Age-Specific Fecundity of Mammalian Populations: A Test of Three Mathematical Models

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Empirical age-specific fecundity distributions are often based on small samples and hence include high levels of sampling error, particularly at the older ages. One solution to this problem is to smooth the distributions using appropriate models. The aim of this article is to compare the utility of three models for smoothing and/or graduating these distributions. The three models examined are 1) the Gamma distribution, 2) the Hadwiger function, and 3) the Brass polynomial. Test data sets consist of four types of primates (including humans), Asian elephants, and Przewalski's horse (an extinct species). The results indicate that all three models work well with a variety of mammalian data. The simplest of these models, the Brass polynomial, cannot be rejected based on available data and appears to be the optimum choice. Zoo Biol 20:487–499, 2001. © 2002 Wiley-Liss, Inc.

Key words: fecundity; mammals; age; mathematical models

INTRODUCTION

Accurate demographic rates for mortality, fecundity, and migration are necessary to evaluate the population dynamics of an endangered species. These estimates are useful to determine whether the size of a population is growing or declining in the wild, and to evaluate alternative management strategies in captivity. Unfortunately, good demographic estimates on endangered species are not generally available. First, data sets for these populations are generally small. As a consequence of the small sample sizes, the resulting rates are imprecise. Second, there may be errors in aging and/or observation of vital events (births, deaths, and migrations). Consequently, the resulting rates may be biased. In general, errors in the data tend to be less severe for captive populations where close observation is possible and more severe for populations in the wild where close observation is difficult. In any event,

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the conventional methods of estimating population dynamics, that is, methods based on stable population theory [Coale, 1972], will amplify any errors in the underlying demographic rates. There are alternative methods of estimating population dynamics [see Gage 1995 for an application of these methods to Przewalski's horse]. However, even the alternative methods require some of the same data as conventional approaches and thus have some of the same problems.

Human demographers faced with these same problems of demographic estimation for the less developed countries have developed model demographic systems to improve estimates of mortality, fertility, and migration. The modeling strategy divides the problem into two parts: the level of the vital rate (mortality, fecundity, and migration) and the age pattern of the vital rate. In general, it is age patterns that require large data sets to estimate because the sample must be broken down by age and sex. When large data sets are not available, the strategy used in human demography is to use a model life table or model fecundity table to establish the shape of the distribution and to use the observed data to estimate the level of the vital rate. One of the obvious problems associated with this methodology is choosing the appropriate age pattern of mortality, fecundity, or migration. Nevertheless, it appears to be the best approach for improving demographic estimates that is currently available.

Model mortality systems have been developed for some nonhuman populations, particularly the primates [Gage and Dyke, 1988; Dyke et al., 1993, 1995; Gage, 1998]. Model fecundity systems are not as well developed [Gage, 1995, 1998]. The aim of this article is to test, on a variety of nonhuman populations, several mathematical distributions that have been used for modeling human fecundity data. This article crosses the human demographic and biological literature. Consequently, it is necessary to define several common terms. Because this article appears in the biological literature the biological terminology will be followed, that is, fecundity refers to realized births, while fertility refers to the capacity to reproduce. The human demographic literature reverses these terms.

Mammalian age patterns of fecundity are thought to fall into two types, those displaying reproductive senescence, and those that do not senesce (Fig. 1). In general, mammalian fecundity displays a significant prereproductive period followed by a rapid increase in fecundity with age to a maximum and finally a decline. It is argued that some mammals do not display the decline in fertility at the older ages, that is, there is no senescent phase [Caughly, 1977 for sheep and Promislow, 1991 for mysticete whales]. Conversely, in at least one species (*Homo sapiens*), there is a menopause followed by a significant postreproductive phase. Because the general methods examined here are borrowed from the human demographic literature, only the senescent pattern of fecundity will be considered. One of the difficulties with modeling the age patterns of fecundity in nonhuman mammals is that all mammals appear to senesce with respect to mortality, but do not have significant postreproductive phases [Caughly, 1977; Gage, 1995; Gage, 1998]. Consequently, the age pattern of fecundity at the older ages is particularly difficult to estimate precisely because the number of animals exposed to the risk of a birth is always very small (few survive to these ages). Thus, age-specific fecundities at the oldest ages incorporate a very large random error. In fact, the lack of evidence for reproductive senescence in the mammals where reproductive senescence is thought not to occur might be because of this problem.

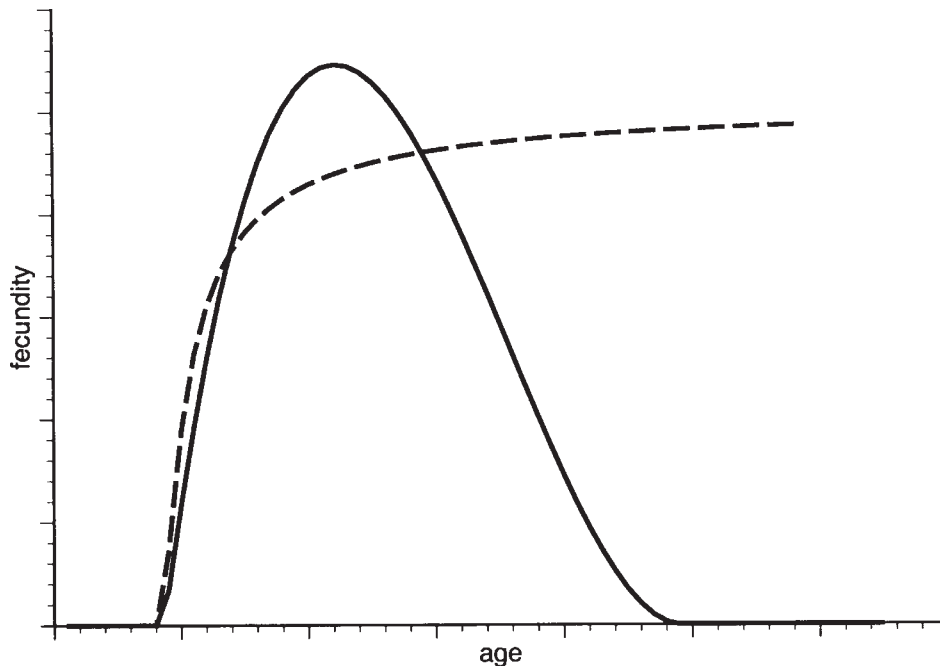The models of age-specific fecundity developed for human populations fall

Fig. 1. The two mammalian patterns of age-specific fecundity. The solid line represents the reproductive senescent pattern, and the dashed line represents the nonsenescent reproductive pattern.

into two or three types: 1) models based on empirical data, 2) mathematical density functions, and 3) combinations of empirical data and mathematical functions. Applications in human demography frequently use models based on empirical data or a combination of empirical data and mathematical functions. This approach requires large amounts of high-quality data to define the characteristic shape of the age-specific fecundity curve. Such data are available for human populations and are enhanced by combining the results across several well-documented populations. As a consequence, random variation in the age-specific fecundity rates are minimized, and the characteristics of the human fecundity curve are well known. Similar empirical data are more difficult to obtain for most other mammalian populations, because of the problems mentioned herein. Furthermore, empirical models must be constructed individually for each species or at least separately for organisms with largely different life history characteristics. Thus, the models examined here are all based on mathematical density functions that can be used to smooth empirically obtained age-specific fecundity distributions derived from small populations.

Methods of smoothing human fecundity distributions have been compared recently by Hoem et al. [1981] using contemporary Danish fecundity data. They examined several methods that do not rely completely on empirical data including 1) cubic splines, 2) the Hadwiger function, 3) the Gamma density, 4) the Beta density, 5) the Brass polynomial, and 6) the Gompertz function. Hoem et al. [1981] also examined several variations of the methods just listed, which are dependent on empirical data. One of these is the Coale and Trussell [1974] procedure, which is perhaps the most widely used method in human demography. Hoem et al. [1981] compared the fit of

all of these methods to contemporary Danish fecundity and concluded the following: the cubic spline provides the best fit; the Coale-Trussell procedure, Gamma density, and Hadwiger function were second but still fit the data well, whereas the Beta density, the Brass polynomial, and the Gompertz function were less accurate [Hoem et al., 1981]. Here the application of the Gamma density, the Hadwiger function, and the Brass polynomial are extended to several nonhuman mammalian populations. I have excluded 1) the cubic spline because it requires good underlying empirical data; 2) the Coale-Trussell procedure because it requires good empirical model fecundity schedules, which are currently unavailable for nonhuman mammal populations; and 3) the Beta and Gompertz functions because they do not fit contemporary human fecundity distributions well. I have included the Brass polynomial despite the less accurate fits reported by Hoem et al. [1981] because this procedure provides parameter values that are directly interpretable with respect to life history characteristics, and because it has been used to smooth nonhuman fecundity distributions previously [Gage, 1995, 1998].

METHODS

The Gamma distribution, modified for fecundity analysis is:

$$m_x = c\left[\frac{1}{\Gamma(b_1)b_2^{b_1}}(x-d)^{b_1-1}\exp\left\{-\frac{(x-d)}{c}\right\}\right]$$

for $x > d$, and where x is age, c is the level of fecundity (measured as a "total fertility rate," TFR, the number of offspring ever born to a female that survives to the end of the reproductive period), d is the length of the prereproductive period, and $\Gamma(b_1)$ is the gamma function of b_1. In this model, the parameters b_{1+2} have no particular demographic interpretation. In general, the gamma distribution is thought to provide a slightly better fit to human fecundity distributions than the Hadwiger function [Hoem et al., 1981].

The Hadwiger function is an adaptation of the inverse Gaussian or Wald density. It is

$$m_x = c\left[\frac{b_2}{b_3\sqrt{\pi}}\left(\frac{b_3}{x-b_1}\right)^{3/2}\exp\left\{-b_2^2\left(\frac{b_3}{x-b_1}+\frac{x-b_1}{b_3}-2\right)\right\}\right]$$

for $x > b_1$ where, x is age, c is the level of fecundity (again measured as a TFR), but the parameters b_1, b_2, and b_3 have no particular demographic interpretation. A common problem with the Hadwiger function, at least for fitting contemporary Danish (human) fecundity distributions, is a tendency to overestimate fecundity at the oldest fertile ages [Hoem et al., 1981].

The Brass polynomial is a simple third-degree polynomial. More complex adaptations of this model have been developed by Brass [1975] and Hoem et al. [1981]; however, these adaptations generally require empirical model fecundity tables. The Brass polynomial is defined here as

$$m_x = c(x-d)(d+w-x)^2.$$

For $x > d$ and $x < (d + w)$, and where x is age, c is a measure of the level of fecundity (but cannot be interpreted as the TFR), d is the lower age at fecundity, and w is the length of the reproductive period [Gage, 1995, 1998].

All three functions are fitted using the same nonlinear least-squares fitting routine [Velleman, 1997]. This routine uses the Fletcher method of minimization, which uses numerical (as opposed to analytical) derivatives. In all cases the "loss" function is defined as the sum of the squared error (sse). The statistically appropriate model is also identified from sse. Comparisons of the Gamma and Hadwiger functions, which have the same number of parameters, can be based directly on sses. Comparisons of the Brass polynomial (three parameters) with the Gamma or Hadwiger functions (four parameters) were carried out using an F-test based on a likelihood ratio [Gallant, 1987]. This is

$$F = \frac{sse_r - sse_f}{sse_f / (n-4)}$$

where sse_r and sse_f are the sums of the squared errors for the reduced model (Brass polynomial), and the full model (the Gamma or Hadwiger), respectively, and n is the number of data points. There are 1 numerator degrees of freedom and $n - 4$ denominator degrees of freedom.

The data used for illustrating and testing the three methods of smoothing and/or graduating fecundity distributions are not a representative sample of mammalian populations. These data sets were chosen primarily on the basis of their availability to the author. Overall, the sample consists largely of primates (including two human fecundity distributions), although several other populations are also presented: Przewalski's horse and Asian elephants (Table 1). The primate data were used in a recent comparison of primate life history characteristics [Gage, 1998].

Human fecundity patterns are frequently classified into two types: "natural" and "controlled" fecundity. This dichotomy is considered to account for most of the variation in human age patterns of fecundity. In human affairs, "natural" fecundity is

TABLE 1. Fecundity data

Population	Type of population[a]	Length of age interval (yr)	No. of age intervals	Source
Marmosets (various)	n	1	14	Unpublished data[b]
M. mulatta (rhesus)	c	1	28	Dyke et al., 1986
Pan t (chimpanzee)	n	4	9	Sugiyama, 1994
Homo s. Costa Rica 1966	n	5	8	Keyfitz and Fleiger, 1971
Homo s. Sweden 1967	c	5	9	Keyfitz and Fleiger, 1971
Przewalski's horse	c	1	21	Gage, 1995
Asian elephants	c	4	10	Unpublished data[c]

[a]Type of population; c, controlled; n, natural.
[b]These are based on data concerning *Callithrix jaccus*, *Saguinus fuscicollis*, and *Saguinus oedipus* at the Oak Ridge Associated Universities Marmoset Research Center.
[c]These are based on data collected from the North American Stud Book.

defined as the fecundity observed in the absence of behaviors consciously intended to limit fecundity, whereas "controlled" fecundity is defined as the fecundity observed in the presence of behaviors consciously intended to limit fecundity [Henry, 1961]. For example, the use of contraceptives to limit exposure to risk of fecundity would result in "controlled" fecundity. By these definitions, the observed fecundity of nonhuman animals is generally "natural." However, among captive animals, caging decisions by human managers (consciously or unconsciously) may limit the exposure of risk of females and hence limit their fecundity. Thus, the samples used here are classified into two types, "natural" and "controlled," depending on whether human interference (in this case conscious or unconscious) could have limited fecundity. The problem of exposure to risk could be controlled statistically where exposure to risk is documented; however, currently there are few data sets (human or nonhuman), that include accurate information on exposure to risk. The classification of the samples is included in Table 1. I have classified the marmosets as "natural" because these data represent an active attempt to accommodate marmosets to captivity. Fecundity in captivity of these species is relatively low; hence, it is likely that every attempt was made to maximize the birth rate of this population given the captive environment [Gage, 1998].

RESULTS

All three methods provide reasonably close fits to the data (Tables 2–4, and Figs. 2 and 3). Based on absolute mean square error , the Gamma function appears to give the best results (Table 5). It provides the closest fit in four of the seven cases and is second best in all other cases. However, formal statistical tests indicate that in general, the more complex Gamma and Hadwiger functions are not statistically justifiable (Table 6). The F-tests indicate that the simpler Brass polynomial (three parameters) can only be rejected in favor of the more complex Hadwiger and Gamma models at the $P < 0.05$ level for the Swedish fecundity data. If Bonferroni's adjustment (a conservative correction for multiple tests) is applied across the seven comparisons, then the Brass polynomial cannot be rejected even for the Swedish fecundity distribution.

Absolute goodness of fit is only one criterion for evaluating the utility of a model. For those models for which the parameters have some interpretable demographic or biological meaning, the values of the parameters can also be considered. The Gamma and Hadwiger functions both parameterize the TFR, that is, the number of offspring ever born to mothers surviving throughout the entire reproductive span. The Brass polynomial also provides a parameter representing the level of fecundity,

TABLE 2. Parameters of the Gamma distribution

Population	c^a	b_1	b_2	d	Loss
Marmoset	7.367	2.340	2.755	1.225	0.07706575
Rhesus	7.206	3.007	4.612	1.478	0.04707600
Chimpanzee	6.760	1.592	10.214	12.612	0.01615345
Costa Rica	6.704	6.094	3.538	8.651	0.00433433
Sweden	2.298	12.918	1.708	4.927	0.00002265
Przewalski's horse	9.653	2.508	5.211	1.074	0.14301433
Asian elephants	1.115	3.214	5.560	2.437	0.00072285

[a]c is interpretable as a total fertility rate.

TABLE 3. Parameters of the Hadwiger distribution

Population	c^a	b_2	b_3	b_1	Loss
Marmoset	7.591	1.233	8.579	–0.498	0.08241881
Rhesus	7.229	1.789	20.429	–5.182	0.05209716
Chimpanzee	7.185	1.002	22.779	6.972	0.01587748
Costa Rica	6.726	2.587	32.307	–2.132	0.00462435
Sweden	2.302	3.738	32.678	–5.673	0.00002430
Przewalski's horse	9.716	1.535	18.482	–4.337	0.15036234
Asian elephants	0.963	0.751	17.557	10.000	0.00246622

$^a c$ is interpretable as a total fertility rate.

c. However, this parameter is not interpretable as a TFR (Table 4) as is the human demographic convention. The estimates of TFR for the Brass polynomial presented in Table 4 were computed by numerical integration of equation 3 between d and $d + w$. In general, TFR estimates of all three models are similar; however, the TFRs estimated by the Brass polynomial are consistently lower than those of the Gamma and Hadwiger functions (Tables 2–4). This is largely because of differences in fecundity estimates of the three models at the older ages (Figs. 2 and 3). The Brass polynomial generally provides lower fecundity estimates at these ages.

The Gamma density and Brass polynomial both include a parameter that might be considered the "age of maturity." The standard life history definition of age at maturity is the mean age at first birth [Stearns, 1992]. However, both models provide estimates of age at maturity as the earliest age of significant reproduction. Using this later definition, the Brass polynomial appears to provide the most reasonable estimate. Comparisons of the value of the parameter representing "age of maturity" with the minimum age of first birth in the observed data indicate that the Brass polynomial provides the best estimate in three cases, whereas the Gamma provides the best estimate in two cases. In the two remaining cases, the models provide very similar results. In one of these, Asian elephants, the estimate of both the Gamma and Brass models is far too low, approximately 2 years, whereas the first observed birth occurs between ages 8 and 12 years.

The Brass Polynomial model also parameterizes the length of the reproductive period. In this case, the length of the reproductive span is estimated as the difference between the age at which fecundity exceeds zero (earliest age of significant reproduction) and the age (older than the earliest age of significant reproduction) at which fertility again reaches zero. This estimate is consistent with the life history definition

TABLE 4. Parameters of the Brass polynomial

Population	c^a	d	w	Loss	TFR
Marmoset	1.750e-3	0.938	14.690	0.12129878	6.791
Rhesus	1.125e-4	2.220	29.044	0.03975706	6.671
Chimpanzee	2.770e-5	9.129	40.515	0.02773600	6.220
Costa Rica	4.590e-5	15.181	35.947	0.00186213	6.387
Sweden	2.455e-5	14.809	32.836	0.00214561	2.378
Przewalski's horse	1.890e-4	1.125	27.146	0.14540089	8.552
Asian elephants	5.710e-6	2.098	38.811	0.00088270	1.080

$^a c$ is a measure of the level of fecundity but not interpretable as a total fertility rate (TFR). TFR is computed by numerical integration of the Brass polynomial between d and $d + w$.
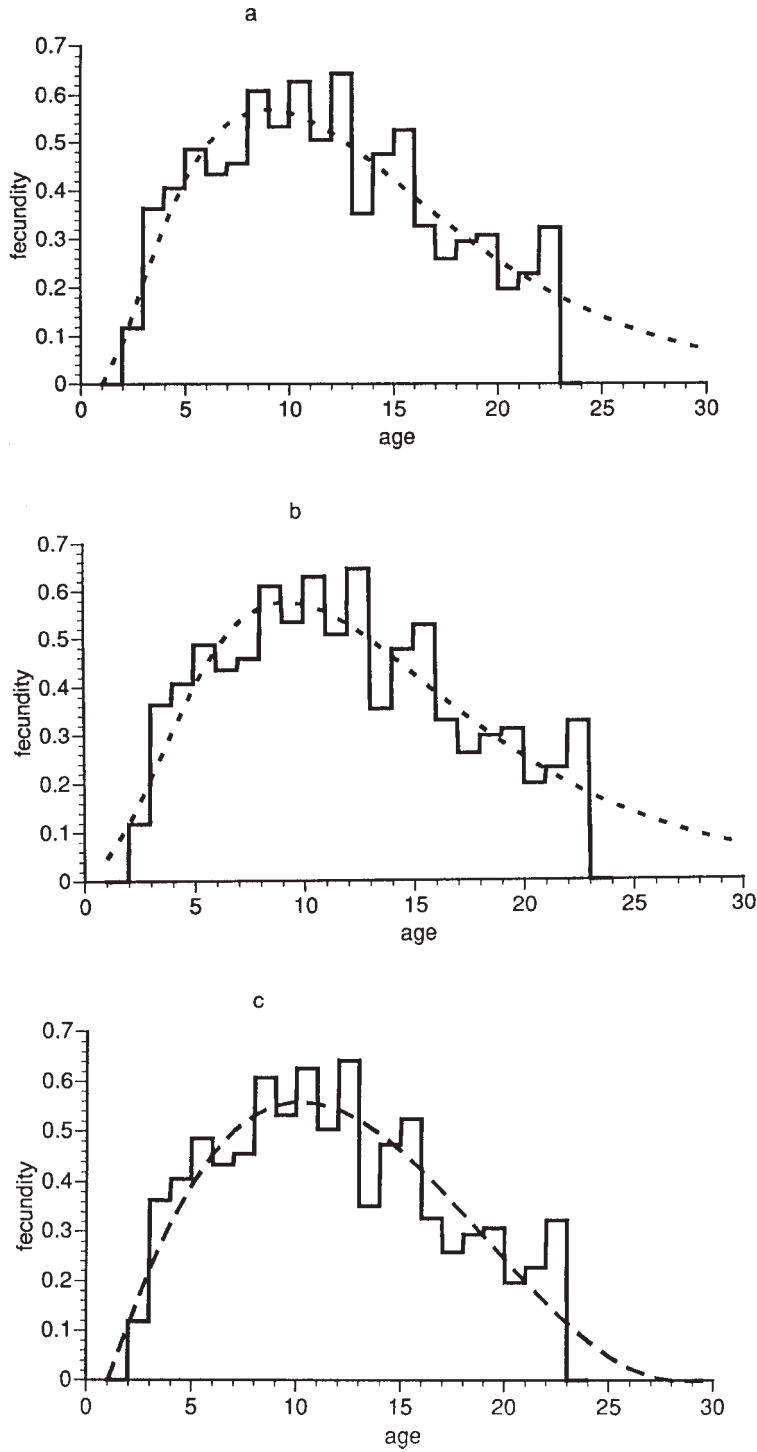
Fig. 2.   The three models (dashed line) fit to the observed Prizwalski's horse fecundity distribution (solid line). **a:** The gamma distribution. **b:** The Hadwiger function. **c:** The Brass polynomial.
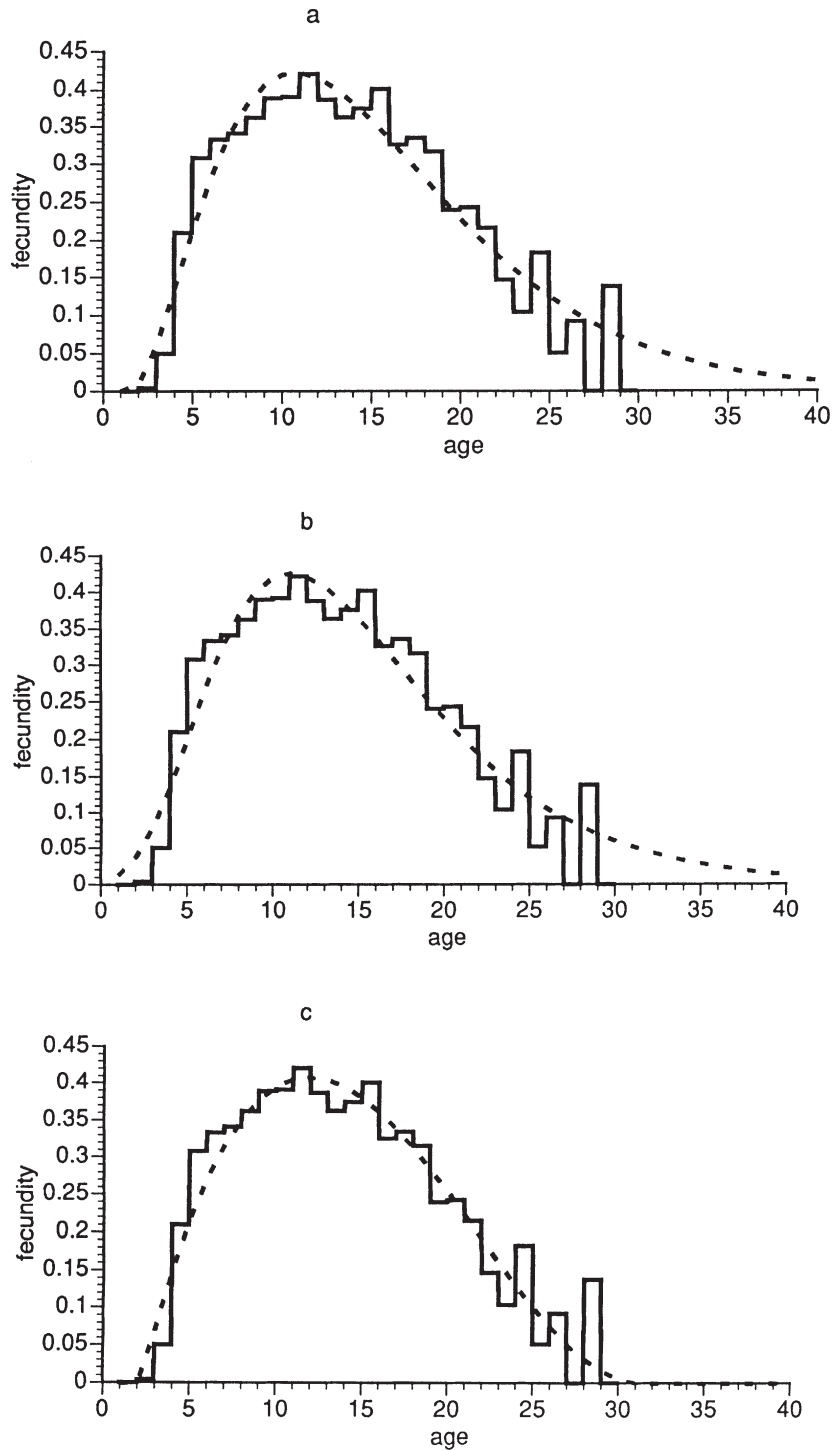
Fig. 3.   The three models (dashed line) fit to the observed rhesus fecundity distribution (solid line). **a:** The Gamma distribution. **b:** The Hadwiger function. **c:** The Brass polynomial.

TABLE 5. Goodness of fit based on the sum of the squared error

Population	Brass polynomial	Hadwiger	Gamma
Marmoset	0.121299	0.082419	0.077066[a]
Rhesus	0.039757[a]	0.052097	0.047076
Chimpanzee	0.027736	0.015877[a]	0.016153
Costa Rica	0.001862[a]	0.004624	0.004334
Sweden	0.002146	0.000024	0.000023[a]
Przewalski's horse	0.145401	0.150362	0.143014[a]
Asian elephants	0.000883	0.002466	0.000723[a]
Mean	0.048440	0.043982	0.041198

[a]Best fit from among the three models.

of the maximum reproductive lifespan [Stearns, 1992]. However, the concept of a maximum reproductive lifespan is only meaningful for mammals that display reproductive senescence. The estimates for humans (approximately 35 years) appear reasonable (Table 4), but little comparable data are available for the other species. In all cases, the Brass polynomial provides an estimate of age at the end of the reproductive career that is greater than the observed age at oldest birth in the data analyzed here. However, the Gamma and Hadwiger models both consistently predict higher fecundity at the older ages, as already noted here, and hence longer reproductive lifespans compared to the Brass polynomial (Figs. 2 and 3). Thus, the Brass polynomial appears to describe the biological characteristics of the observed fecundity distributions better than the alternative models, and provides a more conservative (lower) estimate of the level of fecundity.

DISCUSSION

This comparison of methods of modeling age-specific fecundity for a variety of mammalian populations is limited by the lack of good fecundity data for a variety of species under a variety of environmental conditions. Ideally, accurate data should be used to test the validity of the mathematical models. Unfortunately, accurate data are commonly available only for humans. The data currently available for other animals are limited by the problems of observing demographic events for animals living in the wild or by the potential effects of caging arrangements on fecundity in captivity.

TABLE 6. Values of F based on a likelihood ratio

Population	Brass vs. Hadwiger	Brass vs. Gamma	df[a]	*P* value for Brass vs. Gamma[b]
Costa Rica	0.149	0.143	4	0.725
Sweden	17.459	18.746	5	0.008
Marmoset	0.048	0.057	10	0.815
Rhesus	0.010	0.006	24	0.937
Chimpanzee	0.149	0.143	5	0.720
Przewalski's horse	0.002	0.001	17	0.975
Asian elephants	0.107	0.037	6	0.854

[a]These are denominator degrees of freedom, numerator degrees of freedom is 1 in all cases.
[b]$P < 0.007$ is necessary to reject the Brass model with Bonferroni's adjustment (a correction for multiple tests).

The present study is based on the limited data that are currently available. It is likely that these data underestimate the natural level of fecundity of the species examined in the environments in which they are observed. Observations in the wild will underestimate the level of fecundity because births may be overlooked, particularly those births that die at an early age. In captivity, caging arrangements are likely to reduce the exposure to risk of fecundity of at least some females and hence reduce the observed fecundity rates. The wild versus captive environment is also likely to influence the level of fecundity, with captive animals displaying lower or higher fertility, depending on whether the species does or does not adapt well to captivity.

Bias in the shape of the age-specific fecundity distribution may occur in both wild and captive populations. In wild populations, age may not be well established; in fact, reproductive status might be used to infer age and hence bias the "observed" age distribution of births [see, for example, Sugiyama, 1994]. In captivity, where age is likely to be better established, animal managers may bias age-specific fecundity rates, consciously or unconsciously, by making caging decisions on the basis of age or the achieved fecundity of a female. For example, older females might not be exposed to the risk of fecundity as continuously if managers assume that they would not be productive anyway. Additional data collection and research will be necessary to evaluate the significance of these potential problems.

Conversely, human age patterns of fecundity are remarkably uniform despite extensive self-manipulation of fecundity rates. In general, the only significant variation in the age patterns of fecundity are thought to be caused by "natural" versus "controlled" fecundity [Coale and Trussell, 1974]. Controlled fecundity is characteristic of modern populations, where fecundity is curtailed after a certain number of births are achieved. These differences are reflected in the Costa Rican (natural) and Swedish (controlled) fecundity distributions (Fig. 4). In this regard, the results pre-
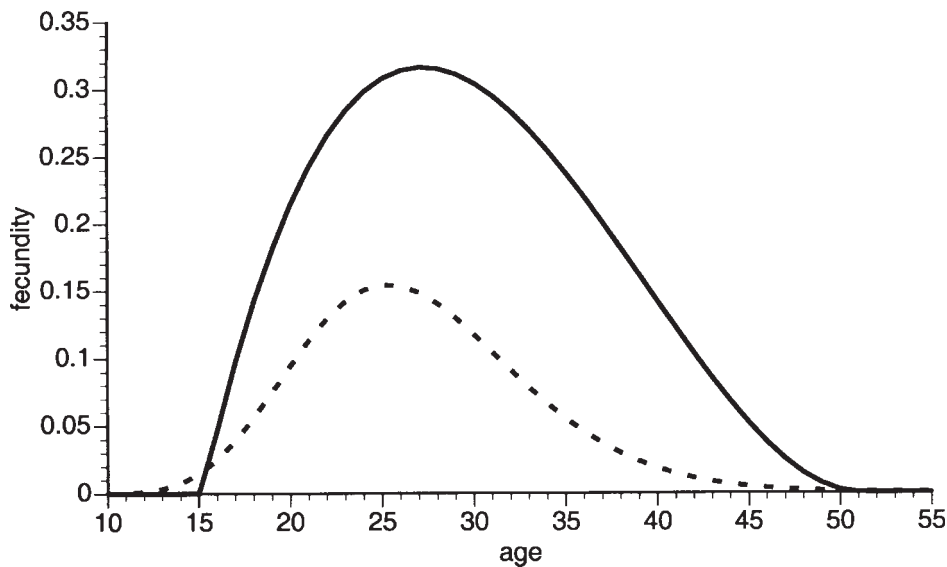

Fig. 4. The Costa Rican data smoothed with the Brass polynomial (solid line) represent the "natural" fecundity pattern and the Swedish data smoothed with the gamma distribution (dashed line) represent the "controlled" fecundity pattern.

sented herein tend to confirm the finding that the Gamma distribution fits modern Danish fecundity (controlled) best [Hoem et al., 1981]. However, the results do not support the conclusion reached by Hoem et al. [1981] that the Gamma provides the best fit to human fecundity distributions in general. The Brass polynomial fits the Costa Rican (natural) fecundity distribution better. Given that human age patterns of fecundity are relatively uniform despite high levels of self-manipulation, it is possible that the mammalian fecundity data examined here are similarly resistant to the potential limitations and bias discussed herein.

CONCLUSIONS

Lacking better data, the data currently available are assumed to reflect the characteristic shape of the age-specific fecundity distribution, and any deviations from this distribution are caused by random sampling error. If this is true, then it is possible to select the mathematical model that best fits mammalian age-specific fecundity distributions (for those species that display reproductive senescence) and use it for improving age-specific estimates of fecundity. Based on currently available data, there is no reason to reject the simple Brass polynomial as a method of smoothing and/or graduating age-specific data. This conclusion should be considered preliminary and regularly reviewed as additional and hopefully better-quality data become available. Nevertheless, the Brass polynomial currently appears to be the optimum method for several reasons: 1) it is the simplest of the models, 2) statistical tests indicate that it cannot be eliminated as an adequate fit to the available data, and 3) it provides parameter estimates that are interpretable as standard life history characteristics, i.e., length of the prereproductive and the reproductive periods. Finally, the Brass polynomial provides the most conservative estimate of TFR and hence is least likely to overestimate the security of an endangered species.

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