ATTENUATION OF NURSING-RELATED OVARIAN SUPPRESSION AND HIGH FERTILITY IN WELL-NOURISHED, INTENSIVELY BREAST-FEEDING AMELE WOMEN OF LOWLAND PAPUA NEW GUINEA

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Summary. Intense, sustained nursing lengths inter-birth intervals and is causally linked with low natural fertility. However, in traditional settings, the effects of such nursing on fertility are difficult to disentangle from those of nutrition. Results from a prospective, direct observational study of reproductive function in well-nourished Amele women who nurse intensively and persistently but who also have high fertility are here presented. Endocrine measures show that ovarian activity resumes by median 11.0 months postpartum. Median duration of postpartum amenorrhea is 11.3 months, time to next conception is 19.4 months, and the inter-birth interval is 28.0 months. Average life time fertility is 6.0. High fertility in Amele women is due both to refractoriness of reproductive function to suckling stimuli, and to maintenance of equivalent age-specific fertility rates across the reproductive life span.

Introduction

The relationship of nursing behavior to reproductive function and birth spacing has received intense scrutiny during the last 15 years. Physiological and demographic data (Howe & McNelly, 1982; Whitworth 1988) have led to the conclusion that, in natural fertility populations, sustained breast-feeding provides the greatest single contribution to length of inter-birth interval (Bongaarts & Potter, 1983; Short, 1984). Nevertheless, the efficacy of sustained intense nursing in suppressing ovarian function varies widely among individuals and populations (Stern et al., 1986; Huffmax et al., 1987a; Lewis et al., 1991). Maternal nutritional status has been implicated in this variation (Bongaarts & Delgado, 1979; Prema et al., 1981; Lunn et al., 1986; Huffman et al., 1987b; Rosetta, 1989). This report presents evidence that, even when they nurse intensively, women of good nutritional status do not experience the same degree of ovarian suppression as do less well-nourished populations with similar nursing patterns.

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Investigation of suckling-induced ovarian suppression in humans has been complicated by interventing variables that modify direct effects of nursing. Factors such as work, social custom and personal preference determine nursing behaviour and thereby affect the nursing-fertility link. Both the frequency and the duration of nursing episodes have been found to influence duration of postpartum amenorrhoea, and it has been repeatedly observed that women who nurse more frequently or in longer bouts experience longer postpartum amenorrhoea than do their peers who nurse less intensively (Ellis, Teas & Bora, 1986; Jones, 1988, 1989). In addition, nutritional status of the mother appears to modulate the effects of nursing. In a marginally-nourished Gambian community, lactating women receiving food supplements showed higher prolactin levels and shorter postpartum amenorrhoea than unsupplemented women (Lums et al., 1980, 1984). Women in Bangladesh with low body weight and weight for height experience longer durations of postpartum amenorrhoea than their peers (Huffman et al., 1987b). In the same population, better-educated nursing women with presumed better nutrition have shorter periods of postpartum amenorrhoea, although they also have earlier supplementation and weaning. The degree to which the influence of maternal nutrition on nursing-induced ovarian suppression is mediated by changes in nursing behaviour (either mother- or infant-initiated) rather than a direct physiological effect of maternal nutrition remains disputed (Scott & Johnson, 1982).

While the linkage of nursing to suppression of ovarian function has been well established (Glasser, McNeilly & Howe, 1986; Howe et al., 1982; McNeilly et al., 1982a; Stern et al., 1986), the precise mediators of this suppression are still controversial. Prolactin release is provoked by nipple stimulation via a neural reflex. Elevated prolactin in nursing mothers has been thought to be responsible for ovarian suppression through direct effect on the ovary, interference in ovarian regulation by the pituitary, and/or impairment of the adequacy of luteal phases after menstrual cycling resumes (Delvoye, Delegne-Destorch & Robyn, 1980, 1982a,b). But recent evidence suggests that other mechanisms for suppression of ovulation, such as nursing-induced disruption of pulsatile secretion of gonadotropins, without prolactin mediation, may reinforce or constitute the primary basis for these effects (McNeilly, 1987; Whitworth, 1988). Nipple stimulation is recognized as an antecedent in all of these functional schemes. Thus, as a measure of nipple stimulation, if not of direct ovarian regulation, regulating prolactin remains a salient physiological measure.

Large population differences in nursing customs—from prolonged and intense to brief or absent—have provided opportunities to probe the influence of these practices on maternal reproductive function and fertility patterns (reviewed by Howe & McNeilly, 1982; Rivers et al., 1985; Vitzthum, 1989). Comparisons among populations has, however, been impeded by differences in important factors such as nutrition and health, which confound the possible contribution of differences in the nursing patterns themselves. Food intake has been compromised in most of the groups studied in non-western countries (e.g. Kung, Gains, Bangladesh, and several West African populations), which has led to the contention that energy restriction can be a more important determinant of fertility than is nursing (Vitzthum, 1986). Although the contribution of intense and prolonged nursing to low inter-birth intervals and low lifetime fertility has been well documented in certain traditional settings (Kotter & Worthman, 1980; Wood, Johnson & Campbell, 1985a; Wood et al., 1985b), the
question of whether intensive nursing practices are also compatible with high fertility has not been addressed.

This report presents a prospective, direct observational study of the relationship of nursing pattern to postpartum resumption of maternal reproductive function in a relatively better-nourished adult population with intense and prolonged breast-feeding, good health care and high fertility. Reproductive function is evaluated from endocrine and demographic measures (prolactin levels, ovarian function, and duration of postpartum amenorrhoea and birth interval) from a cohort of Amele mothers in Papua New Guinea. This, along with one other study (Haffman et al., 1987a), is the only longitudinal investigation of postpartum ovarian function and inter-birth interval that incorporates direct observation of nursing behaviour, rather than self-report.

Materials and methods

Study population

The study was conducted in the period January 1983–April 1984 among the Amele, bush-fallow cultivators of north-east lowland Papua New Guinea. Relevant cultural, demographic, and health-related information has been reported elsewhere (Jenkins, Orr-Ewing & Heywood, 1984; Jenkins & Heywood, 1985; Jenkins, 1989). A total population of around 6000 is distributed in 28 villages over an area of 200 km², with a population density of 30/km². Adult Amele have a relatively good nutritional status, due to a productive lowland farming system (Allen, 1980), as well as their extensive dietary use of high-fat coconut and access through the cash economy (wage-earning and marketing in a town 16–18 km distant) to protein- and calorie-rich foods. In addition, the population has access to health services, a clinic established in the 1950s that provides pre- and postnatal care and contraceptive services, along with comprehensive clinical and surgical care (Jenkins, 1989). Nearly all infants are born at the clinic, and birth weights have risen over the last four decades. The 1982–84 infant mortality rate was 46 per 1000 live births among the Amele and surrounding area (Mele et al., 1989).

Participants were drawn from twelve of the 28 Amele villages to represent the range of microclimates from sea level to 200 m. The study recruited 52 women who had an infant under 1-5 years of age that was breast-fed and who were not using contraceptives. None used contraceptives during the study period. Participants had a mean age of 29 years (range 19–45) and median parity of three (range 1–12); ages of infants observed across the study interval ranged from 0.6 to 34.3 months. Each woman provided a complete reproductive history, long term follow-up of subjects to the present has yielded time of resumption of menses for 39 and closed birth intervals for 33 participants.

Behavioural measure

Nursing activity was measured by direct observation and continuous recording by three investigators; 75% of observations were made by a single observer. Observation sessions included 21 morning-only (mean duration 3.7 hr), 29 afternoon-only (4.9 hr), 52 full-day (8.0 hr) and 2 night-time periods (12.1 hr), for a total of 680 recorded hours on 104 separate occasions with 52 different infant–mother pairs. Average number of
observation sessions per child was 1.9 (range 1–4); each session with individual infants was taken at different developmental ages. Termination of an observation period was determined by time of day (noon or 17.30 hours), or by a break in the daily activity routine, and was thus independent of nursing activity. Onset of a suckling episode (bout) was timed from application of the mouth to the nipple, with removal marking the end of the event and the beginning of the subsequent inter-bout interval. Clock time of onset of a suckling bout was recorded in hours and minutes, and the duration was measured in seconds with a stopwatch. (This presents some difficulty for analysis; see Alason, 1982.) Inter-bout intervals of ≤ 6 seconds were dropped in analysis and added, along with the time of the succeeding bout, to the duration of the previous one. In all, 1549 nursing events were noted.

**Hormone sampling**

Serum samples for prolactin determination were drawn by finger-grip from 38 participants on two separate occasions in conjunction with observations of nursing activity at different stages of infant motor development (Jenkins & Heywood, 1985). A total of 66 blood samples were taken towards the end of sessions of direct observation of daytime nursing, within one-half min of the end of a nursing bout. Sera were frozen immediately upon separation by centrifugation and stored at −70°C until laboratory analysis.

Saliva samples were obtained from 51 of the participants for measurement of gonadal steroids; one sample of 1–4 mL was collected at the time of entry into the study, and one each during subsequent infant motor development stages, for an average of three samples per woman (range 1–2). Samples were stored at −70°C until laboratory analysis. Previous experience with saliva collection in this population had shown that bleeding gums are rare among Amele (Orr-Ewing, Heywood & Coward, 1986). Betel nut is chewed by most women, 10% of saliva samples showed some discolouration and presumably contained chemical residues from betel, but these do not appear to interfere with the steroid assays used; no difference in measures of duplicate samples heavily stained or unstained with betel was found.

**Physical measures**

Each month, mothers were asked whether and when they had menstruated during the previous month. Weight, skinfold measures (triceps, subscapular), and mid upper arm circumference were taken with triple beam balance (CMS, London), Holtain skinfold calipers, and steel tape, respectively.

**Population surveys**

Ongoing demographic surveillance as well as child development and nutrition studies of the Amelé population supplied a full information source, providing larger data bases for calculation of birth interval, completed fertility, and age at introduction of solid foods (weaning) and of denial of the breast (severance). A demographic survey was taken in 1982–84 from a random sample of 522 women (drawn from a complete demographic index of the population), stratified by 10-year age groups of females aged 15 years and over. The reproductive histories obtained by this survey provided the basis for calculations of lifetime fertility patterns among Amelé. Another survey of 663
Amelie and surrounding closely related populations, drawn by the National Nutridon Survey in 1982-83, yielded population data on infant age at weaning and of severance.

Hormone analysis

Serum prolactin. Serum prolactin (PRL) was measured using a fluorescence immunoassay (FILIA) from Pharmacia Diagnostics (Löfgren, 1985), based on the direct sandwich technique employing two monoclonal antibodies directed against different sites on the hormone molecule. The manufacturer's protocol was strictly followed. Performance characteristics for the assay were as follows. Assay sensitivity, determined in the authors' laboratory and defined as 3 SDs above the mean of the zero standard, is 0.01 ng/mL. Exploratory coefficients of variation are 3.2% (pool 1, 0.02 ± 0.00 ng/mL, mean ± SD), 3.7% (pool 2, 54 ± 2.0 ng/mL) and 19% (pool 3, 59 ± 9.9 ng/mL). Inter-assay coefficients of variation are 5.2% (pool 1, 3.5 ± 0.2 ng/mL, mean ± SD), 7.5% (pool 2, 19.4 ± 1.5 ng/mL) and 4.4% (pool 3, 44.7 ± 2.6 ng/mL, n=6). The assay has no significant cross reactivity with LH, FSH, TSH, HCG, or HGH. Recoveries range from 98 to 102%.

Salivary zeotrode. A total of 138 saliva samples were assayed for progesterone (P), employing a modified protocol of a commercially available kit for serum P (Parke, No. 137). Saliva samples were centrifuged, and the supernatant withdrawn and aliquotted as for assay. Standards (50 µL and 450 µL working buffer [phosphate buffered saline with 0.1% BSA]) and 0.5 mL saliva samples and controls were incubated with 10 µL tracer for 30 min, then extracted twice with 5 mL ether and dried under nitrogen. Dried extracts were brought up in 0.5 mL working buffer with 2 min vortexing, 10 min incubation at 37 °C and 1 min further vortexing. Duplicate (100 µL aliquots of reconstituted extracts were placed in 12 x 75 mm polypropylene tubes and counted for recovery, after which 100 µL of tracer and 100 µL antibody (diluted 1:16 in working buffer) were added. Following overnight incubation at room temperature, 100 µL of the second antibody was added. A further incubation for 1 hr at room temperature was followed by 1 hr room temperature centrifugation at 2800 rpm. Supernatants were decanted immediately, and the tubes counted for 10 min each.

Sensitivity of the modified P assay is 19 pmol/L (0.1 pg/mL), defined as binding inhibition equivalent to 2 SDs from the zero standard. The antisera does not measurably cross-react with related steroids. Extraction recovery was 82-100%. Method recovery varied between 99 and 103%. Within-assay coefficient of variation (CV) was 12.4% and 7.5% for the low (171 ± 21 pmol/L, mean ± SD) and medium pools (884 ± 63 pmol/L, n=10), respectively. Inter-assay CV was 9.6% in the low pool and 7.2% in the high (n=8).

Salivary oestradiol (E2) was determined using a modified [125I] radioimmunoassay kit from Ecolab, which has been described elsewhere (Woehlman, Stallings & Hoffman, 1990). Due to limited sample volume, only 113 of saliva samples could be measured for E2.

Statistical analysis

All hormonal and some nursing variables had skewed distributions which were linearised by logarithmic transformation for statistical evaluation. Thirteen women
became pregnant during the hormone sampling period, all post-conception endocrine samples were omitted from calculations of gonadal Steroid means and correlations.

Results

Infant feeding

All Amel infants are breast-fed, and the nursing attitude can be characterised as indulgent demand feeding. Mother-infant pairs are in constant physical proximity during approximately the first 6 months postpartum, after which time mothers arrange work to minimise physical separation and accommodate infant demands. Other caregivers were present in about 30% of all observed nursing events. Supplementary foods are introduced slowly, commencing with watery semi-solids, then mashed starchy staples, and finally principal reliance on a standard diet. Based on the population nutrition survey (n = 662), median age at introduction of supplementary foods is 7-4 months (6-7 to 8-1 months, 5 and 95% confidence intervals). Supplements to breast-milk are initially liquids or semi-liquids rather than solids. Severance is initiated only upon an established subsequent pregnancy or advanced child age (5 years); nutrition survey data indicate that this occurs at median age 36-3 months (34-0 to 39-2 months, 5 and 95% confidence intervals; n = 586).

During the first 18 months of life, infants are breast-fed 1-5-3 times per hour in bouts lasting 1-3 min. Amel believe that breast-feeding is adequate to support infant needs at least through the crawling stage (i.e. to about 12 months of age). This perception may be based on the intensity and extent of lactation: Orr-Ewing et al. (1986) have found that mothers in this population produce sustained high milk outputs with high fat content. Outputs of over 830 g/day are attained by 6-8 months; output peaks at 901 g/day at 9 months with a slow decay thereafter, so that 501 g/day are still produced at 24 months postpartum. However, it is well recognized that breast-feeding alone cannot adequately support an infant beyond the age of 6 months. Indeed, the inadequacy of even Amel mothers' rather high milk outputs to sustain optimal infant growth is demonstrated by poor infant weight gains after the age of 6 months (Jenkins et al., 1984). Nevertheless, mothers rely on breast-milk as the principal diet for infants in their first year.

Breast-feeding frequency, duration, and interval are shown by time postpartum in Fig. 1. The method of correction for bias from truncated intervals employed by Wood et al. (1985b) was applied to calculate mean inter-bout intervals per observation session. This correction increased inter-bout estimates by 25%, a correction notably smaller than the 87% derived for Gaoni (Wood et al., 1985b), due probably to differences in distribution of bout intervals. Mean inter-bout interval per observation session by mother-infant pair was also used so that all pairs were equally weighted. Both mean and median values are plotted because there is marked individual variation in observed nursing patterns that increase with length of lactation and tends to inflate mean values; thus, medians are more representative for the population. Neither nursing frequency decays ($F = 1.9, p = 0.18, \text{slope} = 0.05$) nor inter-bout interval increases ($F = 0.02, p = 0.69, \text{slope} = -0.05$) linearly with infant age. Median nursing frequency rises consistently from 1-5 to 3 times per hour over the first 12 months and then declines to around 2 hr at 2 years. Otherwise, median inter-bout interval declines steadily to half
Fig. 1 Nursing variables—breast length, interval, and duration; median and mean SD, by infant age group. Because individual values show skewness of distribution that becomes more pronounced with time, the mean is a more representative value for the population than is the median.
its initial value over the first year of life, from 34 to 17 min; during the next year, it returns to 22 min. There was no relation between infant morbidity (as measured by maternal recall) and nursing frequency, which discounts the possibility that illness-related fussiness would account for increasing bout frequency over the first year. Bout duration does decrease with time (F = 13.2; p < 0.001; slope = -0.43, r = 0.32); length of nursing sessions is half as long in the second as it is in the first 6 months of nursing. Nursing episodes last over 3.3 min during the first 6 months, and then drop sharply to 1.5–2 min, with a field decrement to 0.6 min in nurseries over 2 years old.

Some previous studies have reported total suckling activity in terms of minutes per hour. To allow for comparison with these reports, total daytime nursing minutes per hour by age group in this study group was as follows: 0–3 months: 7.5 ± 4.1 (mean ± SD); 3–6 months: 8.2 ± 3.2; 6–9 months: 4.1 ± 2.6; 9–12 months: 5.1 ± 1.8; 12–18 months: 6.0 ± 1.8; 18–24 months: 7.2 ± 3.7; > 24 months: 2.4 ± 1.3 (n = 21, 15, 18, 9, 22, 21, 5, respectively). Total hourly nursing time decreases significantly with age (F = 9.34; p < 0.005; slope = -0.66, r = 0.69), a relationship driven by the significant decrease in bout duration over time.

Ovarian function

Serum concentrations of prolactin in nursing Amelie women are shown in Fig. 2 by time postpartum; the standard errors indicate high variance. Circulating prolactin decayed over time (F = 3.3, p < 0.05; slope = -1.55); it remained elevated during the first 12 months of nursing, but fell sharply at 12 to 18 months. Corresponding profiles of ovarian steroids in saliva (Fig. 2) show that E2 levels rose first, indicating resumption of follicular development in some women, followed by a rise in P reflective of returning lutetial activity in increasing numbers of women. Given individual differences in degree of ovarian activity, prevalence of resumed ovarian function may be more informative than group means. Therefore, samples were scored on the basis of whether values of either gonadal steroid were elevated above 3.32 pmol/L for E2 or 45 pmol/L for P, and each individual’s sample series was coded in terms of whether and when detectable ovarian activity appeared. The cut-off for E2 corresponds to a serum concentration of 66.9 pmol/L, somewhat above mean follicular serum levels of 35.9 pmol/L found in normal menstrual cycles, while the P cut-off corresponds to a serum concentration of 98.3 pmol/L, above which some luteal activity is indicated. (Estimated serum equivalents are based on comparison of concentrations in matched saliva and serum samples. Saliva: serum ratio is 0.005 for E2 and 0.015 for P.) Use of these cut-offs would therefore slightly overestimate time of resumed ovarian activity. In Fig. 3, the proportion of women in whom ovarian activity had been detected is plotted by grouped time postpartum. Based on maximum likelihood regression, 50% of women have evidenced ovarian activity by 11 months after delivery. This figure concurs well with prospective verbal reports on return of menses, which when calculated from 39 closed intervals fell as median 11.3 months (mean ± SD 11.3 ± 6.6, range 12–26.6 months). After a correction factor of 2.3 months is applied for censored intervals, the corrected mean length of postpartum amenorrhea is 13.5 months.

Sustained nursing maintains prolactin levels through the first year of lactation, but it does not protect most Amelie women from experiencing concurrent increases in
Fig. 2. Postpartum endocrine changes in Amul mothers mean ± SE by time (for PRL, progesterone and oestradiol). PRL affects degree of and/or maternal hypothalamic-pituitary response to nipple stimulation; gonadal steroids indicate degree of ovarian activity.

Ovarian activity. The expectation that prolactin suppresses ovarian function is at odds with the observation that gonadal activity becomes detectable in the majority of women when PRL levels remain high, although they have begun to decline. While PRL concentrations decrease with time postpartum, they do not correlate with either ovarian steroid (E2, p < 0.69; P, p = 0.92), although both hormones correlated strongly with time (E2, p < 0.003; P, p < 0.001). Because PRL values represent stimulated, immediately post-nursing responses, the important difference may be among women rather than change with time. This possibility was tested by comparing PRL concentrations in women who had resumed ovarian function with those who had not, but no difference was found (independent t = -0.415, p = 0.69). Perhaps a relationship of PRL to gonadal steroids obtains only when PRL concentrations fall below very high levels. However, no significant correlation was found between PRL and either gonadal steroid.
when prolactin was below either 20 (low end of elevated range) or 15 ng/mL (maximum normal range), nor were there differences in genital steroid concentrations between groups defined by either of these cut-offs.

Prolactin decreases most steeply in Amielle women when breast frequency and interval show little change. However, breast length does drop markedly in the latter half of the first year postpartum. Episode duration was correlated with serum PRL concentration (p < 0.001, r² = 0.34), and negatively associated with salivary progesterone. However, analysis identified independent significant effects for inter-bout interval or nursing frequency on PRL level. The model best explaining PRL variance is log mean bout duration, log corrected mean inter-bout interval, mean maternal, trophoblast, skinfold, log infant age, entered in that order (r² = 0.52).

Perhaps subtle shifts in nursing pattern are more responsible for degree of ovarian regression than is prolactin alone. A study of American women has indicated that nursing pattern, rather than a specific projection level, is more closely linked to length of postpartum amenorrhea (Stern et al., 1986). An unobserved nursing dimension—sucking rate and efficiency—may also be an important variable here. (Bowen-Jones, Thompson & Drewett, 1982). A multiple regression model revealed that duration of postpartum amenorrhea was strongly explained by mother's parity and age, inter-bout interval, and time postpartum (p < 0.001, r² = 0.74), and that time retained a high significance for this interaction. Timing of introduction of supplementary feeding, on the other hand, had no influence on duration of amenorrhea (F = 0.255, p = 0.61), nursing frequency (F = 1.89, p = 0.16), or bout duration (F = 0.44, p = 0.54). Length of postpartum amenorrhea was in turn, marginally correlated with length of subsequent births interval (F = 4.4, p = 0.05), but it explained only 16% of interval variance.
ERRATUM

Attenuation of menopause-related ovarian suppression and high fertility in well-nourished, incessantly breastfeeding Amele women of lowland Papua New Guinea

Carol M. Worthman, Carol I. Jenkins, Joy F. Stallings & Dante Lai


By error, an incorrect version of Fig. 2 was published in this article, on p. 433. It should be replaced by the correct diagram, as given below.
Maternal nutritional status

The 52 Amole women in the study were reasonably well-nourished, averaging between 6 and 12 months post-partum, in weight 52.1 ± 7.3 kg (mean ± SD), height 150 ± 5.1 cm, body mass index (BMI: weight/height$^2$) 23.3 ± 2.9 kg/m$^2$, tripeps skinfold 14.6 ± 6.0 mm, subscapular skinfold 20.4 ± 11.6 mm and mid upper arm circumference 26.2 ± 2.4 cm. Nursing patterns may be influenced by maternal nutrition: maternal tripeps skinfold correlated with the number of nursing bouts per hour ($p < 0.005$, $r^2 = 0.45$). Maternal nutritional status also appeared to influence prolactin concentrations, for multiple regression of tripeps skinfold and breast length explained 45% of the variance in that hormone ($p < 0.005$).

Inter-birth interval and life-time fertility

Given the length and intensity of nursing, the period of amenorrhoea is unexpectedly short and contributes to relatively brief inter-birth intervals. The sample of 52 nursing Amole women yielded an adjusted mean birth interval (calculated according to Henry, cited in Wood et al., 1985) of 31.7 months (unadjusted mean, 30.8 months; median 24.0 months; number of closed intervals = 34). Performance of the present small sample is quite similar to that of the population as a whole. Analysis of the large sample of reproductive histories ($n = 520$) yielded an inter-birth interval of 30.9 ± 14.5 months (mean ± SD) and median of 27.6 months. Correction for truncated intervals raised the estimated mean to 31.8 months. For this sample of nursing women, subtraction of a presumed 9 months' gestation period places the estimated median time to next conception at 19.0 months. The median period of lactational amenorrhoea thus accounted for just 59% of the time to next conception. The rather long wait to conception may reflect lactation-induced subfertility, as menstrual cycles may be impaired by continued nursing. It may also reflect some contraceptive use for birth spacing after the completion of the study.

Data from the 1982-84 demographic survey showed that total fertility, or mean number of live births per post-reproductive woman (here, women over age 40) is 2.68 ± 3.2, variance 10.3. This figure includes ten infertile women, or 6% of the sample ($n = 163$). If these are excluded from analysis, mean life-time fertility is 7.14 ± 2.9, variance 7.9. Cumulative fertility (Table 1), the age-specific number of live births, corresponds to the total fertility estimate. Amole women commence childbearing by age 20 and maintain equivalent fertility rates until age 40. Birth intervals (population mean, 30.7 months) varied by neither parity nor maternal age (Table 2). Comparison of variance in inter-birth intervals between the youngest and oldest (40+) age groups showed no difference ($F^2 = 2.14, p = 0.08$), and between parity 1 and 8 + was significant ($F^2 = 2.51, p < 0.005$). Thus, Amole women on average attain a total fertility of nearly seven births by sustaining reproductive output over an excess of 20 years.

Fertility may actually be declining in this population, due presumably to use of contraception, which is readily available through the health clinic. Average parity (Table 3) is lower at nearly all ages in 1984 than it was in 1964 or 1974. Attempts to space children may partly account for the long 7.7-month wait to conception in the longitudinal sample, and the relatively low contribution of postpartum amenorrhoea.
### Table 1. Adjusted age-specific fertility rate and cumulative fertility

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>No.</th>
<th>P-F ratio</th>
<th>Adjusted fertility rate (K = 0.991)</th>
<th>Cumulative fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-19</td>
<td>118</td>
<td>0.943</td>
<td>0.076</td>
<td>0.30</td>
</tr>
<tr>
<td>20-24</td>
<td>102</td>
<td>1.030</td>
<td>0.322</td>
<td>1.87</td>
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<tr>
<td>25-29</td>
<td>88</td>
<td>0.968</td>
<td>0.277</td>
<td>3.26</td>
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<tr>
<td>30-34</td>
<td>76</td>
<td>0.976</td>
<td>0.277</td>
<td>6.64</td>
</tr>
<tr>
<td>35-39</td>
<td>39</td>
<td>0.963</td>
<td>0.288</td>
<td>6.18</td>
</tr>
<tr>
<td>40-44</td>
<td>47</td>
<td>0.977</td>
<td>0.056</td>
<td>5.50</td>
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<tr>
<td>45-49</td>
<td>45</td>
<td>1.013</td>
<td>0.060</td>
<td>6.12</td>
</tr>
</tbody>
</table>

Based on P-F adjusted ratio method for estimating fertility (Brass methods).
Includes all females, ever married or not.

### Table 2. Duration of inter-birth intervals by maternal age and parity

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>No.</th>
<th>Mean interval (months)</th>
<th>SD</th>
<th>Parity</th>
<th>No.</th>
<th>Mean interval (months)</th>
<th>SD</th>
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<td>26.3</td>
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<td>30.3</td>
<td>14.2</td>
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<td>30.2</td>
<td>13.1</td>
<td>3</td>
<td>92</td>
<td>31.2</td>
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<td>30-34</td>
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<td>32.4</td>
<td>14.3</td>
<td>4</td>
<td>76</td>
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<td>20.7</td>
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<td>33.5</td>
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<td>40-44</td>
<td>10</td>
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<td>6</td>
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<td>45+</td>
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<td>7</td>
<td>24</td>
<td>40.7</td>
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<td>Total</td>
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<td>14.8</td>
<td>8</td>
<td>26</td>
<td>28.4</td>
<td>17.2</td>
</tr>
</tbody>
</table>

to time to conception. Secondary infertility may contribute as well. Jenkins (1991), unpublished found that the proportion of secondary infertility rose among Amel between 1964 and 1984, due probably to substantial increases in gonorrhea and other sexually transmitted diseases. These changes in fertility over time may influence validity of the estimate of life-time fertility derived in Table 1. Brass methods for estimating fertility assume a constant fertility rate through time, which is not true for Amel, whose fertility is declining. Thus, the figures probably slightly underestimate total fertility of the older women.
Table 3: Average parity by age at 10-year intervals

<table>
<thead>
<tr>
<th>Age (years)</th>
<th>Average parity</th>
</tr>
</thead>
<tbody>
<tr>
<td>15-19</td>
<td>0.83 1.14 0.10</td>
</tr>
<tr>
<td>20-24</td>
<td>1.64 1.92 1.27</td>
</tr>
<tr>
<td>25-29</td>
<td>2.48 3.01 2.35</td>
</tr>
<tr>
<td>30-34</td>
<td>4.00 4.67 3.96</td>
</tr>
<tr>
<td>35-39</td>
<td>5.21 6.11 5.04</td>
</tr>
<tr>
<td>40-44</td>
<td>6.42 5.41 6.09</td>
</tr>
<tr>
<td>45-49</td>
<td>7.43 7.14 6.84</td>
</tr>
</tbody>
</table>

Discussion

Previous studies on effects of lactation on fertility have focused on the contraception of frequent, sustained nursing to low fertility and the linkage of high fertility to cessation of breast-feeding practices. Amo and his associates have focused on the effects of lactation on the reproductive cycle of women in a community with a high prevalence of breast-feeding. They have found that lactation delays ovulation and inhibits ovulation, leading to a decrease in fertility. This result is consistent with findings in other populations with high prevalence of breast-feeding (Eisenberg et al., 1978; Lunn et al., 1984; Ford & Huffman, 1988).

In other populations, the effect of lactation on fertility has been less pronounced. In these populations, the prevalence of breast-feeding is lower, and the effect of lactation on fertility is less significant. In these populations, the prevalence of breast-feeding is lower, and the effect of lactation on fertility is less significant.

The duration and intensity of nursing among Amo are important factors in the observed effects of lactation on fertility. Long periods of nursing, particularly those that extend beyond the first year of life, are associated with a lower fertility rate. Shorter periods of nursing, on the other hand, are associated with a higher fertility rate. These findings are consistent with studies in other populations with high prevalence of breast-feeding (Eisenberg et al., 1978; Lunn et al., 1984; Ford & Huffman, 1988).

In summary, lactation has a significant effect on fertility in populations with high prevalence of breast-feeding. The effect of lactation on fertility is strongest in populations with long periods of nursing, particularly those that extend beyond the first year of life. In other populations, the effect of lactation on fertility is less pronounced.

References


remains elevated. In contrast to other studies (Konner & Worthman, 1986; Hennart et al., 1985; Mowle et al., 1981; Johnston & Amico, 1986), among Amale PRL does not evidence a correlation with direct measures of nursing intensity (episode frequency and interval), but does correspond to episode duration. This may be due in part to diminution of hypothalamic reactivity to nipple stimulation: PRL begins to fall at 9-12 months, when nursing frequency reaches its peak and inter-bout interval is shortest. Progressive decreases in responsiveness of PRL release to the suckling stimulus have been noted in other investigations of prolonged lactation in well-nourished western populations (Johnston & Amico, 1986; Stern et al., 1986). Moreover, dietary supplementation of marginally-nourished Gambian women has been observed to blunt PRL levels in early lactation, and to depress PRL concentrations at all subsequent stages (Lunn et al., 1990, 1994). While an inverse relationship between maternal weight and both duration of lactation and lactational amenorrhea has been reported in poorly-nourished populations (Prema et al., 1981; Ford & Huffman, 1984), no such association was found among Amale. A similar lack of association has been noted in well-nourished Australian women (Lewis et al., 1991). Amale women may be above a threshold in weight or 'energetic balance', beyond which variation in nutritional status has little effect on reproductive function. Thus, the nutrition-fertility link noted in energy-restricted populations may be attenuated in less restricted ones: maternal fatness (i.e. tripe) was linked in Amale mothers to bout frequency and PRL levels, but the latter did not relate to duration of postpartum amenorrhea.

In addition to possible reduced PRL response to suckling, ovarian or hypothalamic refractoriness to disruption by nipple stimulation and PRL release may contribute to shortened postpartum amenorrhea among Amale. At 6-9 months, when PRL concentrations reached a peak, nearly 40% of women had experienced resumption of ovarian function. No relationship of ovarian steroid concentration to PRL was observed, contrary to other studies (Lunn et al., 1994; Hennart et al., 1985). Among nursing variables, only bout length correlated (inversely) with levels of P and E2. This finding again contrasts with reports of significance for bout frequency or interval for resumption of ovarian function and duration of amenorrhea in other populations in developing countries (Konner & Worthman, 1986; Jones, 1988; Hennart et al., 1985) as well as in better-nourished western women (Ellas et al., 1986, Stern et al., 1986). At short average bout durations (1-2 minutes), episode length possibly reflects inadequacy of nipple stimulation. Notably, nursing frequency did not decrease by time postpartum among Amale, unlike other groups (Wood et al., 1985b; Huffman et al., 1976a), so the frequency of nipple stimulation did not decline during lactation, although the duration did. A distinction between the present study and previous reports that may affect their comparability is that the time of PRL sampling is here specified with respect to occurrence of nipple stimulation: timing the sample immediately after a nursing episode better reflects acute response to suckling, but may be less indicative of relative levels between episodes. Difference in sampling strategy may account for differences in findings between this and other reports, and it is suggested that future studies likewise specify sample timing.

The comparatively light work load of Amale mothers, especially in the first 6 months postpartum, may contribute to early ovarian recovery. Work load can play a role by influencing maternal schedules (Huffman et al., 1980; Panter-Brick, 1991), by
altering energetic balance, or by direct endocrine effects (Shargold, 1984, Benedict, 1955). Factors that influence introduction and degree of supplementation also exert an indirect influence by altering nursing patterns. Timing of introduction of supplementary foods has been observed to affect duration of postpartum amenorrhea; earlier introduction of supplements apparently reduces the duration of amenorrhea by disrupting nursing patterns (Howie et al., 1981; Ford & Hoffman, 1988). Introduction of supplements at 7 months might be expected to lead to decreases in breast-feeding intensity among Amelé; however, timing of supplementation had no effect on nursing variables or length of postpartum amenorrhea. This may be because the first supplements are largely water (e.g., papaya, broth from cooking greens), and because infants take supplements only occasionally after they are first introduced. Jones (1990) found that introduction of solids influenced duration of postpartum amenorrhea, while that of liquids did not.

This discussion has so far assumed good nutritional status in the sample. Amelé have been characterized as a relatively privileged, well-nourished population (Ottowa, 1988), but are they indeed well-nourished? Direct comparisons to American norms yield an ambiguous picture. Contrasted to NCHS norms for women of 25-34 years old (Najjar & Rowland, 1985), the Amelé mothers (mean age 29 years) were below the 5th centile for height and at 15th centile of weight and triceps, but at 25th centile for mid upper arm circumference, 20th for BMI and 50th of subscapular distributions. White populations have a distinctly peripheral fat distribution; non-white populations exhibit greater central (e.g., subcapsular) and lesser peripheral (e.g., triceps) subcutaneous fat distribution (Najjar & Rowland, 1985; Mueller, 1988). It may therefore be more appropriate to compare Amelé with NCHS skinfold norms for blacks; then, for the present sample, triceps was at 20th centile, subscapular over 50th, and BMI and mid upper arm circumference nearly 50th.

Given population differences in myriad factors that determine relative nutritional status, and which may not be reflected in anthropometric measures, norms from a national sample of Papua New Guinea would provide a more realistic index of relative nutritional status. Such norms are not available, and their construction may be complicated by the presence of multiple, genetically diverse ethnicities (Hewwood, 1989). Analysis of anthropometric surveys of two adults New Guinean populations, one coastal and one highland, concluded that: the New Guinean adult is short, light, lean and muscular compared to the European (Norga, Ferro-Imori & Durman, 1982). Means for all body fat and circumference indices in Amelé women were greater than in either of these populations. Further, there was no evidence of maternal depletion, no negative association of weight and age (F=0.09, p=0.70) or weight and parity (F=0.29, p=0.58), which has been reported for other populations in Papua New Guinea (Norga et al., 1983; Trauer, 1991). It may be concluded, therefore, that Amelé women experience little dietary stress, a situation to which good health care and stable, high quality food intake may each contribute.

High fertility among Amelé is explained not only by a reduction in postpartum amenorrhea regardless of intense nursing, but also by a pattern of sustained fertility over the reproductive life span. Consistent with other natural fertility populations, including another group in Papua New Guinea (Wood et al., 1985a), the Amelé have been found to maintain equivalent fertility rates from age 20 until 40. Inter-birth
Intervaldo not vary by age. However, as a population, Amole may not be a case of entirely natural fertility. Although women in the longitudinal sample did not use contraceptives during the time of the study, there is some evidence that they did so after its completion, and that Amole women, as a group, are both attempting to space births and experiencing increasing secondary infertility due to sexually transmitted disease.

Thus, reproductive output is lower than it might be, an observation that reinforces rather than contradicts the point that intensive nursing practices are compatible with high fertility when nutrition and health care are good.

Data presented here, and in other studies, indicate that maternal nutritional status interacts with nursing patterns to alter the ability to maintain prelactation levels and suppress ovarian function. In this regard, the pituitary and the ovary are acting in a slightly dissociated manner, with each responding in significantly independent ways to maternal status and infant stimulation. When one considers this observation teleologically, it actually appears to make functional sense that the ovary should be acutely sensitive to nursing-mediated endocrine suppression when lactation is a heavy energetic burden for the mother, but that lactation could continue under appropriate stimulation if the woman can readily accommodate it energetically, while the ovary escapes to resume activity and potentiate an earlier subsequent pregnancy that the favourable energetic conditions allow. The data further support the growing consensus that no specific nursing parameter—breast frequency, duration, or interval, or even prolactin level—is the regulator of ovarian suppression. These act, instead, as a network of regulating variables which are themselves influenced, as is their potency, by the nutritional status of mother and child.

In sum, the Amole study provides insight into biobehavioural dynamics underlying high fertility in a natural fertility population where prolonged breast-feeding is practiced. The factors regulating postpartum resumption of ovulation are a complex of interrelated variables, which mitigates against any blanket prescription of which single component will be active. Data from the present study do not negate the importance of lactation in birth spacing, for 29% of the birth interval was taken up with postpartum amenorrhea, which otherwise lasts only 6-12 weeks in non-breast-feeding women (see similar results in Rosner & Schulman, 1980). But the findings suggest that policy aimed at optimising birth spacing by urging mothers to maintain lactation (Consensus, 1988) will not provide adequate protection for well-nourished women. Particularly for populations with good nutritional status and health care, contraception will also need to be provided, at the latest, on first postpartum menstruation to extend effectively the time of next conception and maintain fertility at desired levels (Lewis et al., 1991; Bracher, 1992).

Acknowledgments

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