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ONCE UPON A TIME? HUMAN MENSTRUAL SYNCHRONY, OFFSPRING SURVIVAL AND FEMALE REPRODUCTIVE SUCCESS

ABSTRACT: The convergence of the onset dates of human menstrual flow was first documented in 1971 and since then, evidence of human menstrual conversion has been far from anecdotal. However, there is also abundant evidence failing to replicate these results. Criticism hinges on several methodological shortcomings which inherently bias towards synchrony. The purpose of the current study is not to substantiate menstrual synchrony by empirical investigation, but to shift view towards its biological significance. The evolutionary approach posits that concealed ovulation, continuous sexual receptivity, and the potential for menstrual synchrony are all linked to achieve higher gains in paternal investment. However, kinship may have been overemphasized for male helpers and underestimated for females. The phenomenon of partible paternity demonstrates that male provisioning need not be contingent on biological fatherhood. At the same time, human life histories assure the availability of well-qualified allomothers such as grandmothers. It is therefore hypothesized that menstrual synchrony in human females represents a redundant life history artifact which has its origins in our primate heritage as cooperative breeders.

KEY WORDS: Menstrual synchrony – Evolutionary biology – Allocare – Reproductive success

INTRODUCTION

The convergence of the onset dates of human menstrual flow was first documented by McClintock in 1971, and since then, evidence of human menstrual conversion has been far from anecdotal (Skandhan *et al.* 1979, Graham, McGrew 1980, McClintock 1981, Quadagno *et al.* 1981, Brown 1984, Preti *et al.* 1986, Goldman, Schneider 1987, Weller, Weller 1993a–c, Weller *et al.* 1995, Stern, McClintock 1998, Weller *et al.* 1999a, Weller *et al.* 1999b). Menstrual synchrony[1], the observation that females living together menstruate or ovulate together, has elicited great interest in both the scientific community as well as the public domain. Particularly the possibility that the phenomenon may be indicative of human pheromonal

synchrony stems from direct indices of ovulation/estrus, whereas in humans the timing of the onset of menstruation is taken as an indicator (Graham 1991). The majority of studies on synchrony have focused on menstrual onset dates with the underlying assumption that menstrual synchrony is also an indicator or expression of ovulatory synchrony. Although this is a reasonable assumption since the luteal phase of the cycle is more uniform in length than the follicular phase (Bailey, Marshall 1970), this equation of ovulation and menstruation has been harshly contested (Strassmann 1997a). Communal ovulation *per se* has not been studied, except by Stern, McClintock (1998).

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[1]   Menstrual, ovulatory and estrous synchrony are used synonymously. However, the comparison of menstrual with estrous synchrony may not always be appropriate. In nonhuman species evidence for

communication has received a wealth of attention (Preti *et al.* 1986, Schank, McClintock 1992, 1997, Stern, McClintock 1998, Morofushi *et al.* 2000).

However, there is also abundant evidence failing to replicate the aforementioned studies (Pfaff 1980, Jarett 1984, Wilson 1987, Wilson *et al.* 1991, Wilson 1992, Trevathan *et al.* 1993, Arden, Dye 1997, Strassmann 1999, Schank 2000a–b, 2001). Criticism has mainly hinged on sampling bias, miscalculation of the initial difference in menstrual onsets and inappropriate experimental design, especially lack of control for physical proximity, nutrition, or physical activity (Jarett 1984, Wilson 1987, Wilson *et al.* 1991, Wilson 1992, Trevathan *et al.* 1993, Strassmann 1997a, Strassmann 1999). While follow-up studies were careful to circumvent these apparent flaws (Weller *et al.* 1995, Weller, Weller 1997, Stern, McClintock 1998), a recent evaluation still found methodological shortcomings which inherently bias towards synchrony (Schank 2000a,b, 2001). A second aspect which needs to be considered is the question how much synchrony can or should be expected. Variability in group cycle length is due to substantial within-woman as well as inter-female variability (Strassmann 1997a) and can only be overcome when intra-female variability is manipulated through entrainment (Schank 2000a). Due to the popular misconception that menstrual cycles are farther apart than they really are (Strassmann 1997a), the extent of menstrual synchrony can be easily overrated. Arden and Dye (1997) were able to show that variable cycle length alone can cause a shift from synchrony to asynchrony. Hence, synchrony intrinsically represents a proportionally small shift in the timing of a female's cycle. Thirdly, due to varying fertility regimes, menstrual synchrony may not be widely encountered in natural-fertility populations as females are often pregnant or lactating (Short 1976, Strassmann 1997a).

Studies in human females indicate that synchrony only occurs under very limited conditions. Some apparent prerequisites are proximity, an abundance of emotional involvement, as well as female interaction. However, Kiltie (1982) found that merely 39% of societies provide sufficient proximity for women to become synchronous. Three major factors have been empirically documented: Emotional bond, male presence and life history parameters. (a) Spatial proximity, shared activities as well as friendship may be indicative of time spent together and personality similarity. However, intensive social contact by itself may not be conducive to menstrual synchrony (Weller, Weller 1998). Most often, menstrual synchrony has been found among close family members such as sisters (Weller *et al.* 1999a, Weller, Weller 1997), or mother-daughter dyads (Weller, Weller 1993a). All the same, synchrony is not a phenomenon based on familial relationship, but rather on exposure and affiliation (Weller, Weller 1993b, Robinson 1995). Menstrual synchrony has also been documented among close friends (McClintock 1971, Graham, McGrew 1980, Quadagno *et al.* 1981, Goldman, Schneider 1987, Graham 1991, Weller, Weller 1993b, Weller *et al.* 1995,

Weller, Weller 1997, Weller *et al.* 1999a, b), co-residents (McClintock 1971, Skandhan *et al.* 1979, Jarett 1984, Little *et al.* 1989, Weller, Weller 1993a, b) and even among co-workers. However, women in high stress, low interdependency occupations do not synchronize (Matteo 1987; Weller, Weller 1995). (b) The degree of sexual exposure seems to be an important confounder (Weller, Weller 1997), as both length and regularity of the menstrual cycle are related to contact with males (McClintock 1971). In lemurs, sexually active males enhance synchrony (Perret 1995). In humans, lesbian couples do not exhibit synchronous trends (Weller, Weller 1992, Trevathan *et al.* 1993, Weller, Weller 1998). (c) Young women are more prone towards synchrony than older females. This may be indicative of a social regulation of ovulation throughout the lifespan (McClintock 1998). In addition, the presence of menopausal women has a diminishing effect which may be related to the release of a pheromone which counteracts synchronization (Skandhan *et al.* 1979). It has therefore been suggested that menstrual synchrony does not effectively happen in older women, as their cycles have already stabilized (Burleson *et al.* 1991, Weller, Weller 1993b).

The purpose of the current study is not to substantiate menstrual synchrony by empirical investigation, but to shift view towards its biological significance. Obviously, potential benefits of menstrual synchrony have to be related to reproduction (Knowlton 1979, McClintock 1981). The evolutionary approach posits that concealed ovulation, continuous sexual receptivity, and the potential for menstrual synchrony are all linked to achieve higher gains in paternal investment (Turke 1984). The aim of this paper is to expand on the issue of availability of direct infant care and to emphasize the central role of child welfare and the risk of child mortality. It is hypothesized that menstrual synchrony in human females represents a redundant life history artifact which has its origins in our primate heritage as cooperative breeders (Hrdy 2000b), and is largely independent of paternal care and provisioning.

COVARIATES OF MENSTRUAL SYNCHRONY IN NON-HUMAN PRIMATES

Female reproductive success depends on ecological as well as social factors (review in Abbott *et al.* 1998). *Table 1* shows that menstrual synchrony in non-human primates has been documented in a variety of different ecological and behavioural contexts.

Individuals survive or reproduce better in large groups (Kokko *et al.* 2001). A common denominator of all listed species in *Table 1* is the predominance of birth seasonality (Di Bitetti, Janson 2000) and moderate to extensive allocare. Allocare occurs when individuals forego independent reproduction and help others to reproduce. As a reproductive system it is restricted to familial societies in a dangerous environment with high mortality risks, in

TABLE 1. Drawing on zoological evidence, McClintock (1983) lists 36 species of mammals in which menstrual synchrony, suppression and enhancement occurs in female groups. Additional observations are provided by Wallis (1983), Wallis (1986), French, Stribley (1987) and Johnston, Rowell (1987).

Primate species	Behavioral and reproductive covariates
Erythrocebus patas Bramblett (1976), Chism (1986), Harding, Olsen (1986), Hrdy, Whitten (1987), Richard (1985), Rowell, Hartwell (1978)	• no external signs of estrus • harem polygyny; multimale during mating season • extensive allomaternal care
Eulemur fulvus Fleagle (1988), Gachot-Neveu *et al.* (1999)	• multimale-multifemale groups • no signs of marked female dominance • female choice influences male reproductive success
Hapalemur griseus van Schaik, Kappeler (1993), Wright (1990)	• monogamy • females are dominant over males • infant care is characterized by "parking" • alloparenting by father and older siblings
Lemur catta Evans, Goy (1968), Nakamichi, Koyama (1997), Pereira (1991)	• female defense polygyny • high infant mortality rate (30–50%) • females are dominant over males • extensive allomothering
Leontopithecus rosalia Kinzey (1997a), Rylands (1993), Montfort *et al.* (1996)	• one breeding pair per group • high paternal investment • nuclear families, can be extended family
Macaca fascicularis Angst (1975), Welch *et al.* (2001)	• harem polygyny • females have a tendency to have close bonds with their maternal relatives • male-infant interactions increase mating success • male aggression towards females (sexual coercion)
Macaca mulatta Smuts (1987a)	• multimale-multifemale social system • females have a tendency to mate with extra-group males • dominance hierarchies exist in both sexes • social grooming strengthens bonds between females
Macaca silenus Estes (1991), Fleagle (1988)	• multimale-multifemale social system • multiple mating behaviour • low reproductive rates • hierarchical system based upon matriline
Pan troglodytes Estes (1991), Matsumoto-Oda (1999), Nishida (1979)	• fission-fusion society • females adopt many-male strategy or best-male strategy • unrelated females will not show much interaction • allocare
Papio cynocephalus Altmann (1980), Estes (1991)	• promiscuous multimale-multifemale social system • much aggression between males • male consorts aid in the rearing of infants (carrying/grooming) • male consorts become foster parents when the mother dies
Papio hamadryas Estes (1991), Stammbach (1987), Zinner *et al.* (1994), Smith *et al.* (1999)	• harem polygyny • harem-less males serve as "stud" while older male leads the harem • females in conceptive estrus show less synchrony • extensive allocare
Saimiri oerstedi Kinzey (1997b), Mendoza, Mason (1991), Vermeer (1996)	• multimale-multifemale; • little aggression between male members • reproductive cycle is stimulated by social behaviour between adult females • to prevent inbreeding, adult males must be replaced every four years • fathers take no part in raising young • allomothering by older females

which others serve as alloparents (Emlen 1995). Hence, delayed dispersal beyond reproductive maturity, postponed onset of reproduction, and provision of alloparental care by non-breeders are typical characteristics (Solomon, French 1997). Under certain ecological situations, i.e. environmental conditions inconducive to dispersal and independent breeding, menstrual synchrony counteracts overpopulation by acting as an effective birth control measure (Abbott *et al.* 1998, Hatchwell, Komdeur 2000).

The evolution of such a system has been comprehensively analyzed and theorized by Lacey and Sherman (1997). Two competing theories explain the origin on either the basis of altruistic behaviour and kin selection (Cockburn 1998), or emphasize ecological constraints and the scarcity of alternative breeding options which force offspring to delay dispersal and help parents raise new offspring (Hatchwell, Komdeur 2000). It is important to note that cooperatively breeding species show considerable variability in patterns

of within-group reproduction, with plural and singular breeding systems at either end of the continuum. Plural breeding implies that reproductive success is equal among all females within the group, while singular breeding is limited to one dominant female. Singular breeding is achieved through various avenues such as harassment or resource exclusion which may lead to reproductive failure in subordinate females. In addition, olfactory, visual and behavioural cues from dominant females can inhibit sexual behaviour, ovulation and implantation (Abbott *et al.* 1997). Estrous synchrony has been theorized to act as a preventive check to counteract singular cooperative breeding (Hrdy 1981).

THE EVOLUTIONARY BIOLOGY OF MENSTRUAL SYNCHRONY

Ovulatory concealment and extended sexual receptivity are thought to have triggered an increase in paternal investment which in turn has been deemed instrumental in procuring monogamy (Benshoof, Thornhill 1979). Knowlton (1979) was the first to put forth a model of reproductive synchrony, parental investment and evolutionary dynamics of sexual selection. In line with this, Turke (1984) developed a comprehensive scenario which put concealed ovulation, continuous sexual receptivity, the potential for menstrual synchrony and male parental investment into a single theoretical framework. He hypothesized that female reproductive success is enhanced by male exclusive consortship and increased parental effort. Based on the idea that converging cycles are a by-product in females living in small groups and close proximity, coordinated reproduction would have led to enhanced fitness. Ovulation concealment, ovarian synchrony and lactation-mimicry (pendulous breasts) are thus to be regarded as adaptations through which females efficiently counteracted a male sexual monopoly. Knight (1991) further integrated archaeological and ethnographic accounts and stressed the revolutionary potential of synchrony as a means to create gender solidarity. Taking this one step further, Power (1997) hypothesized that such a coalition of non-cycling females would not only have restricted access to cycling females in the sense of an ingroup/outgroup boundary, but that the entire group of females – whether cycling and non-cycling – would have advertised fertility via menstrual signals.

In consequence, the regulation of communal fertility serves four distinct purposes: the reduction of male competition for sexual partners, a counter-strategy against a male sexual monopoly, a stimulus to male provisioning, and generation of solidarity among women. While the outlined model is very plausible, the key features on which the scenario rests, are open to scrutiny. Are concealed ovulation and continuous sexual receptivity unique human traits? Does synchrony enhance female reproductive success? Is exclusive paternal care a major factor in infant survival? And does synchrony stimulate female solidarity?

These questions need to be addressed in light of new primate, evolutionary or ethno-historical evidence.

Is concealed ovulation an exclusively human trait?

Many primate females advertise their fertile times through morphological, olfactory or behavioural changes once or twice per annum and in synchrony with others. In contrast, sexual activity in humans is seen as continuous and not coordinated with fertile times. Concealed ovulation and constant receptivity were thus thought to be unique human traits and the absence of sexual signals was proposed to indicate an adaptive mechanism (compare Alexander, Noonan 1979). The adaptive advantage of constant receptivity was theorized to encompass greater within-group cooperation, monogamy, intensification of paternal behaviour, high protein food acquisition, paternity deception and/or infanticide reduction (for a comprehensive review, compare Pawłowski 1999). However, the disappearance of visible ovulatory signals need not be associated with a selection trend towards new reproductive behaviour, and could simply be the byproduct of bipedalism and environmental conditions (Pawłowski 1999). Moreover, Sillén-Tullberg and Møller (1993) could show that in 68 species of higher primates, only half produced visible signs of ovulation. Furthermore, human sexual behaviour may not be completely independent of hormonal fluctuations. Many women perceive changes during their menstrual cycle, i.e. experience a bimodal pattern of sexual intensification around ovulation at mid-cycle and a secondary peak in the premenstruum (Manson 1986). Findings by Harvey (1987) or Singh and Bronstad (2001) suggest that ovulation-linked odours may be related to human mate selection. Thus, the conclusion of true ovulatory concealment in humans may be unjustified (Burt 1992).

Primate evidence demonstrates that concealed ovulation cannot be attributed to a single mating strategy, and estrus synchrony appears to be associated with a range of mating systems from relative promiscuity, harem polygyny to monogamy (McClintock 1983). However, phylogenetic analyses suggest that concealed ovulation has most likely originated in lineages with polyandrous females. Once evolved, it facilitated the evolution of social monogamy (Sillén-Tullberg, Møller 1993). It is important to note in this context that social monogamy does not imply genetic monogamy. Social monogamy refers to a pair bond without any assumptions about mating exclusivity or bi-parental care. Consequentially, sexual fidelity is not an essential criterion for social monogamy.

Does synchrony enhance female reproductive success?

Intrasexual competition denotes the competition among same-sex conspecifics for access to desirable mates or resources. In most primate species, including humans,

inter-male competition is more intensive than inter-female competition. In general terms, female reproductive success is limited by access to resources, while male reproductive success is limited by access to females. Hence, both monogamy and promiscuity are characterized by a relatively low variance in reproductive success (Starks, Blackie 2000), while polygyny is associated with a high variance in male reproductive success (Say *et al.* 2001). Furthermore, not only is female reproductive success negatively related to the number of harem females, polygyny also has an adverse affect on child survival, even when various mediating factors such as age and sex of the child, or economic status of the parents are controlled for. Resource dilution, co-wife competition, paternal and nepotistic investment are all crucial variables in predicting child health (Strassmann 1997b). Synchrony among co-wives has also been shown to decrease the likelihood of conception (Small 1988). Thus, cycle variability not only facilitates female mate choice (Ostner, Kappeler 1999, Schank 2001) but also promotes higher female reproductive success when the probability of fertilization is low (Gattermann *et al.* 2002).

When paternal investment is high, mating systems drift toward monogamy. And conversely, when paternal investment is low, other factors such as inter-male competition, mate-guarding, coercion or female "gene-shopping" can lead to polygyny (Marlowe 2000). Greater breeding synchrony reduces the opportunity for individual males to monopolize multiple females (Emlen, Oring 1977). And even in species with partial synchronization of brief estrus periods, concealed ovulation minimizes the chances for polygynous mating (Pereira, McGlynn 1997). In line with this, Dunbar (1988) could show that a male's ability to monopolize a group of females depends on both the number of females and the degree of reproductive synchrony. In some cases one male may be inadequate for his harem size and sperm may become a limited resource. Inter-female competition for conception thus influences the demography of one-male units (Zinner *et al.* 1994). Female-controlled polygyny (as defined by Smuts 1987b, Richard 1992) is of particular interest in this context. Via coalitions, females are capable of gaining control over benefits which cannot be otherwise acquired (Smuts 1987b). This can lead to an adjustment of the existing reproductive strategy by mating with peripheral males (Small 1988). Thus, species with synchronized breeding seasons are either particularly monogamous, or favour extra-pair matings. Such multimale-multifemale systems provide genetic benefits which significantly enhance a female's lifetime reproductive success (Newcomer *et al.* 1999, Hrdy 2000a).

Males who do not have to guard females experience less intra-male competition and are therefore able to invest more time to provide for their female companions. This enhanced effort in provisioning bestows various benefits on the female as well as her offspring. However, investment in offspring need not be limited to fathers. There are at least 18 indigenous societies which believe that a child can have more than one father. The phenomenon of "partible paternity" demonstrates that male provisioning need not be contingent on biological fatherhood. This South American, Indian or Polynesian belief bestows a variety of positive side effects on both mother and child. Benefit is most pronounced in the number of pregnancies which come to term, and to a lesser extent, postnatal child survival. The increase in survivability is related to provisioning by secondary fathers (Beckerman, Valentine 2002). This coincides with findings from comparative zoology, where intra-male competition has been known to influence offspring survival, not only in terms of the quality or quantity of the resources made available but also in the quality of paternal care (Qvarnstrom *et al.* 2000).

Is paternal care exclusively geared towards offspring?

Children who grow up in single mother families fare much poorer across a wide range of adolescent and adult outcomes, including educational attainment, economic security, as well as physical and psychological well-being. In contrast, children whose fathers play an active role in their lives develop better and have fewer behavioural problems, even when their fathers do not live at home (Sigle-Rushton, McLanahan 2002). A wealth of studies attests to the importance of paternal involvement, but evidence from primatology and the ethnographic record documents that male-infant caretaking is not exclusively linked to paternity probability. Furthermore, mating behaviour does not always signal parentage, hence, a variety of male reproductive strategies ranging from possessiveness, opportunistic mating to monogamous consortship can lead to paternity across all male ranks (Hrdy 1981, Constable *et al.* 2001, Launhardt *et al.* 2001). Thus, kinship may have been overemphasized for male helpers and underestimated for females (Cockburn 1998). Furthermore, it needs to be understood that the interests of male and female helpers may be quite different.

In general terms, males who exhibit more infant care also gain greater access to desirable females. Thus, the observed "mate-then-care" pattern, may simply be a "care-then-mate" pattern (Tallamy 2000, Menard *et al.* 2001, Welch *et al.* 2001). Within the evolutionary context, male contribution to offspring has often been linked to provisioning. Marlowe (2001) was able to demonstrate that the male contribution to diet – taken as a proxy for provisioning – has important consequences for the female's reproductive span and her overall fertility. With the exception of humans, male primates do not contribute significantly to the food consumed by females and juveniles. This unique male subsistence contribution is therefore said to have evolved as a competitive display. Hawkes *et al.* (1995) or Van Schaik and Paul (1996) have argued that men provide care simply as mating effort. The so-called "show-off" hypothesis argues that men hunt because they receive

fitness returns in the form of extra matings or social benefits. Consequentially, women compensate show-off men by offering them sexual favours, males tolerate a certain degree of infidelity by their wives with the show-offs, and all band members grant preferential treatment to the show-off's children (Hawkes 1990, 1991). In contrast, Smith and Bliege Bird (2000) or Bliege Bird *et al.* (2001) have focused on Zahavi's "costly signalling hypothesis", stipulating that productive males are not exchanging meat for mates, but are using their foraging prowess as a honest, intraspecific signal of quality. Such displays of public generosity indicate phenotypic mate quality and the encountered costs are later recouped through signal benefit.

These studies show that male offspring care may indeed serve ulterior motives, unrelated to paternal behaviour. However, a note of caution must be allowed. A recent investigation by Marlowe (1999) demonstrates that stepchildren receive less care than biologically related children. This implies that stepfathers are less motivated to care for stepchildren and also suggests that provisioning is provided, at least in part, as parenting effort.

Does menstrual synchrony enhance female solidarity?

Social cooperation and coalition formation are evolved strategies which allow individuals greater access to and control of essential resources. Consistent with evolutionary theory, such coalitions are typically formed among kin and compete with other kin-based coalitions (Geary, Flinn 2001). In female-bonded primate species, the formation of stable social networks reduces offspring mortality risks and allows offspring to learn the basic skills involved when living in a complex social community (Barton *et al.* 1995). Females also use intra-sex coalitions to gain protection against male aggression and to influence male group membership (Smuts 1987b).

Interestingly, primates – such as Bonobos – which exhibit particularly strong female solidarity, do not have estrous synchrony. Variations in female social strategies therefore reflect the various ways in which social behaviour is used to achieve reproductive goals. The ecological model links such relationships to spatial patterning in relation to food, and hence to competitive regimes. It also assumes that predatation risk forces females to live in groups. Sterck *et al.* (1997) characterize the ensuing female social relationships as dispersal-egalitarian, resident-nepotistic, resident-nepotistic-tolerant or resident-egalitarian. Thus, it is ecological forces rather than menstrual synchrony that determine the type and strength of female coalitions.

MENSTRUAL SYNCHRONY – AN EVOLUTIONARY STABLE STRATEGY?

A primary goal of any ecological or evolutionary model is to explain the maintenance of behavioural and phenotypic variety in equilibrium populations. An evolutionary stable strategy (ESS) is a behavioural phenotype which cannot be invaded by a mutant strategy and has the highest fitness against all other alternatives (Maynard Smith 1982). The ESS describes a strategy – or combination of strategies – which maximizes individual fitness at equilibrium. As such, it is a prediction of the conditions in a population after evolution has proceeded to a stable equilibrium. This need not be the same as the condition under which population fitness is highest. It is important to keep in mind that any ESS is conditional on the context, and its pay-offs vary systematically with the prevailing conditions in the environment.

Communal rearing has been suggested within the context of human menstrual synchrony, as group cycling would have inadvertently lead to synchronized breeding, which is beneficial in terms of group mothering and the ability to interchangeably breast-feed one another's young (Buckley 1982, McClintock 1981, Stern, McClintock 1998). In the theory of life histories, trade-offs are important. The trade-off between maximizing reproductive success via synchronized communal breeding or individual cyclicity has been addressed previously (Foley, Fitzgerald 1996, Power *et al.* 1997). Computer simulations reveal that synchronization is only beneficial in conditions of relatively low infant mortality or marked reduction in interbirth intervals (Foley, Fitzgerald 1996). In a situation of high child mortality the costs of reproductive synchrony are too high, making individualistic reproduction a more effective strategy to compensate for demographic losses. While Power *et al.* (1997) concur with many of Foley and Fitzgerald's results, they argue that the model does not correspond to the demographic conditions prevailing in recent human past. They assert that seasonal synchrony could have been a viable strategy to prevent harem holding. Seasonality in combination with continuous receptivity may have promoted long-term pair bonding, while synchrony would have further prevented males from monopolizing female consorts.

Argument 1: In times of high infant mortality, individual reproduction is a better strategy than synchronous breeding.
Foley and Fitzgerald's computer simulation (1996) stresses that menstrual synchrony could have been disadvantageous and therefore have become less and less important in societies with high infant mortality (Strassman 1996). The rise in infant mortality following the Neolithic transition is an excellent case in point. However, it is not suggested that this particular event in recent human history is actually responsible for the demise of synchrony. Several factors are intertwined in this dramatic alteration of fertility and mortality regimes. The adoption of the new subsistence mode occurred because hunting and gathering were no longer ecologically or economically feasible (Layton *et al.* 1991). The onset of agriculture not only triggered a cultural

change which brought farming and associated technologies across Europe but the shift in resource base was accompanied by a demographic transition as well.

Sedentism imposed a host of novel health risks due to the introduction of infectious diseases (malaria, measles, mumps, chicken pox, smallpox), zoonoses (anthrax, brucellosis, tuberculosis) and diseases associated with human waste or contaminated water (cholera, typhus, plague – Armelagos *et al.* 1991, Frauendorf 2001). Paleodemographic, paleoepidemiological, and modern comparative population data support the inference that infant survivorship chances may have been particularly poor. Observations in skeletal data attest to a higher prevalence of various defects which can be linked to a less diversified dietary spectrum (Cucina 2002). Similarly, measurements of child health – particularly morbidity, diet and growth patterns – support findings that the subsistence base of many sedentary communities may be inferior (Nathan *et al.* 1996). Cohen (1989) argues that changes in settlement patterns exposed humans to higher mortality risks, which could have only been counteracted by increased birth rates in order to achieve population growth. This may have been accomplished via a replacement strategy, where parents have an additional child to replace one who has previously died (Zhang 1990). A peculiar side effect to adopting a sedentary lifestyle is the marked increase in female fertility and fecundity induced by a switch from a high-protein, meat-based diet to a high carbohydrate, low-protein, cereal-based diet which contributes to a higher body fat/body weight ratio (Henry 1989). Higher reproductive output was also facilitated through the availability of softer foods which allowed earlier weaning. The latter is an important health issue since it is a hazardous period for malnutrition, infections, and mortality (Katzenberg *et al.* 1996). These health risks are directly related to the weaning diet (Alt 2002). Speeding up weaning in natural fertility populations often leads to a premature resumption of childbearing. However, inadequate interpregnancy intervals below 6 months and greater than 59 months are associated with increased maternal morbidity and mortality (Conde-Agudelo, Belizan 2000) as well as adverse pregnancy outcome (Fuentes-Afflick, Hessol 2000). Moreover, the negative effect of a short interbirth interval continues beyond the first year of life into early childhood (Lindstrom, Berhanu 2000).

Argument 2: Humans are not seasonal breeders, even though fertility may show seasonal variations.
While brief mating season has a high potential for estrous synchrony, timing of reproduction in humans is no longer dependent on a seasonal variation of infant survival probability, but is related to multiple factors such as socio-demography (Bobak, Gjonca 2001) or culture (Lummaa *et al.* 1998), an effect best attributed to urbanization and changing norms (Trovato, Odynak 1993). Still, persistent seasonal fluctuations in fertility and mortality can be

observed in virtually every human society. Besides being extraordinarily stable over time, these seasonal cycles are very pronounced when compared to other temporal trends (Lam and Miron 1994). In humans, seasonal patterns in conception and birth can be documented in historical (Lummaa *et al.* 1998) as well as ethnographic data (Chatterjee, Acharya 2000). Overall, birth seasonality is most prominent in many pre-industrial or pastoralist populations (Danubio *et al.* 2002). It is important to note that seasonality patterns are not static but can exhibit marked changes (Russell *et al.* 1993). The "resilience hypothesis" which posits that there are several fundamental causes of seasonality which result in three basic prevailing phenomena – the peak in births early in the year associated with the so-called European pattern, the trough in spring associated with the so-called American pattern, and the September peak that occurs in both patterns – has the highest explanatory power. For a discussion of the environmental, social, and biological correlates of the observed seasonality patterns, see Doblhammer *et al.* (1999).

Events in early life strongly influence adult survival prospects. As such, month of birth has been found to be an important predictor of life expectancy (Gavrilova *et al.* 2001). Similarly, life expectancy at age 50 appears to depend on factors that arise *in utero* or early in infancy and that increase susceptibility to infectious or chronic diseases later in life. These differences in adult lifespan by birth month decrease over time and are significantly smaller in more recent cohorts, which benefited from substantial improvements in maternal and infant health (Doblhammer, Vaupel 2001). A Dutch study found that fecundity may be linked with the female's birth season (Smits *et al.* 2000). Best understood is the phenomenon of death seasonality where the peaks in infant mortality during the summer or winter can be linked to diseases of the circulatory or respiratory system such as pneumonia and influenza or the diseases of the digestive tract due to parasitic infections (Kloke 1998). Such phenomena are most likely the result of seasonal variations in past living conditions, nutritional intake or exposure to infectants. The permanent effect of malnutrition on the development of the immune system during foetal growth has been documented in societies experiencing annual agricultural cycles or natural occurrences such as drought. Thus, people born during a hungry season run an elevated risk of premature death (Moore *et al.* 1997).

Argument 3: Human life histories assure the availability of well-qualified allomothers.
Humans evolved as cooperative breeders (Hrdy 2000b). Cooperative breeding is a reproductive system restricted to familial societies in a dangerous environment with high mortality risks, characterized by delayed dispersal beyond reproductive maturity and provision of alloparental care by non-breeders (Emlen 1995, Solomon, French 1997). Primate mothers allow non-maternal care in order to

increase their own reproductive output. Thus, social networks with other females in the wider community are formed to give social support and provide alloparenting. Overall, they appear to be a feature of an evolved female reproductive strategy (Irons 1983, Taylor *et al.* 2000). The creation of female solidarity through curbing female intra-sexual aggression, while enhancing the female contribution in terms of socio-emotional involvement, is paramount for hominid evolution (Campbell 1993). Species with high allocare levels grow rapidly post-natally and wean their infants at a younger age. Hence, early weaning – in conjunction with a shortening of the intergenetic interval – allows high allocare species to support higher birth rates than low allocare species (Ross, MacLarnon 2000). Alloparenting also conveys benefits to the helper. The "learning-to-mother hypothesis" asserts that parenting skills are learned and that allomothering helps to acquire these skills. Second-hand breeding experience thus greatly enhances reproductive success and inclusive fitness (Woodard, Murphy 1999, Bales *et al.* 2000).

Based on data from human hunter-gatherers, Hewlett *et al.* (2000) could show that allomaternal assistance contributes significantly to larger completed family sizes. Several fringe-benefits, such as reduction of maternal energetic burden, increased socialization and protection of the infant have been suggested in this context (Hrdy 1976, 1979, Price 1991). One of the most spectacular examples of communal rearing can be observed among the Efé hunter-gatherers where infants average 14 different caretakers, including fathers, brothers, sisters, aunts, grandmothers, and even unrelated individuals. Not surprisingly, time spend with alloparents greatly exceeds time spend with the mother (Ivey 2000). In line with evolutionary biology, kin are preferred as allocare providers over non-kin (Sherraden, Barerra 1997). But as the history of wet nursing documents, the societally condoned allocare by non-related individuals can be traced back to prehistoric times. Wet nursing was particularly popular from 1500–1800, when the majority of the European aristocracy, gentry, but also wealthy merchants or farmers regularly relied heavily on such services (Fildes 1988, Stuart-MacAdam, Dettwyler 1995, Hrdy 2000b).

Moreover, human life histories assure the availability of well-qualified allomothers through delayed maturation and long post-menopausal life spans (Hawkes *et al.* 1998). Turke (1988) found that women who have one or several daughters first tend to have higher completed fertility when compared to women who bore sons first. Draper and Hames (2000) could show that number of older siblings as well as sibling set size are strong predictors of fertility, especially for males. In this context it is important to emphasize that alloparenting need not be restricted to active childrearing; older siblings can aid in household chores, light agricultural tasks and the like (Crognier *et al.* 2001). The fact that human females survive longer time periods after menopause has given rise to the "grandmother hypothesis" which posits that older women can increase their inclusive

fitness more by investing in grandchildren and other relatives than in continued childbearing (Hill, Hurtado 1996, Hawkes *et al.* 1998, Alvarez 2000). For example, forager grandmothers will typically provide a large percentage of a family's gathered food during her daughter's early years of child bearing. During this crucial period the mother's constant nursing, holding and carrying of younger infants interferes with her ability to tend to her older children. Hence, the grandmaternal contribution is important for the grandchildren's well-being (Hawkes *et al.* 1998, Mace 2000). Interestingly, as modernization has reduced the number of available caregivers, particularly biological kin, the decrease in the availability of direct care for children may have prompted the drastic reductions in fertility which characterize the demographic transition (Waynforth, Waynforth 2001).

CONCLUSION

It is hypothesized that menstrual synchrony in human females represents a redundant life history artifact which has its origins in our primate heritage as cooperative breeders. In line with Foley and Fitzgerald (1996) or Power *et al.* (1997), menstrual synchrony is not thought of as an evolutionary stable strategy. The mechanisms which have rendered menstrual synchrony functionless are related to a high degree of child mortality and cultural changes pertaining to a reduction in the benefits of reproductive seasonality and a greater reliance on allocare. The evolutionary approach posits that concealed ovulation, continuous sexual receptivity, and the potential for menstrual synchrony are all linked to achieve higher gains in paternal investment (Turke 1984). However, kinship may have been overemphasized for male helpers and underestimated for females. Hawkes *et al.* (1995) and Van Schaik and Paul (1996) have argued that men provide care only as mating effort. The so-called "showoff hypothesis" argues that men hunt because they receive fitness returns in the form of extra matings or social benefits. Thus, the observed "mate-then-care" pattern, may simply be a "care-then-mate" pattern (Tallamy 2000, Menard *et al.* 2001, Welch *et al.* 2001). Moreover, human life histories assure the availability of well-qualified allomothers through delayed maturation and long post-menopausal life spans (Hawkes *et al.* 1998). Turke (1988) found that women who have one or several daughters first tend to have higher completed fertility when compared to women who bore sons first. Similarly, Draper and Hames (2000) could show that number of older siblings as well as sibling set size are strong predictors of fertility, especially for males. In this context it is important to emphasize that alloparenting need not be restricted to active childrearing; older siblings can aid in household chores, light agricultural tasks and the like (Crognier *et al.* 2001). The fact that human females survive longer time periods after menopause is also an important clue. The "grandmother hypothesis" posits that

older women can increase their inclusive fitness more by investing in grandchildren and other relatives than in continued childbearing (Hill, Hurtado 1996, Hawkes *et al.* 1998, Alvarez 2000).

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