

ABSTRACT

Title: MATERNAL INVESTMENT IN DOMESTIC CATTLE.

Cassandra Marie Moore-Crawford, Ph.D., 2005

Directed By: Associate Professor W. Ray Stricklin,
Department of Animal and Avian Sciences

Hypotheses from biology propose that females that are in better condition are better able to provide resources to their offspring through maternal investment. The investment can be either direct nutritional or greater behavioral investment. The objectives of these studies were to determine the influence of several maternal factors on differential maternal investment. In the first study, data sets were taken from the beef records from the Wye Angus cattle at the University of Maryland Wye Research and Education Center, Queenstown, Maryland and Grazinglands Research Laboratory west of El Reno, Oklahoma. The relationship between age of dam and gestation traits were analyzed based on calf sex for each data set. Two of six maternal traits were significant predictors of calf sex.

For the second study, data from the Animal Improvement Programs Laboratory (AIPL) of the USDA, which conducts a national evaluation of birthing difficulty (calving ease), were used. Over 12.4 million dairy records were included in an analysis of sex ratio as a function of parity. Cow productivity influenced future sex ratios. The data support the contention that females in better condition produce

male offspring and also indicate that domestic animals, in this case cattle, still exhibit genetic influences that result from evolutionary influences – even though artificial selection influences have occurred. The determination of what mechanisms actually underlie the differential sex ratios that result from females of different production capabilities is an important question that needs further consideration.

In the third study, feed competitions between a mother, daughter, and non-related cow were conducted to determine the level of maternal investment after a prolonged separation of mother and daughter. Mothers ate for a significantly greater percentage of the total eating time than either daughter or non-related cows. On the second day of the trials there was a non significant trend for the occurrence of mother-daughter alliances. These results indicate that post weaning associations between mothers and daughters may be disrupted by management practices. The Trivers-Willard hypothesis was supported in dairy cattle, but the beef cattle data only provided limited support for this hypothesis.

MATERNAL INVESTMENT IN DOMESTIC CATTLE.

By

Cassandra Marie Moore-Crawford.

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Advisory Committee:
Associate Professor W. Ray Stricklin, Chair
Professor Emeritus Larry Douglass
Associate Professor Jones Harden
Associate Professor Carol Keefer
Dr. Katerina Thompson

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Dedication

To my parents who taught me the value of finishing what I start, no matter how long it takes; to my husband who has made life better with his years of love, devotion, and support; and to my children who have taught me the wonders of asking why, stopping to smell the roses, and not taking myself too seriously.

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List of Abbreviations

% DBH – percentage difficult births in heifers

AI – artificial insemination

AIPL – Animal Improvement Program Laboratory

CE – calving ease

DHIA – Dairy Herd Improvement Association

ESS – evolutionary stable strategy

FCM – fat corrected milk

LMC – local mate competition

LRC – local resource competition

mtDNA – mitochondrial DNA

PTA – predicted transmitted ability

USDA – United States Department of Agriculture

WREC – Wye Research and Education Center

Introduction

Maternal investment is maternal care given to an offspring that in some way reduces the mother's fitness (Kathnelson and Hudson, 1998). In mammals, this maternal care starts while the offspring is in utero, via the nutritional and metabolic support a mother gives a fetus through the placenta. After birth, maternal care continues through the transfer of milk from the mother to the offspring. The time from birth to weaning, is typically the focus of many maternal investment studies. However, maternal investment may extend past weaning. In many groups of animals that are matriarchal in structure post weaning associations convey benefits to the offspring.

It has been document in many species that females may alter the amount of maternal investment they provide to an offspring based on the sex of that offspring. In general, males are more costly to produce than females, therefore only mothers in good condition produce males. Thus, the ethological literature generally contends that mothers in good condition are more likely to produce males. One of the theories behind sex ratio biases was introduced by Trivers and Willard (1973). Trivers and Willard theorized that parents may have the ability to vary the sex ratio of offspring. This idea was based on the assumption that the sex ratio at birth in mammals is a measure of tendency to invest in one sex more than in the other.

Many research articles have been published that attempted to test the Trivers-Willard hypothesis in a variety of wild, feral, and domestic animal populations. Some of this research has supported the Trivers-Willard hypothesis, while the rest have reported conflicting results. The purpose of the research in this dissertation is to determine the validity of the Trivers-Willard hypothesis in domestic animals, specifically domestic cattle. Domestic cattle have been placed under different selection pressures compared to their wild counter parts for the past 6,000 to 8,000 years. Although cattle have been domesticated, the genetic influences that result from evolutionary influences are still present in these populations of animals.

Chapter 1: Review of Literature

In some species, mothers provide different amounts of parental investment depending on the sex of the offspring. The investment can be either direct nutritional (for example milk, higher birth weight, etc.) or greater behavioral investment (more attention through closer spatial proximity, grooming, etc.). In general, males are more costly to produce than females, therefore only mothers in good condition produce males. Therefore, the ethological literature generally contends that mothers in good condition are more likely to produce males. There is also some evidence that the sex ratio at birth in some species is affected by environmental factors, such as number of adult males present and the age of males present (Manning et al. 1997).

Sex ratio is not equal in livestock. This has been recognized for some time. The cause for this imbalance is not completely understood. However, from the study of wild populations there is considerable information and hypotheses that may have relevance to food producing animals. This review will first review the various hypotheses as to why sex ratios may differ, and then summarize the studies from wild populations, and finally, the information from domestic ungulates will be presented.

I. Sex Ratio Hypotheses

The question of why the sex ratio in most species approximates 1:1 when limited quantities of males are needed to fertilize the females has been raised for years. In an efficient system females would outnumber males in relation to the role each plays in reproduction and raising offspring. Natural systems such as these are

rarely seen. However, biases in sex ratios have been recorded in several animal populations.

Several theories have been proposed to explain the various sex ratios seen in populations of organisms (Hardy, 1997). From these theories it is evident several factors are involved which influence sex ratios of offspring. The focus of some sex ratio theories is the amount of investment a parent places in an offspring. Other theories focus on genetic and environmental influences on the sex ratio. Due the presence of such varied theories in the literature, interpretation of sex ratio results can sometimes be complex. A brief history of sex ratio hypotheses is necessary to understand the plethora of ideas that have come out of this area of research.

A. Fisher's Hypothesis

Fisher (1930) was the first to explain why sex ratios may deviate from 50:50. The key idea of Fisher's hypothesis was that effort spent producing each sex is equal. In circumstances when effort was unequal, the sex that required the lesser effort gained a reproductive advantage. However, this advantage might be short lived due to natural selection. This was because the reproductive value of each sex was still equal, since each sex contributed an equal amount of genetic material to the next generation. From this, Fisher concluded that the sex ratio at the end of parental care was dependent upon differential mortality of offspring during the care period. Fisher's hypothesis can be used to explain sex ratios that are skewed in either direction.

B. Hamilton's Local Mate Competition Hypothesis

Hamilton (1967) provided a mathematical model for the prediction of sex ratios in offspring. Hamilton's hypothesis differed from Fisher's in several ways. The first was that Hamilton stated that his hypothesis was influenced by group structure, whereas Fisher's hypothesis was not. In addition, Fisher's hypothesis relied on population wide competition for mates, while Hamilton's hypothesis did not hold this assumption. Hamilton clearly stated that the conditions for which Fisher's assumptions did not hold true were widespread in nature. This fact was a driving force in the creation of Hamilton's hypothesis.

Hamilton's hypothesis was called local mate competition (LMC). One of the assumptions of the local mate competition hypothesis was male siblings would compete against each other for mating opportunities. The ideology of Hamilton's hypothesis was the production of males did not provide a fitness payoff for an individual in terms of the number of grandchildren produced. Sex ratios were biased so that competition for mating opportunities was decreased. This hypothesis contended the sex ratio of offspring depended on the numbers of females contributing offspring to the mating group. Therefore, female biased sex ratios would occur when the number of females contributing offspring to the population was low. When the number of females producing offspring was high, the sex ratio would approach equality. This hypothesis only predicted female skewed sex ratios, unlike Fisher's hypothesis that explained both male and female skewed ratios.

C. *Clark's Local Resource Competition Hypothesis*

A third hypothesis of sex ratios was proposed by Clark (1978) and was called local resource competition (LRC). Local resource competition has been considered a generalization of Hamilton's local mate resource competition (Hoogland, 1981). Clark asserted that competition among mothers and their female offspring skew the sex ratio towards males. In addition, this skew appeared at birth and was not corrected by differential mortality of offspring. The premise of local resource competition was that competition for all resources, including food, territory, and mates were considered as contributing factors that influenced sex ratios. This hypothesis predicted that females should bias the sex of their offspring in such a way that decreased competition between their offspring and themselves. Thus, the local resource competition hypothesis can be considered in situations where one sex dispersed from its natal unit, but the other sex is philopatric. In these circumstances, females bias sex ratios in favor of the dispersing sex. Local resource competition can be used to explain both female and male biased sex ratios.

D. *Trivers and Willard Hypothesis*

All of the theories discussed thus far indirectly assert parents have the ability to manipulate sex ratios. These manipulations may be the result of available resources, mating opportunities, or pressures from natural selection. The first sex ratio hypothesis to directly assert that parents have some influence over the sex ratio of their offspring was Trivers and Willard (1973). Trivers and Willard based their hypothesis upon three assumptions. These assumptions were: 1) The condition of

offspring at the end of parental care is correlated with the condition of the mother during the period of investment; 2) The condition of young at the end of the period of parental investment will continue into adulthood; and 3) Males will have better reproductive success if they are in better condition compared to their female counterparts. Based on these assumptions, Trivers and Willard stated that skews in sex ratio were a measure of the tendency to invest more in one sex over the other.

The Trivers and Willard hypothesis asserted females in good condition would produce male offspring and females in poor condition would produce female offspring. The idea behind this hypothesis was that natural selection would favor genes that adjusted a female's sex ratio to her body condition during the period of parental investment. Natural selection would favor deviations in equal investment in the two sexes not in actual sex ratios. The differences in sex ratios were a consequence of differential investment. In addition, females that were able to adjust their level of investment throughout the care period would produce more offspring in the long run than females that only adjusted their investment levels at the beginning of the care period.

Trivers and Willard also proposed a mechanism for sex ratio differences. One possible mechanism was differential mortality. This differential mortality could be of sperm or of young during the period of investment, including pregnancy. Trivers and Willard reported that adverse environmental conditions for mothers during pregnancy were correlated with a reduction of male offspring in deer and humans. Their hypothesis suggested that in species with a long period of parental investment after

birth, biases in parental behavior towards offspring of different sexes might be expected. This hypothesis predicted a sex ratio bias in both directions, akin to Fisher's hypothesis and local resource competition.

E. Maynard Smith's Hypothesis

A final sex ratio hypothesis is one proposed by Maynard Smith (1980). Maynard Smith presented a mathematical model for the evolution of sexual investment. This hypothesis asserted that primary sex ratios are fixed at 50:50, but parents had the ability to recognize the sex of offspring. Because of this, offspring fitness varies for the two sexes. In essence, an evolutionary stable strategy arose in which male and female offspring were invested in differently. There were three criteria for which these differences were made.

The first of these criteria was that when the probability of survival for one sex was lower than that of the other sex when a finite amount of investment was given, parental selection would favor the sex with the lower survival rate. The second criteria exerted that an evolutionary stable strategy (ESS) of investing in one sex more than the other would arise when one sex experienced a frequency dependent component of fitness. The final criterion of this hypothesis was that when a parent had the ability to recognize the sex of an offspring after a certain amount of investment had been given, an ESS would arise to invest slightly more in the more expensive sex. This hypothesis, unlike LMC, LRC, and Trivers and Willard did not rely on environmental conditions such as maternal condition or local resources. In contrast, this hypothesis depended on natural selection and fitness to vary sex ratios.

This hypothesis was somewhat akin to Fisher's hypothesis. Maynard Smith's hypothesis predicted sex ratios that can be biased both toward males or females, depending on the circumstances. The key point of this hypothesis was that parents invested in male and female offspring differently.

Table 1. Summary of sex ratio hypotheses.

Hypothesis	Predictions of Sex Ratio
Fisher, 1930	Deviations from 50:50 will be corrected by natural selection; either sex can show a bias
Hamilton, 1967 - local mate competition (LMC)	female biased ratios
Clark, 1978 - local resource competition (LRC)	male biased ratios
Trivers and Willard, 1973	male or female bias can exist; differential parental investment
Maynard Smith, 1980	male or female bias can exist; parents invest differently in males and females

II. Sex Ratios from Wild Populations

A. American Bison

American Bison (*Bison bison*) are the sole native North American members of the family Bovidae. Herds of bison are found in the western part of the United States, and are typically managed to some extent. Bison have been used to test sex ratio theories, primarily Trivers and Willard (1973) because they fit many of the assumptions of this hypothesis. American bison are sexually dimorphic, males

compete aggressively for mates and do not contribute investment toward offspring, and cows typically have one calf at a time. These conditions are the same stipulated by Trivers and Willard.

Wolff (1988) studied maternal investment and sex ratio adjustment in American Bison calves. The study took place from May 1987 to August 1987 at the National Bison range in Moise, Montana. This site supported approximately 350 bison maintained in two herds. The activities of each focal dyad were recorded, as well as nursing behavior. The sex ratio of the calves was analyzed in relations to many maternal factors including dominance rank, reproductive status, and age.

Wolff found the sex of a calf was not correlated with dam's age. In addition, the sex ratio of early born and late born calves did not differ significantly and there was no relationship between a mother's dominance and the sex of her calf. However, sons weighed significantly more than daughters did at five months of age. This heavier weight may have been achieved via more frequent nursing. In terms of nursing behavior, sons nursed significantly longer than daughters. Additionally, when nursing calves were allowed to nurse for as long as they wanted, daughters stopped nursing before sons. These behaviors can be interpreted to mean that male American bison calves cost more to rear than female calves. Based on this, Wolff concluded cows in better than average condition produced more sons than daughters.

The analysis of reproductive status showed cows that had a son in one year were more apt to be barren the following year compared to cows that had daughters. However, for those cows that had a calf two years in a row, the sex of the second calf

was not dependent on the sex of the previous calf. As the breeding season drew to an end, bulls tended several cows with young daughters. During this time, mothers with young sons were not tended by bulls; however bulls tended mothers with older sons. These findings suggest sex ratio adjustment was more closely correlated with previous reproductive effort. In addition Wolff suggested that producing a male might reduce a mother's fecundity for the next year.

Rutberg (1986) studied the relationship between lactational status and fetal sex ratios in American Bison. The study was based on the two herds of American Bison maintained at the National Bison range in Montana. During the periods from 1957-1967 culled animals were slaughtered, butchered, and the following information about each individual was ascertained: age of cow, pregnancy status, and lactation status. During the period of 1964-1967 fetuses were sexed as well. Rutberg analyzed this data in relation to the Trivers and Willard hypothesis of sex ratio adjustment.

In the analysis, Rutberg found 86% of non-lactating cows carried male fetuses, while only 48% of lactating cows carried male fetuses. The sex ratio of the entire sample was 51 males to 31 females (1.65:1), as opposed to the ratio of 0.88:1 for calves born into the herd. This means that the culled animals showed a male biased sex ratio, while the herd had a slightly female biased ratio. This skewed sex ratio bias was present in nulliparous as well as multiparous cows.

From these results, Rutberg stated that estimates of sex ratios in utero and birth may be distorted by selective culling of non-lactating females; however this was not believed to be the case in this study. The high rate of male offspring among non-

lactating cows was consistent with Trivers and Willard hypothesis. Rutberg suggested that lactational status may be a measure of condition because non-lactating condition may convey those cows are in better condition than lactating cows because there is no extra energy expenditure.

Green and Rothstein (1991) studied the patterns of maternal investment in American Bison. They tested the hypothesis of adaptive sex ratios in bison using the assumptions of Trivers and Willard (1973). The objectives of this study were: 1) to determine whether mothers showed sex biased parental investment; 2) to determine whether offspring sex was related to female condition; and 3) to examine the assumptions (a) differences in offspring condition at the end of the period of parental investment endured into adulthood and (b) offspring condition was correlated with maternal condition. The study was conducted over 8 years at Wind Cave National Park, South Dakota. This bison population consisted of approximately 230 cows and juvenile and 100 bulls. Data on maternal and offspring condition was collected.

Analysis of the data revealed the frequency of barren females was not related to the sex of the previous calf. Autumn body mass did not differ between the years in which cows bore male versus female calves. Daughter's fecundity did not increase with maternal dominance or maternal age. Offspring sex ratio was not significantly related to short or long term measures of maternal condition. In addition, none of the measures of maternal condition improved the model to predict the sex of a calf. However, maternal dominance was correlated with the dominance rank of daughters, but not with dominance rank of sons. These results provide little evidence for an

influence of maternal condition on sex ratio among the majority of females in the bison herd.

There were several differences between male and female calves in this study. One of the differences between calves was male calves weighed more than female calves by 7 months of age. Another was that male calves were born later in the calving season than females. Additionally, birth intervals were slightly longer after male calves compared to female calves, but this trend was not significant. Another non-significant trend was birth intervals before male calves were longer than before female calves. These results indicate there is little evidence that mothers bias their pre-weaning investment toward sons. However, the later birth of sons suggested either longer gestation or later conception. Green and Rothstein suggested the relationship between maternal and offspring condition differed between sons and daughters. This presumption was in agreement with Maynard Smith's (1980) hypothesis.

In relation to reproductive status, previously barren cows produced a greater proportion of daughters, while previously parturient cows had 50:50 sex ratios. In addition, daughters of previously barren cows ranked higher among their peers compared to daughters from parturient cows. Daughters of previously barren cows showed the trend to have earlier age of first reproduction, have heavier yearling weights, more fecundity between ages 7-9, and were taller compared to daughters from parturient females. Finally, previously barren cows calved slightly later than

parturient cows, and cows that were barren in the year after the birth of an offspring continued to nurse the offspring longer than parturient cows.

Green and Rothstein suggested the prediction that mothers in poor condition should produce mostly daughters received some support in that the proportion of female calves increased for elderly cow. Additionally, the results provided some support for the assumptions that early differences in offspring condition endure into adulthood. When a female was barren before or after the birth of an offspring, she appeared to invest more in that offspring. In addition, mothers may influence the condition of daughters more than that of sons during the first 2 years.

Green et al. (1989) studied post-weaning associations among bison mothers and daughters. This study was conducted at Wind Cave National Park, South Dakota, where there were approximately 230 cows and juveniles and 100 bulls. This is the same population that was studied in the previous article. Data were collected on focal mother-daughter dyads. Several measures of association both between the dyad and the rest of the herd were recorded.

The data revealed mothers and daughters associate preferentially until sexual maturation of daughter at age 3. In addition, daughters spent significantly more time in groups with their mothers compared to control individuals. Yearlings and their mothers followed each other frequently. The primary change in contact maintenance behavior from pre to post-weaning was caused by increased offspring independence and increased maternal effort at maintaining proximity.

Green et al. suggest that long term associations with mothers may benefit daughters because daughters were displaced less often when their mothers were present. In addition, daughters tended to be at the group center when their mothers were present compared to when they were not present. The authors suggested that post-weaning associations may confer anti-predator benefits to daughters as well. Post-weaning associations conveying benefits on to daughters fit both the Trivers and Willard (1973) and Maynard Smith hypothesis.

B. Reindeer

Kojola and Eloranta (1989) studied the influences of several maternal factors on the sex ratio in semi-domesticated reindeer (*Rangifer tarandus tarandus*). The data for this study was obtained from an experimental reindeer herd in Finnish Lapland. Dam body weights were used as a measure of maternal condition at conception. In addition, ages of dam and parity number were examined in relation to offspring sex ratio.

This study showed there were several weight related factors that influenced sex ratio of offspring. Cows that had male offspring were significantly heavier at conception compared to cows that had females. In addition, conception weight to weaning weight ratio was higher for cows that produced female offspring. This was a possible indication that energy demands were higher for females with male calves. Along with this finding, females that weighed less than 60 Kg (approx, 130 lbs) had significantly more females. Additionally, there was a slight non-significant trend for females that weighed more than 70.7 Kg to have more males.

Other factors that influenced sex ratio were age and previous reproductive performance. Older cows in the herd produced a slight excess of female offspring. In addition, age at first breeding influenced sex ratio such that females that were older at the time of first conception had a higher proportion of male offspring. In terms of previous reproductive performance, females that lost a calf within the first month after parturition tended to have an excess of male calves at the next parturition. The majority of the data from this study supported the Trivers and Willard hypothesis. Factors such as female body condition and age were shown to influence the sex ratio of offspring.

Skogland (1986) tested the hypothesis that maternal condition and investment influences the sex ratio of offspring. Data on prenatal sex ratios and maternal size were collected on three herds representing poor, medium, and good range. There was a five-fold difference between the poor and good ranges. These variations in range condition were meant to simulate the variation that exists in range conditions wild populations depend upon.

The range labeled as poor had small sized females and a male biased ratio. The medium range had medium sized females and a sex ratio that was near unity. Finally the good range had large sized females and a female biased sex ratio. Offspring survival was also evaluated. On the poor range offspring survival was approximately 45%, while on the good range offspring survival was approximately 100%. Although there were differences in the survival rates of offspring of these two herds, the poor range post-weaning ratio was similar to the good range prenatal ratio.

Based on these results, Skogland came to three conclusions. The first conclusion was: when mortality rates were high in one sex during the period of parental investment, the sex ratio at the start of the investment would be biased toward that sex. In addition, Skogland added that when the offspring of one sex is more costly to produce or more likely to die during the period of the sex ratio at the end of parental investment would be biased against the more expensive sex. Finally, when offspring of one sex dispersed at the end of parental investment and incurred a greater rate of mortality, females would invest more in the dispersing sex, but produce fewer of them. The data from this study provided support for the notion that food-stressed females of lower average productivity more commonly have a male biased primary sex ratio.

Reimers and Lenvik (1997) studied fetal sex ratio in relation to maternal mass and age in reindeer. In this study 1525 carcasses and embryos were examined. These samples were obtained from six herds between 1976 and 1979 in three regions of Norway and Sweden. Ages of females were determined either via ear tags or tooth wear.

The data from this study revealed no significant differences in carcass mass and sex ratio. In addition, sex ratio did not differ with changes in female parity. Finally, age was not a significant factor for sex ratio. Although no significant results were found in this study, the data supported the Trivers and Willard hypothesis to some extent. The Trivers and Willard hypothesis predicted deviations from 50:50.

Because there is variation among the individuals in a population, these deviations would cancel out over the entire population.

Kojola (1989) studied the relationship between mother's dominance rank and differential investment in reindeer calves. The study was carried out on semi-domesticated mountain reindeer. The importance of maternal rank for male and female offspring, as well as for mothers was evaluated in terms of weight loss during the first post-weaning winter.

In terms of weight changes, male calf body weight depended on maternal rank during the overwintering period. In addition, low status mothers lost more weight during the overwintering period compared to high status mothers. As maternal status increased, mother calf-distance decreased. These results show the strong influence maternal rank had on maternal investment in reindeer calves.

During the overwintering period, reindeer dig for food from under the snow. This is commonly called cratering. Calves of dominant mothers used the same crater more than 50% of the feeding time, while calves of subordinates did so less than 15% of the time. In the second year of the study, female calves shared the snow crater with their mother more often than did male calves.

This study showed that sharing a snow crater with the mother influenced calves winter weight loss. Additionally, the study showed that maternal status could affect post-weaning weight gain in female offspring who were philopatric. Maternal status appeared to have more effect on male weight pre-weaning and on female

weight post-weaning. This study showed evidence of differential maternal care based on sex, because cow weight loss was not influenced by sex of offspring.

C. Red Deer

Kruuk et al. (1999) studied the affect of population density on the variation of sex ratio in red deer (*Cervus elaphus*). The study population was the unmanaged population of red deer on the Isle of Rhum, Scotland. Since this population was not managed, the birth rate continued unchecked for several years. This increase in population density had an effect on many aspects of the red deer ecology.

As population density increased the proportion of males born each year declined. Another change associated with increased population density was a decrease in female fecundity. The changes in population density were seen when high and low density areas were compared. Offspring sex ratio was associated with dominance rank in low density areas, but not high density areas. In addition, sex ratio at birth was correlated with the amount of rainfall during the period of pregnancy; excess rain decreased the sex ratio the following year.

One conclusion reached based on this data was that there were differential fetal losses due to stress during pregnancy. This difference might be evolutionarily adaptive when conditions were favorable. However when nutritional stress was involved, differences in susceptibility of male and female fetuses may have caused population wide skews in sex ratios.

Clutton-Brock et al. (1986) studied the relationship between several maternal factors and sex ratios in offspring. Some of the factors that were studied were

dominance rank and breeding success. The North Block population of red deer on the Isle of Rhum, Scotland was used in this study. The study area contained approximately 180 hinds that were 1 year of age or older. Data were collected during the periods of 1969 and 1984.

The sex ratio among offspring of high ranking females was significantly male biased, but low ranking females showed no deviation from unity. Dominant females calved more frequently and tended to have their offspring survive to maturity compared to subordinate females. In addition, dominant females conceived and calved approximately 5 days earlier than subordinates. This most likely occurred because males tended dominant females first. Difference in survival of offspring for dominants versus subordinates was seen in male offspring. Approximately 64% of dominants sons survived their first year compared to 49% of subordinates sons. This trend was also seen in yearling survival. For yearling survival, 92% of dominants sons survived their second year compared to 70% of subordinates sons.

With respect to breeding success, individuals with dominance ranks above the median had greater lifetime reproductive success compared to subordinate females. In addition, dominance rank of a mother was correlated to the breeding success of her son. Males born to dominant hinds were more reproductively successful than females born to dominant hinds. However, females born to subordinate hinds were more reproductively successful than males born to subordinate hinds.

The data from this study support the Trivers and Willard hypothesis. Clutton-Brock et al. suggested the possibility that all females conceive 60% males, but only

subordinate females lose 1/3 of their sons. The data from this study did not completely support this, but did not refute this hypothesis either. Because the intersection point of male and female fitness on parental investment quality was located close to median rank, Clutton-Brock et al. suggested that sex ratio trend is adaptive.

Gomedio et al. (1990) investigated the subsequent survival and reproductive performance of dams that reared male versus female offspring. Data from a sample of 283 red deer hind from the Isle of Rhum, Scotland were used. The objective of the study was to determine if the relative costs of rearing offspring of different sexes varied with maternal rank.

The overwinter survival and fecundity of hinds declined with age, high rainfall, and low winter temperatures. After the above factors were corrected for, overwinter survival was not related to dominance or sex of the offspring. Subordinate mothers that had reared a male showed lower overwinter survival compared to dominant hinds with sons. However, subordinate hinds with females had the same or slightly higher probability of survival compared to dominant hinds.

In relation to reproductive performance, if an adult female red deer survived the winter, the probability of her calving the next summer was influenced by her dominance not by the sex of her previous calf. Additionally, subordinate hinds were less likely to calve again after rearing a male offspring the previous summer compared to rearing a female. Dominant hinds were more likely to calve again compared to subordinate mothers.

Based on the data from this study, the extra fitness costs of rearing male offspring verses female offspring appeared to be substantial among subordinate mothers, but absent among dominant mothers. Subordinate females could be more strongly affected by differential energy costs of raising male verses female calves because they did not have priority of access to the best feeding sites. In addition, their body condition was generally poorer than that of dominant females. Frequent nipple stimulation which inhibits ovulation may be a proximate mechanism in the relationship between fecundity and sex ratio of offspring since it has been documented that male offspring suckle more often and possibly harder.

Kathnelson and Hudson (1998) investigated maternal investment in wapiti (*Cervus elaphus*). The study was conducted at the University of Alberta's Ministik Wildlife Research Station. The research herd has been managed since 1977, thus weight and reproductive data since this time were available. The objective of this study was to examine relationship between costs of reproduction and maternal investment.

There was a significant skew in sex ratio toward males between the years of 1978 and 1994. However, there was a non-significant relationship between maternal body condition and offspring gender. Females in good condition had male biased sex ratios, while females in poor condition had 50:50 sex ratios. In addition, a hind's previous reproductive performance was non-significant factor on sex ratios.

Male calves in this study weighed significantly more at birth compared to females. Additionally, calf birth weight increased with hind age. There was also a

non-significant trend for males to be born later than females. In addition, younger mothers calved later than older mothers. The birth intervals preceding male calves were significantly longer than those for females. The longer inter-birth intervals preceding male calves were probably due to longer gestation length. Mothers of males spent more time grazing compared to mothers of females. Additionally, there was a non-significant trend for males to nurse longer.

The results of this study indicate hinds invested more in male offspring than female offspring. Mothers allocated more resources to sons pre-natally, which was seen in heavier birth weights and longer gestational lengths, and post-natally as evidenced by longer nursing lengths. The data from this study support the hypotheses of both Trivers and Willard and Maynard Smith.

In addition, the data provided evidence to suggest wapiti hinds adjust sex ratio according to their ability to invest. If mothers of sons suffered different costs of reproduction, this was not apparent from their weight dynamics. This is because mother's age and when she gave birth influenced changes in weight more than offspring gender. The larger amount of time spent grazing by hinds with sons suggests they were compensating for higher energy expenditure. Finally, this study provided evidence for differential maternal care rather than investment based on sex. Maternal care is defined as an increase in offspring fitness without cost to the mother, while maternal investment is defined as parental care that reduces a mother's fitness.

D. *White-Tailed and Mule Deer*

Verme (1989) studied maternal investment in white-tailed deer (*Odocoileus virginianus*). This study was conducted at the Cusino Wildlife Research Station at Shingleton, Michigan. The data used in the analysis was collected from the period of 1959-1983 and is based on 83 individuals that produced 209 litters. The females in this study were confined in pairs in pens and fed a pelleted ration year round.

Multiparous mothers, those greater than three years old, usually gave birth earlier in the calving season compared to primiparous females. In addition, older mothers usually produced larger fawns than primiparous mothers. However, fawn body mass was not influenced by maternal age. It was determined that female fecundity was related both to age and nutritional level. One conclusion from this study was that male offspring were more energetically expensive to rear than female offspring. This was supported by the fact that males whether singletons or twins were heavier at birth and increased their weight advantage through weaning at a greater rate than female fawns.

Kugera (1991) studied the adaptive variation in sex ratio of offspring in nutritionally stressed mule deer. Sex ratios of litters of mule deer were collected during late winter 1984-1989 in eastern California. Kidney-fat index was used as an indicator of total body fat. The relationship between litter category and maternal age, weight, and kidney-fat index were tested.

The overall sex ratio was 1:1.14, which was not significantly different from unity. Mule deer typically have litters of two. The frequency of the twin sex ratio

categories differed from binomial expectation. The expectation is as follows: 1) twin females; 2) mixed twins; and 3) male twins. In this study, twin females occurred more often and mixed twins occurred less often than expected. The weight of mothers with twins was greater than females with singletons or non-breeders. In addition, mothers carrying female twins tended to be the lightest of the three twin categories. Females with the largest kidney-fat index tended to have litters of two males

The twin category distribution in this study indicated that this herd was under nutritional stress. Another indication of this was that the offspring of heavier females and offspring of lighter females tended to be male and female respectively, regardless of litter category. Additionally, the heaviest and fattest mothers tended to produce male biased litters. The data from this study support the Trivers and Willard hypothesis.

Caley and Nudds (1987) reviewed sex ratio literature regarding the genus *Odocoileus* (i.e., white-tailed and mule deer). According to the authors, the sex ratio data for *Odocoileus* is inconsistent with the Trivers and Willard hypothesis, which predicted that females in better condition would bias their offspring toward the sex that has greater fitness variation. One proposed reason for this inconsistency was that members of the genus *Odocoileus* did not show as much variation in reproductive success between sexes as other species did. Indirect evidence suggested that members of *Odocoileus* were not as polygynous as red deer and American bison which are species whose sex ratio data had been consistent with the Trivers and Willard hypothesis. This evidence included smaller male-biased breeding groups,

less intense sexual selection, and smaller testis size. Because many *Odocoileus* species did show male biased sex ratios, the authors suggested that local resource competition may account for this bias in nutritionally stressed females.

E. Fallow Deer

Birgersson et al. (1998) investigated male biased maternal investment in fallow deer (*Dama dama*). Two groups of fawns were studied to find the causes of faster growth in males. These groups consisted of bottle reared and mother reared calves. The study took place in south-central Sweden between June and October 1996. The fawns used in the experiment came from a captive population of approximately 25 hinds.

The average suckling rate during the first 10 weeks was significantly higher for males compared to females. Suckling rate was defined as the total time each fawn suckled from the bottle until the milk was finished. Male fawns were more likely to drink a bottle without interruption compared to females. By 10 weeks of age males had gained more weight than females. Both bottle and mother reared males had significantly more weight gain compared to their female counterparts.

The data from this study suggested that male fawns sucked harder and were motivated to obtain milk more than females. Male fawns received more milk under natural conditions, since there was no difference in suckling time between the sexes for mother reared fawns. One conclusion from this study was that maternal investment seemed male biased, but the bias was directed by the fawn's behavior. This was because harder suckling stimulated more milk production. Their mothers to

a certain extent met the higher nutritional requirement of male fawns. This was evidenced by the fact that mothers who reared males accumulated less body mass during lactation compared to females who reared females. In addition, there were reproductive costs for these females. Their next offspring tended to have later birth dates, as well as lower pre-winter weights.

Braza and San José (1988) analyzed mother-young behavior of fallow deer. During the summers of 1984 and 1985 a population of fallow deer consisting of 14 pairs of mother and young were observed in the Doñana National Park in southwest Spain. The activities of the does and fawns were recorded and categorized as feeding, walking, vigilance, self grooming, mother-young interactions, or social interactions. Differences between the activities of individuals, sexes, and years were examined.

There were no significant individual differences in activities between the two study years. For the different sexes the rate of interactions was positively correlated with fawn's weight for male fawns and their mothers. This relationship was not found for female fawns in general, but was found for two heavy female fawns. Although predictions exist that females invest more in males, the authors suggested that the possibility could exist that there could sometimes be fitness benefits from investing in large female offspring. Evidence for this idea came from the greater interactions and vigilance shown by the mothers with the heavy female fawns.

F. Rocky Mountain Bighorn Sheep

Hogg et al. (1992) studied sex biased maternal expenditure in Rocky Mountain bighorn sheep. The authors defined parental expenditure as, "the transfer

of resources from parent to offspring without regard to control.” The data for this study was derived from the population of bighorn sheep residing in the National Bison Range in northwestern Montana between June 1979 and June 1985. The weight, date of birth, and suckling duration and interval were recorded for lambs, as well as gestation length, date of first ovulation, reproductive status, and age for ewes.

The weight of lambs at the time of capture was significantly associated with lamb sex. Males weighed 11% more than females. The greater birth weights of males were not associated with longer gestation periods. These results provide evidence of greater pre-weaning energetic expenditure by mothers on sons. In addition, substantial maternal control over post-natal expenditure was suggested by the fact that ewes almost invariably terminated suckling bouts.

For ewes that had males versus females there was a significant increase in the delay in return to estrus. The annual effect of greater reproductive effort on return to estrus was cumulative over several years. Ewes that consistently made greater reproductive effort consequently gave birth progressively later over several reproductive episodes. The increased reproductive effort put forth by ewes of ram lambs delayed subsequent conception and birthing. These late-born lambs were less likely to survive to weaning. In addition, there was an association between late conception and subsequent ewe mortality. The data from this study suggest that increased maternal expenditure may entail a fitness cost via reductions in both lamb and maternal survivorship in this population.

Bérubé et al. (1996) investigated reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. During the time of this study, the population density of the bighorn sheep at Ram Mountain, Alberta Canada doubled. Between the years of 1978 and 1988, the population was considered low density, but during the years 1988 through 1992 the population was considered at high density. The sheep in this study were captured in a corral trap baited with salt, and body mass and reproductive status of each ewe was recorded.

Based on the fact that Rocky Mountain bighorn sheep are sexually dimorphic, polygynous, and that male breeding success is determined by dominance, the authors made three predictions. The first prediction was that ewes that weaned males would accumulate less body mass over the summer compared to ewes that weaned females. The second prediction was that ewes of males would incur a reduction in future fecundity or survival compared to ewes that raised females. The finally prediction was that the sex of the lamb would affect the survival of future offspring.

Ewes that conceived females were approximately 3% heavier than ewes that conceived males. Additionally, mothers of daughters were slightly older than the mothers of sons. However, lamb sex did not affect summer mass gain. There was a non-significant trend for ewes to lose more mass after weaning daughters than after weaning sons. These two results were in opposition to the predictions of the authors.

In regards to the predictions about future reproductive success, ewes that weaned sons were less likely to wean a lamb the following year compared to ewes that weaned a daughter. In addition, lambs were less likely to survive to 1 year if

they were born following the weaning of a son than if they were born the year after their mother had weaned a daughter. Population density also had an effect on lamb survival. At low population density, the survival to 1 year of lambs born following a son was 82% of the survival of lambs born following a daughter. However, at high population density, the survival to 1 year of lambs born following a son was 43% of the survival of lambs born following a daughter. The greater cost of sons was accentuated at high population density suggesting that environmental factors can affect the differential fitness costs of lambs of different sex.

The results of this study implied that ewes were unlikely to have sons in consecutive years. This indicates that ewes that raised sons incurred higher reproductive costs. The altering of the sex of lambs produced could be an adaptive strategy for bighorn ewes to avoid sustaining the high cost of sons in consecutive years. The lower survivorship for lambs born after a son could be due to higher maternal expenditure for male offspring leading to poor maternal condition at the time of breeding. In addition, the higher cost of sons was also associated with a low probability of producing male lambs in consecutive years.

G. Northern North American Sheep, Goat, and Deer Species

Hoefs and Nowlan (1994) assessed the sex ratio of offspring from six species of ungulates held in game farms in the Yukon Territory, Canada. The six species were Elk (*Cervus elaphus nelsoni*), reindeer (*Rangifer tarandus tarandus*), mountain goats (*Oreamnus americanus*), Dall's sheep (*Ovis dalli dalli*), Stone's sheep (*Ovis*

dalli stonei), and caribou (*Rangifer tarandus caribou*). The various species were studied for a period of time that ranged from 2 to 23 years.

A distorted sex ratio showing a female bias was documented for all six species. This indicated that well-fed females in good condition produced more females than male offspring. The authors suggested that the distorted sex ratios most likely occurred at conception. In addition, the high quality supplemental feed probably attributed to distorted sex ratios. Captive stock that are given supplemental feed may be similar to domestic animals because it is unrealistic to presume that different ungulates would develop similar reproductive strategies when they have different life histories and behavior.

Rachlow and Bowyer (1994) studied the variability in maternal behavior by Dall's sheep. Dall's sheep in Denali National Park and Preserve in central Alaska were observed from April through July in 1988 and 1989. The authors presented three strategies for partitioning investment in offspring in response to late births and a shortened season for growth. These strategies were: 1) abandon neonates and conserve resources for subsequent reproduction; 2) invest more heavily in late-born lambs and forgo reproduction in the next year; 3) invest more heavily following parturition, but terminate that investment more quickly in an attempt to reproduce and successfully raise offspring in consecutive years.

The onset of spring was delayed in 1989 versus 1988. This caused delayed lambing in 1989. Females nursed lambs at a higher rate in 1989 and total suckling time decreased more rapidly in 1989. In 1989 females spent more time nursing early

in lactation, but also reduced maternal care more quickly. The greater time spent suckling in 1989 may have been maternal strategy to bring about compensatory growth for late-born lambs. The proportion of suckles terminated by females was greater in 1989. These females also denied more suckles in 1989. Both of these phenomena occurred in early lactation. The proportion of suckles terminated by females and the proportion of unsuccessful suckles indicated a more active weaning process in 1989 compared to 1988.

Based on the results from this study, the hypothesis that variability in maternal behavior by Dall's sheep was a simple response to changing quality of diet was rejected. In addition, the notion that differences in maternal behavior between years was a simple response to quality of diet and climate was ruled out. The data from this study strongly suggested that more complex circumstances determine care-giving behaviors of female Dall's sheep. The patterns of maternal care observed in this study could not be explained solely as a result of lambs attempting to solicit more care. Female Dall's sheep in this study responded to proximal variation in resource availability by altering their maternal behavior.

Thomas et al. (1989) studied fetal sex ratios in caribou. The researchers sampled fetuses from two sub-species of caribou, barren-ground caribou and Peary caribou. The samples of barren-ground caribou were from the years 1974 through 1979, while the samples of Peary caribou were obtained between 1980 and 1987.

The overall sex ratio for both subspecies did not differ from 50:50 based on maternal age. In barren-ground caribou, the proportion of male calves born to young

females (ages 2-4) was low, while the proportion of male calves born to old females (age >10) was high. Additionally, 3-year-old barren-ground caribou females were most likely calving for the first time. Since caribou 1.5 - 4 years old are still growing, producing female offspring would permit faster maturation of young mothers if the energetic costs of producing females were lower than for males.

No body condition indices were found that were related to sex ratio. However, there was a non-significant trend for female barren-ground caribou to be slightly heavier when carrying female fetuses. Male fetuses were heavier than female fetuses. Barren-ground caribou females carrying male fetuses exhibited a significant difference among age class for kidney fat index. The trend was that fat indices decreased with age, while weight increased. Mothers with female fetuses showed similar age differences.

The sex ratio of calves produced by caribou depended on the age structure of females. This study showed an age effect, but not a body condition effect. The data from this study supports the Trivers and Willard hypothesis of sex ratios. In addition, the results of this study indicate that data obtained for confined individuals may not apply to wild populations.

Byers and Moodie (1990) investigated sex specific maternal expenditure in pronghorn (*Antilocapra americana*). A population of approximately 120 individuals was studied at the National Bison Range at Moise, Montana. Between the months of May and June in the years 1981 through 1985, pronghorn fawns were captured

between the ages of 0 to 6 days. Weight, sex, and suckling data were recorded for these individuals.

The median age at weighing and distribution of ages weighed did not differ by sex. There was a non-significant trend for males to be slightly heavier than females. During the first 6 weeks of life, suckling rates of males and females differed. Across all ages, female fawns had higher rates of rejected suckle attempts compared to those of males. Twins and singletons suckled at equal rates, but singleton females nursed at significantly higher rates than singleton males. In addition, there was a non-significant trend for female fawns with siblings to nurse at higher rates than male fawns with siblings during weeks 2-6. Female fawns were more active than male fawns. Male fawns tended to spend more time eating than female fawns. This difference approached significance.

The results from this study indicate that male fawns did not receive more resources than females. However, the male fawns allocated these resources differently as was indicated in their heavier weights. Since dominance status has an influence on reproductive success, female fawns were expected to demand more resources from mothers during the period of dominance formation. However, no offspring sex difference in maternal investment found. The results of this study suggested that the degree of adult dimorphism and absolute level of maternal investment have interacted over evolutionary time to adjust sex differences in scheduling of growth in polygynous mammals.

H. Other Ungulates Species

Berger and Gompper (1999) investigated the affects of predation on the adult sex ratio of several species of ungulates. They listed five causes of gender specific survival. These were: 1) biased maternal investment; 2) predisposition of males to greater mortality due to accelerated growth rate in conjunction with other factors; 3) dispersing sexes experiencing greater mortality than philopatric sexes; 4) less starvation related mortality in females due to adipose reserves; and 5) high intensity of intrasexual competition between males that leads to greater morbidity and mortality.

In populations without predators, there was no relationship between sex ratios and sexually dimorphism. However, in populations with predation, live females were more plentiful than males in 74% of the species surveyed. On a per species basis, males were preyed upon more heavily. Body mass was not related to the difference in sex ratios between live and killed animals. This means that predators were choosing to kill either larger or smaller individuals.

Based on this meta-analysis, there was a distinction between proximate and ultimate factors responsible for adult sex ratios that are not obvious. Therefore the challenge for future research is to evaluate which life history traits predispose sexes to differential mortality and the extent to which predation may shape these traits. Heavy male predation may be related to high proportion of males being conceived or male biased sex ratios seen at birth and maturity of many species

Kojola (1998) reviewed the data of several reports discussing sex ratio and maternal investment in ungulates. The purpose of the review was to provide a standardized arena to test sex ratio hypotheses in ungulates. Population sex allocation was defined as the sum of the allocation of the individuals in the population. The author purported that a common flaw in testing predictions of sex ratio is the application of both Trivers and Willard (1973) hypothesis and Fisher's (1930) hypothesis, because Trivers and Willard's hypothesis predicted variation among families, while Fisher's hypothesis predicted sex allocation over the entire population.

The sex ratio of offspring was usually associated with the nutritional status of females of browsers. Browsers were defined as species with breeding group sizes of more than 6 individuals. The results from grazers, which were defined as species with breeding group sizes of 3-5 individuals, were inconclusive. In many of the studies analyzed, there was a positive correlation between browsers' quality and the proportion of sons. However, in several of the studies no connection was found. Quality could be factors such as dominance rank, reproductive status, or weight.

The differential costs of rearing a son versus a daughter appeared to shape offspring sex ratio in ungulates. Clark's (1978) local resource competition hypothesis provided a likely explanation for the population sex ratio variation. This was plausible because the proportion of the more expensive sex, females, decreased under the increased food limitation in species using more defendable forage browse. Based on the results of this meta-analysis, there was a great need for more research to

investigate sex ratio adjustment as being adaptive. A lack of proximate mechanisms weakens adaptive adjustment hypotheses.

Forthman et al. (1993) studied the behavioral development and parental investment in captive bongos (*Tragelaphus eurycerus*). The study took place in the Los Angeles zoo. Five calves and their dams were studied. Descriptive data were presented because of the small sample size. The mean weight for males was higher than females. In addition, calves of old or dominant dams had the highest initial rates of suckling. However, male calves did not have longer suckling bouts than females. There was no relationship between "thief suckling" or suckling attempts and sex of calf. The neonatal weights demonstrated a trend consistent with females investing more in males. Other results from this study showed no sex differences or a bias toward females.

Hewison and Gaillard (1996) studied the relationship of birth sex ratios and local resource competition hypothesis in roe deer. Roe deer are unlike the animals that fit the profile of the Trivers and Willard (1973) hypothesis because they are neither highly sexually dimorphic nor polygamous. Data were collected between 1983 and 1990. In total 1181 embryos were examined. Maternal conditions were based on eviscerated body weight. The objective of the researchers was to examine the tendency for mothers to produce litters biased toward one sex or the other in relation to body weight. This trend was looked for both within populations and between populations.

The sex ratio increased as maternal condition increased. In addition, increasing sex ratio was linked to decreasing maternal condition. Females with twins were heavier than those with singletons. This trend was more pronounced in lower body weight populations. The sequence of investment was for this species was: 1 male, 1 female, 2 males, 2 females as body condition increased. The sequence suggests that roe deer tend to produce an excess of males when resources are limited. These results support Clark's (1978) hypothesis of LRC. Based on these results, sex ratio variation may be an adaptive trait in this species. A proximate mechanism for this strategy may be delayed implantation of up to 5 months. The existence of delayed implantation may explain why LRC has a strong potential influence on sex ratio manipulation in roe deer.

Pélabon et al. (1995) questioned whether sex biased maternal care was limited to total maternal expenditure in polygamous ungulates. In order to answer this question, the researchers reviewed the data of several published article that dealt with sex ratio biases and maternal condition. In their study, Pélabon et al. used birth weight as a measure of maternal expenditure. In addition, they defined maternal care by the ratio between male and female neonatal weight after log transformation. In total, 32 populations of 18 species or subspecies of polygamous ungulates were analyzed.

A relationship between sex biased care and total maternal expenditure was not found in this study. Different examples of sex ratios from various populations demonstrated that no simple relationship could be expected between maternal

expenditure, sex biased care, and polygynous mating systems among ungulate species. From the available information, environmental conditions and the relative effects of maternal care on male and female lifetime reproductive success seemed to be the best predictors of sex biased care.

III. Sex Ratio in Domestic Ungulates

A. Sheep and Goats

Skjervold (1979) studied the causes of variation in sex ratio and sex combination in multiple births in sheep. Data from the Norwegian sheep recording system from the period of 1974 through 1977 were used for this analysis. The overall average sex ratio was 48.9. There were several factors that had a significant effect on sex ratio. These factors included breed, age of dam, nutritional level of the flock, size of litter, the number of lambs weaned the previous year, and lambing season. In addition to these finding, there was also a small but consistent proportion of same sex twins.

Based on the data from this analysis, the sex ratio of sheep was influenced by environmental factors. A possible mechanism for variations in sex ratio suggested by Skjervold was differential mortality of male embryos or fetuses. The data from this study suggested that sex ratio estimates may provide information about the quality of the environment individuals were raised in.

Alley et al. (1995) studied a group of feral goats (*Capra hircus*) and investigated the behavioral perspective of maternal investment. The herd of goats consisted of 60 does and three bucks, which was observed for a period of five

months. This herd grazed on paddocks near Woodville, New Zealand. The frequency and duration of suckling bouts was recorded, as well as kid activity and mother-kid distances.

The overall sex ratio did not differ from unity, but the sex ratio of twins was female biased. In addition, the weight of dams at conception was correlated to the sex ratio of singleton lambs, but the weight of dams producing twins was heavier compared to dams of singletons. The distance between mother and offspring did not differ between the sexes.

With regards to sex differences in maternal investment, singleton males had higher birth weights than singleton females, and grew faster until the age of 3 months. Singleton males suckled more frequently than singleton females, but the duration of suckling bouts did not differ between the sexes. Additionally, singleton males were less likely to have a nursing bout terminated by the dam compared to singleton females. Thus males were more likely to have a successful nursing bout compared to females. In addition, female kids spent more time grazing and less time playing in comparison to their male counterparts.

Suckling behavior is often used as a measure of milk intake, and therefore could be used as a measure of maternal investment. However, suckling behavior could only be used as a measure of maternal investment if it is correlated with milk intake. Based on the data from this study, measures of suckling behavior during the first three months of life did not provide evidence of sex biased maternal investment. According to Byers and Moodie (1990) the sex that receives the least maternal care

should be expected to spend more time foraging. The data from this study supported this notion, as well as Trivers (1972) parental investment hypothesis. Variations in birth rate and growth rate may be indicative of differential allocation of maternal resources or a reflection of how the two sexes utilize these resources.

B. Pigs

Meikle et al. (1993) studied the relationship between maternal dominance rank and sex ratio in domestic pigs (*Sus scrofa domesticus*). Six groups of multiparous pigs were formed over an 11-month period of time. Agonistic encounters of displacements, shoves, bites, and chases were observed to determine a dominance hierarchy. Each pig was assigned to either the high ranking or low ranking half of her group. In order to analyze the relationship between dominance rank and sex ratio only live born piglets were used.

The data from this study indicate that maternal rank had a significant effect on sex ratio. High ranking females produced male biased litters. The proportion of males born to high ranking females was greater compared to low ranking females. The overall sex ratio was close to unity. The researchers found no rank related effect on fertility or fecundity.

The data from this study supports Trivers and Willard (1973). Meikle et al. suggested that since there was an equal number of offspring born to high and low ranking females, the difference in proportion of males born to high ranking females may be related to differential mortality of blastocysts prior to implantation. The cause of this differential mortality may be environmental stress. This environmental

stress could have taken the form of nutritional stress because low ranking individuals did not have the same access to food as high ranking individuals. The environmental stress could have also caused an increased adrenal activity because of agonistic encounters. These two possible mechanisms are not mutually exclusive, thus more investigations are needed to determine if they are the causes of differential fetal mortality.

Meikle et al. (1996) studied the relationship between dominance rank and parental investment in domestic swine. Five groups of gilts and six groups of sows were used in this study at the Southern Illinois Swine Research Center. Due to the variety of individuals used, this study allowed for the analysis of a wide range of ages and parities in the relationship between social dominance and maternal investment. Observations of agonistic encounters were used to establish the social structure of the pigs. The analysis of the relationship between parental investment and social rank only included live born piglets.

The mean proportion of males born to high ranking sows was greater than the proportion of males born to low ranking sows. In addition, the proportion of males born to a sow was correlated with the percentile dominance rank of females. The same relationship for proportionality of males held true for gilts as well. Parity and age were positively correlated with litter size, with age accounting for a significant proportion of the variance of litter size. The proportion of males born did not change with increasing parity or age for high ranking or low ranking females.

For high ranking females, there was a positive correlation between maternal age and the mean body mass at birth of sons and daughters. This was not true for low ranking females. This result indicates that there were age related differences in the abilities of high and low ranking female swine to invest in offspring. In addition, these differences may contribute to the overall rank related difference observed in secondary sex ratios. There was also a positive correlation between parity and the mean body masses of sons and daughters at birth for high ranking but not low ranking females.

The results from this study did not support the hypothesis of an age or parity related increase in the proportion of investment in sons. They also did not support the hypothesis that increasing maternal parity is associated with a decrease in maternal investment in sons. Based on the results from this study it may be warranted to pay closer attention to the variation observed in each female's offspring sex ratio over the course of her reproductive lifespan, since the mechanism for sex ratio variation is not clearly understood.

Drickamer et al. (1997) investigated the relationship between the proportion of males in a litter to sibling female anogenital distance. This investigation also studied the affect of various factors on conception failure. Data was collected at the southern Illinois University Swine Center at Carbondale, Illinois. Anogenital distances were collected on all live gilts from 154 litters born between January 1995 and August 1996. However the proportion of males in a litter included live and dead piglets.

There was a significant effect on the influence of a sow's birth litter sex ratio on reproduction success ratio. Females that were from male biased litters had lower reproductive success compared to females from litters with a low proportion of males. A higher proportion of males in a litter resulted in a larger mean anogenital distance for the females in that litter. Based on the results of this study anogenital distance and litter sex ratio for gilts could be used to indicate potential reproductive failure in replacement gilts. Gilts meeting certain criteria could be raised as market animals as opposed to replacement gilts, thus increasing profits for producers.

C. Horses

Cameron et al. (1999) studied the relationship between birth sex ratios and mare condition at conception in Kaimanawa horses (*Equus caballus*). Kaimanawa horses are feral horses that inhabit the Kaimanawa Mountains and plateaus of central North Island, New Zealand. This population of horses, consisting of approximately 400 individuals, has been observed since 1994. Body condition scores were assigned to mares throughout their eleven month gestation. Body condition scores were used because they have a high correlation with body fat percentage.

There were significant differences between the conditions at conception of mares that had female foals compared to mares that had male foals. Mares were in significantly poorer condition when they conceived their female foal. Thus mare condition at conception was a significant predictor of offspring sex. There was no significant variation in sex ratio between primiparous and multiparous mares or whether a mare had foaled in the previous year or in the year the foal was born.

This study confirmed the applicability of Kaimanawa horses as an ideal test of the Trivers-Willard hypothesis, because they meet the conditions of the hypothesis. The results strongly support the predictions of the Trivers-Willard hypothesis. Although a mechanism for sex ratio variation is not clearly understood, the researchers were inclined to state that the birth sex ratio reported were unlikely the result of differential death of fetuses or neonates by mares in poorer condition. This was because the variations in the birth sex ratio were too large to be accounted for by differential fetal loss alone. The data from this study suggested that the sex ratio variation occurred near conception and before sexual differentiation occurs.

Cameron and Linklater (2000) investigated bias maternal investment in mares (Kaimanawa horses - *Equus caballus*) as it related to their body condition. A group of 55 feral horses located on the central North Island, New Zealand were studied for four breeding seasons. The age of mares was estimated in years based on tooth wear patterns and foals were categorized by day of age groups. Body condition scores were assigned to the mares. In addition, mare terminated suckling bouts and unsuccessful suckling attempts were recorded.

Mares that foaled in one year were less likely to foal the subsequent year. This phenomenon was not influenced by the sex of the previous foal. Mares in good body condition lost more weight with a male foal compared to individuals with a female foal. However, mares in poor body condition gained less weight after having a female foal compared to a male foal. Therefore the differential reproductive cost of raising a son or daughter depended on body condition at conception. Thus mares in

good condition favored their sons, while mares in poor condition favored their daughters. In addition, there was a longer interval between foaling and conception for females in good condition than for males.

Mares in good condition incurred more costs in rearing a son; these costs were in body condition, as well as future reproduction. However, mares in poor condition incurred more costs in raising a daughter. The results of this investigation showed that there were no differences in maternal behavior based on sex at the population level. This indicates that mechanisms that cause sex ratio variation worked at the individual level.

D. *Cattle*

Skjervold and James (1978) studied the causes of variation in the sex ratios in dairy cattle (*Bos taurus*). The data used for the analysis were from the Norwegian dairy herd recording association. The years that were studied were 1972 through 1977. Annual records, which included both whole and partial lactations, were converted to whole lactations. Several environmental factors were studied in relation to sex ratio. These factors included parity, average herd milk production, herd size, age at first calving, calving interval, and milk yield.

The overall sex ratio was 52.24, which is in line with other studies. This sex ratio indicated no large deviation from equal numbers of the sexes. There was no great influence of parity on the sex ratio. However, for parity two and parities three through 5 the herd level of production during previous lactation had a significant influence on the sex ratio. The sex ratio was higher for herds with higher milk

production, but high yielding cows had a lower proportion of males. In addition, the season of calving only had a significant effect on primiparous individuals. Heifers that calved in the spring had a higher proportion of males compared to heifers that calved at other times of the year. Other than this, calving season had little effect on the sex ratio. For parity two and parities three through five, the sex ratio was higher for a single insemination compared to multiple inseminations.

There was an increase in sex ratio as herd size increased. The sex ratio increased with age of first calving for parities one and two. This means that older first time mothers had more male calves. In contrast, cows calving for the first time at a young age had a smaller proportion of male calves. Calving interval had a significant effect on subsequent sex ratio. Those individuals with short calving intervals had the lowest sex ratio.

This study used milk yield used as a measure of environmental stress. Based on the data from this investigation, there was a difference between herd (group) level of production effect on sex ratio (positive) and individual level of production effect on sex ratio (negative). One of the hypotheses put forth by the authors of this study was that variations in sex ratio were caused by differential fetal mortality. They purported that more male fetuses were lost early on in gestation. The authors reached the conclusion that sex ratio could be used as an indicator of environmental stress, since a low sex ratio indicates that improvements to management systems are needed.

IV. Summary

In reviewing the literature pertaining to sex ratios in ungulate species, several things became apparent. The first is that sex ratio skews do occur in wild, feral and domestic animal populations. The interpretations of these sex ratio skews are often difficult and typically can be explained by one or more of the prevailing sex ratio theories. In addition, the conflicting reports that exist with regard to whether a specific sex ratio hypothesis is supported by various species further complicate the interpretation of research results. It is clear that further investigation is needed to understand the factors that skew these ratios in various animal populations and to find the mechanisms that drive these skews.

Table 2. Summary of research supporting Trivers-Willard hypothesis in ungulates.

Supporting Data	Species
Alley et al. (1995); Cameron et al. (1999); Clutton-Brock et al. (1986); Green et al. (1989); Green and Rothstein (1991); Kathnelson and Hudson (1998); Kojola and Eloranta (1989); Kugera (1991); Meikle et al. (1993) Reimers and Lenvik (1997); Rutberg (1986); Thomas et al. (1989); Wolff (1988)	American Bison; Caribou; Domestic Pigs; Feral Goats; Kaimanawa Horses; Red Deer; Reindeer

Table 3. Summary of research supporting other sex ratio theories in ungulates.

Sex ratio hypothesis	Supporting Data	Species
Clark, 1978 - local resource competition (LRC)	Hewison and Gaillard (1996)	Roe Deer
Maynard Smith, 1980	Green et al. (1989); Green and Rothstein (1991); Kathnelson and Hudson (1998)	American Bison; Red Deer

Chapter 2: Maternal Investment and Sex Ratios in Beef Cattle

Abstract

Hypotheses from biology propose that females that are in better condition are better able to provide resources to their offspring. It is well known in animal agriculture that cows that range in age from approximately 4 to 8 years are in their peak milk production years. The objective of this study was to determine the influence of several maternal factors on the sex of offspring. Two data sets were used. The first data set was taken from the beef records from the Wye Angus cattle at the University of Maryland Wye Research and Education Center, Queenstown, Maryland. The birth records from this data set spanned approximately 50 years. The second data set was taken from records produced during a cow-calf production forging study conducted at Grazinglands Research Laboratory west of El Reno, Oklahoma. The birth records from this data set spanned approximately 5 years. The relationship between age of dam, previous reproductive effort, and calf sex was analyzed for each data set. There were no significant differences found between age of dam and calf sex.

Introduction

It has been document in many vertebrate species that females may alter the amount of maternal investment they provide to an offspring based on the sex of that offspring (Hardy, 1997). This differential investment can be either direct nutritional (for example milk, higher birth weight, etc.) or greater behavioral investment (more attention through closer spatial proximity, grooming, etc.). Trivers and Willard (1973) proposed a hypothesis of differential parental investment in relation to the sex

ratio of offspring. This hypothesis presented the concept that parents may have the ability to vary the sex ratio of offspring.

The Trivers-Willard hypothesis was based on the assumption that the sex ratio at birth in mammals is a measure of tendency to invest in one sex more than in the other. From this assumption, Trivers and Willard stated that females in better condition tend to invest in sons. As evidence of this, they reported that adverse environmental conditions for mothers during pregnancy were correlated with a reduction of male offspring in deer and humans. Their hypothesis suggested that in species with a long period of parental investment after birth, biases in parental behavior towards offspring of different sexes may be expected. Thus parents in better condition would be expected to show a bias toward male offspring.

Since this hypothesis was introduced, there have been many empirical studies that have tested its validity. Wolff (1988) studied American bison and reported that cows that had sons in one year were more apt to be barren the following year compared to cows that had daughters. In addition, sons nursed significantly longer than daughters. This lends support to the idea that sons are more costly to produce and Wolff suggested that American bison cows in better than average condition produce more sons than daughters.

Retrospective studies have also been performed to test the validity of the Trivers-Willard hypothesis. Skjervold (1979) studied the causes of variation in sex ratio and sex combination in multiple births in domestic sheep. One of the sources of variation in the sex ratio was the number of lambs weaned in the previous year. The more lambs a ewe weaned in the previous year, the fewer male offspring she

produced. This additional evidence supports the idea that good body condition is necessary to produce male offspring. From these results, Skjervold (1979) suggested that sex ratio estimates may provide some information about the quality or the stress effect of the environment in question.

Several studies have been conducted that lend support to the Trivers-Willard hypothesis. Austad and Sunquist (1986) reported that female opossums given supplemental food did not have more offspring than females denied supplemental food, but supplemented females' offspring were larger at all stages of development and their litters were male biased. Milligan and Brigham (1993) reported that the date of birth had a significant effect on the sex of the young in Yuma bats and suggested that older females benefit by producing males. Season of birth and age of dam were factors that affected sex ratios in Skjervold's (1979) research.

The aforementioned research reports all suggested that body condition is an important factor in the sex ratio of offspring. However, it is unclear as to the role of other factors such as age since Wolff's (1988) results contradict Skjervold's (1979) and Milligan and Brigham (1993). There may be other factors that contribute to sex ratios in mammals including maternal investment. According to Trivers and Willard (1973) parents should invest differentially in the different sexes. If parents do invest differentially in the different sexes, then Skjervold's (1979) belief that sex ratios are an indication of environmental stress may be correct. In these circumstances, the environmental stress sex ratios are indicating would be the quantity and quality of maternal investment.

The study of domestic animal in relation to biological hypotheses, such as the Trivers and Willard hypothesis, is lacking in the literature. The Trivers-Willard hypothesis was based on species where: 1) sexually dimorphism exists; 2) males compete for females; 3) males contribute very little to investment; and 4) offspring are born one at a time. Domestic cattle meet these criteria because they are sexually dimorphic; males typically weigh 30% to 40% more than females depending on the breed of cattle, and males will compete with each other in order to breed with females. In addition, cows typically give birth to one offspring at a time with no parental investment given by the bull. Another advantage of using domestic cattle to test the validity of the Trivers and Willard hypothesis is that domestic cattle are numerous and readily available to study. Beef cattle records are routinely kept on traits related to both mother and offspring.

The aim of this study was fill the gap in the literature regarding the application of the Trivers-Willard hypothesis to domestic cattle. Specifically we conducted an assessment of maternal factors in relation to offspring sex ratio in beef cattle. Based on the Trivers-Willard hypothesis, mothers in good condition will produce sons. Maternal factors that were used to test the relation between good condition and offspring sex ratio were: 1) age of dam; 2) year of calving; 3) calving ease score of the previous calving; 4) sex of the previous calf; 5) birth weight of the previous calf; and 6) the time interval between two subsequent calvings. As age of dam increased it was expected that more male calves would be born. There were no expectations for year of calving. As calving ease score for the previous calving increased it was expected that more female calves would be born. If the sex of the previous calf was

male, it was expected that the next calf would be a female. As the birth weight of the previous calf increased it was expected that the next calf would be a female. As the time interval between subsequent calvings increased it was expected that the next calf would be a male.

Materials and Methods

Wye Data

The first data set was taken from the beef records from the Wye Angus cattle at the University of Maryland Wye Research and Education Center (WREC), Queenstown, Maryland. The Wye Angus herd was founded in 1937 with 18 heifers and one bull (Lingle et al., 1976). The first crop of calves was born in 1939, and since that time more than 9,000 calves have been born into the Wye herd. The Wye Angus herd became the University of Maryland beef cattle research herd in 1980. Birth records for these animals have been maintained since the establishment of the herd. Records on individual animals at the Wye Research and Education Center are maintained in separate databases. Some of these data bases include pedigree information, breeding information, calf weaning information, and calf crop information. In each database, individuals were identified by a unique eight digit identification number in which the first four numbers represented the year the individual was born, and the last four numbers represented the individual's herd number.

Wye Data Processing

The records from the master database, which included information on the dam of each individual in the herd, were merged with the pedigree database by cow identification number. This created a data set that included both the birth date of the dam and calving dates. These variables allowed for the calculation and creation of a dam age variable. This newly created dataset was then merged by cow identification number with the breeding database. The merged databases created a data set that included the following data: calf identification number; cow identification number; age of dam; dam age in years at the time of calf's birth; sex of calf (1=male, 2=female); and year of birth of the calf. Records that were incomplete were dropped from the data set. The final dataset included 9197 records spanning from the years 1939 to 1998.

Wye Data Analysis

These records were used to determine 1) the influence of age of dam on the calf sex ratio, and 2) the influence of year of calving on calf sex ratio. A multiple logistic regression (SAS) was used to analyze the data set that was described in the previous section.

El Reno Data

The second data set was taken from records produced during a cow-calf production forging study conducted at Grazinglands Research Laboratory west of El Reno, Oklahoma between 1993 and 1997. The cows used in this study were produced over a three year period (1989-1991) from Angus-Hereford dams bred

either to Charolais, Gelbvieh, Angus, or Hereford sires and had a least one calf prior to the study. Ninety-nine cows were assigned within age and breed of sire to one of the three forage systems. Twenty-one additional cows were kept as replacements for any cows lost due to death or culling over the three year period. All replacements came from these cows, and no replacement heifers were saved. Cows that died during calving were replaced at the beginning of the breeding season. Any cows open for two consecutive years were culled and replaced when checked for pregnancy at weaning.

Body weights and body condition score (1 to 9; Richards, et al. 1986) of cows were taken at the beginning of the breeding season (approximately May 15) and at weaning (approximately Oct. 15) each year (Table 4). Calf weights were taken at birth, at the beginning of the subsequent breeding season, and at weaning. Calving ease (1-5) were recording for each calving (Table 5).

Table 4. Descriptions of body condition scores.

Body Condition Score	Description
1	Emaciated
2	Poor condition
3	Thin condition
4	Borderline condition
5	Moderate
6	High moderate
7	Good
8	Fat
9	Extremely fat

Table 5. Descriptions of calving ease scores.

Calving Ease Score	Description
1	No problem or unobserved
2	Slight problem
3	Cow needed assistance
4	Considerable force used to deliver calf
5	Extremely difficult birth

El Reno Data Processing

For each dam in this dataset, the following variables were retained: current calf sex, the sex of the calf at the present calving; next calf sex, the sex of the calf at the subsequent calving; calving interval, the amount of time in days between the present calving and the subsequent calving; current calving ease (CE) score, the calving ease score of the present calving; cow birth body condition score, the body condition score of the dam at birth for the current calf; and cow weaning body condition score, the body condition score of the dam at weaning for the current calf. Records that were incomplete were dropped from the data set. The final dataset included 331 records for the years 1993 through 1997.

El Reno Data Analysis

These records were used to determine 1) the influence of age of dam on the sex of the next calf, 2) the influence of calving interval on sex of the next calf, 3) the influence of current calf birth weight on the sex of the next calf, 4) the influence of calving difficulty on the sex of the next calf, and 5) the sex of the previous calf on the sex of the next calf. A multiple logistic regression (SAS) was used to analyze the data set that was described in the previous section.

Results

Wye Data

The age range of cows in the Wye data set ranged from 2 to 20. When the sex ratio of offspring was regressed by the age of the cow, no significant differences were found. The sex ratio did not significantly depart from unity during the age of peak milk production (Table 6) (Figure 1).

Sex ratio of offspring was also regressed by year of calving. The sex ratio did not significantly depart from unity based on this criterion either. An interesting trend that occurred in this analysis was that sex ratios did not go further than 60% in either direction whether the calving pool was small or large for a particular year (Figure 2).

Table 6. Summary of Logistic Regression Analysis of Wye Data Predicting Calf Sex.

Variable	B	SE	Odds Ratio	Wald statistic
Dam age	.01	.01	1.01	.88
Year of calving	.00	.00	1.00	.88

* $P < .05$; ** $P < .01$

El Reno Data

The sex ratio of all calving records did not significantly differ from unity ($P > .05$). Several maternal factors were also analyzed to determine their ability to predict the sex of the next calf of a dam. The age of dam, calving interval, and calving ease score for the current calf were not significant predictors of the sex of the next calf. Current calf sex and current calf birth weight were significant ($P = .05$) in predicting the sex of the next calf (Table 7). As each of these factors increased, the probability of the next calf being a male increased.

Table 7. Summary of Logistic Regression Analysis of El Reno Data Predicting the Sex of the Next Calf.

Variable	B	SE	Odds Ratio	Wald statistic
Sex (1)	-.47	.24	.62	3.76*
Birth Weight	-.04	.02	.96	3.81*
Calving Interval	.00	.00	1.00	.04
Calving Ease Score				3.27
Calving Ease Score (1)	-.05	.67	.95	.01
Calving Ease Score (2)	-6.04	9.91	.00	.37
Calving Ease Score (3)	-1.87	1.10	.15	2.91
Dam age	0.50	.13	1.05	.15

* $P = .05$; ** $P < .01$

Percentage of Male Versus Female Calves Born to Wye Data Dams by Age of Dam (n=9197)

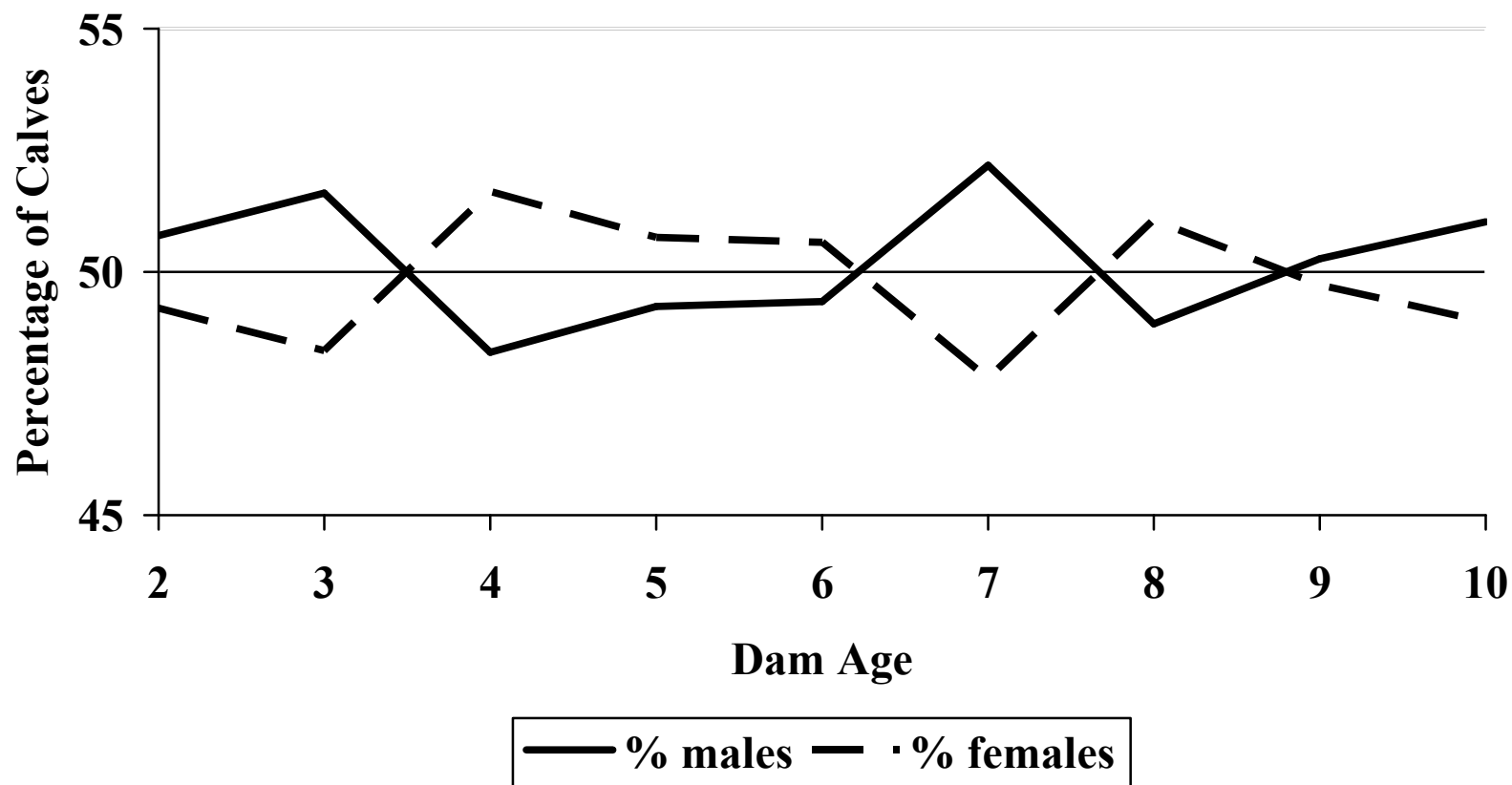


Figure 1. Wye data percentage of male versus female calves by dam age.

**Wye Data Percentage of Male Versus Female Calves Between
1939 and 1998 (n=9197)**

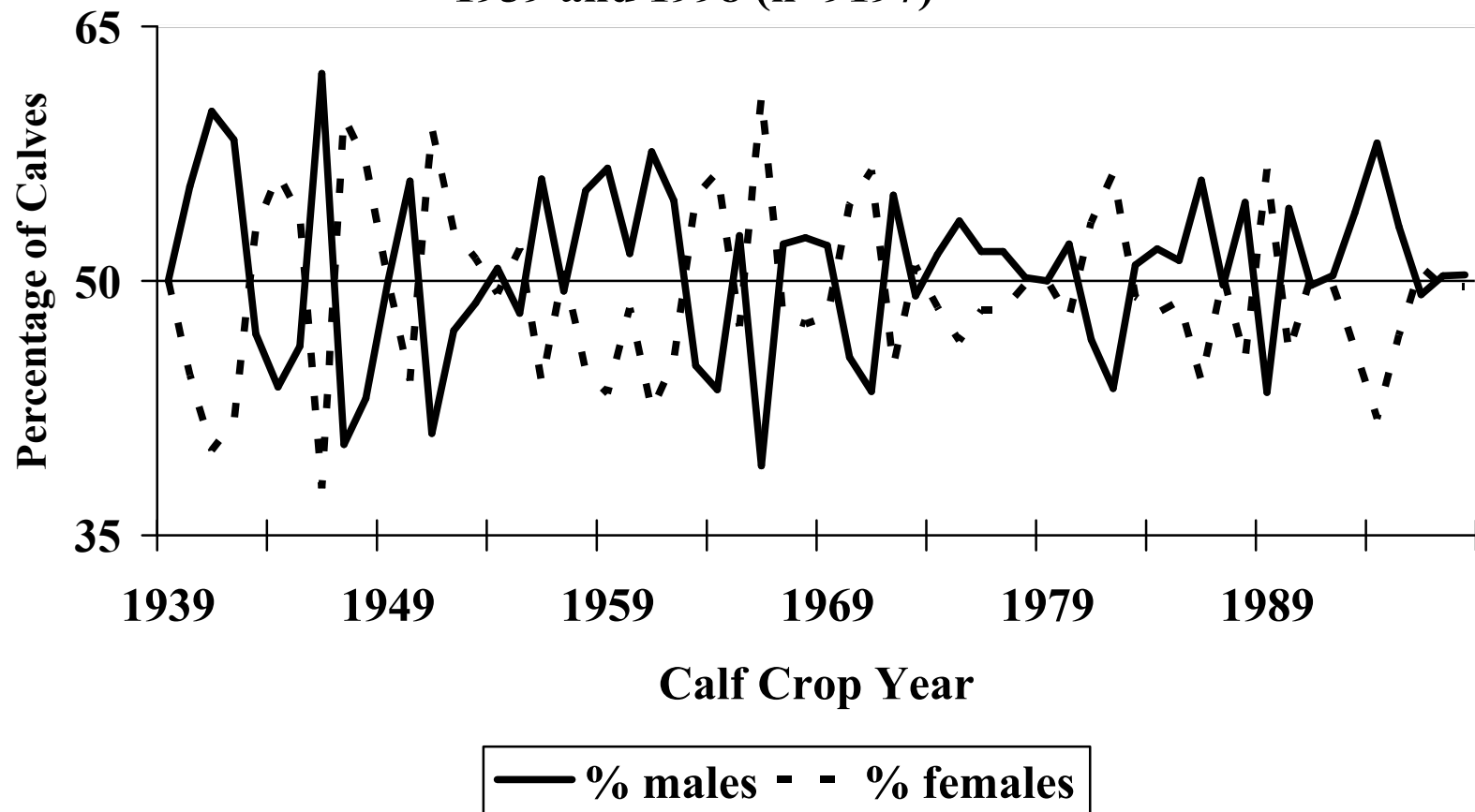


Figure 2. Wye data percentage of male versus female calves born between 1939 and 1998.

**Percentage of Male versus Female Calves Born to El
Reno Data Dams by Age of Dam (n=331).**

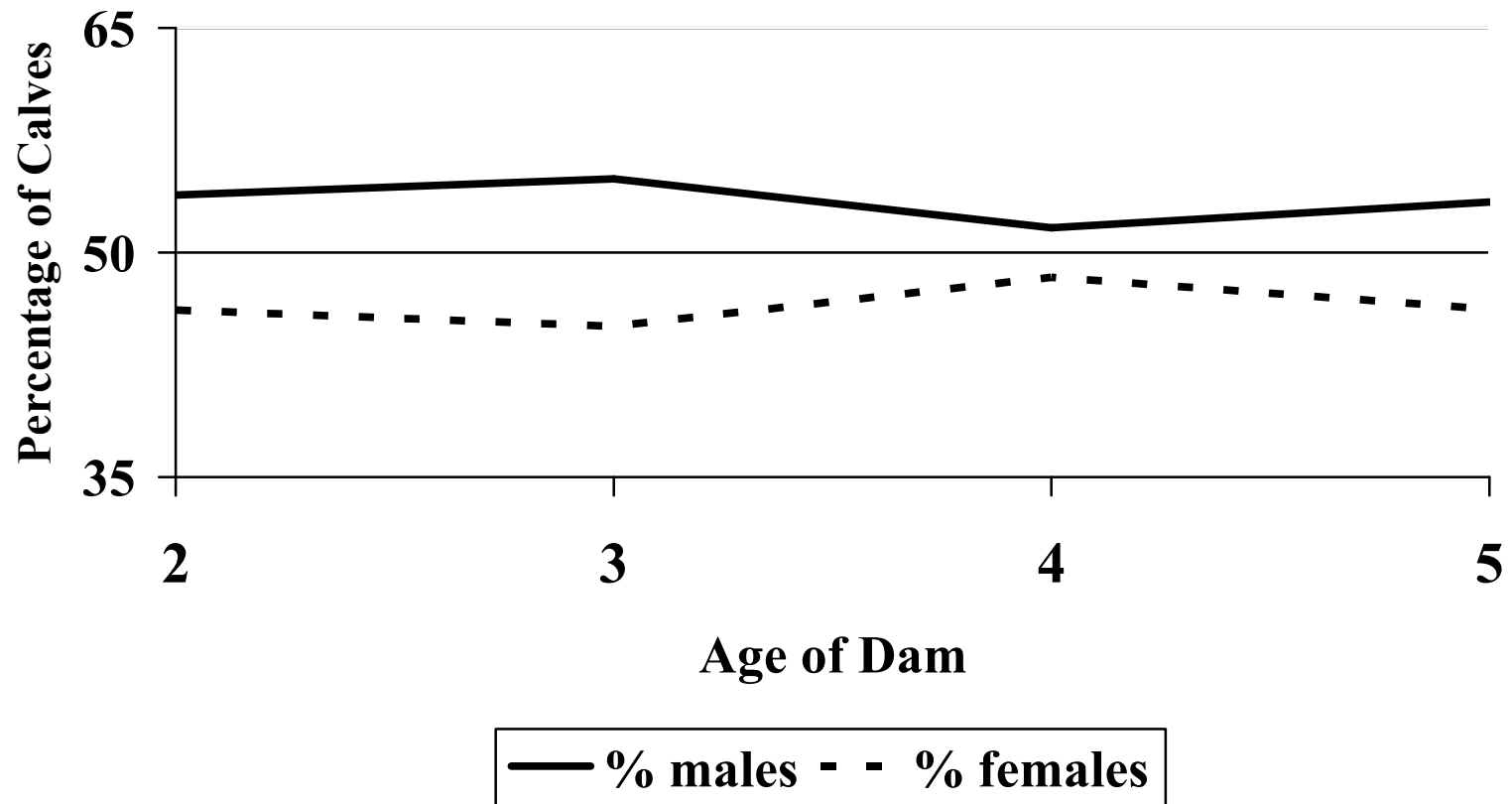


Figure 3. El Reno data percentage of male versus female calves by age of dam.

Discussion

It is well known in animal agriculture that cows that range in age from approximately 4 to 8 years are in their peak milk production years. Additionally, these cows typically have some advantages in their social groups because of seniority and weight. However, analysis of the Wye and El Reno, Oklahoma data do not indicate any bias in sex ratio by age of dam. The results from these data sets also indicate that year of calving, calving interval, and sex of the current calf do not affect the sex of the next calf. Additionally, birth weight of the current calf and calving ease score for the current calf were significant predictors of the sex of the next calf.

Two plausible explanations for the difference in results in the above data sets compared to the data sets reports from wild populations exist. They are: 1) Resource dependence does not occur in domestic animal populations; or 2) The results from the wild populations are inaccurate. Each of these explanations takes into account the inherent difference between domestic and wild animals.

Resource Dependence

Trivers and Willard (1973) contended that females in better condition would produce more male offspring if all assumptions were held. In the case of the current data sets, all of the females were not significantly different in condition score from each other at the time of breeding. Resources in domestic populations tend not to vary drastically so that the condition of the animals is not significantly altered. For some herds, food rations are carefully calculated and measured via radio frequency neck collars or ear tags. The lack of resource dependence in domestic populations would attribute to lack of skewed sex ratios in domestic populations.

The sex ratio bias that was described by Trivers and Willard was meant to describe an individual level bias not a population level bias. This sex ratio bias is based on the ability of a dam to provide maternal care relative to that of other dams in the population (Hewison et al. 2002). In domestic animals in general, and cattle specifically, it is hard to determine if individual dams have the ability to assess their maternal care relative to other dams, because all of the animals in the herd receive the same treatment. Any one pregnant dam receives the same type and amount of ration as other pregnant dams in the herd. This inability to assess maternal care may be another resource dependent obstacle that prevents a biased sex ratio from developing in beef cattle herds.

Age has been debated as a predictor of sex ratio (Saltz, 2001 and Hewison, et al. 2002). Although the argument can be made both ways as to whether maternal age predicts sex ratio, maternal age could be reviewed as a resource. This is because the greater the age of the dam, the more maternal experience she tends to have. This is another resource that domestic cattle are not dependent upon. In a typical beef cattle herd, the median age of dams is about four. These animals on average have had only two calves, so their maternal experience is low.

In cattle there is no period of resource abundance where dams would evaluate level of body reserve at the time of conception as a reliable predictor of future reserves around the time of birth and parental investment. Typical cattle management precludes a variation in abundance of feed at the point of conception. The lack of food resource variation that wild animal populations experience, may lead to the different results obtained from the analyses of these populations.

Finally, resource dependent biased sex ratios may be negated by local resource competition (Monard et al., 1997). Resource dependence predicts male biased sex ratios for females in good condition. Local resource competition predicts a female biased sex ratio for females in good condition. It is probable that both of these mechanisms are working at the same time, since resource dependence works on the level of the individual, while local resource competition works at the level of the population. Since each of these models suggests sex ratio skews in opposite directions, these two mechanisms need to be separated into their component parts in order for a full understanding of sex ratios in any species.

Wild Population Inaccuracies

Many of the wild population sex ratio reports come from data sets with a low number of study animals. The statistics for these data are often complicated and difficult to interpret. This factor along with the fact that Trivers and Willard (1973) are often misinterpreted, may contribute to the disparity between sex ratios in wild populations versus domestic populations. For example, many researchers have set about to prove or disprove Trivers and Willard based on an animal species that does not meet all of the assumptions of their hypothesis. Because the assumptions were violated from the onset, it is nearly impossible to determine whether the outcome proved or disproved the Trivers-Willard hypothesis.

One reason for the discrepancies between wild population data and domestic animal data may come from the fact that many of the wild population studies are based on the same population of animals. For example, of the research studies that pertain directly to sex ratios and American Bison (*Bison bison*) Rutberg (1986) and

Wolff (1988) studied the population at the National Bison Range in Moise, Montana. Two other bison studies (Green et al., 1989 and Green et al., 1991) used bison at Wind Cave National Park in South Dakota. Each of these studies reports herd sizes between 320 to 350 animals. Each of these studies report similar results in that: cows in better than average condition produced more sons than daughters (Wolff, 1988 and Rutberg, 1986); females in poor condition produce mostly daughters (Green et al., 1991); and females provide for their daughters through post weaning associations (Green et al., 1989).

Another example of the overuse of one population of wild animals to study a similar problem is the red deer population in the North Block of the Isle of Rhum, Scotland. Three studies which used this population of animals to investigate sex ratios are Clutton-Brock et al. (1986), Gomendio et al. (1990), and Kruuk et al. (1999). The life histories of the red deer on the North Block of the Isle of Rhum, Scotland have been maintained for several years. In 1973, culling practices were halted and the population increased from approximately 60 adult females to approximately 180 adult females (Kruuk et al., 1999 and Clutton-Brock et al. 1986). Again, these studies found similar results in relation to the Trivers-Willard hypothesis. Using the same group of animals for similar studies will tend to yield similar results. This may be a prime reason why wild population data differs so much from wild animal population data.

The results from the aforementioned studies support the Trivers-Willard hypothesis in varying degrees, but the data from two populations of domestic cattle did not support this hypothesis. The domestic cattle populations are different from

the wild population data of bison and red deer in many ways. The first difference occurs with the number of animals in each of the studies. The data using the Wye Angus cattle consisted of more than 9,000 records, as opposed to the 150 to 300 animals that were used in the red deer and bison populations respectively. Based on the discrepancies with the results, there is an implication that there is some inherent difference between small populations versus large populations when it comes to sex ratios. If this difference exists, it must be investigated in future studies.

Another difference between the wild populations and the domestic animal populations is in the management of the animals. The wild populations had minimal or no management as opposed to the intensive management of the domestic cattle. It may be possible that the level of management may affect sex ratios of animals. For example, Rutberg (1986) suggested that non-lactating animals were over represented in the culled animals. It was also shown that non-lactating females had a higher proportion of male fetuses. Based on this, differences in level of management of study populations should be considered when trying to investigate Trivers-Willard hypothesis within any population of animals.

The results from the current study demonstrated that domestic cattle are a valuable asset in the study of ethological hypotheses. However there were several limitations of this study, the first of which is that it was a retrospective analysis of birth records from two different herds of cattle. Although the number of records used in this study was numerous, they were not representative of beef cattle in current production systems. In addition, the numerous incomplete calving records from the Wye data prohibited analysis of maternal condition code with relation to sex ratio.

Conclusions

The Trivers-Willard hypothesis was not supported by these data. Sex of offspring in the herds of beef cattle studied were not a function of or determined by the ability of the mother to provide optimally for the offspring. It appears as though these cattle were not resource dependent. The sex ratio biases reported in naturally mating populations may be the consequence of environmental stressors that result in differential mortality of embryos, thus influencing sex ratio, that are not present in domestic beef cattle production systems. The fact that no significant differences were found in either of these large data sets was surprising. A larger sample of birth records that is more representative of beef cattle warrant further investigation. Understanding the role of maternal investment on the sex ratio of beef cattle would have economic and welfare implications for beef production systems.

Chapter 3: Maternal Investment and Sex Ratios in Dairy Cattle

Abstract

More productive cows were determined to have fewer male offspring in future calvings. Over 12.4 million dairy records were included in an analysis of sex ratio as a function of parity. The percentage of male calves increased after the first parity. The mean percentage of male calves for parities 7 through 10 was 52.30, and the mean percentage of males for parities 11 through 20 was 46.30. When only births that were followed by a subsequent calving were included for all parities, 1.8 million birth records were available, and the percentage of males was greater for parities 1 through 6 (52.19, 52.49, 52.53, 52.39, 52.38, and 52.38 respectively). The average percentage of males for parities 7 through 13 was 56.34. Because cows that were of lower fertility and lower milk-producing ability were more likely to be culled, the cows included in the consecutive calving data set were more productive cows. The Trivers-Willard hypothesis first reported in 1973 proposed that females with good body condition, high social status, access to resources, etc. should be expected to produce more males, and a number of studies of wild and feral populations have reported sex ratios in support of Trivers-Willard. In this study, age of dam, lactation number, calving interval, and milk production level were significant predictors of the sex of the next calf. These data support the contention of Trivers-Willard and also indicate that domestic animals, in this case cattle, still exhibit genetic influences that result from evolutionary influences – even though artificial selection influences have occurred. A question considered to be of great importance is the determination of

what mechanisms actually underlie the differential sex ratios that result from females of different production capabilities.

Introduction

The question of why the sex ratio in most species approximates 50:50 when limited quantities of males are needed to fertilize the females has been raised for years. In an efficient system, females would outnumber males in proportion to the role each plays in reproduction and raising offspring. Natural systems such as these are rarely seen. However, biases in sex ratios have been recorded in several animal populations.

Several theories have been proposed to explain the various sex ratios seen in populations of organisms (Hardy, 1997). From these theories it is evident several factors are involved that have some bearing on offspring sex ratios. The focus of some sex ratio theories is the amount of investment a parent places in an offspring. Other theories focus on genetic and environmental contributions to the sex ratio. Due to the presence of such varied theories in the literature, interpretation of sex ratio results can sometimes be complex.

The first sex ratio hypothesis to directly assert that parents play a role in the sex ratio of their offspring was Trivers and Willard (1973). Trivers and Willard based their hypothesis upon three assumptions. These assumptions were: 1) The condition of offspring at the end of parental care was correlated with the condition of the mother during the period of investment; 2) The condition of young at the end of the period of parental investment would continue into adulthood; and 3) Males would have better reproductive success if they were in better condition compared to their

female counterparts. Based on these assumptions, Trivers and Willard stated that skewness in sex ratio were a measure of the tendency to invest more in one sex than the other.

There have been many studies conducted to test the validity of the Trivers-Willard hypothesis in wild, feral and domestic animal populations (see dissertation literature review). Many of these studies focus on the differences in maternal factors that have an impact on offspring sex ratios. Some of the maternal factors that have been examined are body condition, social dominance, reproductive status, age, parity, and production level. However the focus of the majority of the research in this area has been on wild animal populations.

The role of domestic animals has been neglected in the great deal of research dedicated to testing the validity of the Trivers-Willard hypothesis. Domestic animals in general and domestic cattle specifically, are often good candidates to test biological hypotheses for the simple fact that they are numerous in number and are easily accessible compared to wild and feral populations of animals. Domestic dairy cattle are somewhat sexually dimorphic compared to their wild counterparts; males typically weigh 30% to 40% more than females depending on the breed of cattle. Under the proper conditions, males compete aggressively for mates, do not contribute investment toward offspring, and cows typically have one calf at a time. These conditions are the same stipulated by Trivers and Willard, making domestic cattle good candidates for testing this hypothesis.

The aim of this study was to fill the gap in the literature on maternal investment and sex ratios in domestic cattle. Specifically we conduct an assessment

of maternal factors in relation with offspring sex in dairy cattle. Based on the Trivers-Willard hypothesis mothers in good condition will produce sons. Maternal factors that were used to test the relation between good condition and offspring sex ratio were: 1) age of dam; 2) level of production; 3) calving ease score of the previous calving; 4) sex of the previous calf; 5) lactation number; and 6) the time interval between two subsequent calvings. As age of dam increased it was expected that more male calves would be born. As level of production increased it was expected that fewer males would be born. As calving ease score for the previous calving increase it was expected that fewer male calves would be born. If the sex of the previous calf was male it was expected that the next calf would be a female. As lactation number increased it was expected that the next calf would be a male. As the time interval between subsequent calvings increased it was expected that the next calf would be a male.

Materials and Methods

Data

Animal Improvement Programs Laboratory (AIPL) of the USDA conducts a national evaluation of birthing difficulty (calving ease). These evaluations have been done by this agency since 1999. The calving ease (CE) data primarily comes from Dairy Herd Improvement Association (DHIA), but some data are received from artificial insemination (AI) organizations (Van Tassell et al., 2003). The national dataset includes more than 12 million calving record of Holstein cows calving since 1980. Biannual updates of the calving ease records are provided by Dairy Records

Management Systems (Raleigh, NC). Calving ease scores are on an ordinal scale of one (no problem) through five (extreme difficulty) (Table 8).

Table 8. Distribution of calving ease (CE) scores by parity.

	First Parity		Second Parity		Third and later parities	
CE Score	Frequency	%	Frequency	%	Frequency	%
1 – No problem	654,050	71.42	368,405	71.81	295,443	71.93
2 – Slight problem	111,756	12.20	61,394	11.97	47,689	10.57
3 – Needed assistance	98,975	10.81	54,578	10.64	41,886	11.83
4 – Considerable force	33,508	3.66	19,063	3.72	15,361	4.23
5- Extreme difficulty	17,464	1.91	9606	1.87	7623	1.80
Total	915,753	49.86	513,046	27.93	408,002	22.21

Database Design

Calving ease records are stored in relational database tables that are linked to both production and pedigree tables to minimize the storage of redundant information. The primary CE table contains CE data for individual calving records (herd, sire, dam, CE score, parity, calving date, multiple birth code, calf sex code, and data source). Dam ID in this table is stored as numeric animal keys and each animal in the production table is assigned a unique animal key, which allows for the cross reference of multiple ID (e.g., American ID and ear tag).

Data Processing

The records from the CE table were merged with the pedigree table by animal key. This created a data set that included both the birth date of the dam and calving dates. These variables allowed for the calculation and creation of a dam age variable. This newly created dataset was then merged by animal key with the production data

tables. At this junction fat corrected milk (fcm) was calculated ($fcm = (0.4 \times \text{milk produced}) + (15 \times (\text{milk fat}/100) \times \text{milk produced})$) (NRC, 2001). The final dataset included 1,847,164 records. By the nature of the variables that were of interest for this study, only dams that had at least two consecutive lactations were included in the dataset. For each dam in this dataset, the following variables were retained: previous calf sex, the sex of the calf at the present calving; next calf sex, the sex of the calf at the subsequent calving; fat corrected milk (fcm), the milk production level for the previous lactation; lactation number; calving interval, the amount of time in days between the present calving and the subsequent calving (dams with calving intervals greater than 730 days were dropped from the dataset), previous CE score, the calving ease score of the previous calving; next CE score, the calving ease score of the subsequent calving; and month of birth of calving.

Data Analysis

These records were used to determine 1) the influence of age of dam on the sex of the next calf, 2) the influence of calving interval on sex of the next calf, 3) the influence of lactation number on the sex of the next calf, 4) the influence of calving difficulty on the sex of the next calf, 5) the influence of previous production level on the sex of the next calf; and 6) the sex of the previous calf on the sex of the next calf. A multiple logistic regression (SAS) was used to analyze the data set that was described in the previous section. The analysis was based on the previous data set where dam age was between 18 and 96 months.

Results

When the sex ratio of all calving records was analyzed (n=12.4 million), the sex ratio for the first parity was 50:50. However, the sex ratio of all other parities deviated from a 50:50 ratio ($P < .05$) when sex of calf was regressed by age of dam, calving interval, lactation number, calving difficulty, previous production level, and sex of the previous calf (Table 9). In addition, the sex ratio over all parities was also skewed (Table 10) when the working data set (n=1.8 million) was regressed using the same variables ($P < .05$). Several maternal factors were also analyzed to determine their ability to predict the sex of the next calf of a dam. The sex of the previous calf, previous calving ease score, and month of calving were not significant predictors of the sex of the next calf. However several maternal variables including dam age, lactation number (parity), calving interval, and previous milk production level were significant predictors of the sex of the next calf ($P < .05$) (Table 11). As dam age (Figure 4) and previous milk production level (Figures 5) increased, the probability of the next calf being male decreased. As lactation number (Figure 6) and calving interval (Figure 7) increased, the probability of the next calf being male increased.

Table 9. Sex ratio by parity (all records).

Parity	Females (%)	Males (%)	N
1	50.21	49.79	3,234,090
2	47.99	52.01	3,667,982
3	47.75	52.25	2,448,523
4	47.68	52.32	1,435,445
5	47.68	52.31	824,638
6	47.69	52.31	418,834
7 through 10	47.70	52.30	334,023
Total	48.44	51.56	12,424,675

Table 10. Sex ratio by parity (consecutive lactations).

Parity	Females (%)	Males (%)	N
1	47.81	52.19	915,797
2	47.51	52.49	513,046
3	47.47	52.53	259,453
4	47.61	52.39	113,334
5	47.62	52.38	30,826
6	47.62	52.38	9,734
7 through 10	45.18	54.82	4,920
Total	47.66	52.34	1,847,159

Table 11. Summary Logistic Regression Analysis Predicting the Sex of the Next Calf in Dairy Cattle.

Variable	B	SE	Odds Ratio	Wald statistic
Production Level	.00	.00	1.00032	6.19*
Age of dam	.00	.00	1.00	4.66*
Lactation number	.02	.01	1.02	7.29**
Calving interval	.00	.00	1.00029	188.09**
Current calf sex (F)	.00	.00	1.00	1.71
Calving ease score (1)	.00	.00	.99	.88
Calving ease score (2)	.00	.00	.99	1.18
Calving ease score (3)	.01	.00	.98	1.21
Calving ease score (4)	.018	.01	.98	1.62

* P < .05; **P<.01

Percentage of Male versus Female Calves by Age of Dam (n=1,847,159)

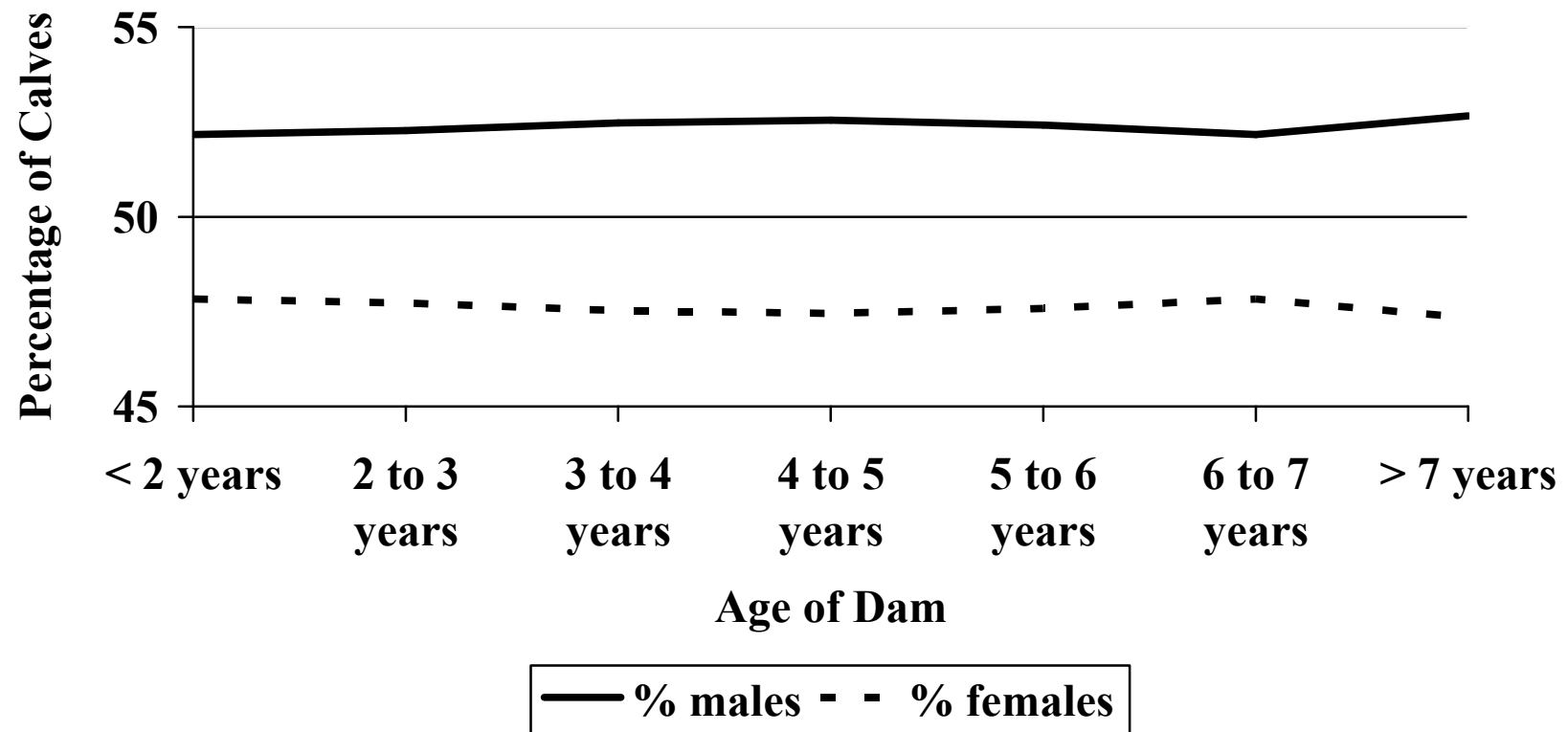


Figure 4. Calving ease data percentage of male versus female calves by age of dam.

Percentage of Male versus Females Calves by Previous Milk Production Level (n=1,847,159)

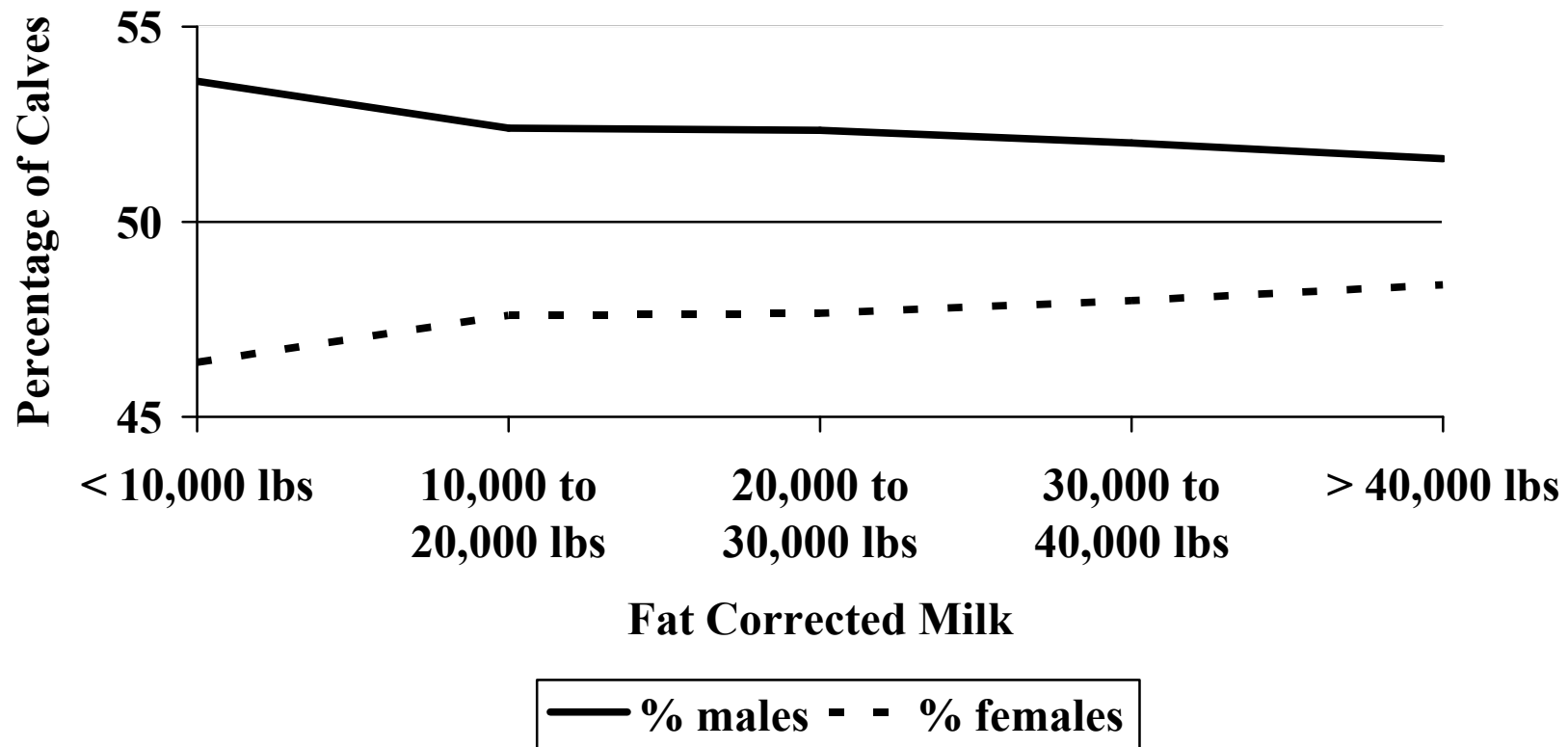


Figure 5. Calving ease data percentage of male versus female calves by fat corrected milk.

Percentage of Male Versus Female Calves by Lactation Number (n=1,847,159)

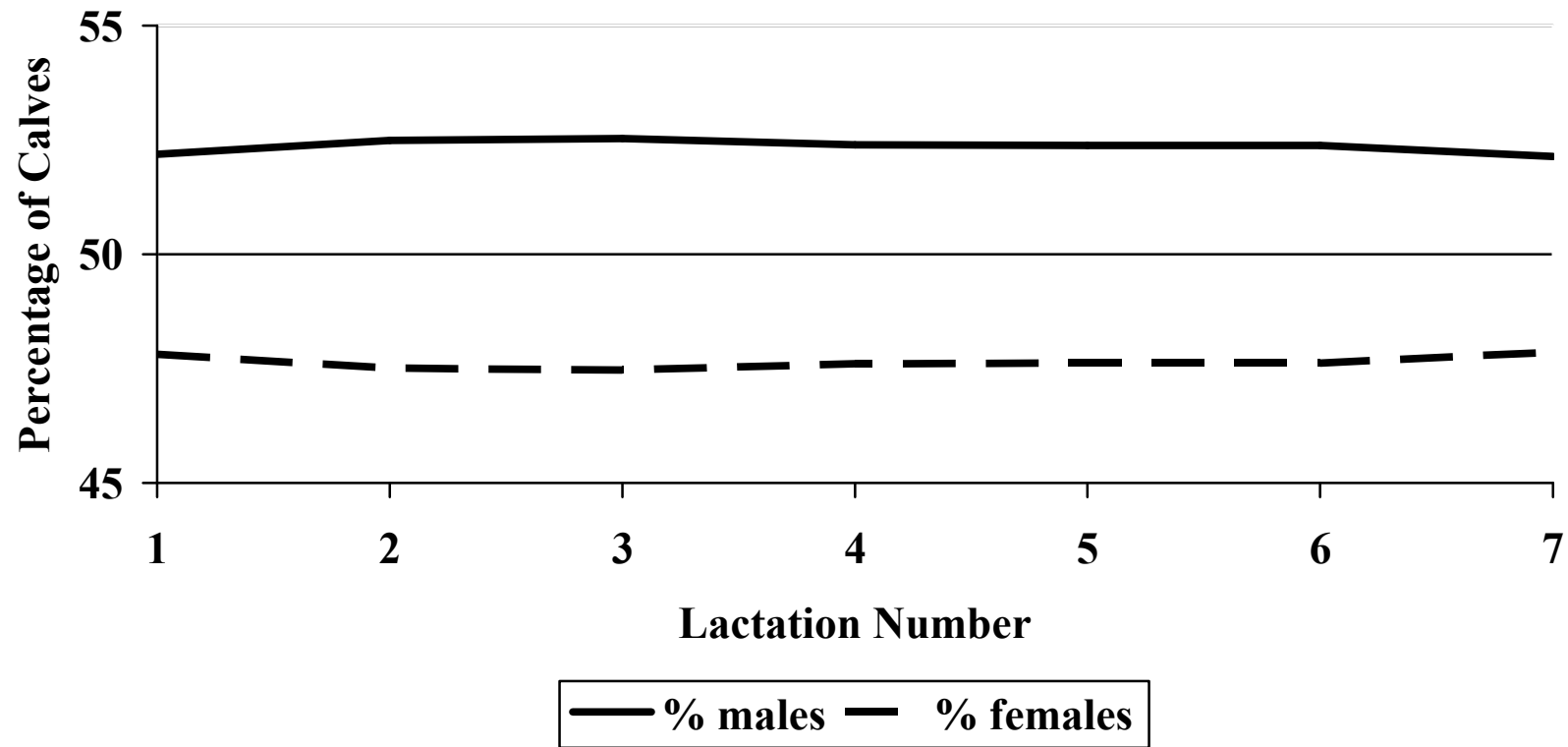


Figure 6. Calving ease data percentage of male versus female calves by lactation number.

Percentage of Male versus Female Calves by Calving Interval (n=1,847,159)

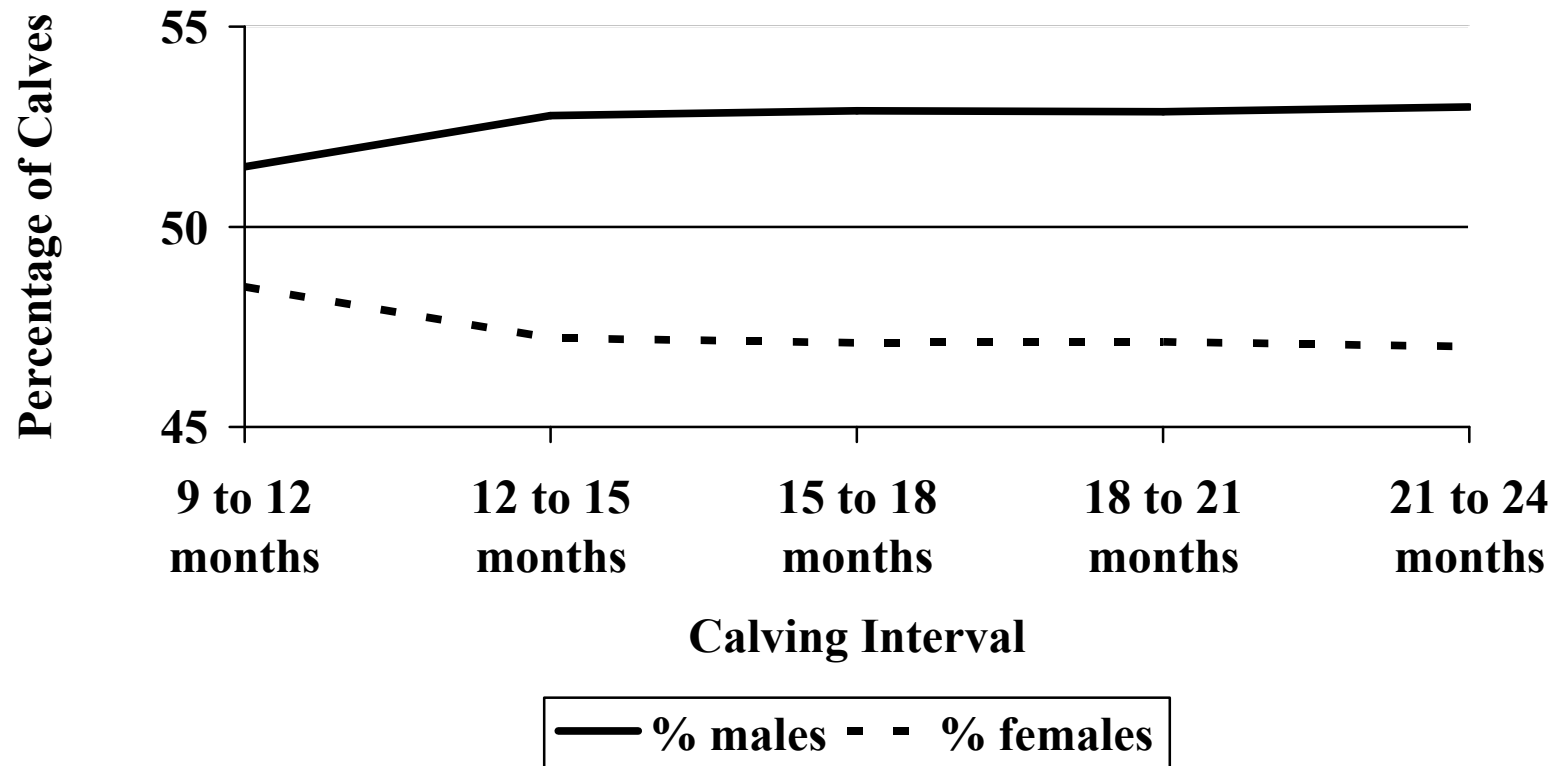


Figure 7. Calving ease data percentage of male versus female calves by calving interval.

Discussion

The current study found that month of calving, previous calf sex, and previous sex of calf were not significant predictors of the sex of the next calf. Other maternal factors, such as previous milk production level, calving interval, age of dam, and lactation number were significant predictors of the sex of the next calf. The results from this study support the Trivers-Willard hypothesis.

Calving interval was a significant predictor of the sex of the next calf. As calving interval increased the probability of a male calf also increased. This is logical, because as more time passes, a dam has more opportunity to replace body reserves that were lost during lactation. These data coincide with the results of the Skjervold and James (1979) study, and supports the Trivers-Willard hypothesis (1973). In the current study productivity level was a significant predictor of the sex of the next calf. This result is in line with the results of the Skjervold and James (1979) study, which looked at the group production level in relation to sex ratio.

Based on the results of these data it appears as if the sex ratio of dairy cattle starts off at equity. However after the first lactation, approximately half of the cows are not returned to the herd for a variety of reasons. Some of these reasons include: failure to re-breed: sold to another herd not participating in the calving difficulty evaluation; or culling from the herd based on past performance. The approximately 50% of cows that are retained and produce another calf have a skewed sex ratio (52.01). At each parity level a certain amount of cows are removed from the production group, and the ones that remain continue to produce a sex ratio skewed toward male calves. Since the sex ratio at each parity level is approximately 50:50

for the current calf, it seems as if cows that have males are removed from the production herd at a higher rate than cows that produce female calves. This phenomenon may be the cost of bearing a male calf. A theoretical depiction of this cost is illustrated in figure 9.

Producers may be inadvertently placing artificial selection pressure on cattle to skew their sex ratio. The results from this study indicate that females that had male calves were removed from the herd in larger numbers than females that had female calves. Cows that bear male calves have a greater risk of culling, because the larger birth weight of males often cause physical damage to the reproductive system during parturition. This results in cows that do not conceive at the expected time, so they are culled. In addition, cows that bore males often return to estrus later than cows that bore females calves, because their bodies must regain the mass that was lost during pregnancy. The artificial selection placed on cattle by producers in conjunction with the innate evolutionary programming may be one reason various sex ratios are seen throughout cattle populations.

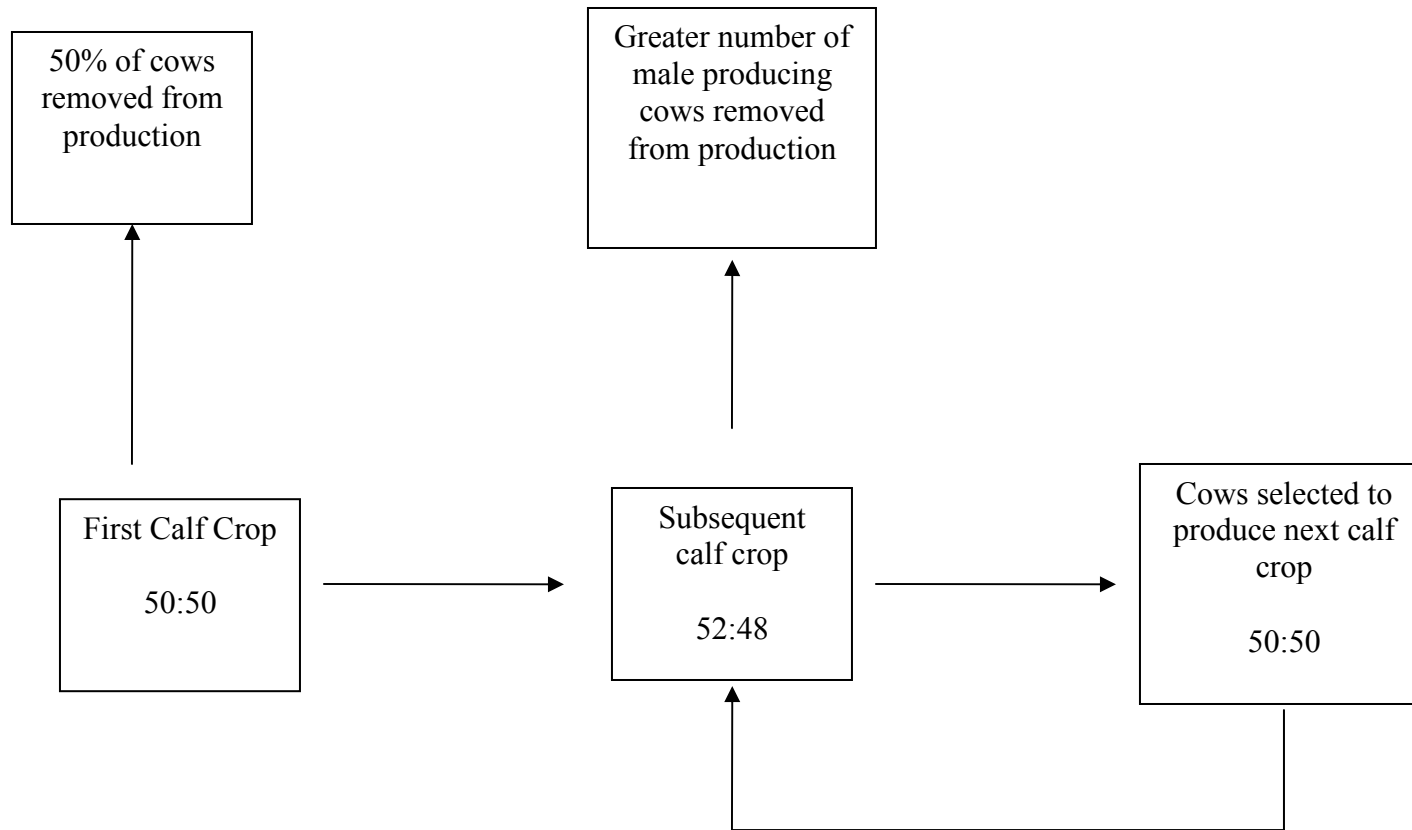


Figure 8. Theoretical depiction of the cost of producing a son.

Conclusions

The results from this study support the validity of the Trivers-Willard hypothesis in dairy cattle. Cows that were more productive had more male offspring. Since productivity can be used as a measure of maternal condition, it is possible that this maternal trait could be used to predict the offspring of domestic cattle. However, because of the interactions of other maternal factors, such as age and parity number that impact production level, care must be taken in using these traits as prediction tools.

The data support the contention that females in better condition produce male offspring and also indicate that domestic animals, in this case dairy cattle, still exhibit genetic effects that result from evolutionary influences – even though artificial selection pressures have occurred. Within domestic animal populations both natural selection and artificial selection are working in concert. The determination of what mechanisms actually underlie the differential sex ratios that result from females of different production capabilities is an important question that needs further consideration.

Chapter 4: Beef Cow Maternal Investment in Adult Daughters after Prolonged Periods of Separation

Abstract

Maternal investment in daughters is known to continue in some species into the daughter's adulthood. The objective of this study was to determine if the dam's presence affects a daughter's ability to compete with a third unrelated beef cow for limited feeding space. Ten mother-daughter pairs and 10 unrelated cows were selected from the USDA Beltsville Agricultural Research Center herd. All cows were individually acclimated to the test pen and a floor-feeding device that had two compartments each with a 5-liter bowl closely positioned and each containing a calf creep feed. Total feeding duration for each cow was measured during an observation. The eating time by dams was not different in the presence of 3 and 5 yr old alien cows. Eating time for daughters was influenced by the unrelated cow's age. Time spent eating by alien cows was related to their age. These results are generally consistent with the benefits of seniority from age in competition bouts. There was no significant difference in feeding time between the daughter and the alien when the two were of similar age. However, when the alien was older, her feeding duration was significantly greater than the daughter's. These results indicate no advantage to the daughters from the presence of their dam. Interestingly in this study, the longer feeding duration of the dam, sometimes in the presence of an older, unrelated cow, may suggest some advantage to the mother while feeding in the presence of her daughter.

Introduction

Maternal investment is defined as maternal care given to an offspring that in some way reduces the mother's fitness (Kathnelson and Hudson, 1998). This investment can be either direct nutritional (for example milk, higher birth weight, etc.) or greater behavioral investment (more attention through closer spatial proximity, grooming, etc.). There has been a plethora of research conducted on both wild and domestic species regarding maternal investment (see dissertation literature review). It has been shown that maternal investment occurs during both the pre and postnatal period. Much of maternal investment research has focused on postnatal investment. In domestic cattle, postnatal investment is primarily seen in the form nutrient transfer via suckling and protection of the calf from predators and menacing herd mates. Another type of postnatal investment that occurs in cattle is the association that is sometimes formed between mother and daughter after weaning. This association aids the younger daughter in access to prime foraging areas, while the mother is protecting her investment for future generations.

In order for domestic cattle to confer care after weaning in current management practices, an ability to recognize kin must be present. The evolutionary basis of kin recognition is that it allows individuals a genetic advantage to confer differential treatment based on relatedness (Hamilton, 1964). Green et al. (1989) found that mother and daughters associated preferentially until the daughter becomes sexually active. These mothers and daughters did not experience any type of separation. It appeared as if long-term associations benefited daughters because they

were displaced by group members less often than control cows, and were often at the group center when their mothers were present.

Within domestic animals, Hinch et al. (1990) found that when ewes were age 8, and had an older lamb age 2.3, and a younger lamb age 1, the ewes nearest family member was either lamb. Mother-offspring associations were present, but there was no evidence of sibling associations. This leads to the suggestion that the lamb maintains mother-offspring association. Stookey and Gonyou (1998) determined that recognition in pigs is based on familiarity by association when piglets are separated for a prolonged period of time. Pigs that were familiar with each other fought less than unfamiliar pigs.

Environmental condition can affect post-weaning associations. L'Heureux et al. (1995) determined that associations between mothers and their year old offspring occurred in bighorn sheep at high population density, but not at low density. Yearlings only associated with ewes that were lactating. Females that associated with ewes gained from the association in terms of greater mass gain or mass at the end of the summer. The data suggested that prolonged associations are a form of maternal care rather than maternal investment. The difference between these two is that maternal care involves a benefit for the offspring, while the mother does not incur a cost. Maternal investment involves a benefit to the offspring and the mother incurs a cost for these benefits.

In general post weaning association between mothers and female offspring appear to convey benefits to both the mother and the daughter. In typical beef cattle operations, heifers are removed from their mothers after weaning and placed in cohort

groups until their first breeding at the age of two or three years. At this time, daughters are reunited with their mother, if they are still members of the herd. It is during this reunion that post weaning associations may occur between mothers and daughters.

Although there is considerable literature regarding post weaning associations in ungulate species, the study of these associations has not been well documented in beef cattle. Swanson (1988) established that kin recognition occurs in beef cattle; however kin recognition and post weaning associations have not been studied within the constructs of beef production systems. Specifically, it has not been established whether cattle have the ability to recognize one another after a separation of several months.

The aim of this study was to determine if maternal investment in the form of post weaning associations exist in beef cattle after a prolonged separation. As kin recognition increased, it was expected that mothers and daughters would have feeding times that differed from a third unrelated cow when tested with a feeding apparatus that only allowed two individuals to feed simultaneously. The feeding times between the mother and daughter were not expected to differ from one another.

Materials and Methods

Animals

Ten mother- daughter pairs and ten unrelated cows from the USDA - Beltsville Agricultural Research Center (BARC) in Beltsville, MD were used in this experiment in May 2002. The age of the mother ranged from four to five years, while

the average age of the daughters was two to three years. The ten unrelated cows were either three or five years old.

The BARC herd is a fall-calving herd. The study was conducted during the month of May and all cows and heifers were on pasture but in separate breeding groups. Thus, the majority of mothers in this study had been separated from their daughters with little or no direct contact with their daughter since weaning. The cows used in the study were sorted from their respective breeding groups and held in a pasture paddock near the working pens and finishing-experimental pens at the BARC Beef Unit during the three days involved in this experiment. Day 1 involved a familiarization of the cows to the experimental pen and days 2 and 3 were experimental days.

All animals in this study were acclimated to the experimental pen (6 x 12 m) which contained a feeding device designed to limit eating activity to only two individuals at a time. The feeding apparatus was a wooden structure that contained two adjacent 4.7-liter stainless steel bowls. A calf creep feed fed to suckling calves at BARC was placed in each bowl. The calf creep feed used because of its palatability and familiarity to the animals. Acclimation of individual cow was accomplished by allowing each cow to explore the paddock where the trials took place and were removed after they fed from the apparatus for thirty seconds. Timing did not commence until individuals placed their head in the bowl. After all of the animals were acclimated to the apparatus trials were conducted.

Procedures

One mother-daughter pair and one unrelated alien cow were placed in the paddock. A trial consisted of a 5-minute period in which the total time each individual animal ate from a bowl was recorded. When all three cows were present with their heads at the bowl, all three were recorded as eating. Thus, while there were only 2 bowls and the experimental period was 5 minutes, the total eating time for an experimental period could exceed 10 minutes. There were three observers during each trial. Each observer had a stopwatch and was assigned to an individual cow at random. Each mother-daughter dyad was tested twice each day for two consecutive days with a different alien cow each time. The area around the feeder was video taped. Agonistic interactions between all individuals in a trial were also recorded. Alliances were considered to occur when two animals spent more time feeding simultaneously, while excluding third animal. An alliance could also occur if two animals fed from the same bowl in tandem.

Data Analysis

The data obtained from the experiment outlined above were used to determine: 1) if kin recognition occurs in beef cattle; 2) the effect of prolonged separation on the mother-daughter bond in beef cattle; 3) if post weaning associations occur in beef cattle and; 4) maternal assistance feed access occurs. An analysis of variance (SAS) was used to analyze the difference between feeding times of the individuals described in the previous section. A mixed procedure model that included alien age (3 versus 5 yrs), relationship (alien, dam or daughter), and the alien age-by-relationship interaction as fixed effects was used to determine effects of these

variables on the time spent feeding by each animal during observation periods.

Random effects included the mother-daughter pair, the alien cow, the testing block the pairs were assigned to, and the interaction between, the mother-daughter pair, the alien cow, and the block assignment.

Results

In this study, dams ate for a significantly greater amount of time than either daughter or alien cows ($F=14.70$; $P<.05$). The amount of time spent eating was strongly related to the age of the individual. When alien cows were age five they ate for a significantly greater amount of time compared to daughters (Table 12).

However, when the alien cow and the daughter were the same age, there were no differences in the amount of time they spent eating. The age of the alien cow did not influence the amount of time the dam spent eating. On the second day of the study, there was a non significant trend for the occurrence of mother-daughter alliances.

Table 12. Results of timed feeding competition between mother, daughter, and alien cows during a 5-min experimental period with two feeding spaces.

Relationship	Mean Time Spent Eating per Observation (Min)		ANOVA F		
	Alien Age		Alien Age(A)	Relationship (R)	A×R
	3	5	.98	14.70*	1.12
Mother	3.12	3.18			
Daughter	1.49	.94			
Alien	1.69	2.21			

* $P<.05$; ** $P<.01$

Discussion

This study found no advantage to daughters with regard to access to limited feed when their dam was present. The management practices of separating daughters from dams after weaning isolation may account for results found in this study. In order for dam-daughter association to occur after prolonged separation, kin recognition must occur. The work of Swanson (1988) supported the notion that some degree of kin recognition occurs in beef cows. In traditional beef production systems, dams and daughters are separated at about 7 months after calving. This was also true for the animals used in this study. The dam-daughter pairs were maintained in separate groups for approximately one year prior to the experiment. Acclimation time for daughters and dams were purposely omitted from this study to determine if immediate kin recognition and post weaning maternal investment would occur.

Swanson (1988) reported that young daughters (2 years old) are repelled by mothers as a mechanism to protect current calves. In addition, Espmark (1971) found that yearling reindeer were actively driven off by gravid does. Yearlings persisted in maintaining the association with their mothers for up to three months after the birth of a calf. This mechanism may have been used in this study, because calves had been recently weaned from the dams and were within calling distance. Other dams had younger calves that were still nursing and had more motivation to seek out their calves than the food source.

The social structure of cattle also played a role in the results of this study. Typically, mothers and young offspring are the core of a herd. This herd will also include older female offspring, as well as other female maternal relatives. In cattle,

older individuals are dominant to younger individuals and individuals that weigh more are dominant to individuals that weigh less. Reproductive status also affects the social status of individuals in a cattle herd. In this social structure daughters are typically subordinate to their dams, even though the daughter may outweigh the dam.

On the second day of the study there was a trend for mothers and daughters to form alliances while eating, which indicates that mothers may recognize their daughters after a prolonged separation due to management practices. This is an important trend because it means that separation for a long period of time, does not affect the relationship between a mother and daughter. This recognition may come from the imprinting that occurred shortly after the birth of the calf. In several species of ungulates, dams maintain post weaning associations with their adult daughters. These associations benefit daughters, because eventually they will inherit their mother's social rank when she leaves the herd. Post weaning associations can also confer benefits to dams because the dam daughter pair can work in tandem to feed on forage while be vigilant for predatory threats. Although this study did not show significant alliances between dams and daughters, the basis for these alliances was established. The reason that we chose to test only the initial response after prolonged separation was that we contend that the results by Swanson (1988) already document post weaning associations. Specifically, we designed the current study to determine if a brief reunion following a prolonged separation would also result in deference or maternal investment to adult daughters.

Conclusions

Older mothers spend a greater amount of time compared to daughter and alien cows. This trend persisted even when the alien cow was close in age to the mother. Adult daughters did not receive a benefit from the presence of their mother, because daughters had the lowest eating times. The presence of an adult daughter may confer advantages to dam while feeding. When the alien cow was older than the daughter cow, the alien cow ate for a longer period of time. Access to limited feeder space was based almost entirely on age. The non significant trend of mother daughter alliances on the second day of testing provides weak evidence of some kin recognition between the mother daughter pairs. This is because the related pair spent more time eating simultaneously. The second day of testing represents a period where “re-familiarization” between dam and daughter could have occurred, thus one could speculate that had the dams and daughters been together longer, as was the case with Swanson (1988), that there would have been greater advantage shown to daughters. Such an investigation would be worth conducting.

Chapter 5: General Discussion

Three studies were conducted to evaluate maternal investment in domestic cattle. Within beef cattle, age of dam, year of calving, calving interval, and current calf sex were not significant predictors of the sex of the next calf; however calving ease score of the current calf and the birth weight of the current calf were significant predictors of the sex of the next calf. In the second study of dairy cattle, calving interval, lactation number, milk production level, and age of dam were significant predictors of the sex of the next calf. The results of the third study provided weak evidence of post weaning associations between mothers and daughters separated for a prolonged period of time of approximately one year. These results indicate that maternal investment occurs in domestic cattle and differential maternal investment may be given based on the sex of the calf.

Domestic Cattle

Domestication of animals occurred under artificial selection, where man instead of the environment selected specific traits. Cattle are important domestic animals because they provide meat, milk and milk products, and draft power. The cattle that we recognize today were domesticated 8,000 – 10,000 years ago (Epstein and Mason, 1984). Domestic cattle breeds differ in milk and carcass yield; this is the reason we have milk, beef, and dual breeds. The presence of feral cattle herds around the world indicates that cattle can live in a wild state and are not that different from their wild counterparts. Based on this, domestic cattle would be good candidates for ethological study.

Conducting the literature review for this dissertation revealed that domestic animals are not typically used in research in which the goal is to test a biological principle or hypothesis. This is not to say that domestic animals are not used in research. Domestic animals are often the research subjects in experiments designed to test production traits in agriculture and are less often used as subjects in behavioral studies. The lack of research using domestic animals prompted the series of studies covered in this dissertation to determine if biological phenomena exist in domestic cattle. The results indicate that maternal investment does exist in domestic animals and that other biological hypothesis can be tested and validated using domestic cattle as subjects.

Difference between Dairy and Beef Cattle

The dairy cattle data had several maternal factors that were significant in predicting offspring sex, while the beef data had only two maternal factors that were significant. Within the beef cattle data there was a significant trend ($P=.05$) that as calving ease score increased and the birth weight of the current calf increased, the sex of the next calf was more likely to be a female. Dairy and beef cattle are the same species of animal (*Bos taurus*) and readily interbreed. Dairy cattle have been selected to produce large amounts of milk, while beef cattle have been selected for a high carcass yield. This is one example of the differences between dairy and beef cattle.

Within the literature there are contradictory reports of findings within the same species. Data from Shaw and Carter (1989) who studied American Bison in Wichita Mountains Wildlife Refuge, southwestern Oklahoma did not support the Trivers-Willard hypothesis. Their study showed that lactating females produced

more females than males; however non-lactating females did not produce more males as suggested by Rutberg (1986). Rutberg theorized that non-lactating females were in better condition, and thus should produce a greater proportion of male offspring. In addition, the group of animals studied by Shaw and Carter did not exhibit a strategy of being barren in alternate years as predicted by Rutberg. There is no clear explanation for the contradictory results of these two studies; however each of these studies had different methodologies. Shaw and Carter observed the sex of the calf born each season in relation to lactational status, while Rutberg observed the sex of the fetus of culled bison in relation to their lactational status. The different modes of collecting the data may explain the different results that were obtained in these studies.

There are inherent difference between dairy and beef cattle. The first difference is the way they are managed. Dairy cattle are more intensively managed compared to beef cattle. In addition, dairy cattle are slightly more sexually dimorphic than beef cattle. This means that the differences in adult weights and build between males and females are greater in dairy cattle than beef cattle. Although differences exist between dairy and beef cattle, these differences are small. Further investigation of maternal investment in beef cattle is warranted, since a limited number of maternal factors showed significance in predicting the sex of the next calf.

Trivers-Willard Hypothesis and Domestic Cattle

Trivers and Willard (1973) proposed females could increase their fitness by producing male offspring when conditions are conducive and female offspring when conditions are not conducive. This system would lead to differential maternal

investment based on the sex of the offspring. Even in animal populations where there are no apparent skews in the sex ratios of offspring, there are differences in the birth and weaning weights of males and female offspring. Typically males are born heavier and weaned later than their female counterparts. This suggests that differential maternal investment is occurring. This type of maternal investment appears to occur in domestic cattle, because male calves typically weigh five percent more than their female counterparts. This trend continues though weaning and into adulthood.

Based on the results of the first study, age of dam, year of calving, calving interval, and current calf sex were not significant predictors of the sex of the next calf in beef cattle. Calving ease score of the current calf and birth weight of the current calf sex were significant predictors of offspring sex. There was limited support of differential maternal investment based on the sex of the calf in beef cattle. The Trivers-Willard hypothesis was not definitely supported by the results of this study. Several studies that have investigated age of dam, previous reproductive effort, and time of season have also shown that these factors are not significant predictors of the sex of the calf (Table 13).

Table 13. Summary of research testing the Trivers-Willard hypothesis with non-significant results.

Variable	Research Study	Species
Dam age	Kojola and Eloranta (1989); Meikle et al. (1993)	Reindeer; Domestic pigs
Previous reproductive effort	Shaw and Carter (1989); Green and Rothstein (1991); Cameron et al. (1999); Côté and Festa-Bianchet (2001)	American Bison; Kaimanawa Horses; Mountain goats
Time of season	Wolff (1988); Lindström et al. (2002)	American Bison; Soay sheep

There appeared to be evidence of differential maternal investment based on the sex of the offspring in dairy cattle. As calving interval and lactation number increased, the probability of the next calf being male increased. This is in agreement with the predictions of the Trivers-Willard hypothesis. As milk production level and age of dam increased the probability of the next calf being a male decreased. These results also support the Trivers-Willard hypothesis. Differential maternal investment based on the sex of the calf was shown in domestic dairy cattle in this study. The results from this study also support research in the literature. Dam age, previous reproductive effort, such as calving interval, and parity (lactation number was used as an indicator of parity in this study) have been found to be significant predictors of the sex of the offspring (Table 14).

Table 14. Summary of research testing the Trivers-Willard hypothesis with significant results.

Variable	Research Study	Species
Dam age	Skjervold (1979); Green and Rothstein (1991); Côté and Festa-Bianchet (2001)	Domestic sheep; American Bison; Mountain goats
Previous reproductive effort	Wolff (1988); Kojola and Eloranta (1989)	American Bison; Reindeer
Parity	Wauters et al. (1995)	Roe deer

Although the Trivers-Willard hypothesis does not make predictions for maternal investment after weaning, it would seem that associations between offspring and mothers after weaning are an aspect of maternal investment. The results from the third study did not support the presence of post weaning associations after a prolonged separation of mother and daughter pairs in beef cattle. On the second day of the study there was a non-significant trend for mothers and daughter to

spend more time eating together. Green et al. (1989) found that daughters benefited from post weaning associations with their mothers until the age of three years. In addition, Swanson (1988) found that mother and adult daughter domestic cattle maintained associations. If the mother daughter pairs were observed for a longer period of time after their reunion, the results of this study may have been different.

As demonstrated in the literature review of this dissertation, mothers of several species of ungulates display differential maternal investment based on the sex of their offspring. Typically mothers that are in better physical condition or have better social status tend to produce a larger proportion of male offspring. Many of these studies have produced results that validate the Trivers-Willard hypothesis. The data from domestic cattle also lend support to this hypothesis.

Limitations and Future Research

The results from the studies conducted in this dissertation brought to light several limitations of the experiments. One limitation of these experiments was that the maternal factors measured in the first study of beef cattle were not identical to the maternal factors measured in the second study of dairy cattle. The results of the beef cattle study did not support the Trivers-Willard hypothesis, while dairy cattle data did support the Trivers-Willard hypothesis. The same exact traits need to be measured and used as predictors of the sex of the next calf to truly determine if there are differences between dairy and beef cattle. Another limitation of these experiments was the number of individuals used in the third study. In order to determine if post weaning associations between mothers and daughters are maintained over prolonged

periods of separation, a group of more than ten mother-daughter pairs should be investigated.

Another limitation of these studies originates from the hypothesis that was being tested. The Trivers-Willard hypothesis has been tested in a variety of species for more than thirty years. In that time, weak evidence has shown a positive correlation between maternal condition and sex ratio in ungulates (Sheldon and West, 2004). One of the problems with the Trivers-Willard hypothesis is the use of terms “good condition” and “poor condition”. These terms are subjective and are often difficult to quantify in an empirical study. Sheldon and West (2004) found stronger evidence of a relationship between maternal condition and sex ratios when dominance status was used as a measure. Grant (2003) proposed that social dominance be used instead, since condition often indicates dominance status. The interrelationships of maternal hormones, particularly testosterone, and social dominance on sex ratios would be an interesting study to conduct in cattle. It has been shown that dominance and serum testosterone level are correlated (Grant, 2003) and dominant red deer produce a greater proportion of male calves (Clutton-Brock et al., 1984 and 1986).

Although Trivers and Willard (1973) suggested the differences in sex ratios were caused by differential mortality of embryos, a mechanism for this has yet to be discovered. One area of focus for future sex ratio research would be possible mechanisms responsible for skewing sex ratios. These mechanisms can be placed into one of two categories: actions that occur prior to conception; and actions that occur after conception. Recently, circulating glucose levels has been suggested as a possible mechanism of sex ratio variation (Cameron, 2004). A measure of circulating

glucose levels around the time of conception in relation to the sex of the calf that is subsequently born would be another study that needs further investigation based on the finding of the studies conducted in this dissertation.

In addition, a more extensive study of the same traits that were looked at in dairy cattle should be applied to beef cattle. Although dairy cattle and beef cattle belong to the same species and are capable of interbreeding, the results from the two studies conducted in this dissertation yielded different results. The study on the beef cattle did not support the Trivers-Willard hypothesis, but the hypothesis was supported in the dairy cattle populations. The number of dairy cattle analyzed was significantly greater than the number of beef cattle and was more representative of dairy cattle. A study akin to the one performed on the AIPL calving ease database is warranted. This could be accomplished by using dystocia data from either the United States Meat Animal Research Center (US MARC), Clay Center, Nebraska or Fort Keogh Livestock and Range Research Laboratory, Miles City, Montana.

Conclusions

The first two studies in this dissertation focused on several maternal factors in relation to the sex of the offspring. Within beef cattle, age of dam, year of calving, calving interval, and current calf sex were not significant predictors of the sex of the next calf. Calving ease score of the current calf and birth weight of the current calf were significant in predicting the sex of the next calf. As both of these factors increased the probability of the next calf being male decreased. The beef cattle studied in this dissertation did not appear to invest differential in their offspring based on the sex of the calf. Based on this, the data from the study of beef cattle did not support the Trivers-Willard hypothesis.

Within the dairy cattle, there appeared to be evidence of differential maternal investment based on the sex of the offspring. As calving interval and lactation number increased the probability of the next calf being male increased. As milk production level and age of dam increased the probability of the next calf being a male decreased. These results support the Trivers-Willard hypothesis in dairy cattle. The domestic dairy cattle in this study displayed differential maternal investment based on the sex of the calf.

The third study of this dissertation focused on post weaning associations in beef cattle. The results provided limited evidence of post weaning associations between mothers and daughters separated for a prolonged period of time. Within mother-daughter pairs, mothers appeared to have an advantage in having a younger daughter around. These mothers could have possibly been recouping some of the fitness lost while rearing the daughter. The lack of immediate post weaning

associations indicate that maternal investment may not be extended if mothers and daughters are separated for a lengthy period of time.

Maternal investment is a phenomenon that exists within domestic cattle in varying degrees. Although cattle have been under the influence of domestication for several thousands of years, they still exhibit evolutionary influences. Both natural selection and artificial selection are working in concert within domestic cattle populations. Domestic cattle may differ from their wild counterparts in some ways; however, the presence of significant results that validate a biological hypothesis indicates that domestic cattle are valuable in the study of ethological principals.

Glossary

Artificial Insemination (AI) – the technique of placing semen from the male into the reproductive tract of the female by means other than natural service

Culling – the practice of eliminating less productive or less desirable cattle from a herd

Embryo transfer – the removal of fertilized ova (embryos) from one cow (donor dam) and placing these embryos into other cows (recipient cows), usually accompanied by hormone-induced super ovulation of the donor dam

Evolutionary Stable Strategy – a strategy when incorporated by an entire population creates an equilibrium where any possible mutation of the strategy can not improve an individual's outcome

Maternal Care – an increase in offspring fitness without cost to the mother

Maternal Effects – the environmental influence of a dam on the phenotype of the offspring

Maternal Investment - maternal care that reduces a mother's fitness

Microsatellite DNA - repetitive stretches of short sequences of DNA used as genetic markers to track inheritance in families

mtDNA – mitochondrial DNA; DNA that is found in the mitochondria organelle that is passed from mother to offspring

PTA – predicted transmitted ability; the best estimate of an animal's inferiority or superiority

Sex Ratio – the proportion of males to females in a population

Trivers-Willard Hypothesis – based on their 1973 paper; the idea that females in better condition will produce more male offspring

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