# Estimating the Average Age of First Birth in Marine Mammals

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The average age of sexual maturity and the average age of first birth should not be estimated with identical models. The two parameters often differ by at least 1 y because, among marine mammals, ovulation and parturition take place in different years because of the relatively long gestation period. Furthermore, the assumptions necessary to estimate the average age of sexual maturity cannot be made to fit the data used to estimate the age of first birth. Equating the two models is essentially equivalent to assuming that each ovulation will result in a birth. The described procedure lends itself well to age-specific data. Comparisons between populations should be with a Chi-square goodness-of-fit test.

*Key words:* reproduction, marine mammals, sexual maturity

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On ne devrait pas se servir des mêmes modèles pour estimer l'âge moyen de maturité sexuelle et celui de la première parturition. Souvent, les deux paramètres différent d'au moins un an parce que, chez les mammiféres marins, l'ovulation et la parturition ont lieu dans des années différentes par suite d'une période de gestation relativement longue. En outre, les hypothèses nécessaires à l'estimation de l'âge moyen de maturité sexuelle ne peuvent être adaptées aux données utilisées pour estimer l'âge de première parturition. Égaliser les deux modèles équivaut essentiellement à supposer que chaque ovulation aboutira à une naissance. Le mode opératoire décrit ici se prête bien à des données spécifiques à l'âge. Les comparaisons entre populations devraient se faire par le test du khi carré.

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FOR many species of marine animals, ovarian and tooth specimens are available, which can be used to generate the average age of sexual maturity (DeMaster 1978a; Laws et al. 1975). When using DeMaster's (1978a) model to estimate the average age of sexual maturity, one necessarily assumes that animals that have not ovulated at age $x$ have not ovulated before age $x$. One must also assume that animals that have ovulated at age $x$ will ovulate every year thereafter. These two assumptions are often true for pinnipeds (Chapman 1973; DeMaster 1978b; Laws 1956; Oritsland 1970; Sergeant 1966; Smith 1973; and Stirling 1971) and the sea otter (*Enhydra lutra*; A. Johnson, NFWL, 4454 Business Park Blvd, Anchorage, AK, personal communication). However, for species like the walrus (*Odobenus rosmarus*; Burns 1965; Fay 1955), the polar bear (*Ursus maritimus*; Lentfer 1976; Lentfer et al. 1981), and most cetaceans, the long period of gestation and nursing precludes annual ovulations. Therefore, to estimate the age of sexual maturity in animals that do not ovulate annually with the procedure described by DeMaster (1978a), only those animals that were "available" for breeding (that is, without young or at the point in maternal care where mating usually takes place) should be included in the estimate.

For species of marine mammals where data on reproductive success are derived from the presence or absence of live young or fetuses, the assumptions of the model used to estimate the age of sexual maturity (DeMaster 1978a) are not reasonable. That is, animals that have not given birth at a given age could have given birth previously, and animals that have given birth at age $x$ cannot be assumed to give birth at all subsequent ages. In this paper a method is described that is appropriate for estimating the average age of first birth for marine mammals for which data on the presence or absence of live young or fetuses are available. However, it should be remembered that only animals that are "available" for reproduction should be considered in the analysis.

The average age of first birth is estimated as follows:

$$(1) \quad \hat{y}(x) = t(x)/n(x)$$

where $x$ = the age of the female,
$\hat{y}(x)$ = the estimated proportion of females of age $x$ that are reproductive,

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$t(x)$ = the number of females of age $x$ that are pregnant or with young of the year, and
$n(x)$ = total number of females of age $x$ observed.

The estimated probability of giving birth at or before age $x$, $z(x)$, is

$$(2)\quad \hat{z}(x) = \hat{y}(x) + [1 - \hat{y}(x)]\,[\hat{z}(x-1)].$$

The probability of giving birth for the first time at age $x$, $r(x)$, plus the probability of giving birth at or before age $x - 1$, $z(x - 1)$, equals $z(x)$. Thus, the estimated probability of reproducing for the first time age age $x$ is

$$(3)\quad \hat{r}(x) = \hat{z}(x) - \hat{z}(x-1).$$

The average age of first birth is then estimated by:

$$(4)\quad \bar{x} = \sum_{x=0}^{w} x\,\hat{r}(x),$$

where $w$ = the minimum age where $z(x) = 1.0$.

The derivation of this procedure necessarily assumes that the probability of reproducing at age $x$ is independent of the probability of reproducing at age $x - 1$, given that the adult female was available in both years. For data where individuals are only included once in the analysis, this assumption should be satisfied. For many species, $y(x)$ will be independent of $z(x - 1)$ after a threshold age is reached (DeMaster 1978b) and for these animals, including resightings of the same individual, should not significantly bias the estimate of $r(x)$. It is also assumed in this estimation procedure that $\hat{y}(x)$ and $\hat{z}(x)$ are unbiased estimates of $y(x)$ and $z(x)$.

The estimated variance of the average age of first reproduction is derived as follows (equations 6, 7, and 8 are derived by use of the Delta method, Seber 1973).

$$(5)\quad \operatorname{var}\hat{y}(x) = \frac{\hat{y}(x)\,[1 - \hat{y}(x)]}{n_x - 1}$$

$$(6)\quad \operatorname{var}\hat{z}(x) = \operatorname{var}\hat{z}(x-1) + \operatorname{var}\hat{y}(x) + [\hat{y}(x)]^2 \operatorname{var}\hat{z}(x-1) + [\hat{z}(x-1)]^2 \operatorname{var}\hat{y}(x)$$

$$(7)\quad \operatorname{var}\hat{r}(x) = \operatorname{var}\hat{z}(x) + \operatorname{var}\hat{z}(x-1)$$

$$(8)\quad \text{and } \operatorname{var}(\bar{x}) = \sum_{x=0}^{w} x^2 \operatorname{var}\hat{r}(x).$$

The derivation of the variance of $\bar{x}$ assumes that $\hat{z}(x - 1)$ and $\hat{y}(x)$ are independent, that var $\hat{z}(x)$ and var $\hat{z}(x - 1)$ are independent, and that the var $\hat{r}(z)$'s are independent. These assumptions should be met if the previous assumption that the $y(x)$'s are independent is met.

Table 1 (hypothetical data) presents this precedure as it is used to estimate the average age of first birth and the variance associated with this average. DeMaster (1978a) estimated the average age of sexual maturity with this same data set. Under the assumptions for determining the age of sexual maturity, the age of first birth is overestimated ($\bar{x}$ = 3.34 vs. $\bar{x}$ = 3.09). These assumptions are equivalent to assuming that each ovulation will result in a birth. This overestimate occurs because the probability of giving birth at or before age $x$, ($z(x)$), under the assumptions of the sexual maturity model ($z(x) = t(x)/n(x)$; DeMaster 1978) is always less than or equal to the estimated $z(x)$ under the assumptions appropriate for estimating the age of first birth (equation 2). Therefore, using the equations appropriate for estimating the age of sexual maturity on data concerning the presence or absence of young or fetuses has the effect of increasing the probability of giving birth for the first time at the older ages relative to the younger ages, which subsequently inflates the estimated age of first birth. A second problem with not distinguishing between the age of sexual maturity and first birth is that for many marine mammals the age at which mating and parturition takes place differs by at least 1 y. This difference exists because the gestation period in most marine mammals is in excess of 8 mo (Asdell 1964). Therefore, the age of sexual maturity and the age of first birth should be clearly distinguished because the assumptions for the two estimates are different, and because the age of the animal when it is sexual mature is often different from the age of the animal when it first gives birth.

TABLE 1. Calculation of the average age of first birth in a hypothetical population of females. Average age of first birth equals 3.092 yr, SE ($x$) = 6.77 yr.

| Age in years, ($x$) | No. females observed, $n(x)$ | No. females with young, $t(x)$ | Proportion of reproductive females, $y(x)$ | $P$ (give birth at or before age $x$), $z(x)$ | $P$ (1st birth at age $x$), $r(x)$ | $x\,r(x)$ |
|---|---|---|---|---|---|---|
| 0 | 35 | 0 | 0 | 0 | 0 | 0.0 |
| 1 | 30 | 6 | 0 | 0 | 0 | 0.0 |
| 2 | 25 | 6 | 0.24 | 0.240 | 0.240 | 0.480 |
| 3 | 20 | 13 | 0.65 | 0.734 | 0.494 | 1.482 |
| 4 | 20 | 16 | 0.80 | 0.947 | 0.213 | 0.852 |
| 5 | 15 | 12 | 0.80 | 0.989 | 0.042 | 0.210 |
| 6 | 15 | 12 | 0.80 | 0.998 | 0.009 | 0.054 |
| 7 | 10 | 8 | 0.80 | 1.000 | 0.002 | 0.014 |
| 8 | 10 | 8 | 0.80 | 1.000 | 0.000 | 0.0 |
| | | | | | | 3.092 |

Estimating the average age of first birth in practice will involve at least one other assumption. In cases where the number of adult females with live young is used, one must assume that the mortality rate of the offspring from birth until it is seen with its mother is negligible. In cases where adult females are classified as pregnant or not, one must assume that intrauterine mortality is negligible. In this situation, it is probably best to use for the age of the adult female the age at parturition, and not the current age.

Another point that should be considered is how senescene may affect the estimated average age at first birth. In practice, the decline in reproductive success with age will not affect the estimate because this reduction in $y(x)$ occurs well past the age where $r(x)$ equals 1.0.

A simulation analysis of this procedure suggests that with sample sizes of roughly 125 animals in each age-class for which $r(x)$ is not zero, differences of 3 yr between populations will be detected. Therefore, for most studies where at least five indeterminant ages (ages where $0 < z(x) < 1.0$) will be encountered at least 600 "available" individuals will have to be sampled to obtain a confidence interval of 3 yr (95% confidence interval = $1.96\, x\, [\mathrm{var}\ (\bar{x})]^{0.5}$). In most studies this sample size is unrealistic. In many situations a comparison between two populations or between one population at two different times is more useful than a confidence interval. The categorical nature of this type of data lends itself well to contingency table analysis, and eliminates the assumption of normalcy that is associated with ANOVA tests. Therefore, a contingency table analysis is recommended for comparing two different populations or one population at two different points in time because it will be more sensitive to differences than the standard $t$-test.

The estimation procedure described in this note should be particularly useful in mark–recapture studies where data on production of young are available, but accompanying ovarian data are not available. Where ovarian data are available, the average age of sexual maturity will be more sensitive to differences between populations than the average age of first birth for similar sample sizes.

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