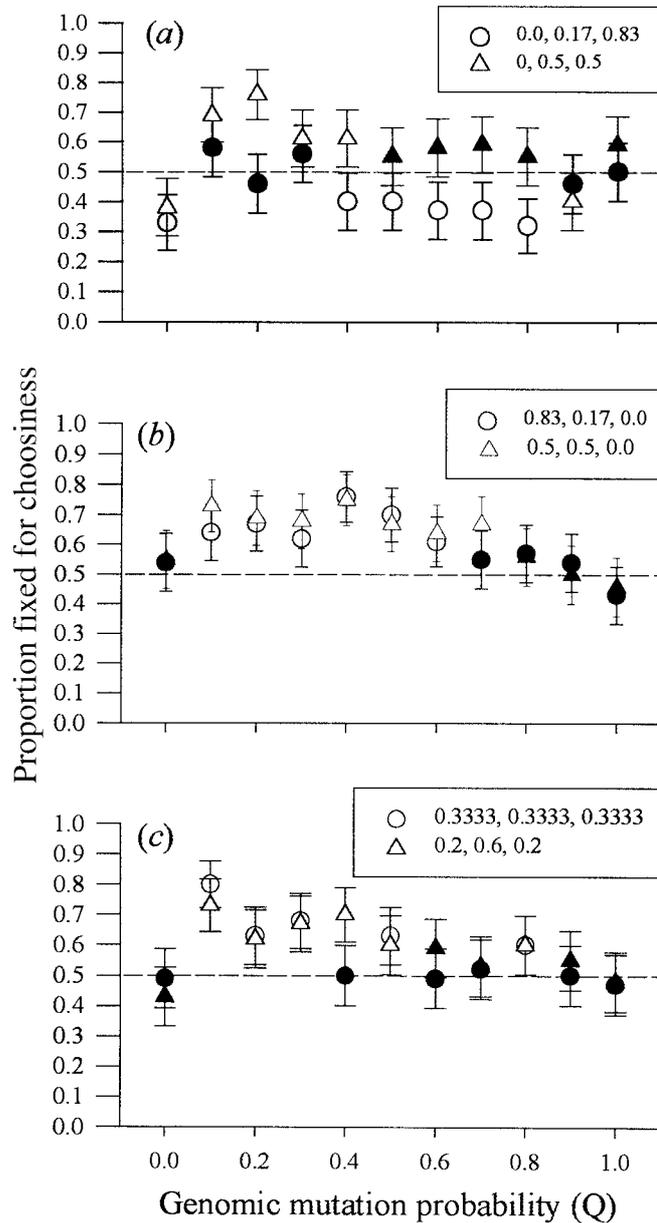


Fig. 1. The evolution of female preference based on male age. Values in each part represent the proportion of choosy females that prefer to mate with age classes 1–3, respectively. The proportion of simulations for which choosiness was fixed is represented by open symbols if the proportion was significantly different than 0.5 ($\chi^2 \geq 4.0$, d.f. = 1, $P < 0.05$). Error bars represent 95% confidence intervals. (a) Preference for intermediate age and older males; (b) preference for intermediate age and younger males; (c) equal preference for all three age classes and strong preference for intermediate age class with equal preference for the other two age classes.

choosiness was fixed more than expected at only 5 of 11 genomic mutation probabilities. In all other cases, the proportion of simulations for which choosiness was fixed was not significantly different from 0.5. Again, choosiness was most likely to become fixed at low and intermediate genomic mutation probabilities.

When there was a viability cost associated with exhibiting a preference, choosiness was rarely if ever fixed (Fig. 2). All models for which there was a 2% viability cost for choosiness resulted in a fixation rate for choosiness of less than 10%, except for models with highest genomic mutation probabilities. The fixation rate for choosiness for the latter was less than 25% in all cases. A reduction in the viability cost to 1% or 0.5% had no significant effect on the proportion of times choosiness was fixed in the population (Fig. 2).

DISCUSSION

Our results suggest that, in species in which males contribute only sperm, female preference based on male age is more likely to evolve in a population if preferences are directed towards younger and intermediate age males. Preferences for older males were rarely selected over random mating; therefore, older males may not be better mates. Our results are at odds with those of Kokko and Lindström (1996), who suggested that a strong female preference for older males is likely to evolve under a wide range of conditions, but support the conclusions of Hansen and Price's (1995) trade-off model, which suggested that females should prefer to mate with younger to intermediate age males.

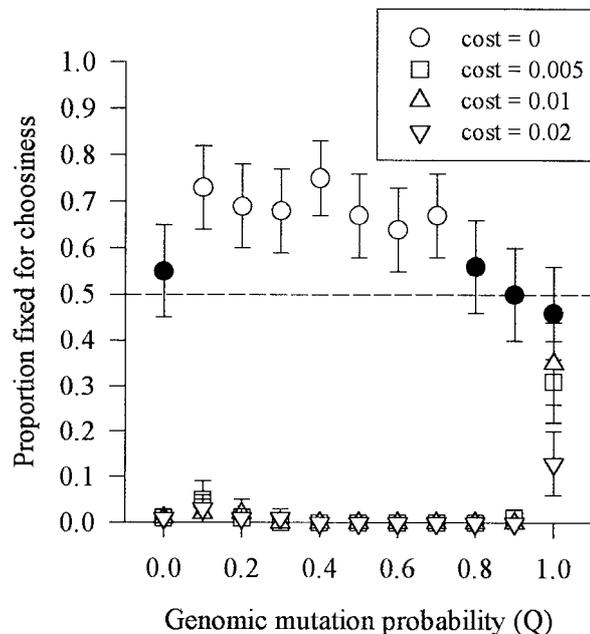


Fig. 2. Effect of viability cost of female mate choice on the evolution of female preference based on male age. Female preferences were set at 0.5, 0.5 and 0 for age classes 1–3, respectively. See legend to Fig. 1 for an explanation of symbols.

Selection for female preference for younger to intermediate age males may be stronger than suggested by the results of our model. We assumed that male genetic quality remains constant with age. However, Crow (1997) suggested that mutation rates may be higher in older males than in younger males. Assuming that mutations have deleterious effects, male genetic quality may decrease with age. In fact, in *Drosophila melanogaster*, Price and Hansen (1998) found a decrease in larval viability and male mating ability in offspring sired by older males when compared to offspring sired by younger males, suggesting that male genetic quality does decline with age. Similarly, 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). Therefore, it appears that male genetic quality may decrease with age. A decrease in individual males' genetic quality with age would act to strengthen the female preference for younger to intermediate age males that we found in our model.

In our model, the evolution of female preference for younger and intermediate age males appears to occur only at low to intermediate genomic mutation probabilities. Based on the genomic mutation rate of a *Drosophila* population estimated by Houle *et al.* (1992), Kokko and Lindström (1996) estimated an average genomic mutation probability of ≥ 0.34 . Therefore, the intermediate mutation probabilities necessary for the evolution of female preference based on male age may occur in some species. Without mutations ($Q = 0$), choosiness is unlikely to evolve, because genetic variation is quickly removed from the population by selection. As a result, the variation among males that would make female preferences advantageous does not exist. However, environmental variation may maintain genetic variation among males that might allow choosiness to become fixed at low mutation probabilities. At high mutation probabilities, choosiness is also unlikely to evolve as a result of 'good genes', because a male's genetic quality would not be strongly correlated to the genetic quality of his offspring, especially at the highest mutation probability. Interestingly, however, Kokko and Lindström (1996) found that female preference for older males was most likely to evolve at the highest mutation probability when offspring resemble their parents the least.

The differences in our results and those of Kokko and Lindström (1996) appear to be due to the manner in which survival was related to viability (Table 1, Fig. 3). Because the differences in the two models were most pronounced at the highest mutation probability, we examined how the relationship between survival and viability affected population age structure and age-specific survival probabilities at $Q = 1$. Differences between the two models in the relationship between survival and viability (see Table 1) led to different age structures and age-specific survival probabilities (Table 2). In our model, in which individuals with the highest viabilities survived to the next generation, the age structure was biased towards individuals in the oldest age class and against individuals in the youngest age class. Furthermore, probability of survival to maturity (i.e. age class 1) was low, whereas the survival probabilities for the older age classes were quite high (Table 2). In contrast, in Kokko and Lindström's (1996) model, in which viabilities were related to the probability of survival to the next generation, the age structure was biased against the intermediate age class. Probability of survival to maturity was higher than in our model, and adult survival probabilities were substantially lower (Table 2).

The differences between the two models in age-specific survival probabilities were related to different patterns of variation in mean viability among male age classes with each model. Therefore, the mechanism for the evolution of female preference for older males may

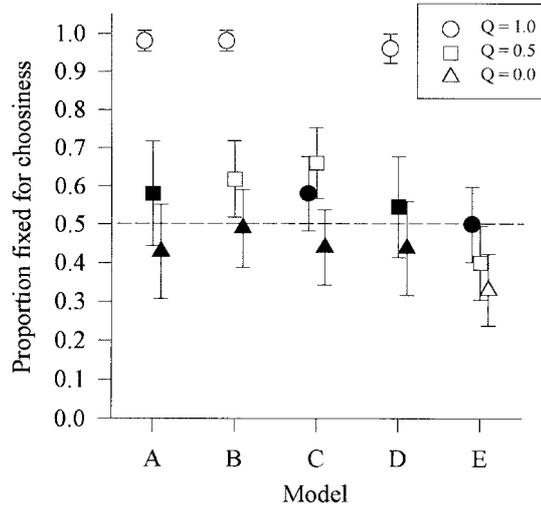


Fig. 3. The effect of model structure on the evolution of female preference for older males. Preferences for males of age classes 1–3 were set to 0, 0.17 and 0.83, respectively. See legend to Fig. 1 for an explanation of symbols. Model A: Kokko and Lindström (1996) model (K and L). Model B: K and L, but maximum age 5 years. Model C: K and L, but maximum age 5 years and survival determined as *n* best viabilities. Model D: K and L, but female preferences determined as in the current model (see methods and Table 1). Model E: current model.

Table 2. Male age structure and age-specific survival probabilities for different relationships between viability and survival

	Age class 1	Age class 2	Age class 3
Age structure			
Proportional to viability	26.7	11.5	21.8
<i>n</i> best viabilities	13.5	12.4	34.2
Age-specific survival probability			
Proportional to viability	0.22	0.43	0.63
<i>n</i> best viabilities	0.11	0.91	0.93

Note: Kokko and Lindström (1996) modelled survival as proportional to viability, whereas in the current model individuals with the *n* best viabilities survived. Age structure and age-specific survival probabilities are generational averages based on two replicates. The age structures of the replicates for each model did not differ from one another by more than a fraction of an individual. Age-specific survival probabilities are the probability of surviving to a particular age class and were calculated as follows: age class 1 = (# age class 1)/120, because 120 male offspring were produced; age class 2 = (# age class 2)/(# age class 1); age class 3 = (# age class 3)/(# age class 2), because in *n* best model there were a maximum of three ages in age class 3.

depend on the relative probabilities of juvenile and adult survival. In Kokko and Lindström’s (1996) model, where juvenile survival was relatively high and adult survival was relatively low (Table 2), the oldest males had the highest and the youngest males had the

lowest mean viabilities (Fig. 4a). Therefore, female preference for older males was likely to evolve as a result of a ‘good genes’ process. In contrast, in our model, where juvenile survival was relatively low and adult survival was relatively high (Table 2), males from different age classes did not differ in mean viability (Fig. 4b). As a result, female preference for older males was unlikely to evolve.

In contrast to the results of our model, many empirical studies have suggested that females do prefer to mate with older males, even when males contribute only sperm (e.g. Zuk, 1988; Manning, 1989; Simmons and Zuk, 1992; Grahn and von Schantz, 1994; Simmons, 1995). The conflicting results of our model and those of empirical studies suggest that such a preference did not evolve as a result of increased viability of offspring from matings with older males, in species in which juvenile survival is low and adult survival is high, males provide only sperm and females prefer older males. As a result, our model suggests that female preference for older males in such species may be best explained by models of sexual selection other than ‘good genes’. Especially if sexually selected male traits are correlated with male age, female preference for older males may result (Hansen and Price, 1995). In species in which males provide more than just sperm, older males may be more experienced providers of parental care or may invest more in their offspring. As a

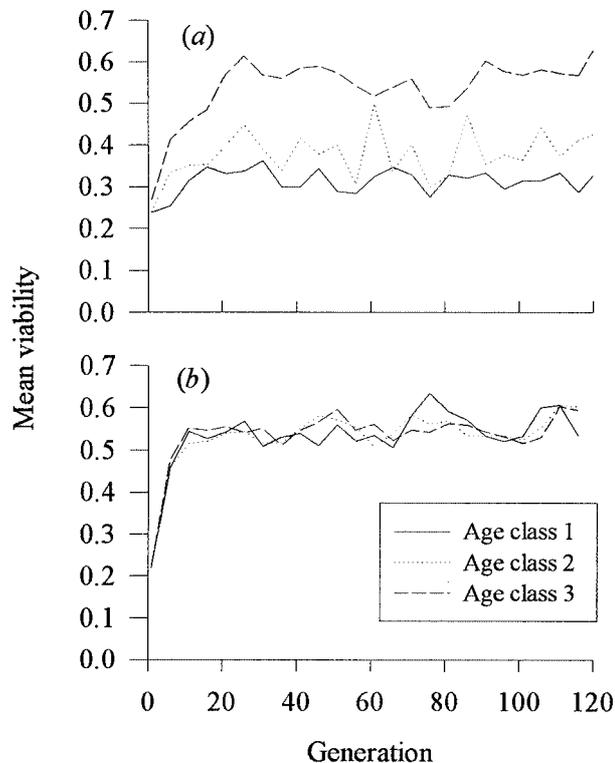


Fig. 4. Mean viabilities for different male age classes for (a) the model of Kokko and Lindström (1996) and (b) the current model. Preferences for males of age classes 1–3 were set to 0, 0.17 and 0.83, respectively, and the genomic mutation probability (Q) to 1.0.

result, female preference for older males may be more likely to evolve in species with male parental investment than in species without such investment.

Costs associated with female mate choice may reduce the likelihood that female preferences are expressed. Kokko and Lindström (1996) found that female preference for older males could evolve, but was less likely to do so, when there was a viability cost for being choosy. In contrast, our results suggest that female preference based on male age is unlikely to evolve in species in which males provide only sperm if there are even slight viability costs associated with female mate choice. Experimental studies have indicated that costs, including increased predation risk and increased energy expenditure, are often associated with female mate choice in many species (e.g. Gibson and Bachman, 1992; Milinski and Bakker, 1993; Rowe, 1994; Reynolds and Côté, 1995; Godin and Briggs, 1996; Grafe, 1997). In some species, females become less choosy as the costs of mate choice increase, as predicted by our model. For example, female sticklebacks (*Gasterosteus aculeatus*) are less discriminating about mates as the energy costs of searching increase (Milinski and Bakker, 1993). Female guppies (*Poecilia reticulata*) also become less choosy when predators are present (Godin and Briggs, 1996). However, in some species, females continue to exhibit a preference for particular males even if there is a cost associated with mate choice. One possible explanation is that males provide more than just sperm. For instance, in redlip blennies (*Ophioblennius atlanticus*), females will endure increased interspecific harassment to mate with older males (Reynolds and Côté, 1995). However, older males guard nests more vigilantly and for longer than younger males, and eggs in their nests have higher hatching rates than those of younger males (Côté and Hunte, 1989). Another explanation for the expression of female mate preference even when there is a cost for mate choice is that the costs are even lower than the cost levels that we modelled. In the sage grouse (*Centrocercus urophasianus*), increases in energy expenditure associated with female mate choice are minimal and predation results in a less than 0.1% decrease in the annual survival rate of choosy females (Gibson and Bachman, 1992).

In summary, in comparison with Kokko and Lindström (1996), our results suggest that female preference for older males may evolve as a result of 'good genes' in some cases, but not in others. The mechanism for the evolution of female preference for older males in species in which males provide only sperm differs depending on the survival probabilities of juveniles and adults. The importance of age-specific survival probabilities to understanding the process by which female preference for older males evolved emphasizes the need for the integration of studies on life-history evolution and sexual selection (see Partridge and Endler, 1987).

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