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An organism's brood size is a critical component of its fitness. As such, brood size (the number of offspring produced per reproductive cycle) is expected to be optimized by natural selection over evolutionary time, to the extent that the proximate determinants of brood size are heritable and unlimited by phylogenetic and other constraints. Haukioja et al. (1989) recently adopted this perspective in attempting to explain the present brood size of humans (*Homo sapiens*). Most human births produce a single baby, but a minority (contemporary estimates range from 0.6% [Vogel and Motulsky, 1986] to 5.0% [Nylander, 1979]) produce two or more. The majority of these multiple births are of twins (Bulmer, 1970). In modern times, the higher birth rate from twins more than compensates for their slightly higher postnatal mortality (Bulmer, 1970), prompting Haukioja et al. (1989) to ask "why are twins so rare in *Homo sapiens*?" They compiled and analyzed an unusually complete data set from late 18th and early 19th century Finnish communities (before the advent of modern medical care) and compared the reproductive success of parents of singletons with that of parents of twins. Haukioja et al. (1989) were unable to reject the hypothesis that the reproductive success

of parents of singletons was identical to that of parents of twins.

The present frequency distribution of human brood size at birth presumably reflects primarily prehistoric evolution (Haukioja et al., 1989). If brood size actually was selectively neutral during prehistoric human evolution (consistent with the result of Haukioja et al. [1989]), then stochastic processes such as drift and mutation would be expected to produce a broad range of average brood sizes among genetically isolated populations (Hartl, 1980). However, the frequency of multiple births is uniformly low worldwide (see above), although a tendency for some racial differentiation exists (Bulmer, 1970). Instead, the consistently low frequency of multiple births across populations suggests that deterministic evolutionary processes (natural selection) affect the species as a whole.

A modal human brood size of a single offspring is not surprising, given that the other higher primates seldom or never produce more than one offspring per brood (Harvey et al., 1987). Moreover, comparative studies of teat number and brood size predict a brood size of one in humans (Gilbert, 1986; Diamond, 1987). Nonetheless, the tendency to conceive more than one

embryo per pregnancy runs in families, suggesting that the trait is heritable and, thus, responsive to selection; this is true for polyovulation and, perhaps, for monozygotic twinning (Parisi et al., 1983). Some evidence suggests that selection would operate against multiple births. First, infanticide against one or both members of a twin birth was reported in 14 of 60 (23%) societies surveyed by Daly and Wilson (1984), and it occurred on five different continents. The killing of both twins in a brood (as reported for the Ayoreo [Bugos and McCarthy, 1984]) involves lost parental investment by the mother (in gestation time and nourishment of two embryos), while the loss of only one of the two leaves the parent with a living, but probably premature and underweight, offspring. Second, the demographic data presented by Haukioja et al. (1989) showed no advantage to producing twins in Finland only two centuries ago; if that population had a higher standard of living than that of humans in prehistory, then the Finnish sample may overestimate the capacity of aboriginal humans to raise twins. Third, the polyovulation and monozygotic twinning that produce twins also produce all other types of multiple births (Gedda and Brenci [1986] discuss a case of sextuplets). A comprehensive evaluation of selection on brood size at birth should include the contribution of all multiple births to parental fitness, but Haukioja et al. (1989) considered only that of twins. Brood size correlates negatively with per capita birth mass and gestation period but positively with total brood mass (Bleker et al., 1988), suggesting that there are increasing costs to both offspring and mother with increasing brood size. If these costs fall disproportionately on births of three or more, then selection may oppose all multiple births, even when twinning alone is selectively neutral.

In the face of probable selection against multiple human births, the appropriate question becomes "why are twins so common?" I suggest that, while selection opposes multiple births it favors multiple attempts to conceive during each estrous cycle. This selection derives from the low probability that a given ovum will produce an embryo that will survive more than one month after conception (see Birney and Baird [1985] for a conceptually similar hypothesis). Genetic abnormalities and other defects prevent many conceptions from leading to a viable pregnancy; estimates of this failure rate range from 16% (French and Bierman, 1962) to 72–77% (Hubinout, 1980). Of embryos that do implant, 8–25% are apparently aborted in the first month, with genetic abnormalities again implicated in the majority of cases (Johnson and Everitt, 1984; Wilcox et al., 1988). By producing more than one ovum, parents increase the probability that at least one will produce a neonate; Melis et al. (1987) provided clinical demonstration of this effect.

The insurance value of extra ova in this scenario is functionally identical to that of insurance eggs laid by some birds that typically raise only one chick to fledging (Anderson, 1990). While brood size in these birds is reduced to one chick by siblicide shortly after hatching, most modern multiple human conceptions are reduced to a single fetus before birth. Sonograms of women in the first trimester show that twins are conceived 2–4 times more often than they are born; in most cases, the smaller fetus disappears by the third trimester, apparently resorbed by the mother (Robinson and Caines,

1977; Schneider et al., 1979; Varma, 1979). The possibility that the surviving fetus contributes to the "brood reduction," as occurs in pronghorn antelopes (O'Gara, 1969) and sharks (Wourms, 1977), has apparently not been investigated, although postnatal dominance relationships in human twins are well known (Moilanen, 1987), and twin pregnancies sometimes end with birth of a live infant and its "macerated" (presumably by the surviving fetus) sibling in some other primates (Benirschke, 1986).

This "insurance ova" hypothesis thus views the birth (as distinct from conception) of aboriginal human twins as an error occurring at low frequency in a system that compensates for embryo mortality. The frequency of the error in some populations is less than 1% (Vogel and Motulsky, 1986; World Bank, 1988 table 29), yet is more than five times higher in others (Nylander, 1979). Selection should minimize the frequency of multiple births in all populations under this hypothesis, but environmental factors that affect regulation of embryo number may vary on too short a time scale for selection to track them, increasing the probability of error. For example, Nylander (1979) showed that western Nigerians in lower social classes produced twins in 6.2% of births, while those in higher classes had only 1.5% twin births. Nylander (1979) linked the probability of multiple birth to diet; members of lower classes eat the local diet, particularly yams containing estrogen-like compounds (Hardman, 1969), while the higher classes eat a European-style diet lacking yams, and have twinning rates typical of humans living in Europe (World Bank, 1988 table 29). Twinning rates also increase with maternal age (Bulmer, 1970), but this may actually indicate an adaptive increase in polyovulation, compensating for genetic defects in ova which are also age-related.

The "insurance ova" hypothesis makes two clear predictions. First, the rate of ovum production should exceed the rate of birth. Data consistent with this prediction are described above. However, twin ovulation has been detected in only 5–10% of menstrual cycles (Brewer and Jones, 1941; Ritchie, 1985), suggesting that some costs (such as the risk of multiple birth) increase with polyovulation. Certainly the normal rate of polyovulation does not approach the ovaries' capacity, as is demonstrated by women under hormone therapy (Ritchie, 1985). Second, because polyovulation contributes insurance against genetic defects (because the embryos are genetically different) as well as against nongenetic developmental failures while monozygotic fission insures only against nongenetic failures (because the embryos are genetically identical), polyovulation should be the method used to produce multiple embryos. This prediction is confirmed for most populations in the sense that most twins are dizygotic rather than monozygotic (Bulmer, 1970). However, the existence of monozygotic twinning at any frequency greater than zero cannot be explained by the hypothesis.

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