

REPRODUCTIVE SYNCHRONY AND THE ESTIMATION OF MEAN DATE OF BIRTH FROM DAILY COUNTS OF NORTHERN FUR SEAL PUPS

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ABSTRACT

Two methods for estimating the mean date of birth from daily counts of northern fur seal pups (*Callorhinus ursinus*) are presented and applied to data collected on the Pribilof Islands in 1951, 1962, 1963 and 1983. The mean date of birth over the four years was July 9. Reproduction is highly synchronized and consistent from one year to the next. Pupping occurs over a five week period with over 50% of the pups being born during the first two weeks of July.

Key words: northern fur seal, *Callorhinus ursinus*, seal pups, pupping, pup mortality, reproductive synchrony.

The mean date of birth is a useful parameter to estimate. It can be used to assign mean ages to pups or to compare the timing of birth between years and between different populations. Other uses of mean date of birth include estimating pup production when only a fraction of the pupping season is observed (B. Le Boeuf, personal communication) and testing hypotheses about interuterine mortality and the timing of the previous year's breeding (Stirling 1971).

The best estimate of mean pupping date is the date corresponding to the arithmetic mean of the number of pups born each day. Unfortunately following individual animals and recording births as they occur is difficult at the best of times and near impossible on high density breeding areas, so that obtaining a random sample to estimate this mean is not generally practical. A simpler approach to quantify reproductive timing is to choose a portion of the breeding area and count all the pups present. Mean pupping date for this portion can be estimated from cumulative daily counts of pups made over the breeding season.

In this study, I present and apply two methods for estimating the mean date

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of birth from daily counts of northern fur seal pups (*Callorhinus ursinus*) made in 1951, 1962, 1963 and 1983. I use the cumulative pup counts to describe and compare reproductive synchrony on the Pribilof Islands. My intent is to estimate the mean date of pupping for northern fur seals and to test if pupping patterns remained the same from year to year.

METHODS

Sigmoid method—The first procedure is essentially a curve fitting routine that assumes the number of pups P_t counted per day t on a study site, increases in a sigmoid fashion. I explored two sigmoid equations, the logistic

$$P_t = A/(1 + ce^{-kt}) \quad (1)$$

and the Gompertz equation

$$P_t = Ae^{-ce^{-kt}} \quad (2)$$

where A , c , and k are the asymptote, the constant of integration, and the growth rate constant, respectively (Zach *et al.* 1984). These equation are used purely for data fitting, not as an indication of underlying population mechanisms. Note that the number of pups that die between counts is ignored at present and that immigration and emigration of pups are assumed to be negligible.

The median date of birth (B) for each study site is estimated at one half the asymptote, such that $P_t = A/2$ where $t = B$. Making these substitutions into Eqs. 1 and 2 yields

$$B = \frac{-\ln(\epsilon/c)}{k} \quad (3)$$

where the constant ϵ equals 1.0 when solving for the logistic equation and $\ln 2$ ($=0.69315$) for the Gompertz equation. Fifty percent of the pups are born before day B . In the case of the logistic equation which is symmetrical, B is both the mean and median birth date; but when applied to the Gompertz equation, B is just the median.

The variance of B is estimated by the delta method (Kendal and Stuart 1977):

$$\text{var}(f[p_1, p_2, \dots, p_n]) = \sum_{i=1}^n \sum_{j=1}^n \frac{\partial f}{\partial p_i} \frac{\partial f}{\partial p_j} \sigma_{p_i} \sigma_{p_j} \rho_{p_i p_j} \quad (4)$$

where n is the number of parameters, $\frac{\partial f}{\partial p_i}$ is the partial derivative of $f(p_1, p_2, \dots, p_n)$ with respect to parameter p_i , σ_{p_i} is the standard deviation of p_i , and $\rho_{p_i p_j}$ is the coefficient of correlation between p_i and p_j . Thus, for Eq. 3, since $\frac{\partial B}{\partial k} = (\ln \epsilon - \ln c)k^{-2}$ and $\frac{\partial B}{\partial c} = (ck)^{-1}$ it follows that

$$\text{var}(B) = \left(\frac{1}{ck}\right)^2 \sigma_c^2 + 2 \frac{\ln \epsilon - \ln c}{ck^3} \sigma_c \sigma_k \rho_{ck} + \left(\frac{\ln \epsilon - \ln c}{k^2}\right)^2 \sigma_k^2 \quad (5)$$

Estimates of A , c and k are obtained by fitting the logistic and Gompertz equations to the daily pup counts using a nonlinear curve fitting routine such as NONLIN in the SYSTAT (1988) statistical package. The output of NONLIN includes standard errors and a correlation matrix of parameters needed to estimate the variance of B .

Summation method—The second procedure for estimating the mean date of pupping is referred to as the 'summation' method. It assumes the probability, $p(t)$, of a pup being born on day t at a given study site is

$$p(t) = \frac{P_t - P_{t-1}}{P_T} \quad (6)$$

where $P_0 = 0$, and P_T is the maximum number of pups counted at the end of the period $t = 1, 2, \dots, T$. The mean date of birth is derived from

$$\begin{aligned} B &= \sum_{t=1}^T t p(t) \\ &= \sum_{t=1}^T t \frac{P_t - P_{t-1}}{P_T} \\ &= P_T^{-1} \left(\sum_{t=1}^T t P_t - \sum_{t=1}^T t P_{t-1} \right) \\ B &= T - \sum_{t=1}^{T-1} \frac{P_t}{P_T}. \end{aligned} \quad (7)$$

The last step in Eq. 7 is obtained by expanding the summations, combining like terms and using the fact that $P_0 = 0$. Missing values of P_t are estimated from

$$P_t = \frac{P_{t-1} + P_{t+1}}{2}.$$

For two or more consecutive missing counts, the number of pups can be approximated by linear interpolation.

The variance of B for the summation procedure is also estimated by the delta method (Eq. 4). But instead of two parameters as in the sigmoid method, there are now T parameters to contend with. Partial derivatives of Eq. 7 are $\frac{\partial B}{\partial P_T} =$

$\sum_{i=1}^{T-1} P_i P_T^{-2}$ and $\frac{\partial B}{\partial P_i} = P_T^{-1}$ for $i = 1, 2, \dots, T-1$. Assuming multinomial variation and independent daily counts, the covariance term in Eq. 4 (*i.e.*, $\sigma_{p_i} \sigma_{p_j} \rho_{p_i p_j}$) equals

$$\begin{aligned} \text{cov}(P_i, P_j) &= \text{cov}(P_j, P_i) \\ &= P_i \left(1 - \frac{P_i}{P_T} \right) - P_j \frac{P_j - P_i}{P_T} \quad i < j. \end{aligned}$$

However, variance in the numbers of pups counted on any single day, $\text{cov}(P_i, P_i)$, is attributable to both binomial variation and miscounting variation:

$$\text{cov}(P_i, P_i) = P_i \left(1 - \frac{P_i}{P_T} \right) + \alpha P_i.$$

Counting errors increase with the numbers of pups present and are assumed to be proportional to the numbers counted (*i.e.*, αP_i) where, using a running means approach,

$$\alpha = \frac{1}{T-2} \sum_{s=2}^{T-1} \frac{(P_{s-1}^2 + P_s^2 + P_{s+1}^2) - \frac{1}{3}(P_{s-1} + P_s + P_{s+1})^2}{2P_s}. \quad (8)$$

Estimating the variance of B in this manner should provide a reasonable indication of the reliability of B .

If no pups die and there are no errors in counting, the numbers of pups counted each day will rise continuously to an asymptote. Under these conditions P_T (the denominator in Eq. 7) is the maximum number of pups counted at the end of the period $t = 1, 2, \dots, T$. Since counting errors do occur, the ratio P_t/P_T will exceed 1.0 if the maximum number of pups counted occurs before time T . One way to correct for this is to set $P_T = \max P_t$ for $t = 1, 2, \dots, T-1$.

A computational difficulty with the summation method is that values of $p(t)$ can be negative because of errors in counting pups (see Eq. 6). This is not considered a major problem however because the final formulation of B (Eq. 7) is expressed in terms of the summation of daily counts. Such a derivation tends to reduce the effects of counting errors on the estimate of B .

Another point to consider in both the sigmoid and summation methods is how to interpret B . Presumably counts are made at the same time each day during a breeding season. If for example counts are made at 2 pm each day then $B = 1$ would refer to 2 pm of day 1 and $B = 1.5$ would be 12 hours later (*i.e.*, 2 am on day 2). Estimates of B are therefore based upon the time of day pups were consistently counted during the breeding season.

Pup mortality—The above methods assume that no pups died between observations. This means both procedures calculate the mean birth date of pups that were alive on the days of counting, thereby resulting in an under-estimate of the true mean date. This can be corrected if dead pups (D_k) are counted on days $k = 1, 2, \dots, T$.

If dead pups are counted daily, the expected number of pups ($\hat{P}_t$) that would have been counted on day t if all had survived is

$$\hat{P}_t = P_t + \sum_{k=1}^t D_k. \quad (9)$$

which is the count of live pups, plus the daily accumulation of dead pups lying on the beach.

If dead pups are not counted each day, but the mortality rate m is known and assumed to be independent of the time of birth, then the total number of pups (D_{total}) that would have died over the period $t = 1, 2, \dots, T$ can be calculated from

$$D_{\text{total}} = \frac{m}{1 - m} P_{\text{alive}} \quad (10)$$

where P_{alive} is the number of live pups counted at the end of the breeding season, and m is the fraction of pups born that were dead on day T . The number of pups (D_k) that die on day k will equal the product of the total number of dead pups (D_{total}) and the daily mortality rate. Pup mortality curves can be constructed from periodic counts of dead pups (see Results for example).

If the daily mortality pattern is not known, the number of pups that died each day can still be estimated by prorating the total number that died from $t = 1, 2, \dots, T$ according to

$$D_k = \frac{P_k}{\sum_{t=1}^T P_t} D_{\text{total}}. \quad (11)$$

Substituting Eqs. 10 and 11 into Eq. 9 yields

$$\hat{P}_t = P_t + P_{\text{alive}} \frac{m}{1 - m} \frac{\sum_{j=1}^t P_j}{\sum_{k=1}^T P_k}. \quad (12)$$

In this formulation, the expected pup count is sensitive to errors in P_{alive} , the number of pups alive at the end of the breeding season. One means of improving the estimate of P_{alive} is to let it equal the mean number of pups counted over the last few days of observations.

Fur seal pup counts—Northern fur seal pups were counted on study sites from June to August in 1951 (Kitovi amphitheatre, Bartholomew and Hoel 1953), 1962 and 1963 (Kitovi study site, Peterson 1965), and 1983 (East Reef study site, unpublished data from the files of the National Marine Mammal Laboratory, Seattle, WA). No other daily counts of northern fur seal pups are available. The Kitovi sites are located on St. Paul Island and the East Reef site is on St. George Island. In 1983 the pups were counted daily between 11 am and 12 noon from an observation blind overlooking the rookery (R. Gentry, personal communication). Unfortunately written records do not indicate what time of day pups were counted at the other study sites, although I think it can be safely assumed that pups were consistently counted at the same time each day within a given year. In all likelihood counts were made at about midday. Nevertheless counts between years might vary by as much as 8 h depending upon whether they were made at the beginning of the day or at the end of it.

The daily mortality pattern is estimated from counts of dead pups made by Kenyon *et al.* (1954) in 1951 on Vostochni rookery (*cf.* York 1985). The study site was bounded by painted rocks and covered an area of 15,000 square feet. Accumulated carcasses were counted from an elevated walkway that bisected the study site. Counts began when the first pup was born and continued at 5-d intervals.

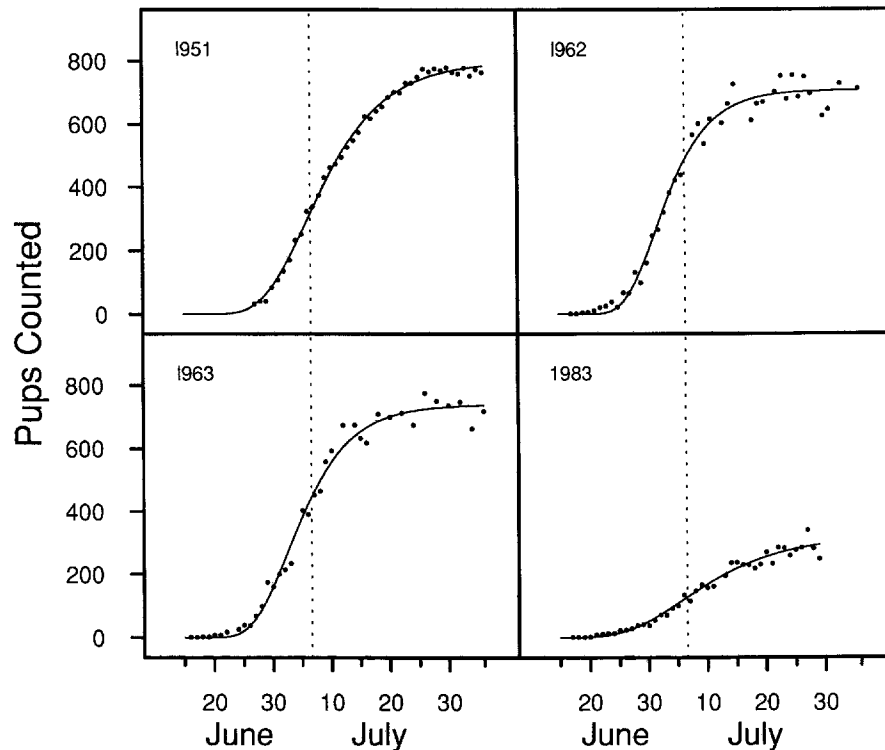


Figure 1. Daily number of live pups counted on four study sites from June 15 to August 5. Data are from Kitovi amphitheatre (1951), Kitovi Study Site (1962 and 1963), and East Reef Study Site (1983). The field counts were fit with Gompertz curves (Eq. 2, Table 1). An estimated median date of birth (July 6, $t = 22.53$, uncorrected sigmoid model) is shown by the dotted vertical line.

RESULTS

The number of pups counted on the four study sites are superimposed with Gompertz curves in Figure 1. The numbers of pups born each day are derived from the Gompertz model, and are scaled by the maximum number born and expressed as a relative number in Figure 2 to facilitate comparing the four data sets. Model parameters and the estimated mean dates of birth are reported in Tables 1 and 2 for the sigmoid (Eq. 3) and summation (Eq. 7) methods, respectively.

Fitting sigmoid curves to the four sets of 'uncorrected' pup counts suggests that the mean date of birth lies between July 3–5 and July 9. The earlier dates are based upon the 1962 and 1963 counts done by Peterson (1965); while the later date is estimated from the 1951 survey of Bartholomew and Hoel (1953) and the 1983 NMML data set. The logistic and Gompertz models fit the daily pattern of pup counts well, and indicate a median date of birth on July 6. Because the results of both models are similar and the squared deviations of samples values were slightly smaller for the Gompertz model, Table 1 only contains Gompertz results.

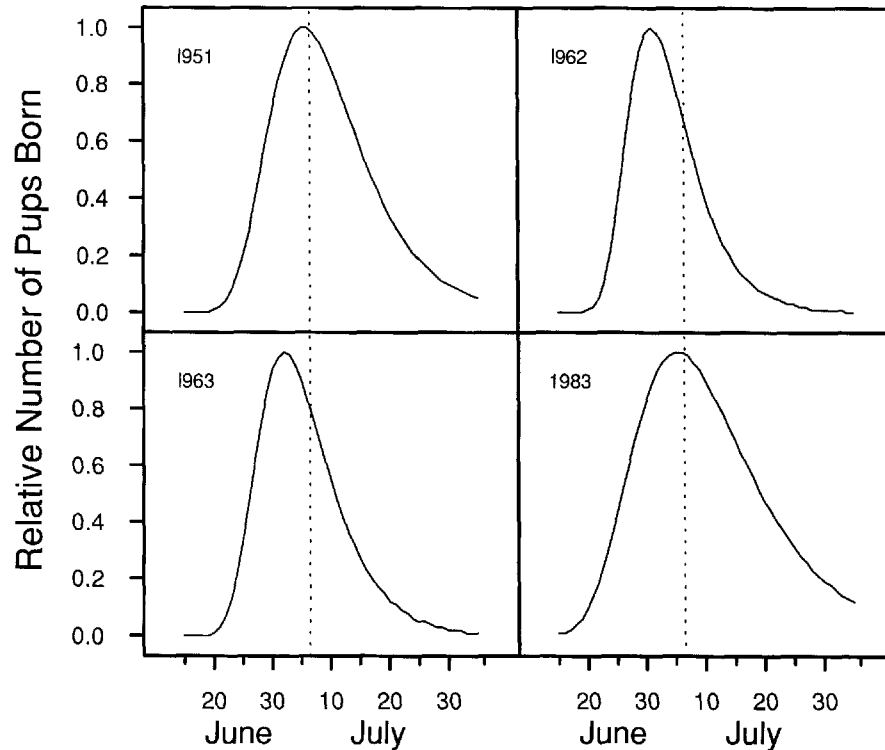


Figure 2. Relative number of pups born each day on four study sites from June 15 to August 5. Data are from Kitovi amphitheatre (1951), Kitovi study site (1962 and 1963), and East Reef study site (1983). The number of pups born each day was derived from the fitted Gompertz model (Table 1, Fig. 1) and scaled for the purpose of comparison. An estimated median date of birth (July 6, $t = 22.53$, uncorrected sigmoid model) is shown by the dotted vertical line.

The summation method suggests the mean date of birth occurs two days later on July 8. The later date reflects the sensitivity of the summation estimates to the magnitude of P_T in Eq. 7. Unlike the sigmoid curves which are less sensitive to outliers, the summation method is sensitive to errors in the maximum number of pups counted by an observer. The reliability of the estimate B resulting from the sigmoid procedure or the summation method depends upon the accuracy of the daily counts during the later part of the season when peak numbers of pups are present. Reliability can be affected by prevailing weather conditions, such as wind and driving rains that cause pups to seek shelter behind logs and under rocks (Ohata and Miller 1977).

Revised estimates of the mean date of birth correcting for natural mortality are found in Tables 1 and 2. Annual estimates of mortality rates were taken from Trites (1989). The total number of pups that died over the period $t = 1, 2, \dots, T$ was estimated using Eq. 10 and multiplied by the cumulative mortality curve in Figure 3 to determine the numbers of dead pups counted on any given day.

Table 1. 'Sigmoid' estimates of the median birth date (B) with 95% confidence intervals for pups born on 4 study sites in 1951, 1963, 1964, and 1983 where day $B = 1$ represents June 15. Pups were counted on n days ending day T . The estimates were derived using the raw daily counts (uncorrected) and the daily counts corrected for annual pup mortality m . Model parameters A , c and k , and associated standard errors are from the Gompertz model (Eq. 2) fit using NONLIN (SYSTAT 1988). The correlation between c and k is ρ_{ck} and MS is the mean squares of the residuals. The mean number of pups counted in the last five days of counts is P_{alive} and the difference between uncorrected B and mortality corrected B equals ΔB .

Sigmoid model	Parameter	1951 Kitovi Amp.	1963 Kitovi	1964 Kitovi	1983 East Reef
Uncorrected	A (se)	799.42 (6.03)	707.91 (10.30)	739.24 (11.84)	319.95 (14.74)
	c (se)	18.56 (1.36)	29.43 (8.14)	22.90 (4.67)	9.63 (1.85)
	k (se)	0.133 (0.022)	0.193 (0.015)	0.169 (0.011)	0.104 (0.011)
	MS	212.47	1,152.66	1,011.94	266.92
	ρ_{ck}	0.975	0.984	0.976	0.967
	B (σ_B)	24.70 (1.01)	19.44 (1.81)	20.66 (1.85)	25.37 (6.06)
	95% CI	22.74–26.68	15.89–22.98	17.03–24.28	13.50–37.24
	B date	July 9	July 3	July 5	July 9
	A (se)	925.43 (8.35)	784.5 (12.22)	804.47 (13.47)	328.59 (16.05)
	c (se)	13.70 (0.86)	18.77 (3.71)	17.48 (3.07)	9.39 (1.81)
Corrected	k (se)	0.133 (0.003)	0.162 (0.011)	0.150 (0.009)	0.101 (0.011)
	MS	241.12	1,174.61	929.60	265.39
	ρ_{ck}	0.973	0.977	0.977	0.969
	P_{alive}	768.24	683.40	724.80	286.82
	m	0.158	0.124	0.076	0.036
	B (σ_B)	26.37 (1.27)	20.43 (2.06)	21.50 (1.96)	25.70 (6.44)
	95% CI	23.88–28.85	16.39–24.46	17.65–25.35	13.08–38.31
	B date	July 10	July 4	July 5	July 10
	n	40	41	37	42
	T	52	52	52	45
Both	ΔB	1.67	0.99	0.84	0.33

The general pattern of births were compared among years by contingency analysis (using only days when pups were counted in all four years) and found to be significantly different (Pearson $\chi^2_7 = 425.3$, $P < 0.001$). Kolmogorov Smirnov tests suggest the difference between 1951, 1963 and 1964 was not significant ($ks = 0.15$, $n = 4$, $P = 0.95$), but that the pattern of pupping in 1983 differed significantly from previous years ($ks = 0.65$, $n = 20$, $P < 0.001$). Point estimates of B were smaller in 1963–64 compared to 1951 and 1983. However, the differences in mean and median birth dates were not deemed significant based on overlapping confidence limits (see Tables 1 and 2).

DISCUSSION

Analysis of harvest statistics and behavioral studies have provided information on the arrival times of adult and juvenile northern fur seals on the Pribilof Island rookeries (Jordan and Clark 1898; Bartholomew and Hoel 1953; Peterson 1965, 1968; Gentry 1981; Bigg 1986). Analysis of the cumulative pup counts adds further information about pupping and timing of the fur seal's life cycle.

The number of pregnant females returning each summer to give birth on the small Bering Sea islands has ranged from 450,000 in the 1950s, to just under 200,000 in the mid 1980s (Lander 1980, Roppel 1984, York and Kozloff 1987, Trites 1989). Reproduction has remained highly synchronized and consistent from one year to the next (Figs. 1 and 2). This phenomenon may reflect climatic seasonality and is likely a strategy that maximizes reproductive success (Peterson 1965, 1968; Ims 1990).

Parturition in northern fur seals occurs on average 0.8 d after arriving ashore and appears to be triggered by their arrival on the rookery (Peterson 1965, Bigg 1984, Gentry and Holt 1986). Thus the abrupt rise in the number of pups born per day in late June reflects the return of pregnant females (Fig. 2). The return schedule is positively skewed, indicating a tendency to be late rather than early. The late arriving pregnant females are probably young and primiparous with a less developed homing instinct than older females (Bigg 1986).

Pupping occurs over a 5-week period. Over 50% of the Pribilof pups were born during the first two weeks of July (56–77%) with over 75% born within a three week period (75–91% between June 28–July 20). The general pattern of births was consistent in all four years studied. Further evidence that this pattern remains the same across years is that daily counts of females at East Reef Rookery peak during the week ending July 13 and have done so for the past 16 yr (Gentry and Francis 1981; R. Gentry, personal communication).

In 1951 pup mortality peaked on July 25 (Fig. 3), 14 d after the median birth date of July 11 (Kitovi 1951; Fig. 1, Table 2). Although the live and dead pups were not counted on the same study site, they were made in the same year and should be comparable. Female fur seals typically spend the first seven days ashore nursing their pups before departing to feed at sea (Gentry and Holt 1986). During the mother's absence the pup receives no care from any other animal. In 1951, the first feeding trip to sea lasted an average of

seven days ($\sigma = 1.1$, $n = 11$, Bartholomew and Hoel 1953, Gentry and Holt 1986). Comparing Figures 1 and 3, it would seem that most pup mortality occurs while the pup is left unattended for the first time, with the greatest number of deaths occurring just prior to the female returning to nurse her pup.

Because of the large variation in daily counts, it cannot be concluded that the small differences of 1–4 d in mean date of birth from 1951 to 1983 were significant. However, there are several reasons to expect differences in the timing of birth. For example, slight differences in timing could exist between rookeries given that adult females show a high site tenacity to their rookery of birth, and the timing of birth may be genetically determined. Another consideration is that the age composition of the rookeries may have changed with time due in part to the commercial harvesting of females that occurred from 1956–68 (Lander 1980). A rookery with many older pregnant females should show an earlier mean date of birth than a rookery of young females, because the older females return first to the breeding islands (Bigg 1986). Thus the female harvest may explain the possible shift in mean date of birth at Kitovi from July 11 in 1951 to July 7 in 1963–64 (Fig. 2).

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