less impressive than when they employed the probably more saturated (but to us invisible) wavelength band in the near UV (Fig. 1, A and B).

Cone oil droplets contain such high concentrations of carotenoids that the redder droplets have absorbances of 50 to 90 and the paler droplets more than 3 (*18*). Even the latter, however, implies a significant absorption in the near UV. How, then, does UV light reach the photoreceptors? One possibility is that rods, which lack oil droplets, are mediating the response. Although in pigeons the accessory members of double cones also lack an oil droplet, their outer segments contain a visual pigment with λ_{max} at long wavelengths, near 570 nm (*6*). Nevertheless, UV sensitivity may involve receptors more specifically sensitive to short wavelengths than either rods or long wavelength cones. In turtles, there are two subclasses of colorless droplet, one of which is transparent in the near UV (*19*). Moreover, recent evidence from pigeons indicates the presence of a cone with λ_{max} at 400 or 415 nm (*10, 20*). These findings suggest that UV vision by hummingbirds could be mediated by a photopic mechanism, and a receptor with λ_{max} in the near UV is not precluded (*12*).

The sensitivity of birds to UV light invites speculation about its adaptive significance, a tack that implies that the human retina represents the standard of performance against which diurnal visual systems should be measured. By this reasoning if an animal can see in the UV, there must have been some special evolutionary pressures that created the capacity, and the roots can be discovered by digging into the behavioral ecology of the species. There is also an alternative view, whose origins are to be found in the writings of Walls (*2*). The early mammals were most likely nocturnal creatures, and color vision in the mammalian line has become largely degenerate. The Old World primates, ourselves included, are the most notable exceptions, but in our evolutionary line cones and color vision have secondarily resurged, hand in hand with the adoption of diurnal habits. Moreover, all of the contemporary groups of placental mammals have lost the retinal oil droplets, and oil droplets once lost have never been recovered in evolution (*2*). Oil droplets provide a very selective form of filter, enabling individual cones to be screened. In principle, therefore, they may be arranged so as to permit the retinas of birds and reptiles to maintain the utmost in visual acuity without sacrificing all cells that are sensitive to the shortest wavelengths in the environment. Although we clearly must know more about the retinal distribution of avian UV receptors—for example, whether they are present in the foveas—one is reminded that in an evolutionary sense our color vision system has most likely been reconstructed from a photopically less capable retina, from which some of the original parts were lost forever. In this view, our retina is therefore making the best of a suboptimal situation, and it is the avian retina that comes closer to being the diurnal retina par excellence. This realization should leave us more open to the discovery of unsuspected visual capacities in other animals. More specifically, the interplay of several spectral classes of oil droplets with several cone pigments and the presence of receptors functioning in the near UV suggest that avian color vision possesses a richness that lies beyond our ken.

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Nursing Frequency, Gonadal Function, and Birth Spacing Among !Kung Hunter-Gatherers

Abstract. *Mothers among !Kung hunter-gatherers nurse briefly and frequently, with brief intervals between nursing bouts (mean ± standard error, 13.19 ± 1.28 minutes). The low levels of 17β-estradiol and progesterone in the serum of the mother are correlated with infant's age and with interbout interval, but not with total nursing time. Maternal gonadal function is apparently suppressed by a timing-dependent, prolactin-mediated effect of breast stimulation. Interbout interval may be a key variable in lactation infertility. If so, it solves the puzzle of !Kung birth spacing.*

Nursing markedly lengthens birth spacing in a number of noncontracepting, nonindustrial populations. Mean postpartum amenorrhea is less than 2 months in women who do not nurse, but at least 10 and up to 18 months in nursing women. In addition, the interval from the onset of menses to conception is lengthened by nursing (*1*). In some noncontracepting, nonabstinent populations where very late weaning is the custom, birth spacing is longer than 3 years.

One probable mechanism by which nursing influences fertility is a direct or indirect effect of prolactin on gonadal function (*2–9*). Prolactin is promptly secreted in response to nipple stimulation in human females, increasing 2- to 20-fold in plasma during 5 to 15 minutes of mechanical stimulation of the nipple (lactating or not), with a half-life in the plasma of 10 to 30 minutes (3). Nursing women maintain higher prolactin levels (2, 4-6) and lower gonadal hormone or gonadotropin levels (5, 6) postpartum than do nonnursing women. Prolactin declines more slowly in women who nurse more than six times a day than in women who nurse less frequently, those who nurse frequently showing no significant decline during the first 12 months postpartum (4). In women observed over a period of time postpartum, decline in nursing frequency and serum prolactin and recovery of gonadal and gonadotrophic hormone secretion occur in concert (5).

In a substantial minority of amenorrheic women the concentrations of prolactin in the serum are excessive, and these women can be treated with a dopamine receptor agonist that lowers serum prolactin, thus restoring gonadal function (9). Controversy continues over the routes of prolactin effects on gonadal function, with both antigonadotrophic (6, 7) and antigonadal (8) effects receiving support.

Among the !Kung, hunter-gatherers of Botswana and Namibia, the long intervals between births—44.1 months in traditional bands (10)—has puzzled investigators. Prolonged postpartum abstinence from coitus is unlikely, fetal wastage is low, and contraception is unknown; the !Kung believe conception takes place during menses by the mixing of semen with menstrual blood (10-14). Speculations have linked !Kung birth spacing to nutritional infertility (11), but there has been no direct support for this hypothesis, and competing hypotheses have not been explored. We now report (i) that the !Kung have an unusual temporal pattern of nursing, characterized by highly frequent nursing bouts with short interbout intervals; (ii) that serum estradiol and progesterone are low in nursing, noncycling women; and (iii) that levels of these hormones in nursing women are correlated with the infant's age and the mean time elapsed between nursing bouts.

The !Kung, like other hunting and gathering peoples, play a key role in anthropological theory; they are thought to represent some aspects of the subsistence ecology, demography, and social organization of Pleistocene human groups. These as well as other features of their society, culture, and health have been extensively described (10-13), including the care and development of infants (14). Infants are always in immediate physical proximity with their mothers until age 2 years or older, and separations are brief until they are about age 3½, when they are weaned during a new sibling's gestation.

Observations from dawn to dusk (Fig. 1) revealed that nursing occurred for a few minutes at a time, several times an hour, throughout the daylight hours. A sample of 45 infants examined with a higher-resolution procedure (15, 16) confirmed the pattern. The percentage of 15-minute periods when mother-infant pairs did not nurse was low throughout the first 80 weeks of infant life ($\leq$ 25 percent), even though observations were not begun during nursing bouts (17).

With these findings in view, we examined the temporal pattern of nursing and the major gonadal steroid hormones, 17β-estradiol (E_2) and progesterone (P), in the same women. A group of 17 !Kung mother-infant pairs, with infants ranging in age from 12 to 139 weeks (mean 63.9 ± 9.9) were observed for 6 hours in three 2-hour sessions on separate days, from 0830 to 1030, 1230 to 1430, and 1630 to 1830; nursing was recorded to the nearest 30 seconds. Overall mean values for nursing variables were 4.06 ± 0.41 bouts per hour; 7.83 ± 1.27 minutes per hour; 1.92 ± 0.18 minutes per bout; 13.19 ± 1.28 minutes between bouts; with 55.16 ± 3.79 minutes (mean ± standard error) being the maximum interval. The age of the infant was unrelated to the bout length or nursing time, but was strongly related to the interval between bouts (r = .71, two-tail; $P < .005$).

Two blood samples were drawn from the women at 1000 on separate days during the observation week (17). Concentrations of E_2 and P in the same serum samples were determined by Celite partition chromatography and radio-

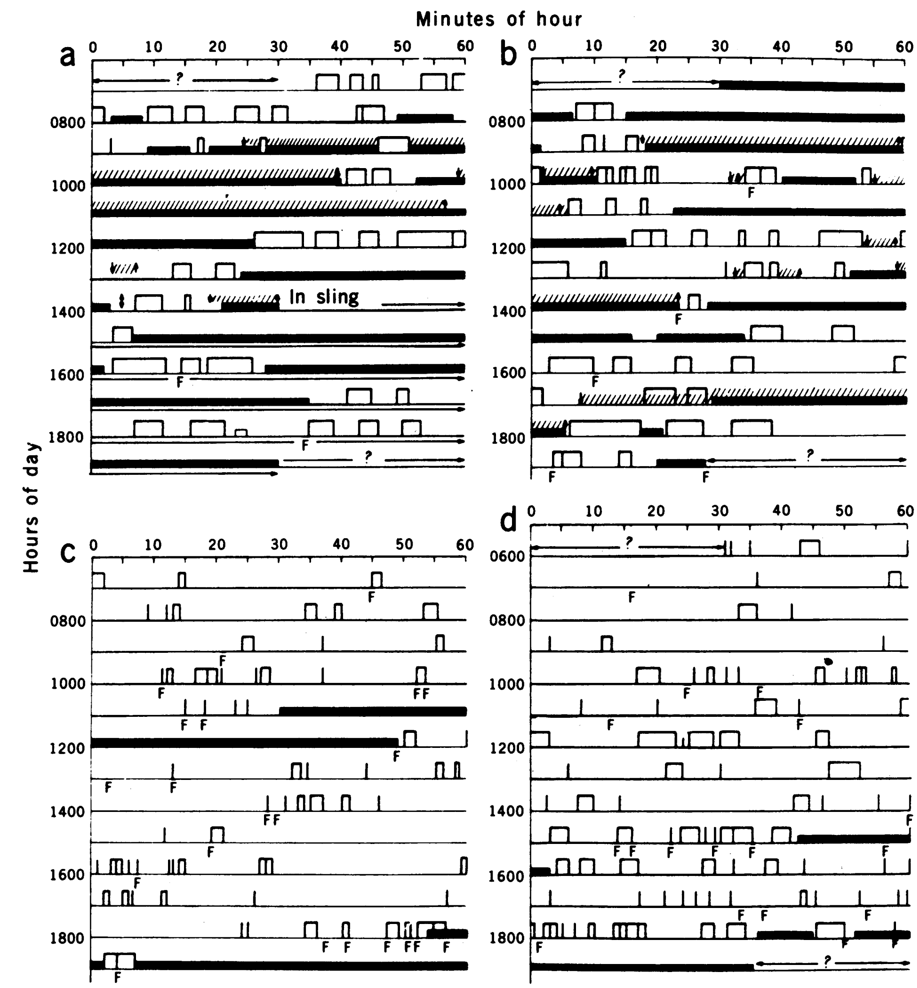

Fig. 1. Four dawn-to-dusk (13 hours) continuous nursing observations of !Kung infants. (a and b) Newborn boy at 3 and 14 days, respectively; (c) 52-week-old girl; (d) 79-week-old boy. Open bars and tall vertical lines, nursing; closed bars, sleep; *F*, fretting or crying. Slashed lines represent the time held by mother, recorded for newborn only, with arrows for picking up and setting down. All variables except fretting were recorded to the nearest 30 seconds. Tall vertical lines indicate nursing bouts of less than 30 seconds duration. The longest observation period without a nursing bout was 98 minutes, in the 3-day-old, during sleep. Sleep is frequently interrupted by half-awake nursing bouts. The same observation protocol was used for the three 2-hour observations of 17 mother-infant pairs. For 16 of the mothers, hormone levels were available for analysis in relation to nursing pattern.

immunoassay (*18, 19*). In a related study (*20*), the menstrual cycles of eight !Kung women were examined, and their serum concentrations of E_2 and P in different cycle phases were available for comparison (Fig. 2). Both E_2 and P were significantly lower in the 12 noncycling nursing women than in the eight cycling women during follicular phase, when both hormones were at a low ebb (E_2, $P < .01$; P, $P < .01$; Wilcoxon two-sample test, two-tail). For the noncycling nursing women, the mean E_2 was 24.7 ± 6.6 pg/ml and mean P was 186 ± 61 pg/ml, values comparable to those found in hyperprolactinemic amenorrheic Western women (*18, 21*). Four of the values for P were below the sensitivity of the assay, and all nursing women with infants under 2 years of age had low values of P (*22*).

A product moment correlation matrix for the nursing sample ($N = 16$) showed that E_2 and P were significantly related to each other ($r = .84$, two-tail, $P < .001$), to infant's age (for E_2, $r = .58$, $P < .02$; for P, $r = .61$, $P < .02$; two-tail), and to the mean interbout interval (for E_2, $r = .67$, $P < .01$; for P, $r = .71$, $P < .01$; two-tail); but they were not to the bout length or nursing time, or to parity or sex of infant. (Taking the log transform of the hormone values leaves the relation of age and interbout interval to E_2 highly significant, but reduces their relationship to P to marginal significance.)

No systematic observations were made at night. However, it is customary and apparently universal for !Kung infants to sleep on the same skin mat with their mothers until they are weaned. Interviews of 21 mothers nursing infants as old as 3 years indicated that nursing during the night is also universal. Of the 21 mothers, 20 reported being waked at least once each night by the infant for nursing. All 21 reported that the infant nursed during the night without waking the mother, from two to "many" times or "all night" (Fig. 1). Since the prolactin level rises at night in the course of its daily rhythm (*23*), gonadal suppression during sleep may not depend on nipple stimulation.

Because the !Kung diet is sometimes low in calories, nutritional infertility cannot be ruled out. However, if poor nutrition were the principal route of gonadal suppression, we might have expected to see correlations of hormone levels with minutes per hour of nursing, bouts per hour, or bout length, but these explained little of the variance. Age in weeks and mean interbout interval showed high correlations with hormone levels and with each other. Although causal inferences cannot be finally made from correlations, our present working model hypothesizes that the key change as the infant grows is the lengthening of the interval between bouts. Late in the child's second year, its play occasions longer separations from the mother. When the child is 2 years old, the regression line of interbout interval on age reaches a level which is approximately equal to the half-life of prolactin in human plasma. Prolactin, which, presumably, has been tonically high previously, is allowed to fall low enough for a long enough time so that its antigonadal or antigonadotrophic effects are impaired, and cycling may be reinstated. Subsequent pregnancy may be further postponed by other effects of suckling, such as erratic or anovulatory cycles, with short luteal phases or otherwise impaired luteal competence (*24*), and, conceivably, interference with implantation (*25*). After lactation amenorrhea, such effects, together with some nutritional infertility and some fetal wastage, could lengthen the birth interval to more than 3 years. We believe that this solves the puzzle of !Kung birth spacing.

Such highly frequent nursing occur-

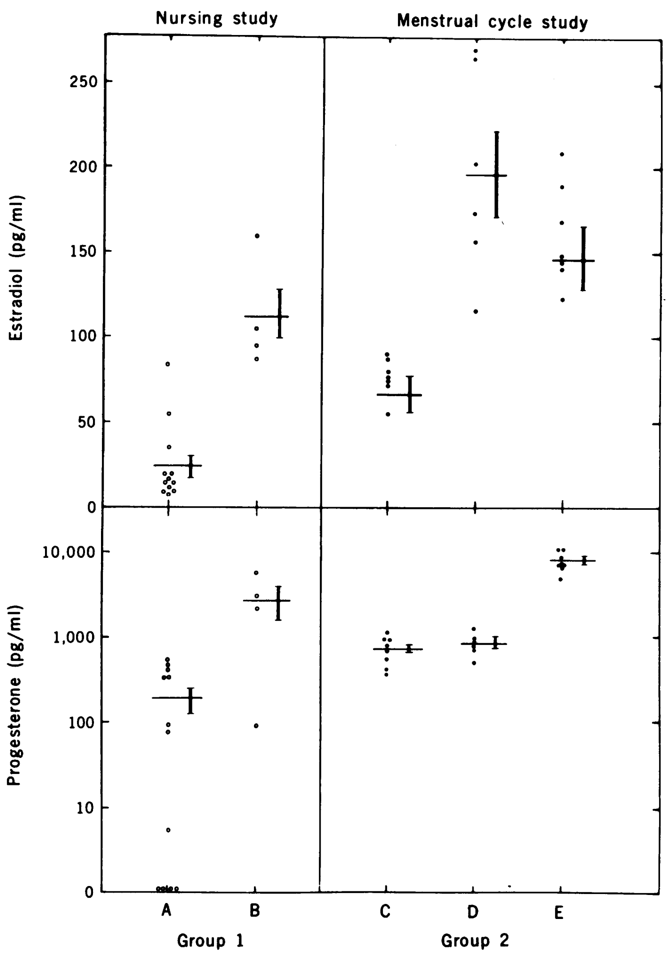

Fig. 2. Steroid levels in !Kung women, by nursing and cycling status. Serum estradiol (E_2) and progesterone (P) determined (*19*) from samples in two related studies: one of 16 nursing women (12 amenorrheic), each sampled on 2 days without regard to cycle phase (columns A and B), and one of eight cycling women, each sampled five times a month for two full monthly cycles. (Samples overlapped to the extent of two nursing women who were subjects in both studies.) Column A shows values for 12 women in the nursing study who were not cycling (group 1); column B, four women in the nursing study who were cycling (group 1); and columns C to E, eight women in the menstrual study followed longitudinally twice through the three-cycle phases (group 2; among these eight were three who were nursing infants). Eact point represents the mean of two to four samples collected at 1000 on different days. P values, but not E_2 values, are drawn on a logarithmic scale. The mean values for E_2 and P (picograms per milliliter ± standard error) and their product moment correlation in each column are as follows: nursing noncycling, $E_2 = 24.7 \pm 6.6$, $P = 186 \pm 61$, $r = .54$; nursing cycling, $E_2 = 112.3 \pm 16.3$, $P = 2653 \pm 1112$, $r = .87$; fallicular phase (column C), $E_2 = 66.8 \pm 10$, $P = 678 \pm 87$, $r = -.04$; ovulatory phase (column D), $E_2 = 196.5 \pm 789 \pm 97$, $r = .20$; and luteal phase (column E), $E_2 = 146.1 \pm 7.3$, $P = 7553 \pm 21$, $r = .17$.

ring naturally in a human population, especially in one of the environments of human evolutionary adaptedness, raises a basic challenge to our understanding of human lactation. Apart from fertility, variables that might be affected by highly frequent nursing include lactation success or failure; infant digestive distress, sleeping patterns, and glucose dynamics; milk composition; and maternal mood and attitudes toward nursing.

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16. Manual nipple stimulation by the infant also occurs. It appears first at 41 weeks, but is rare until the second half of the second year, when it occurs in 14.4 percent of the 15-minute observations, lasting a few seconds to a minute, with or without simultaneous nursing. Manual stimulation of the nipple causes prolactin release, but the efficacy of such brief stimulation is unknown (*3*).
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Bronchodilatation: Noncholinergic, Nonadrenergic Mediation Demonstrated in vivo in the Cat

Abstract. *The composite vagus nerve was stimulated during intravenous infusion of 5-hydroxytryptamine in cats subjected to pharmacologic autonomic blockade with atropine, propranolol, and phentolamine. Bronchial caliber, as assessed by changes in pulmonary resistance, demonstrated a marked dilatation, and dilatation could still be demonstrated after preliminary treatment with reserpine. By stimulating the component branches of the vagus nerve, it was determined that the parasympathetic branch is responsible for this phenomenon.*

Although the physiologic role of bronchial smooth muscle is still speculative (*1*), the neural control of its tone is a subject of active research because of the importance of this muscle in disease. Traditionally, bronchial smooth muscle tone has been thought to be mediated through the autonomic nervous system. Stimulation of parasympathetic cholinergic fibers in the vagus nerve clearly causes bronchoconstriction; stimulation of sympathetic adrenergic fibers through β receptors is generally found to be bronchodilatating (*2*), although stimulation through α-adrenergic receptors, if present, would result in bronchoconstriction (*3*). Vagally mediated bronchodilatation has been reported occasionally (*3*) and dismissed as either anomalous or the result of stimulation of stray sympathetic dilator fibers (*4*).

A noncholinergic, nonadrenergic inhibitory nervous system that mediates bronchial smooth muscle relaxation has been reported (*5*). Evidence for such a system is based on pharmacologic and anatomic observations in vitro; the proposed neural mediator is adenosine triphosphate (*6*). This "purinergic" nervous system is thought to serve several autonomic functions, especially the relaxation that precedes a normal peristaltic wave in the intestinal tract (*7*). Since the lung, like the gut, has endo-

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