Sex allocation theory: implications for animal food industry

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Animal source foods (ASFs) have been an integral component of human diet since ages in various forms like meat, milk, fish, eggs, cheese, yogurt, etc. Approximately half of all the major nutrients (proteins, carbohydrates and fats) and major servings of some essential vitamins and minerals in human diets are derived from ASFs[1]. Development of high-yielding breeds and implementation of scientific husbandry practices have been instrumental in sustaining the animal food industry despite the ever-growing need for nutritious food. Carefully designed feeding regimen and management practices have further helped in harnessing maximum yield from the dairy and food animals.

Female of the egg-laying birds and milk-yielding animals is valued more than the male, whereas male of the meat-producing animals is valued more than the female due to higher yields obtained from the former. Hence, male calves born in the dairy industry and female chicks (female calf in meat industry) born in the egg industry are culled. This represents loss of half of all the pregnancies in some industries and is unavoidable due to the inherent ability of each sex offspring born being equal[2]. This loss can be minimized by increasing the chances of obtaining offspring of the desired sex. Attempts to obtain female offspring with each pregnancy in dairy animals using fluorescent activated sorting of spermatozoa have been fairly successful and are being used in few farms in the developed nations[3]. Such methods have not been developed for other animals, as the costs incurred are high. Even though sperm sexing has been highly successful and sophisticated instruments are developed, it cannot be utilized effectively until the technology becomes affordable by the farmers. Further, extensive *ex vivo* handling of spermatozoa during various steps of sorting deteriorates the quality of the genetic material[4,5].

Any method that can increase the probability of obtaining the desired sex offspring with minimal cost and technology inputs can be of tremendous value both for the animal husbandry farmers and consumers. One potential method can be derived from exploiting the knowledge accumulated by evolutionary biologists about the parental ability to select the sex of the offspring[6,7]. The probability of obtaining offspring of either sex is theoretically equal in most of the sexually reproducing species[8]. However, Charles Darwin observed a frequent deviation from this value under certain circumstances. He was unable to explain it and concluded that, 'I formerly thought that when a tendency to produce the two sexes in equal numbers was advantageous for the species, it would follow from natural selection, but now I see that the whole problem is so intricate that it is safer to leave its solution for the future.' This problem was solved by Trivers and Willard[6], who contemplated that mothers in better condition would be advantaged by biasing their investments in favour of more variable sex. Similarly, mothers with limited resources would be benefited by investing more in the reproductively stable sex. In most of the polygynous species, males have highly variable reproductive success as only elite males father disproportionately large number of offspring. Contrary to this, most of the females sire at least a few offspring, irrespective of the social rank or body condition. Hence, a female in good condition and a female in poor condition can maximize their reproductive success by investing in a male and a female offspring respectively. This hypothesis is appropriate for small litter-bearing species and depends on three assumptions: (1) that the maternal condition determines the condition of the offspring at the end of parental investment; (2) that the condition of the offspring at the end of parental investment tends to endure into adulthood, and (3) that the reproductive success of the adults will be influenced by this difference in body condition. These three assumptions hold true for food and meat animals as well. A number of studies in many different systems have demonstrated the validity of this hypothesis, ranging from house mice[9], deer[10], dairy cattle[11] to even humans[12,13].

Knowledge gained from more than 1000 studies designed to test the Trivers and Willard hypothesis (TWH) and few studies in developmental biology have suggested the possible mechanisms behind maternal ability to adjust the offspring sex. Cameron[14] analysed all the published studies testing TWH and concluded that sex ratio adjustments occur around conception and a potential mechanism for this was suggested based on the two important characteristics of conceptuses. First, interferon-tau, which signals pregnancy to the mother, was differentially expressed by male and female foetuses as early as at the blastocyst stage[15]. This can give a potential opportunity for the mother to bias the investment based on the sex. Second, *in vitro* growth of female conceptus was inhibited with increase in the concentration of glucose in the growth medium, whereas growth of male conceptus was increased suggesting that glucose influenced the development of male and female blastocysts differently[16]. These findings have been further strengthened by the reports that feeding of diet rich in fatty acids significantly increased the male births in laboratory mice[17,18]. Although the term maternal condition was not defined clearly in TWH, Cameron[14] suggested that the body condition score (BCS) measured close to conception can be used as the maternal factor that influences offspring sex. Studies have tested various measures that can affect maternal condition like damage, population density, food supply, maternal dominance, parity, etc. Among all these factors, maternal BCS around conception was found to significantly support the TWH, as further shown by the studies conducted in ruminants[11,14,19].

The wealth of theoretical and empirical work on sex allocation theory can have implications in increasing the ASF production without additional cost inputs. Animal diets designed to influence the maternal BCS around the time of conception can skew the sex of the offspring in the desired direction. This can minimize the loss due to culling of the undesired offspring. One such example can be derived for broiler industry from a recent report where a modified feeding regime was used for kakapo to achieve optimal breeding body weight and at the same time preventing the male-biased brood sex ratio[20]. Development of any similar method that can temporarily increase/decrease the blood glucose level during artificial insemination in food animals may help in manually skewing the sex ratio in the desired direction. Even though the knowledge of the factors that influence maternal condition and subsequent sex selection is not complete, the existing data suggest that maternal diet is a principal factor in determining maternal condition. Once such results can be obtained commercially, the benefits to mankind will be huge and can help in sustaining the increasing demands for quality food.

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ACKNOWLEDGEMENTS. I would like to thank Dr Pradeep Swamy (Assistant Professor of Veterinary Public Health at Veterinary College, KVAFSU, Bidar) and Dr Naveen Kumar (Assistant Professor of Animal Genetics and Breeding at Veterinary College, KVAFSU, Shimoga) for extensive discussions on sex allocation since 2005. Opinions expressed here are only those of the author and not necessarily those of any institute where the author was employed during the study period.

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