Evolutionary adaptations

Aristotle's theory of mammalian teat number is confirmed

Jared M. Diamond

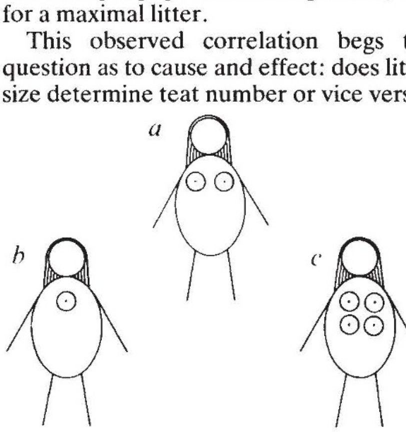
Animals which have small litters, both those that have solid hoofs and those that carry horns, have their mammae by the thighs; and there are two of them. Animals that have large litters or are polydactylous . . . have numerous mammae placed at the sides upon the abdomen — for example, swine and dogs. (Aristotle, *The Parts of Animals* Lesbos, about 350 BC).

Le nombre des mamelles et leur situation sont extrêmement variables . . . Il est d'ailleurs ordinairement en rapport avec le nombre des petits que les femelles peuvent mettre bas. (G. Cuvier, *Leçons d'Anatomie Comparée* vol. 5, p.155; Baudoin, Paris, 1805).

MAMMARY glands are so central to ecology and life history in the order Mammalia that they give the order its name. We think anthropocentrically of the normal teat number as two but, as Aristotle noted, it varies greatly among species: some primates have six, and rodents have up to fourteen. What accounts for this interspecific variation? Why, for instance, does the human female have design *a* rather than *b* or *c* (see figure)?

Aristotle suggested that teat number is related to litter size, a view followed by Cuvier but varously espoused or disputed by twentieth century scientists. A recent analysis by A.N. Gilbert (*Proc. natn. Acad. Sci. U.S.A.* **83**, 4828–4830; 1986), resting on a massive database, now supports Aristotle. Gilbert assembled values, for 266 rodent species, of teat number T (ranging from 2 to 14), mean litter size $\bar{L}$ (ranging from 1 to 8) and maximum litter size L_{max}. There is a significant positive correlation between $\bar{L}$ and T: $\bar{L} = 0.39 \pm 0.46T$, $P < 0.001$, $r = 0.72$. Averaged over all species, the ratio $\bar{L}/T$ is 0.53 ± 0.01, and L_{max}/T is 0.92 ± 0.02. Thus, there are two teats per pup for an average litter, one for a maximal litter.

This observed correlation begs the question as to cause and effect: does litter size determine teat number or vice versa?



Theoretical designs for human mammary gland arrangement. *a*, The accepted number; *b*, no excess capacity for twins; *c*, too extravagant.

At a proximate level, teat number does affect surviving litter size, as milk production is critical to pup survival and there is a sharp increase in pup mortality when litter size exceeds teat number. The value $L_{max}/T = 0.92$ means that natural selection has produced mammals with a safety margin of teats, enough to provide one per pup in the occasional large litter.

At an ultimate level, there have been many theoretical discussions of the evolution of litter size, which is generally seen as constrained by factors such as latitude, length of breeding season, body size and metabolic rate. By ignoring teat number, such analyses tacitly assume that it easily evolves in response to the driving variable of litter size. However, Gilbert suggests that this may not be true. For instance, within a few generations it is feasible to select animals for increased litter size but not for increased teat number, which is a rather constant species characteristic.

If we now return to our question concerning human females, they are seen to fit Gilbert's rodent-based theories perfectly. For $T = 2$, the relations $\bar{L} = 0.53T$ and $L_{max} = 0.92T$ predict that our maximum litter size should be 1.84 (after rounding to an integer, twins) and our mean litter size 1.06 (usually singletons). In fact, singletons are our norm, twins a not uncommon exception (5 per cent of all births in some populations) and triplets vanishingly rare. Thus, our selected design *a* in the figure is to accommodate the occasional twin birth, whereas the other designs are rejected because they lack a safety margin (*b*) or are extravagant (*c*). □

Jared M. Diamond is Professor of Physiology at the University of California Medical School, Los Angeles, California 90024, USA.

Edward A. Doisy (1893–1986)

EDWARD A. DOISY died on 23 October 1986, one month before his 93rd birthday. His numerous scientific achievements centred around his masterful selection of methods for the isolation of trace natural products of biological significance. Needless to say, the methods available to Ed Doisy in the early part of this century were crude compared to those available today. His major contributions were made while residing in the city of St Louis, where he worked first at Washington University (1919–1923) and then at St Louis University (1923–1965).

Edward Doisy was born in Hume, Illinois, on 13 November, 1893. He studied chemistry at the University of Illinois and then went to Harvard to work under the guidance of Otto Folin, receiving his doctoral degree in 1920.

He was appointed an instructor in biochemistry at Washington University School of Medicine in 1919 and became associate professor in 1923, when he moved across town to become the first professor and chairman of a new department of biochemistry at St Louis University, a position he held until his retirement in 1965.

At Washington University he began his work on the isolation of natural products by the purification of insulin by isoelectric precipitation. He then developed an interest in ovarian function and the nature of the ovarian hormone through collaborative studies with the anatomist Edgar Allen. By judicious application of bioassays for oestrus in rats and his skill in the purification of trace compounds, he was the first to obtain oestrone, one of the female sex hormones, in crystalline form from urine in 1929. A few years later, he isolated from several tons of sow ovaries the more potent ovarian hormone oestradiol. These discoveries opened up the field of fertility to biochemical study, the consequences of which are still being exploited.

In 1936, following the discovery of vitamin K as a new fat-soluble compound that promoted coagulation of blood in chicks and rats by Henrik Dam, Doisy undertook the isolation of this lipid vitamin from various sources, including alfalfa and fermented fish meal. In 1939, he succeeded in crystallizing vitamin K from alfalfa meal and vitamin K_2 (now called menaquinone-7) from fermented fish meal. He subsequently synthesized homologues in both the vitamin K_1 and K_2 series. Doisy received the Nobel Prize in physiology and medicine, jointly with Dam, the discoverer of vitamin K_1, in 1943 for his work on the isolation and synthesis of vitamins K_1 and K_2. No doubt his contributions to the oestrogen field played some role in the award.

During World War II, he worked for the Office of Scientific Research and Development and isolated several new antibiotics. After the end of the war, Doisy began to study bile acids and succeeded in isolating novel bile acids from the rat.

His many students and associates remember Edward Doisy as a single-minded and astute judge of research problems that could be solved with the techniques available, and an excellent mentor who both recognized scientific skills in young people and helped to develop them to the utmost. Robert E. Olson

Robert E. Olson is Professor of Medicine at the State University of New York at Stony Brook, Stony Brook, New York 11794-8160, USA.