THE NUBILITY HYPOTHESIS

The Human Breast as an Honest Signal of Residual Reproductive Value

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A new hypothesis is proposed to explain the perennially enlarged breasts of human females. The nubility hypothesis proposes that hominid females evolved protruding breasts because the size and shape of breasts function as an honest signal of residual reproductive value. Hominid females with greater residual reproductive value were preferred by males once reliable cues to ovulation were lost and long-term bonding evolved. This adaptation was favored because female-female competition for investing males increased once hominid males began to provide valuable resources.

KEY WORDS: **Female-female competition; Male care; Perennially enlarged breasts; Residual reproductive value.**

Human females are unique among primates in having noticeably larger breasts than males even when they aren't pregnant or lactating. In other primates, breasts enlarge during pregnancy and lactation with the expansion of mammary tissue, which also occurs in humans. But the perennially enlarged breasts of humans are due to fat deposits around the mammary glands. There appears to be a consensus that breast size correlates more with amount of fat than amount of mammary tissue (Hytten and Leitch 1971; Niefert et al. 1985). However, there is no clear consensus

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on how and why human breasts came to be perennially enlarged. The nubility hypothesis proposes that this adaptation resulted from sexual selection for signaling nubility.

It has been suggested that men find breasts attractive because they are honest signals of fat reserves, which reflect a woman's ability to survive lean times, give birth, and invest in offspring (Cant 1981; Gallup 1982; Huss-Ashmore 1980). In addition, when fat reserves fall below a certain threshold, women become anovulatory (Cohen 1980; Frisch 1978), so men should prefer women with adequate stores of fat. However, if this were the whole story, men should find breasts no more erotic than fat anywhere else on a woman's body. Even if the fat on breasts is different because it is used specifically to support lactation, one still needs to explain why such fat is concentrated there. But how did breasts become attractive at all if hominid females originally had large breasts only when pregnant or lactating, and therefore not ovulating? Smith (1984) argued that females with large breasts were not as closely guarded. Hence they were freer to carry on clandestine affairs, which paid off in social, material, or genetic benefits. This situation relaxed selection against perennially enlarged breasts until, eventually, they had the advantage of obscuring a female's reproductive state. Although this may explain why enlarged breasts were not repulsive, it does not explain why they would be preferred by males.

Low et al. (1987) argue that fat stored on the breasts (and hips) is a deceptive signal (but see Anderson 1988; Caro and Sellen 1990; and for replies, Low et al. 1988, 1990). They suggest fat makes hips appear wider, which is attractive because a wide pelvis means easier offspring delivery, and fat makes the mammary glands appear larger, which is attractive because larger mammary glands did originally indicate superior lactation ability. Women with insufficient glandular development do have trouble lactating and have more asymmetric breasts (Niefert et al. 1985). Women with more asymmetric breasts were found to have lower fecundity (Møller et al. 1995) and to be less attractive to men (Singh 1995). Manning et al. (1997) found that women with large breasts showed less asymmetry than expected allometrically, even though they had more body fat and higher levels of estrogen, which increases asymmetry. They concluded that women who can produce symmetrical breasts despite associated costs, advertise their "good genes."

Several authors have argued that there is no reason to invoke sexual selection (including Anderson 1988; Smith 1986). Some have argued that natural selection for fat stores to support gestation and lactation is sufficient to explain the enlarged human breast (Caro and Sellen 1990; Mascia-Lees et al. 1986). The same would apply to hips since fat there is used to support lactation (Rebuffe-Scrive et al. 1985). But as others have pointed out, fat stores indicate a female's ability to nourish offspring and, therefore, would be subject to sexual selection to the extent male choice had any influence on female reproductive success (Huss-Ashmore 1980; Lancaster 1986). I will argue that the human breast is an erotic stimulus and that this is relevant to explaining why fat is deposited there. What I seek to explain is not why females have fat stores (which are clearly advantageous for ovulation and lactation), nor why human females have larger fat stores than other primates (Kaplan 1997), but why fat is stored around the mammary glands, and why only humans have perennially enlarged breasts which males find attractive.

THE HYPOTHESIS

The nubility hypothesis proposes that perennially enlarged breasts evolved in hominid females as an honest signal of age and, thus, residual reproductive value. Residual reproductive value is the expected future reproductive output of an individual (Fisher 1958). For example, a female at the very beginning of her reproductive career has high residual reproductive value since all of her reproduction is ahead of her. If males have short-term access to many mates, they should prefer females of the age at which age-specific fertility peaks, but if males have long-term access to only one or two females in a lifetime, residual reproductive value is what should be valued most. If a male acquires a mate who is already halfway through her reproductive years, he has lost half the number of offspring he might have had with a nubile female. Because prepubescent and postmenopausal females are infertile, they should be less attractive to males, but when long-term bonding occurs, so too should females nearing the end of their reproductive careers. While others have noted the link between size and shape of breasts and reproductive condition (Anderson 1988; Gallup 1982; Low et al. 1987; Smith 1984), no one has emphasized age. I propose that fat is stored in protruding breasts because advertising age is the primary function of perennially enlarged breasts.

Breasts advertise age by their size and shape: if not protruding at all, the girl is prepubescent; if protruding and firm, the woman is mature but young; if sagging, she is old. Breasts sag with age because the supporting fibrous tissue stretches and slackens (The Diagram Group 1983). Gravity will eventually take its toll and protruding breasts will not stay firm forever. For this reason, the larger breasts are, the faster gravity should make them sag. The result is that males can judge the age of a female with large breasts better than they can a female with small breasts; accordingly, males should prefer larger breasts. If pair-bonds became extended in time, and there was significant male care or provisioning which influenced female fitness, it would pay a female to attract the best provider. Since after puberty protruding breasts would eventually begin to sag, a female of maximum residual reproductive value could advertise her youth, and attract more males from which to choose, if she had protruding, firm breasts.

Why is fat stored around the mammary glands? After all, protruding appendages placed anywhere would be subject to the same forces of gravity and so function to signal age. Signals tend to evolve from traits which are already correlated with something related (Dawkins and Krebs 1978; Krebs and Dawkins 1984). In this case, any trait that was already correlated with cycling could be used to signal the onset of puberty. And signaling puberty would become important if cues to ovulation were lost because males would no longer know if a female was old enough to ovulate. If there were no sexual swellings or behavioral cues to ovulation, the clearest signal of cycling would have been pregnancy (and menstruation). A swollen stomach and swollen breasts would have signaled a female was old enough to ovulate, so fat was stored in the breasts because swollen breasts already signaled cycling. This cue was extended to be continuous and prior to pregnancy, which made protruding breasts attractive because they no longer signaled temporary non-ovulation but rather the beginning of cycling. Even if breasts were initially too small to signal nubility, they could have become attractive because even small, protruding breasts advertised puberty.

DISCUSSION

Because all females who haven't died will reach puberty, they will have an equal amount of youth to advertise. The nubility hypothesis does not, therefore, propose that it is nubility per se that breasts are advertising, but rather ability to signal nubility honestly. All 17-year-old females were not equally capable of allocating energy to such signals. The cost of such allocation might be reduced mobility, or the cost of converting energy to fat rather than other tissue. It might be costly to allocate fat to the breasts when it is needed elsewhere; excessive fat in breasts can even inhibit the flow of milk (McCary 1973), and there is an increased risk of cancer with increased levels of estrogen required for breast development (Boyle 1988). The cost might be the tradeoff between advertising age and revealing asymmetry: females allocating fat to protruding breasts would signal nubility but also reveal asymmetry. Once a mutant gene for perennially enlarged breasts appeared it could become fixed as long as even weak signals were favored over no signal. The nubility hypothesis is ultimately a "good genes" argument—females with greater vigor were more capable of allocating energy to signals of youth.

There should be a tradeoff for females between the advantages and disadvantages of large breasts. A female would benefit later in life by having smaller breasts since her age would be more difficult to judge. I propose, however, that males prefer large breasts precisely because they are honest signals. How could a trait evolve which favored its carrier when young, only to work against her when she is old? As long as early gains exceed later losses, such a trait would be selected for. A high level of testosterone, for example, may help males win contests even as it shortens their lives (Daly and Wilson 1983). If pair-bonds are of long duration, a female who acquires a high-quality, provisioning male at the beginning of her reproductive career, and keeps him throughout her most fertile years, will have an advantage over a female who acquires such a male only later in life. Small-breasted females might be more attractive as they get older, but by then may be less fertile and may have used up some of their childbearing years with a poorer male. From my observations of the Hadza of Tanzania, a foraging society in which women suckle on demand and wean after 2–3 years, breasts can usually stay fairly firm through the years of peak fertility, even after two or three children. Large breasts, therefore, would not begin to sag and work against a female until after peak fertility.

Many have argued that American men are unusually interested in large breasts, concluding that men in many other cultures may not be interested in breasts (Anderson 1988; Masters et al. 1988; McCary 1973). It should be no surprise if we find the ideal breast size varies cross-culturally, but breasts are reported to be an erotic stimulus across a wide range of cultures (reviewed by Ford and Beach 1951). Even though men's interest in breasts may increase where women are clothed, the interpretation that men in nude cultures do not find breasts erotic is erroneous. Based on numerous interviews I conducted with the Hadza, men find breasts erotic, even though women usually do not cover their breasts. They fondle breasts during intercourse and like "a handful of firm breast," as they put it, "like teen-aged girls have." Such fondling is reported in numerous other nude cultures (Ford and Beach 1951). The contention that eroticism only occurs where breasts are covered would imply that men do not find vaginas erotic in completely nude cultures, and that there are no sexual signals among other species. I suggest that firmness is the main criterion of attractiveness, and since firmness means less if breasts are small, that males prefer large, firm breasts cross-culturally.

How large should breasts be? Since men prefer symmetrical breasts (Singh 1995), and since larger breasts reveal asymmetry more than small breasts (Møller et al. 1995), we would expect men to prefer large breasts so as to judge symmetry. But I suggest an additional reason: the breast is a supernormal stimulus which men find attractive when larger than average because, when firm, it is a more reliable signal of youth. The upper limit on size would be the point at which breasts would not be firm even at puberty, and the point at which natural selection would check runaway sexual selection.

The nubility hypothesis is contingent upon considerable female-female competition for mates as a result of considerable male investment with long-term bonds. Thus, perennially enlarged breasts must have evolved after male provisioning abilities increased and cues to ovulation were lost. Breasts develop around the time of menarche, a couple of years before ovulation becomes regular (Short 1976; Lancaster 1986). For most preliterate societies, marriage occurs within three years of menarche (Whiting et al. 1986). This suggests that human females have evolved to attract males early enough so as to choose a mate who will probably be bonded for a year or so before the first child is born, which should raise the male's confidence of paternity and likelihood of investment.

If there were no long-term bonds, males should prefer females of the age at which fertility peaks. Chimpanzee males appear to show most interest in females at peak fertility, several years after peak residual reproductive value (Goodall 1986). The evidence is equivocal regarding the most preferred age in humans, though men clearly prefer women younger than themselves (Buss 1994; Kendrick and Keefe 1992). Males in other primate species may not prefer nubile females either because ovulation is advertised, because there are no long-term bonds with considerable male investment, or because females are dispersed in separate territories where there is less opportunity to judge relative female quality. Another reason why human females are unique in having perennially protruding breasts may be bipedalism. Breasts always extend straight down if females are in a quadrapedal position, so protruding breasts would not function as a gauge of age in quadrapedal species. In addition, the existence of menopause provides all the more reason for males to prefer females who advertise their age. Without menopause, bonding with and provisioning an old female would not necessarily be selected against, especially if older females have an advantage in terms of better parenting skills. But once menopause evolved, bonding with an older female and staying until she dies would have been strongly selected against.

Perhaps the evolution of human breasts owes nothing to their signal value. If so, the adaptation discussed here is only in the mind of males who use breast size and shape to gauge the age of females. If the nubility hypothesis is correct, however, we might find other signals of female nubility in species with male provisioning and long-term bonds. There are signals of age in many species: puberty signals such as horns and manes, signals of old age such as the hair on silverback gorillas and cheek pouches of orangs, and signals of youth such as the differently colored young of many animals.

CONCLUSIONS

The nubility hypothesis posits that perennially enlarged breasts evolved because they were honest signals of residual reproductive value. Fat deposits in the breasts are adaptive stores of energy which are drawn upon during pregnancy and lactation. But this fat might have been distributed more evenly across the body with less erotic value. The nubility hypothesis explains why fat deposits are stored in protruding breasts, why they are erotic, and why they evolved only in humans. What is needed for a preliminary test is cross-cultural data on the correlation of breast size and shape with age, parity, lactation, exercise, and reproductive success, as well as male preferences for female age and breast type. I predict (1) that firmness is positively correlated with residual reproductive value; (2) that males, cross-culturally, prefer large, firm breasts; and (3) that females who have a relative advantage in attracting males at the beginning of their careers achieve higher reproductive success than females who have a relative advantage only later in life.

Frank Marlowe is research has focused on paternal care and mating effort among Hadza hunter-gatherers. He is also interested in mate preferences, mating systems, and life history theory.

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