University of Alberta

GENDER-BIASED MATERNAL INVESTMENT IN WAPITI (*Cervus elaphus*)

by

SANDRA LYNNE KATHNELSON ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

DEPARTMENT OF RENEWABLE RESOURCES

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The undersigned certify that they have read and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Gender-Biased Maternal Investment in Wapiti (*Cervus elaphus*)** submitted by SANDRA LYNNE KATHNELSON in partial fulfillment of the requirements for the degree of Master of Science.

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DEDICATION

Early on, my interest in nature and science was nurtured and developed by two very special people, both respected scientists in their fields.

My late grand-father, Edwin G. Swenson, first introduced me to the joys of walking quietly through forests, observing animals; I carried his memory with me throughout my work in the field. I know he would be pleased at the completion of this degree, although he would feel it necessary to remind me (one more time!) that 'a university education does not make a person better than anyone else'...Grampa, I will remember this.

My father, Jerry Kathnelson, guided me through my first effort at scientific research when he helped me to conduct an experiment for a grade eight science fair. He continues to lend support, both moral and technical, and is my favorite and most respected editor. He has seen me through my undergraduate and now my master's degree, and I know I will always be able to go to him for help and advice.

This work is dedicated to both my grand-father and my father, and a great part of it belongs to them.

ABSTRACT

Gender-biased maternal investment may be an adaptive strategy in species where reproductive success is more variable in one gender, and may be influenced by maternal investment. In this study, patterns of maternal investment were examined in a herd of captive wapiti, *Cervus elaphus*, to determine whether mothers were biasing investment towards male offspring, as would be predicted by theories of parental investment.

In captive wapiti, sex ratios were skewed towards males. Wapiti mothers appeared to modify sex ratios in relation to their ability to invest; mothers in good body condition, as compared to others in their age class, produced more males than females, while mothers in poor condition produced equal numbers of each gender. Wapiti mothers also allocated more resources to individual male than to individual female offspring. Birth weights of males exceeded birth weights of females, and gestation lengths appeared to be longer for male than for female calves. Nursing bouts between mothers and sons were longer than bouts between mothers and daughters, indicating that mothers allowed male calves to obtain more milk. Some preference was also shown towards males with respect to measures of maternal care.

Costs of reproduction were examined, to determine if the increased expenditure on male offspring translated into higher costs for their mothers. No differences were found in terms of female weight changes during lactation or interbirth intervals between mothers of males and females. However, mothers of males did spend more time grazing than mothers of females. This would appear to be a form of compensation for their increased investment in male calves.

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And most important, thanks from the bottom of my heart to the little clan who are my 'home'. That I have made it through the past three years, while managing to stay relatively sane, is a tribute to the patience, tolerance and great sense of humour of a very special person, Todd Ree. He has been as committed to my project as I have, offering love and help along the way. Last, but in no way least, thanks to two wonderful creatures, Murphy & Bentley, whose unconditional love (not to mention hilarious antics) remind me daily of why I enjoy studying animal behaviour.

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1.0 Introduction

To contribute genes to future generations, parents must successfully raise offspring which will in turn reproduce successfully. Parental investment may be defined as any action by which a parent increases the likelihood of survival of a current offspring at the expense of the parent's ability to invest further in future offspring (Trivers 1972). Investment theory addresses the problem of how parents should invest in offspring in order to maximize their own lifetime reproductive success. In species where the investment of fathers is limited to the contribution of gametes and mothers provide all post-natal care, maternal rather than parental investment may be considered.

Much of investment theory has dealt with the role of offspring gender in determining investment strategies. Fisher (1930) argued that the only stable strategy involves average parents making equal investments in their male and female offspring. This would result in an even sex ratio if sons and daughters cost the same to raise, or a sex ratio skewed towards the least expensive gender. Although Fisher's model of equal investment in the genders has received support (Williams 1979, Metcalf 1980, Le Boeuf et al. 1989, Kretzmann et al. 1993, Smiseth and Lorentsen 1995), there have been many cases of deviation from equal investment (Clutton-Brock et al. 1981, Kovacs and Lavigne 1986a, Trillmich 1986, Silk 1988, Kojola and Eloranta 1989).

The idea that gender-biased investment could be an adaptive strategy was first put forward by Trivers and Willard (1973). They proposed that if variance in reproductive success was greater in one gender, and could be affected by parental investment, parents able to make a large investment should bias production towards that gender. This model is particularly applicable to polygynous mammals, where a male's reproductive success often depends upon his ability to compete for females (Geist 1971, Clutton-Brock et al. 1982) and variance in reproductive success is generally considerably higher in males than in females (Trivers 1972, Krebs and Davies 1987, Clutton-Brock 1988, but see Hrdy and Williams 1983). In these circumstances it is likely that an increase in body condition will more strongly influence the reproductive success of males, by making them better competitors, than it will the reproductive success of females. Given these effects, a mother in good condition (able to invest a large amount) would leave more grandchildren by producing a son than by producing a daughter. Similarly, the best strategy for a mother in poor condition (able to invest only a small amount) would be to produce a daughter, since a female's reproductive success will not be as adversely affected by this decrease in condition (Trivers and Willard 1973). In some species, for example when daughters share maternal home ranges, mothers are better able to influence the reproductive success of daughters than that of sons (Verme 1969, Simpson and Simpson 1982, Silk 1988, Lloyd and Rasa 1989, Green and Rothstein 1991). In these cases mothers able to make large investments would be predicted to invest more in their daughters than in their sons.

Evidence for the Trivers and Willard model of gender-biased investment would take the form of adaptive modification of offspring sex ratios (without the associated higher cost of the lower–frequency gender predicted by Fisher's theory of equal investment). Mothers able to make large investments would be predicted to bias production towards the gender which will benefit the most from this investment (Silk

1988), which in the case of many polygynous mammals is the male. Several factors have the potential to affect a mother's ability to invest in her offspring. Maternal body condition and size often are positively correlated with offspring size and survival (Reiter et al. 1981, Clutton-Brock et al. 1982, Le Boeuf and Reiter 1988). Sex ratios vary in the predicted direction with maternal condition in mice, *Mus musculus* (Rivers and Crawford 1974), hamsters, *Mesocricetus auratus* (Labov et al. 1986), mule deer, *Odocoileus hemionus* (Robinette et al. 1957) and roe deer, *Capreolus capreolus* (Wauters et al. 1995) and with maternal size in southern elephant seals, *Mirounga leonina* (Arnbom et al. 1994). A female's access to valuable resources may be determined to some degree by her social status; dominant females may be in better condition than their subordinates and thus be able to invest more in offspring. High-ranking females bias production of offspring towards the preferred gender (the one which benefits most from the mother's high rank) in red deer, *Cervus elaphus* (Clutton-Brock et al. 1984), rhesus monkeys, *Macaca mulatta* (Simpson and Simpson 1982, Meikle et al. 1984, Gomendio 1990) and pigs, *Sus scrofa* (Meikle et al. 1993, but see Mendl et al. 1995). Maternal age may also affect the ability to invest in offspring. Because female condition may be highest in prime-aged animals, and subsequently decrease with age (Clutton-Brock 1991), there may be a corresponding decrease in the ability of aging mothers to invest in offspring. However, the theory of terminal investment (Clutton-Brock et al. 1982) predicts that very old mothers should invest large proportions of their resources in offspring, since they have fewer potential reproductive opportunities remaining, thereby reducing the cost of reproduction in terms of future fecundity (Trivers 1974). The idea of terminal investment is supported by studies of maternal investment in bison, *Bison bison* (Green 1986) and California gulls, *Larus californicus* (Pugesek 1983). Older mothers produce a greater proportion of males in caribou, *Rangifer tarandus* (Thomas et al. 1989) and roe deer (Wauters et al. 1995). The effects of age may be confounded by the effects of maternal experience. Breeding performance improves with experience in Antarctic fulmars, *Fulmarus glacialoides* (Weimerskirch 1990) whereas past experience increases certain aspects of parental care in convict cichlid fish, *Cichlasoma nigrofasciatum* (Lavery 1995). An additional factor affecting a female's ability to invest is her previous year's reproductive effort, since this may impact on her current condition. There is a tendency for females who are barren one year to produce predominantly male offspring the next in bison (Rutberg 1986) as well as red deer (Darling 1937). In addition, female bighorn sheep, *Ovis canadensis*, rarely produce males in consecutive years (Festa-Bianchet 1989).

There is an alternative form of gender-biased maternal investment. Rather than modify offspring sex ratios according to their ability to invest, mothers may invest more in individual offspring of the preferred gender (Reiter et al. 1978, Maynard Smith 1980). To ensure that sons develop into successfully reproducing adults, mothers may be required to invest more in each of their male calves than they do in their female calves, since daughters receiving only an average amount of maternal care will be likely to reproduce successfully. The converse would be true in species where females benefit more than males from increased maternal investment.

Gender-biased investment according to the Maynard Smith (1980) model could be demonstrated by showing that mothers allocate more resources to offspring of one gender.

Mothers invest in offspring both during gestation and in the period from parturition through until weaning. Components of pre-natal investment include birth weight and length of gestation, while post-natal investment can be gauged by calf weight gains, weaning dates, milk transfer from mother to offspring, as well as certain aspects of maternal behaviour.

Evidence of male-biased pre-natal investment has been found in several polygynous species. There are longer gestation periods for male than for female offspring in red deer (Clutton-Brock et al. 1982) and horses, *Equus caballus* (Berger 1986). Birth weights of males exceed those of females in Galapagos fur seals, *Arctocephalus galapagoensis* (Trillmich 1986), grey seals, *Halichoerus grypus* (Kovacs and Lavigne 1986a, 1986b, Anderson and Fedak 1987, Smiseth and Lorentsen 1995), southern elephant seals (McCann et al. 1989, Arnbom et al. 1994), northern elephant seals, *Mirounga angustirostris* (Reiter et al. 1978), otariids (Otariidae) and walruses (Odobenidae) (Kovacs and Lavigne 1992), red deer (Clutton-Brock et al. 1982), wapiti, *Cervus elaphus* (Johnson 1951), fallow deer, *Dama dama* (Braza et al. 1988), black-tailed deer, *Odocoileus hemionus columbianus* (Mueller and Saldleir 1980) and Rocky Mountain bighorn sheep (Hogg et al. 1992). Others, however, have failed to detect this difference (Byers and Moodie 1990, Bowen et al. 1992).

Measures of post-natal investment which have supported higher investment in male offspring were growth rates (red deer: Blaxter and Hamilton 1980, phocid seals (Phocidae): Kovacs and Lavigne 1986a, grey seals: Kovacs and Lavigne 1986b, Anderson and Fedak 1987, otariid seals and walruses: Kovacs and Lavigne 1992), milk intake (red deer: Clutton-Brock et al. 1982, horses: Duncan et al. 1984, African elephants, *Loxodonta africana*: Lee and Moss 1986, Galapagos fur seals: Trillmich 1986, bison: Wolff 1988, Rocky Mountain bighorn sheep: Hogg et al. 1992, but see Festa-Bianchet 1988a, McCann et al. 1989, Byers and Moodie 1990, Kretzmann et al. 1993), and weaning dates (northern elephant seals: Reiter et al. 1978, zebu cattle, *Bos indicus*: Reinhardt and Reinhardt 1981). Certain behavioural indices may be used as indicators of maternal care, since they may demonstrate a mother's preferential treatment of offspring of one gender (Smiseth and Lorentsen 1995). Investment through maternal care is essential; poor maternal care has been linked to decreased offspring survival and increased predation (Hewson and Verkaik 1981, Ozoga and Verme 1986). Gender-biased maternal care occurs in sheep (Festa-Bianchet 1988a) and grey seals (Smiseth and Lorentsen 1995).

Central to the study of maternal investment is the idea of reproductive costs. Investment, by definition (Trivers 1972), implies a cost to the mother in terms of either future survival or fecundity. There are a number of ways by which the cost to a mother of rearing an offspring can be assessed, including direct measurement of her subsequent survival and her reproductive success in the following breeding attempt. Red deer females who raise male calves are less likely to survive the next winter than those raising female calves (Clutton-Brock 1991), and when they survive are more likely to be barren the following year (Clutton-Brock et al. 1981). Similarly, bison females who raised sons displayed reduced reproductive performance in the following year (Wolff 1988). Reproductive costs may also be assessed by measuring factors which could indirectly affect a female's survival and fecundity, for example her weight loss over the period of offspring dependence. Reindeer, *Rangifer tarandus*, mothers raising sons lose more weight during lactation than those raising daughters (Kojola and Eloranta 1989). Reproductive costs have also been measured using interbirth intervals, or the length of time between births of successive offspring. Longer interbirth intervals following male offspring have been reported for African elephants (Lee and Moss 1986).

Wapiti refers to a group of subspecies of *Cervus elaphus*. Like the red deer, which has been the focus of much research relating to maternal investment (Clutton-Brock et al. 1982), the wapiti is a sexually dimorphic, polygynous ungulate. Red deer satisfy the three main assumptions of the models of gender-biased investment. In farmed red deer, the weight of a female at the time of conception is correlated with her offspring's weight at the end of the period of maternal investment (Blaxter and Hamilton 1980), satisfying the assumption that maternal condition affects juvenile condition (Trivers and Willard 1973). Differences in juvenile condition persist into adulthood, since early growth affects adult dominance in farmed red deer stags (Suttie 1983). The third assumption, that variance in reproductive success is higher for males, has been verified in a population of wild red deer (Clutton-Brock et al. 1982). The same assumption may be valid for farmed populations, where only a few 'high quality' males do the majority of the breeding, while all females breed. Because of the similarities between red deer and wapiti in their ecology and social structure it is reasonable to assume that wapiti also meet these assumptions. Female red deer invest preferentially in male offspring (Clutton-Brock et al. 1982, Clutton-Brock et al. 1984); it is therefore worth investigating whether the same is true of female wapiti.

The objective of this study is to investigate patterns of maternal investment in wapiti, and to determine whether females invest more in their male offspring, either by the adaptive modification of sex ratios (Trivers and Willard 1973) or through the allocation of more resources to male than to female offspring (Maynard Smith 1980). The costs of reproduction will also be examined, since drawing conclusions relating to patterns of maternal investment may only be meaningful if that investment entails a cost in terms of future fecundity or survival. There is still a great deal of controversy surrounding the study of maternal investment, partly because of the often contradictory results obtained by different studies of the same species. Researchers have cautioned against short-term studies investigating maternal investment (Green and Berger 1990) and called for more long-term work which would span the reproductive life-span of individuals. The opportunity for such work is afforded by the existence of long-term (1977-1993) records of weight and reproductive performance of the herd of farmed wapiti at the Ministik Wildlife Research Station. The fact that this herd is captive allows for close observation of individuals and the measurement of many parameters not readily obtainable from wild populations. Indeed, captive groups may provide the best opportunity for the study of maternal investment (Small and Smith 1984).

To achieve the objectives stated above a dual approach was adopted, combining the use of long-term records kept at the Ministik station, supplemented by research conducted there during the 1994 calving season. The long-term records were used to answer questions relating to sex ratios and measures of pre-natal investment (length of gestation, birth weights), as well as to address the issue of reproductive costs. Patterns of post-natal investment were investigated using behavioural observations to study nursing behaviour and other aspects of maternal care.

2.0 Methods

2.1 Study area, animals and management practices

This study was conducted at the Ministik Wildlife Research Station at the University of Alberta. The station is situated 52 km southeast of Edmonton, Alberta, Canada, on aspen parkland range. A research herd of wapiti, ranging in size from 8 to over 70 animals, has been managed at the station since 1977. With the exception of some males acquired over the years as breeding stock, the herd has descended from animals obtained from the Sybille Research Station in Wyoming and the YaHa Tinda Ranch near Banff, Alberta in 1976. In 1994, the last year of the study the herd consisted of 35 adult female wapiti (hinds) and 3 breeding males (stags), as well as 6 two-year-old females (jinnocks) and 8 yearling females.

Animals are free-ranging on a series of pastures with a total area of approximately 65 ha, and are supplementally fed when range conditions deteriorate at the end of summer as well as throughout the winter. Thus, the condition of the Ministik herd may be better than that of a wild population, since they are not subject to the same nutritional stress which wild populations may experience in the winter. As in the wild, calving begins in late May and peaks in early June, although some calves are born in July and occasionally as late as August. While most hinds give birth unassisted, staff will intervene after prolonged periods of labour, or when the position of the calf precludes normal delivery. Consequently, mortality rates due to calving difficulty may be lower than in wild populations. In the wild, hinds may continue to associate with their calves until they give birth again (Altmann 1963), although milk production begins to decrease in September (Bubenik 1982). At Ministik weaning occurs (calves and mothers are separated) in September, to allow hinds to recover some condition before breeding, and also to allow calves some time to recover from the stress of weaning before being shipped to sale (usually in November). During the breeding season, from mid-September through to late December, one stag is placed with each breeding group of between 10 and 20 females. All females are exposed to stags at the same time. Each year all male calves along with a portion of the remainder of the herd are sold at auction. The purpose of the cull is to keep the number of animals at the facility down to the level dictated by available pasture. In the past, the herd has been managed with an emphasis on natural conditions, and non-breeding animals were not removed (Hudson et al. 1991). More recently there has been a trend towards increasing production; very recent removals from the herd may have been biased towards animals with poor breeding performance. Animals are handled on a regular basis to weigh them and administer routine veterinary treatment. This is facilitated by a series of corrals and corridors leading to a weigh cell and a restraining cell, which is used when close contact with an animal is required. Exceptions to routine management practices described above may occur when certain animals are used in research trials; animals managed in ways which would affect their suitability for this study were not used for data collection.

Data analyzed for the purposes of this study were obtained from records of weights and reproductive performance at Ministik from 1977 to 1994. All behavioural data were collected between May and September 1994.

2.2 Records of reproductive performance

Between 1978 and 1994, there were approximately 315 live calves (including one set of twins) born at Ministik to 65 individual hinds. Birth dates for most calves born at Ministik are known, since hinds are checked regularly during the calving season. The timing of those calving events not directly observed could often be estimated quite accurately using the date the hind was last checked, behaviour of the hind (both pre- and post-parturient) as well as neonate behaviour and appearance. Thus, birth dates are generally accurate to within 1-2 days, and any errors in estimation should not bias the data in one direction.

Approximately 24 hours after birth, calves are handled to determine gender and obtain weights. Thus what will be referred to as 'birth weights' in the data set are actually weights measured at 24 hours. The delay in obtaining the first calf weight minimizes disturbance immediately following parturition which could jeopardize mother-offspring bonding. Weights are obtained by placing calves in slings and suspending them from a scale suspended from a tree. Some calves were not caught and weighed until they were older than 24 hours; if a weight could be obtained within ten days of birth, birth weight was calculated using the equation

$$Y = 0.9975 + 0.0555X$$

where Y is multiple of birth weight and X is age in days. This equation was used by Hudson et al. (1991) to describe the relationship between birth weight and weight of calves up to ten days of age. Birth weights have been omitted from the data set for any calves which were not weighed by the age of ten days. From calving through to weaning, calves and their mothers are weighed every 1-2 weeks. Throughout the remainder of the year, all animals are weighed monthly.

2.3 Condition

Commonly used measures of an animal's body condition include body fat (eg. subcutaneous back fat, femur marrow fat, kidney fat), body condition scores, body size and body weight (Thomas et al. 1989, Chan-McLeod et al. 1995). Body weight was chosen for use in this study as an index of body condition, since for ungulates the two are usually correlated within gender and age classes (Adamczewski 1993). In addition, it is easily obtainable from live animals (unlike many measures of body fat) and is an objective measure needing no prior experience to measure (unlike body condition scores). There is a potential drawback to this method in that it does not take into account an animal's body size. An individual's current condition, however, may not be accurately represented by measures of body size such as shoulder height and jawbone length, since skeletal development likely occurred under different environmental conditions (Downing 1980). In red deer, a mother's body weight is more important in predicting calf birth weight than the skeletal size (Clutton-Brock et al. 1982), while in roe deer, body weight, not size, affects fertility and sex ratio (Wauters et al. 1995). Thus body weight may be the most appropriate measure of condition in studies of maternal investment in ungulates.

The condition of a female at the time of conception will likely affect her ability to invest in her offspring, therefore a female's condition at this time should be considered important with respect to maternal investment. The weight used to assess the condition of a hind was calculated as the average of all weights recorded for her during the rutting season (September, October and November) in a given year. Since weights may be correlated with condition only within age classes, females were placed into condition classes by comparing their average rut weight to that of other animals in the same age class (2, 3, 4-6, 7-9, 10-12, >13 years). In addition to being compared to each other, females were also compared to themselves in other reproductive years. Any hind who bred successfully more than once was assigned to a condition class for each reproductive effort, relative to herself in each of her other reproductive years. Maternal condition at the time of conception was then related to the gender of the offspring.

2.4 Reproductive costs and plane of nutrition

It is likely that the costs of reproduction may only be evident under certain (stressed) ecological conditions (Boyce & Perrins 1987). The normal management practice of supplemental feeding at Ministik allows most females to maintain high levels of condition, thus reproductive costs to females may not be apparent. It was desirable, for the purposes of this study, to produce some variation in female condition during the period of post-natal maternal investment. Plane of nutrition of breeding hinds was manipulated as follows. In May 1994, just prior to calving, hinds were divided into two treatment groups which were subsequently managed separately until weaning in September. Both groups were free-ranging, but the 'supplement' group was given supplemental feed (oats and alfalfa pellets), while the 'pasture' group was not. Due to poor pasture conditions at the end of August, both groups were provided access to round bales of grass hay for the last 13 days of the study. This was not thought to have had any effect on the difference in condition between the two groups, which had by that time become apparent.

2.5 Behavioural data collection

Data on nursing bouts and behavioural interactions were collected from May to September 1994. Twenty-three mother-calf pairs (15 male, 8 female calves) were used as subjects for the behavioural observations. Twelve of these (7 males, 5 females) were in the supplement group and eleven (8 males, 3 females) were in the pasture group. Nursing bout data were collected from 28 mother-calf pairs (18 males, 10 females).

To facilitate identification of individuals, all study animals were fitted with uniquely-coloured collars, such that each hind-calf pair wore collars bearing the same colour pattern. Collars (canvas strips covered with coloured tape and connected using plastic fasteners) were fitted around the necks of hinds in May, prior to calving. Matching collars were placed around calves' necks at 24 hours of age, while they were being weighed. Several of the hinds have worn collars during previous studies; this does not appear to disturb the animals nor does it interfere with normal behaviour. Collars were checked and adjusted during weekly weighings to maintain proper fit. Collars were occasionally lost in the field, but individual recognition was always possible using other cues (ie. ear-tags, physical appearance, association with known individuals).

Data were collected by an observer on foot in the field, using binoculars when necessary, at distances varying from 5 to 40 m from the focal animals. The animals are well-habituated to human presence, and people at these distances are tolerated without noticeable changes in behaviour. Observations were scheduled throughout the daylight hours (0500-2200), though most occurred during times of peak animal activity (0500-0900, 1800-2200). Focal dyads (hind-calf pairs) were chosen for observation based on activity level and calf age. Each of the 23 dyads was observed once for each of two types of observations, instantaneous and focal-animal (Altmann 1974), during each of four calf age classes: 0-3 weeks, 4-6 weeks, 7-11 weeks and 12-16 weeks. Where necessary, distances between animals were estimated using animal lengths and landmarks as aids. Although 96% of the observations were conducted by the author, two other individuals assisted in the collection of data. A comparison was made to verify that behaviours were observed and recorded in the same manner by all three observers.

2.5.1 Nursing bouts

Lactation entails a tremendous energetic cost, accounting for at least 75% of the total energy expended on reproduction (Oftedal 1985). Consequently, it may be considered the most critical form of post-natal maternal investment. Nursing bout length is often used as a key measure of a female's investment in her offspring (Clutton-Brock et al.

1982, Lee and Moss 1986, Wolff 1988, Hogg et al. 1992), and has been shown to be correlated with milk intake (Trillmich 1986, but see Mendl and Paul 1989). It has been suggested that gender-related differences in investment, rather than indicating differential allocation of resources by the mother, could be the result of differential extraction of resources by offspring of one gender (Clutton-Brock 1991). Nursing bout length may only be a true indication of the magnitude of maternal investment, therefore, if control of nursing lies primarily with the mother. The issue of control of this type of investment can be considered by focusing on which individual, mother or calf, initiates and which terminates a bout. *Ad libitum* sampling (Altmann 1974) was used to record the duration of all observed nursing bouts, as well as which individual initiated and terminated them. A nursing bout was defined as any period of more than 5 seconds during which a calf suckled from its mother, and bout length was calculated to the nearest second by subtracting the length of all pauses (interruptions less than 60 seconds in duration) from the total length of the bout.

2.5.2 Contact maintenance

Care provided to offspring by parents is a form of investment, and has been shown to bring about costs to parents in terms of growth and future fecundity (Balshine-Earn 1995). One particularly important aspect of maternal care is contact maintenance with offspring, components of which are proximity, spatial transitions, behavioural synchrony and contact interactions (Green 1992).

In terms of the spatial relations between mothers and their offspring during the first few weeks following birth, ungulate species employ two anti-predation strategies (Lent 1974). In ‘follower’ species, mothers protect their young by maintaining close proximity immediately following birth. In contrast, wapiti are said to be a ‘hider’ species (Geist 1982), in that calves remain hidden in vegetation for the first 1-2 weeks of life, and are inactive except during the brief visits made by the mother for the purpose of nursing. The success of the hider strategy relies on mothers remaining at a distance from their calves during this initial hiding phase, and decreased offspring survival may result from mothers staying too close (Ozoga and Verme 1986). Maintaining the proper proximity may be considered a form of maternal investment since in the initial hiding stages mothers incur a high energetic cost resulting from traveling back and forth to allow the calf to nurse (Carl & Robbins 1988). Later on, close contact with older, more active calves must be maintained to protect against predation and prevent separation. Spatial transitions (the manner in which hinds and calves approach and leave each other) aid in maintaining contact between mother and calf. A mother may also maintain closer contact with her calf by synchronizing her behaviour with that of the calf. This could mean an increase in activity and a reduction in foraging at a time when energetic costs are high due to lactation (Green 1992). Certain contact interactions may also help to ensure mother-calf bonding, keep the calf close to its mother and/or encourage it to follow its mother. These interactions include grooming, nuzzling and vocalizing.

Two types of sampling techniques were used to collect data relating to contact maintenance in this study. Instantaneous sampling (Altmann 1974) was used to collect information on mother-offspring proximity and synchrony of behaviour. Mother-c pairs were observed for periods of two hours, with the activity of both hind and calf as well as the distance between them recorded onto data sheets at two minute intervals, yielding 61 data points for each observation period. Distance classes and categories of dyad behaviour are listed in Appendix 1. Focal-animal sampling (Altmann 1974) was used to provide information on spatial transitions and contact interactions. Focal dyads were observed for periods of one hour, wherein all activities of and interactions between mother and calf were recorded using a 'Realistic Micro-16' microcassette tape recorder. These tapes were later transcribed and the frequencies of all variables (see Appendix 2) were tabulated.

2.6 Milk intake and nutritional dependence

Although observational studies are often used to estimate milk intake, there is some question as to whether time spent nursing is an accurate indicator of milk transfer (Mendl and Paul 1989). Rate of milk intake changes with wapiti calf age and weight (Hudson and Adamczewski 1990). To estimate the amount of milk relative to the amount of forage consumed by calves, fecal alkanes were measured. Alkanes are saturated aliphatic hydrocarbons found in plant cuticular wax. Because they can be partially recovered in feces, alkane levels in feces may be used to estimate forage intake (Dove and Mayes 1991). Since milk contains no alkanes, the concentration of alkanes in a calf fecal sample should indicate the relative portions of the calf diet made up by forage and by milk. The alkane analysis will provide a means of comparing the ratio of milk to forage in the diets of male and female calves. Although the results of the alkane analysis cannot be used to directly measure milk intake, they may be combined with behavioural observations of time spent foraging by calves to provide an estimate of the relative amount of milk in the diet. In addition, since weaning does not occur naturally in this population, looking at the change in the relative amounts of milk and forage in the diet as calves age will give an indication of nutritional independence. The rates at which male and female calves move from milk to forage as their main source of nourishment will be compared. Fecal samples were collected every 2-3 weeks from individual calves while they were confined for weighing. On or about the same day fecal samples were also collected from two hinds to use as a comparison (since their diet presumably included no milk). Samples were placed in open plastic containers which were then wrapped in paper bags and frozen. Prior to analysis, fecal samples were dried and ground. Alkanes were then extracted and the fecal concentration of C31, a common, naturally-occurring alkane, was determined using gas chromatography, following a procedure based on the methods of Dove and Mayes (1991).

2.7 Costs of reproduction

By definition, maternal investment implies a cost (Trivers 1972) in terms of a female's future survival and fertility. If females are not able to regain good condition during the period following parturition, as well as maintain it during lactation, they may compromise their ability to breed in the fall rut (cost in terms of fertility) or survive the approaching winter (cost in terms of survival) (Oftedal 1985). The average daily weight gain (ADG) of females, from immediately after parturition until weaning, was used to gauge the cost of reproduction. ADG for each female in each year was calculated as the slope of the linear regression of weight on days since birth, using all weights recorded between parturition and weaning. For females who did not calve, the mean birth date for that year was used as a simulated date of parturition.

To determine whether reproduction brings about a cost for hinds at Ministik, ADG of three categories of females were compared: barren females (who did not calve, either because they failed to conceive or because they aborted their fetus), parturient-non-lactating females (who calved, but whose calves were removed for hand-rearing immediately following birth) and parturient-lactating females (who calved and raised their calves through to weaning). There were a number of parturient females whose calves died shortly after birth; these were excluded from the second group because of the likelihood of illness, which could affect maternal weight dynamics. The first group of females should suffer no costs of reproduction, the second group should suffer only the costs of gestation and parturition, while the third group should suffer the costs of gestation, parturition and lactation.

Costs of reproduction may be examined to determine whether maternal investment is gender-biased; a higher investment in offspring of one gender would bring about a higher cost. To determine whether the costs of reproduction for mothers of male and female offspring are the same, ADG of hinds who successfully raised male and female calves were compared.

The investment by a mother in an offspring is related to the length of time following the birth of that offspring before she is able to reproduce again (Silk 1988). The interbirth interval has been used to measure the cost of reproduction (Small and Smith 1984, Lee and Moss 1986, Silk 1988, Gomendio 1990, Green and Rothstein 1991). The interbirth interval, or the number of days between births in successive years, was calculated for each female who bred in successive years, and this number was related to the gender of the offspring born at the start of the interval.

2.8 Statistical analyses

Except where otherwise indicated in the text, the binomial test (or when n>30, the normal approximation to the binomial test with correction for continuity), was used to compare ratios of male to female calves to 1:1 sex ratios (Zar 1984), and the chi-square test of independence was used to examine relationships between sex ratios and factors which are thought to influence them. All parametric analyses were carried out using analysis of covariance (ANCOVA). The factors included in some or all of the models were calf gender and nutritional treatment, and the covariates were maternal age, calf age, maternal rut weight, calf birth date and year. Repeated-measures ANCOVA was used in the analysis of contact maintenance data, which were collected in behavioural observations made during four calf age classes. Means reported in the text are accompanied by standard error of the mean (SE). The software package Systat (Systat, Inc. 1992) was used for all parametric analyses, all tests are two-tailed, and the significance level chosen for hypothesis-testing was 0.05.

Data sets to be analyzed using parametric statistics were first tested for normality, using the Lilliefors test. Some data sets violated the normality assumptions. Since preliminary analyses showed that transforming the data (using square root and arcsine transformations) did not reliably improve normality, nor change the results, and because of the robustness of analysis of covariance to deviations from normality, the untransformed data were used for final analyses.

The software package G•Power (Buchner et al. 1996) was used to calculate power (post-hoc) of some statistical tests, in cases where a Type II error (failure to reject a false null hypothesis) was likely due to small sample size. The outcome of these power analyses are discussed in the text in cases where non-significant results may have been the product of small sample sizes.

3.0 Results

3.1 Sex ratios

Between 1978 and 1994, there were 177 male and 140 female elk calves born at the Ministik Wildlife Research station. This sex ratio for all years pooled is significantly different from unity (Z_c=2.036, $0.02<p<0.05$). In only one year, 1992, was the sex ratio significantly different from 1:1, although in 13 out of 16 years there were more males born than females (Table 1).

To determine whether individual females produced more offspring of either gender, ratios were also examined within individual progenies. Progeny sizes observed in

Table 1. Sex ratios of calves born in each year from 1978 to 1994

Year	# males born	# females born	p value
1978	2	1	ns
1980	4	2	ns
1981	2	1	ns
1982	5	3	ns
1983	5	4	ns
1984	1	6	ns
1985	6	3	ns
1986	7	7	ns
1987	11	8	ns
1988	12	14	ns
1989	13	6	ns
1990	18	17	ns
1991	16	23	ns
1992	32	16	$p<0.05$
1993	19	16	ns
1994	24	13	ns
total	177	140	$p<0.05$

NOTE: Due to the low numbers of calves born each year between 1978 and 1991, the chance of detecting a difference between the observed and 1:1 sex ratios ranged from 6%-59% for data collected in those years. For 1993 data there was a 9% chance and for 1994 data an 86% chance of detecting a difference. (Power was calculated for chi-square tests of goodness of fit, but should be similar for binomial tests.)

this study ranged from 1 to 14 calves. Because of inadequate sample sizes, sex ratios for each progeny size could not be examined. There were thirty-six hinds who produced four or more calves each during the study; the offspring of these mothers were used to examine this problem. Observed sex ratios of the first four calves born to these hinds were compared to a binomial distribution (for n=4, with equal probability of either gender). There was no significant difference between observed and expected sex ratios (Chi-square goodness of fit test: $X^2=4.41$, 4 df, $p>0.25$). The analysis was repeated using the sex ratios of the last four calves, and again there was no significant difference between observed and expected ratios ($X^2=6.22$, 4 df, $p>0.25$).

For each year in which a hind calved, she was placed into one of two condition classes (good or poor) based on her weight during the previous rut compared with weights of other animals in the same age-class. Although there was no significant relationship between maternal condition and offspring gender ($X^2=2.57$, 1 df, $0.10<p<0.25$), the sex ratio of offspring born to females in good condition was significantly skewed towards males while the sex ratio of offspring born to females in poor condition was not significantly different from unity (Table 2).

Any hind who bred successfully more than once was assigned to one of three condition classes (good, average or poor) for each reproductive effort, based on her weight in that year relative to her weight in her other reproductive years. When condition was assessed in this manner, there was no significant relationship between condition and offspring gender ($X^2=0.995$, 2 df, $p>0.50$), although there was a tendency for mothers in better condition to have a higher proportion of males (Table 3).

Table 2. Offspring sex ratios in relation to maternal condition, where condition is assessed by comparison with rut weight of other same-aged individuals

Maternal condition	Number of calves born		Z_c	p value
	male	female		
good	90	58	2.61	$p<0.01$
poor	74	75	0.0	$p>0.50$

Table 3. Offspring sex ratios in relation to maternal condition, where condition is assessed by comparison of an individual's rut weight to her weight in other reproductive years

Maternal condition	Number of calves born		Z_c	p value
	male	female		
good	49	38	1.08	p>0.20
fair	54	39	1.47	0>0.10
poor	39	38	0	p>0.50

Parturient hinds were divided into 3 age classes, representing young (2-3 years), prime (4-12 years) and old animals (>13 years). Although young and prime mothers tended to produce more males than older mothers, the sex ratios in each class were not significantly different from unity (Table 4) and hind age was not found to significantly affect sex ratios (X^2=0.608, 2 df, p>0.50).

To examine the effect of the previous year's reproductive effort on gender of the current year's offspring, parturient hinds were categorized with respect to their reproductive status in the previous year. Whether a hind had been barren, had a calf which subsequently died, successfully raised a male calf or successfully raised a female calf in the previous year had no effect on sex ratios (X^2=1.0756, 3 df, p>0.75; Table 5).

3.2 Measures of pre–natal investment

Mean calf birth weight (n=249) was 18.92 kg ± 0.17 kg. Analysis of covariance showed that calf birth weight was significantly higher for males (19.62 ± 0.23 kg) than for females (18.08 ± 0.23 kg) ($p<10^{-6}$), increased with hind age (p<0.04) and with female rut weight (p<0.00034), and increased from 1982 to 1994 (p<0.0006).

Mean calf birth date (n=303) was julian day 154 (June 3). There was a non-significant tendency (p>0.20) for female calves to be born earlier than males (June 2 vs. June 5). Older mothers calved earlier than younger mothers (p<0.0002), and birth date became progressively later from 1978 to 1994 (p<0.0001). Birth dates were earlier for hinds with heavier body weights at the time of conception (p<0.002).

Table 4. Offspring sex ratios in relation to maternal age

Maternal age class	Number of calves born male	female	Z_c	p value
2-3 years	50	38	1.18	p>0.20
4-12 years	117	92	1.67	p>0.05
>13 years	10	11	0	p>0.50*

* There is only a 7.4% chance of detecting a difference of this magnitude with this sample size (power was calculated for a chi-square test of goodness of fit, but should be similar for binomial test).

Table 5. Offspring sex ratios in relation to previous year's reproductive status

Previous year's reproductive status	Number of calves born		Zc	p value
	male	female		
barren	10	12	0.214	p>0.50*
calf died within 10 days of birth	9	7	0.252	p>0.50**
successfully raised female calf	55	45	0.905	p>0.20
successfully raised male calf	66	49	1.509	p>0.10

* There is only a 7.6% chance of detecting a difference of this magnitude with this sample size (power was calculated for a chi-square test of goodness of fit, but should be similar for binomial test).

** There is only a 6.9% chance of detecting a difference of this magnitude with this sample size (power was calculated for a chi-square test of goodness of fit, but should be similar for binomial test).

The interbirth intervals preceding the births of calves were known in 220 cases, for 50 different hinds. With the effects of hind age and year controlled for, intervals preceding births of male calves (365.76 ± 1.63 days) were significantly longer than those preceding births of females (363.26 ± 1.16 days) ($p<0.007$).

3.3 Measures of post–natal investment

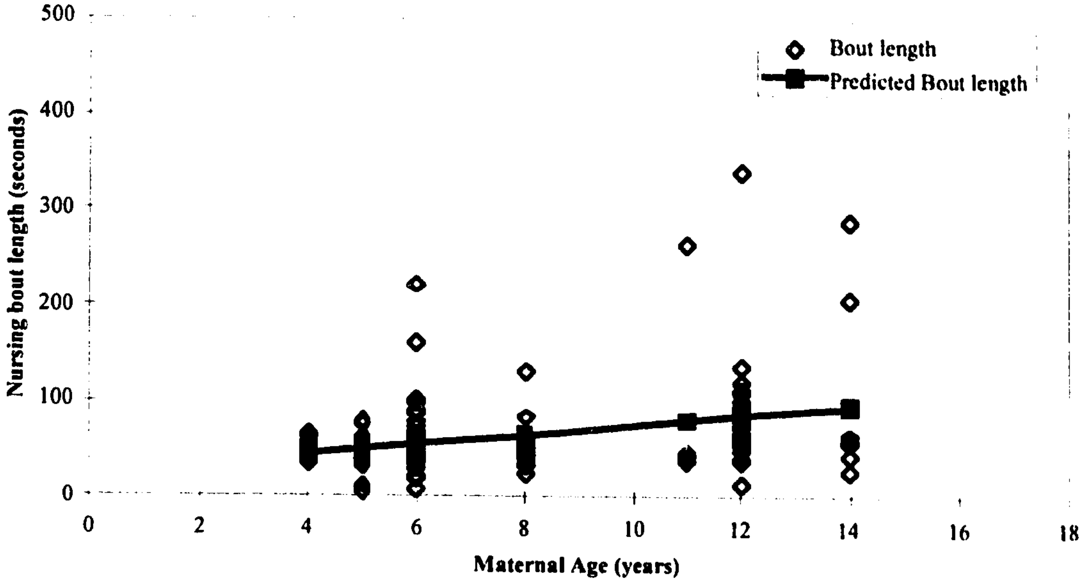
3.3.1 Milk transfer

3.3.1.1 Nursing bouts

A total of 616 instances of nursing were observed; for 382 of these both the beginning and end were observed, and thus the exact length of the nursing bout (to the nearest second) was known. Mean nursing bout length (n=382) was 65.6 ± 2.6 seconds. ANCOVA was used to test for gender differences in nursing bout length, while controlling for hind age, calf age, birth date and nutritional treatment. Mean nursing bout duration for male calves was 67.1 ± 3.4 seconds, longer than for female calves (63.1 ± 3.9 seconds; $p<0.02$). As calves aged, the lengths of their nursing bouts decreased significantly ($p<10^{-7}$). Overall there was a tendency for older hinds to nurse their calves longer than younger hinds. Due to a significant interaction between hind age and calf gender this relationship was significant for mothers and daughters, however mothers and sons showed an opposite but non-significant trend (Figure 1).

In 163 cases it was clear which individual was responsible for initiating a given nursing bout. Hinds initiated bouts by approaching calves, sometimes vocalizing, and often striking with front legs at bedded calves to make them stand and nurse. Calves

(a) nursing bouts between mothers and daughters



(b) nursing bouts between mothers and sons

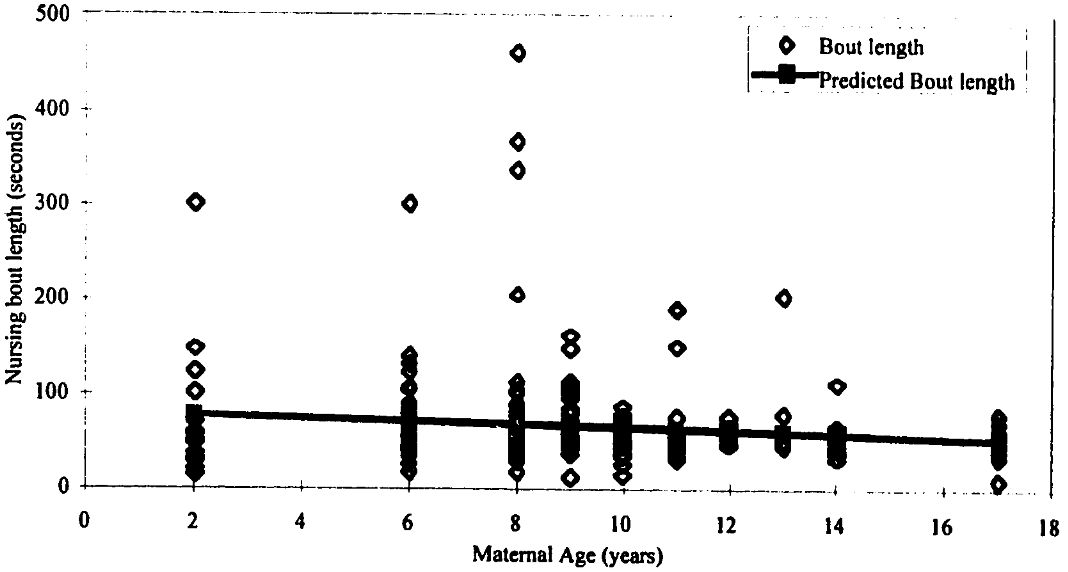


Figure 1. Interaction between calf gender and maternal age in the analysis of nursing bout length. The relationship between nursing bout length and maternal age is (a) significant and positive for bouts between mothers and daughters (n=140), and (b) non-significant and negative for bouts between mothers and sons (n=242).

initiated bouts by approaching their mothers and beginning to nurse. Overall, hinds initiated 68.3% and calves 31.7% of bouts. Mothers initiated 62.6% of bouts with sons, while they were responsible for initiating 77.8% of bouts with daughters; this difference was not significant (Chi-square test of independence: $\lambda^2=3.59$, 1 df, $p>0.05$).

For 551 bouts the individual responsible for terminating the bout was known. Calves were said to terminate bouts when they were seen to stop suckling without having been rejected by the hind. Hinds terminated bouts by walking away from their still-suckling calves, often aggressively rejecting further attempts by the calf to nurse. Overall, mothers terminated 93.3% of bouts. Male calves terminated 6.8% of bouts while female calves terminated 6.6%. It seemed that only very young calves were allowed control of nursing bout duration; calves who terminated bouts were 17.4 ± 3.6 days old, while the mean age of calves involved in bouts terminated by mothers was 47.7 ± 1.1 days. Since mothers terminated bouts with male and female calves at the same rate, if male calves attempted to nurse more often than females, they could potentially extract more resources from their mothers (without this being a choice of investment by mothers). Of all recorded attempts at nursing, attempts by males accounted for 35.9% and attempts by females for 64.1%. This corresponds nearly exactly to the numbers of male and female calves in the study (35.7% females, 64.3% males).

3.3.1.2 Alkane analysis

The analysis of fecal alkanes was restricted to animals in the pasture group. Thirty fecal samples, collected on four different days from nine calves were analyzed for alkane content. Analysis of covariance was used to examine the effect of calf gender on the amount of forage relative to milk in calves' diets, while controlling for effects of hind age and calf age. There was no difference ($p>0.84$) in the relative concentrations of milk and forage in the diets of male (239.3 ± 42.0 mg C31/kg fecal sample) and female calves (238.6 ± 45.4 mg C31/kg fecal sample). This could, however, be the result of small sample size; calculation of the power of this test showed less than a 54% chance of detecting a 'medium-sized' effect (Buchner et al. 1996). The amount of forage relative to milk in calves' diets increased significantly with calf age ($p<10^{-5}$). To look at the rate at which calves gained nutritional independence (our best estimate of rate of weaning), the slopes of regressions of fecal levels of C31 on calf age were analyzed. Females moved from milk to forage in their diets at a slightly faster rate than males, however this difference was not significant ($p>0.10$). Calves born later in the season moved from milk to grass at a significantly faster rate ($p<0.013$).

3.3.2 Calf growth rates

Growth rates of calves were assessed by measuring their ADG between birth and weaning. Analysis of ADG of 20 calves born in 1994 showed that, after accounting for the effects of nutritional treatment, maternal age and birth date, there was no difference between growth rates of male (858 ± 14 g/day) and female (890 ± 25 g/day) calves ($p>0.112$). However, the calculation of the power of this test showed that there was less than a 37% chance of detecting a 'medium-sized' difference (Buchner et al. 1996) in growth rates between the genders. Only nutritional treatment had a significant effect on calf growth. Calves in the supplement group grew at a mean rate of 912 ± 12 g/day while calves in the pasture group grew an average of 820 ± 11 g/day; this difference was significant ($p<0.0004$).

3.3.3 Contact maintenance

3.3.3.1 Proximity

The number of scans per observation spent by mothers and calves within 0, 5, 10, 20 and 40 m of each other, as well as the number spent more than 20 m and 40 m apart were analyzed to determine if mothers and sons maintained different proximity than mothers and daughters. There was no difference attributable to calf gender, once variation due to nutritional treatment, calf birth date and maternal age had been accounted for. The nutrition of mothers affected the proximity between mothers and calves. Mothers in the supplement group spent more time within 10 m ($p<0.02$) and within 20 m ($p<0.007$) of their calves, and less time at distances greater than 20 m ($p<0.007$) than did mothers in the pasture group (data presented in Appendix 3).

As ungulates which use the 'hider' strategy to decrease risk of predation, wapiti mothers should spend very little time in close proximity to young calves. During the first age-class (0-3 week old) mothers were observed within 5 m of their calves in only 3.8 ± 1.2 scans per observation period. There was a significant difference in the amount of time spent at this distance by mothers of males and mothers of females, once nutritional treatment, calf birth date and maternal age had been accounted for. Mothers were seen within 5 m of their male calves (n=15) in 2.8 ± 0.8 scans, however for mothers of daughters (n=8) this proximity was observed in 5.6 ± 3.1 scans ($p<0.05$).

3.3.3.2 Synchrony of behaviour

Three mutually exclusive behavioural states were recorded during instantaneous sampling periods: foraging, resting and active. Considering both mother and calf, there were nine possible categories of dyad behaviour, representing the nine pairwise combinations of behavioural states (see Appendix 1). The number of scans per two-hour observation (out of a total of 61) during which each category of dyad behaviour occurred was treated as the dependent variable, and subjected to repeated-measures ANCOVA to determine the effects of calf gender while controlling for the effects of nutritional treatment, maternal age and calf birth date. Where significant results are presented in the text, the corresponding data appear in Appendix 4.

In scans where calves were resting, hinds rested 68.2% of the time, foraged 29.3% of the time and were active 2.5% of the time. Mothers synchronized their behaviour to that of their resting calves significantly more often in the supplement group than in the pasture group ($p<0.003$). In addition, due to an interaction between calf gender and nutritional treatment, in the pasture group mothers and daughters rested together more often than mothers and sons ($p<0.01$), while in the supplement group the opposite relationship existed ($p<0.04$). Mothers foraged while their calves rested more often in the pasture than the supplement group ($p<0.0004$), and there was the same type of interaction between nutritional treatment and calf gender. In the pasture group, mothers of resting males foraged more often than mothers of resting females ($p<0.005$), while in the supplement group there was an opposite, non-significant trend. The frequency with which mothers were active while their calves rested was affected only by maternal age; this category of dyad behaviour occurred more often with younger than with older mothers ($p<0.05$).

When calves were active, hinds were active in 21.6% of scans, rested in 33.1% and foraged in 45.3%. Calf gender had no effect on how often mothers and calves were active together, however mothers in the supplement group were more often active with their calves than mothers in the pasture group ($p<0.01$). The frequency with which hinds rested while calves were active was not affected by any of the factors. Hinds in the supplement group foraged more often while their calves were active than mothers in the pasture group ($p<0.006$), however there was no effect of gender.

Of the scans in which calves foraged, their mothers foraged in 63.5%, rested in 33.6% and were active in 2.9%. Levels of synchronous foraging were higher in the pasture than the supplement group ($p<0.02$). In addition, in the pasture group mothers foraged more often with their male than female calves ($p<0.03$) whereas there was no significant effect of gender in the supplement group. The frequencies with which hinds either rested or were active while their calves foraged were not affected by any of the factors.

3.3.3.3 Spatial transitions

The frequency of leaves and approaches by hinds and calves across three distance boundaries (1, 5 and 10 m) were combined to give overall frequencies. An index recommended by Hinde and Atkinson (1970) was used to determine which member of the mother-calf dyad was contributing more to maintaining proximity between the two. The index, which is calculated as follows,

$$\text{index} = 100\ [\text{APP}_{\text{calf}}/(\text{APP}_{\text{calf}}+\text{APP}_{\text{hind}}) - \text{LEAVE}_{\text{calf}}/(\text{LEAVE}_{\text{calf}}+\text{LEAVE}_{\text{hind}})]$$

will have a negative value if the mother is making a larger contribution and a positive value if the calf is contributing more. The overall mean (n=23) for this index was 9.1 ± 4.0. Neither calf birth date nor maternal age had any effect on values of this index, however there were tendencies for female calves to contribute more than male calves to maintaining contact with mothers (females: 14.7 ± 8.8, males: 6.1 ± 4.0; $p>0.08$), and for calves in the pasture group to contribute more than calves in the supplement group (pasture: 17.0 ± 5.3, supplement: 1.8 ± 5.3; $p>0.06$).

3.3.3.4 Contact interactions

Occurrences of vocalizations and nuzzling were too infrequent to allow for analysis, thus grooming was the only contact interaction analyzed. The time spent by mothers grooming calves was recorded during one-hour observations, and averaged 178 ± 27 seconds/hour. Analysis of covariance showed no significant difference in the time spent by mothers grooming male and female calves, after accounting for the effects of maternal age and nutritional treatment. Similarly, a mother's age had no effect on the amount of time she spent grooming her calf. However, the amount of time spent grooming calves by mothers in the supplement group (249 ± 40 sec/hour) was greater than in the pasture group (101 ± 17 sec/hour; $p<0.009$).

3.4 Costs of reproduction

3.4.1 Average daily gain

The data set used for this analysis consisted of 190 measures of ADG, for 55 different females in 12 years. Analysis of covariance was used to establish the effect of reproductive status on maternal weight loss from calving through to weaning, while controlling for maternal age, nutritional treatment and year. ADG decreased with hind age ($p<0.007$), and was significantly affected by year and nutritional treatment ($p<10^{-6}$). Reproductive status played a significant role in determining ADG ($p<0.003$). Multiple means comparisons showed that hinds whose calves were taken away at birth had significantly lower weight gains than both hinds who successfully raised their calves and hinds who did not calve at all, however there was no difference between the ADG of the latter two groups (Table 6).

Subsequent analysis of ADG of only those hinds who successfully raised calves was performed to determine the relative costs of raising male and female calves. Once the effects of hind age, year, nutritional treatment and calf birth date were controlled for, there was no difference between ADG of mothers of male calves (286 ± 19 g/day) and ADG of mothers of female calves (260 ± 21 g/day) ($p>0.8$).

Table 6. Average daily gains (ADG) for hinds in three categories of reproductive status

Reproductive Status	ADG (mean ± SE)*	n
Barren	0.312 ± 0.04a	12
Parturient-non-lactating	0.112 ± 0.06b	8
Parturient-lactating	0.274 ± 0.01a	161

*means followed by different letters are significantly different ($p<0.05$), as determined by Tukey's test for multiple means comparison

3.4.2 Interbirth intervals

The interbirth intervals following the births of calves were known in 217 cases, for 50 different hinds. ANCOVA was used to determine the effects of gender on interbirth interval, while controlling for the effects of maternal age and year. It took an average of 362.0 ± 1.7 days for a mother to give birth again following the birth of a male calf, and 364.7 ± 1.5 days following the birth of a female calf; this difference was not significant ($p>0.32$). Neither maternal age nor year had any effect on interbirth interval.

3.4.3 Grazing behaviour

Grazing behaviour was observed during the two-hour instantaneous sampling observations, and the number of scans (out of 61) during which an animal was seen grazing (including browsing and eating hay) was recorded. Feeding on pellets/oats was not included, since only animals in the supplement group had access to grain.

3.4.3.1 Calves

The number of scans during which calves were observed grazing, averaged over the four age classes, was 11.7 ± 1.1 ($n=23$). When maternal age, calf birth date and nutritional treatment were accounted for, there was no difference between the number of scans in which male and female calves grazed ($p>0.6$). Only maternal age and nutritional treatment had significant effects on calf grazing. Calves of older mothers grazed more than calves of younger mothers ($p<0.025$). In the supplement group, calves were seen grazing in 9.2 ± 1.1 scans, while in the pasture group, they grazed in 14.6 ± 1.5 scans ($p<0.01$).

3.4.3.2 Hinds

Hinds grazed an average of 20.8 ± 1.7 scans per observation (n=23). Analysis of covariance showed that mothers in the pasture group grazed significantly more than mothers in the supplement group (26.8 ± 2.0 vs 15.4 ± 1.5 scans/observation, $p<0.003$). There was a significant interaction between nutritional treatment and calf gender. Overall, mothers of males spent more time grazing (21.5 ± 2.5 scans) than did mothers of females (19.6 ± 2.0 scans) ($p<0.015$); this relationship held true for the pasture group however there was an opposite, but non-significant trend for the supplement group (Figure 2). Maternal age also had a significant interaction with calf gender. While older mothers of male calves spent less time grazing than younger mothers, the opposite was true of mothers of females (Figure 3), however neither of these relationships was significant.

4.0 Discussion

Wapiti hinds in this study invested more in their male offspring than they did in their female offspring. Sex ratios changed according to maternal body condition. In addition, mothers allocated more resources to sons, both pre-natally in terms of birth weights and gestation lengths, and post-natally, in terms of nursing bout length and some forms of contact maintenance. No bias in 'traditional' measures of reproductive costs were found to confirm that maternal care was translated into investment. However, the results seem to contradict Fisher's theory of equal investment, and instead lend support to those of Trivers and Willard (1973), Reiter et al. (1978) and Maynard Smith (1980).

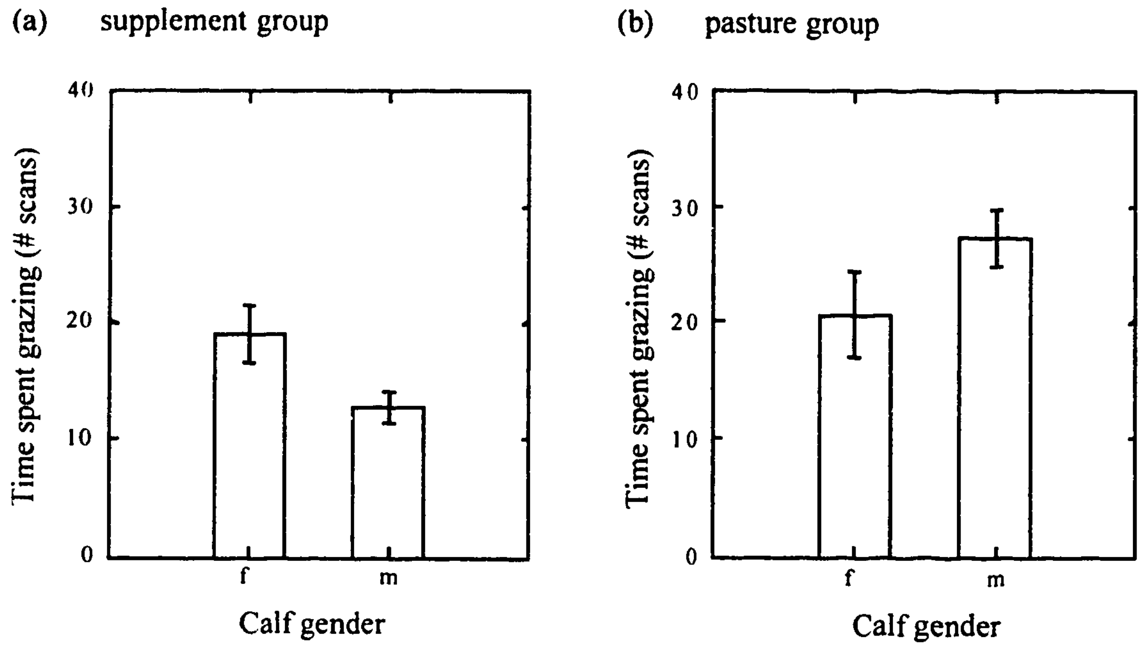
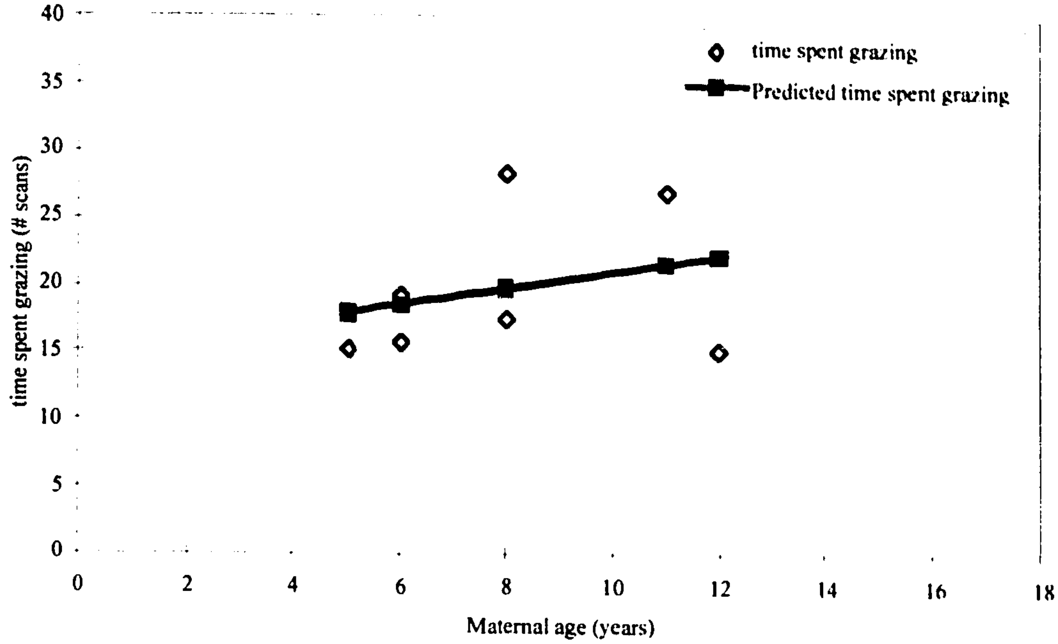


Figure 2. Interaction between calf gender and nutritional treatment in the analysis of time spent grazing by hinds. In the supplement group (n=12), mothers of females graze more than mothers of males (a), whereas in the pasture group (n=11), mothers of males graze more than mothers of females (b).

(a) mothers of female calves



(b) mothers of male calves

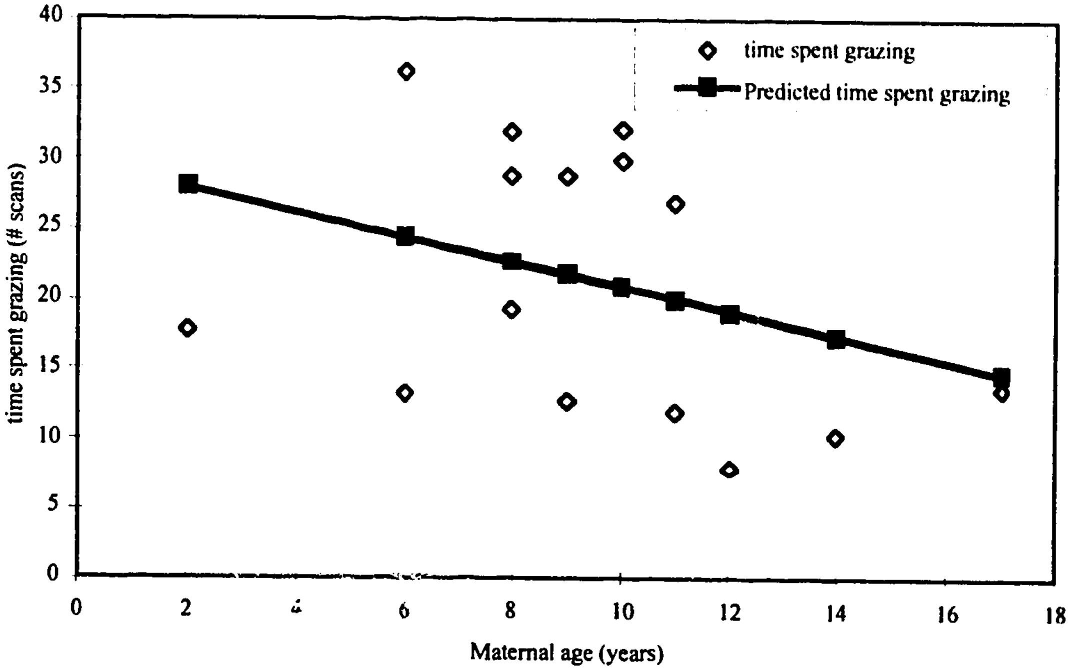


Figure 3. Interaction between calf gender and maternal age in the analysis of time spent grazing by hinds. The relationship between maternal age and time spent grazing is (a) positive for mothers of females (n=8), and (b) negative for mothers of males (n=15).

4.1 Adaptive modification of sex ratios

This study provided evidence to suggest that wapiti mothers adjust sex ratios according to their ability to invest, in agreement with the predictions of investment theory and with the findings of several other studies (Rivers and Crawford 1974, Robinette et al. 1957, Simpson and Simpson 1982, Clutton-Brock et al. 1984, Meikle et al. 1984, Labov et al. 1986, Gomendio 1990 [illegible] et al. 1993, Arnbom et al. 1994, Wauters et al. 1995). Among wapiti mothers with the ability to invest highly in offspring, sex ratios were skewed towards males, while mothers able to make only small investments produced even numbers of male and female offspring. This type of modification of offspring sex ratios accounts for the overall sex ratio being significantly male-biased.

Possible mechanisms by which females might exert control over offspring gender have often been considered. Trivers and Willard (1973) proposed that female control of offspring gender in mammals must occur through differential mortality by gender of either sperm, embryos or young offspring, since mammalian gender is determined by male gametes. Whether it is in fact possible for sex ratios to be altered is an issue which has not been clearly resolved (Clutton-Brock and Albon 1982). There is, however, evidence for differences in both motility and viability between X and Y spermatozoa (Guerrero 1975, Roberts 1978, Harlap 1979, all cited in Verme and Ozoga 1981), and uneven sex ratios have frequently been attributed to the timing of insemination relative to ovulation, with a higher proportion of males being conceived later in the cycle in humans (Guerrero 1975, Harlap 1979) as well as white-tailed deer (Verme and Ozoga 1981).

Although it is beyond the scope of this study to identify the mechanism by which sex ratios are modified, the data do allow certain inferences to be drawn. If the male-biased ratios were the result of selective loss or resorption of female embryos, one would expect to see a large number of male calves born the length of one estrous cycle later than the average birth date. Wapiti females who fail to conceive or who abort embryos take at least 21 days to return to estrus (Haigh and Hudson 1993). Although this study indicated a tendency for males to be born later in the season than females, this difference was neither significant nor long enough to be explained by this mechanism. The most probable mechanism for the male-biased sex ratios observed in this study is the timing of fertilization. It is possible that wapiti, like white-tails, conceive more males when they are bred late in the day of estrus. In red deer, dominant mothers produced higher proportions of sons than daughters (Clutton-Brock et al. 1984). The timing of breeding relative to the onset of estrus may be a function of individual behavioural traits related to dominance. Hudson et al. (1991) suggested that male-biased sex ratios among young wapiti females could be related to breeding behaviour. Hind dominance may affect breeding behaviour in such a way as to delay fertilization. Of the factors investigated in this study, only maternal body condition and age were related to sex ratios. Similarly, these two factors may be correlated with dominance. Dominance hierarchies would be required to determine whether sex ratios at Ministik are related to social rank, and close observation of interactions between stags and hinds during the rut would allow the timing of insemination relative to the onset of estrus to be determined.

4.2 Pre-natal investment

During gestation, wapiti mothers allocated more of their resources to male than to female fetuses, as indicated by the two measures of pre-natal investment investigated.

As in many other studies of maternal investment (Reiter et al. 1978, Mueller and Sadleir 1980, Clutton-Brock et al. 1982, Kovacs and Lavigne 1986a, 1986b, Trillmich 1986, Anderson and Fedak 1987, Braza et al. 1988, McCann et al. 1989, Hogg et al. 1992, Arnbom et al. 1994, Smiseth and Lorentsen 1995), the results of this study showed that male birth weights were significantly higher than female birth weights. However, in polygynous species, there should be strong selection on males to attain large body sizes, and heavier birth weights could simply be the result of gender differences in allocation of resources to growth. Although birth weight may be used as an indication of gestational effort (Lee et al. 1991), conclusions about differential maternal investment should not be based on male-biased birth weights alone (Clutton-Brock 1991).

The second measure of pre-natal investment investigated was the length of gestation. Since conception dates were not known, gestation was examined indirectly through analysis of interbirth intervals. The interbirth interval consists of two components: the time taken to return to estrus following the previous reproductive effort plus the length of gestation for the current reproductive effort. Intervals preceding births of male calves were found to be longer than those preceding births of female calves. This difference could indicate one of two things: either hinds who take longer to return to estrus tend to conceive higher proportions of males or there is a longer gestation period for male calves. The first possibility is not consistent with the patterns observed in this study. Animals who take longer to return to estrus generally do so because they are in poor condition, yet the mothers in poor condition in this study produced as many females as males. Longer interbirth intervals preceding male wapiti calves are likely due to longer gestation periods. The same male-biased, pre-natal investment was found for red deer (Clutton-Brock et al. 1982) and for horses (Berger 1986).

4.3 Post-natal investment

4.3.1 Milk transfer

Post-natal investment by wapiti mothers at Ministik also appears to be male-biased, as evidenced by the fact that male calves nursed for longer periods of time than female calves. This finding is in agreement with many other studies of maternal investment which found evidence for higher milk intake by male offspring in red deer (Clutton-Brock et al. 1982), and other species (Duncan et al. 1984, Lee and Moss 1986, Trillmich 1986, Wolff 1988, Hogg et al. 1992).

Clutton-Brock (1991) cautioned that gender-biased investment may arise by selection on offspring of one gender to extract more resources from parents, and not merely by preferential allocation of resources by parents. To establish whether longer nursing bout length for males is attributable to male behaviour or maternal behaviour, control of this type of investment must be examined. Mothers were responsible for terminating over 90% of nursing bouts, and they terminated bouts with males and females at the same rate. Although males are slightly larger, and presumably stronger than females, it is doubtful that it is any more difficult for a hind to terminate a bout with a male than a female calf. It is therefore unlikely that males could prolong nursing bouts by resisting their mothers' attempts to reject them, thus extracting more resources than female calves. Pressure on male calves to extract more resources from their mothers could cause them to make more frequent attempts to nurse than female calves. Although nursing bout frequency was not directly measured, a rough comparison between genders can be made by looking at all recorded nursing attempts. Attempts by male and female calves to nurse occurred in very close relation to their respective frequencies in the population. The observed differences in nursing behaviour seem to favour the idea of male-biased investment by wapiti hinds over that of differential extraction of resources by male calves.

Maternal age affected nursing bout length for female but not male calves. For mothers of females, nursing bout length increased significantly with maternal age, whereas there was no significant relationship for mothers of males. This interaction may be related to the concept of terminal investment (Clutton-Brock et al. 1982). Mothers of female calves may adaptively alter their investment in relation to their age and future reproductive potential. Younger mothers should invest in their daughters in such a way as to conserve resources for their future reproductive efforts. Older mothers, with fewer reproductive opportunities remaining, should choose to invest more in their daughters. It is possible that mothers of male calves are investing maximally, regardless of age, and may be unable to increase their investment in terms of milk transfer. That wapiti mothers with daughters, but not sons may be adjusting their level of investment to their age is supported by the analysis of time spent grazing by mothers. Time spent grazing by mothers of female calves increased with maternal age, whereas the opposite relationship was seen for mothers of male calves. Though neither relationship was significant, the patterns observed suggest that older mothers of daughters incur greater costs than younger mothers of daughters, in accordance with the theory of terminal investment (Clutton-Brock et al. 1982).

The length of nursing bouts was used as an indicator of the amount of milk transferred from mother to offspring. There are two potential problems with the use of bout length in this manner which should be addressed. The first problem concerns which parameter of nursing bouts should ideally be measured. Both the length and the frequency of nursing bouts have been used to gauge pre-weaning maternal investment. Hogg et al. (1992) measured both suckling duration and intervals between bouts in Rocky Mountain bighorn sheep, and used both of these measures to calculate a suckling rate in seconds/day. They found that bout duration was positively correlated with the length of the interval preceding that bout, and used this relationship to explain the discrepancies between their findings (that male lambs suckled more) and those of Festa-Bianchet (1988a), who found that nursing bouts were longer for female lambs. They argued that although bouts for males in Festa-Bianchet's (1988a) study were shorter, if they occurred more often males might have been receiving more milk. Intervals between bouts in this study were not often known, due to the inability to observe all bouts, and thus ascertain the length of time between bouts. However, in a study of lactation in the Ministik population, Kozak et al. (1995) found that milk intake in wapiti calves is typified by a small number of bouts and a large intake per bout. Consequently, bout length and not frequency may be the most appropriate measure.

The second problem involves how well the time spent nursing is correlated with the amount of milk taken in during that time. Although Trillmich (1986) demonstrated a good correlation between nursing bout length and milk intake in the Galapagos fur seal, it is possible that in some species, rate of milk removal may differ between individual offspring. Mendl and Paul (1989) found a negative correlation between time spent nursing and juvenile growth rates for mice and domestic cats, *Felis catus*, and suggested that time spent nursing might be a measure of milk demand rather than milk intake. This would indicate that offspring unable to obtain sufficient amounts of milk (ie. weaker offspring, or offspring of mothers with low milk production) would spend more time nursing. Neither of these explanations seems plausible in this case. Rate of milk intake by captive wapiti calves was shown to increase as calves matured (Hudson et al. 1991), and so in this study the analysis of bout length corrected for effects of calf age. Even so, female wapiti calves might still be slightly smaller, and thus weaker than males of the same age. However, it was not the weaker individuals (the females) in this study who spent more time nursing. Therefore the idea that weaker individuals need longer amounts of time to obtain the same amount of milk is not applicable here. It is also unlikely that male calves spent more time nursing simply because their mothers had lower milk production; mothers of male and female calves experienced similar weight dynamics during lactation, and likely had similar milk production.

The analysis of fecal alkane content did not provide conclusive evidence to confirm the difference in milk intake between male and female wapiti calves suggested by behavioural observations of nursing bouts. This could be due to the low power of the statistical test resulting from the small sample size (see Section 3.3.1.2). Alternatively, the inability to detect a difference could be due to the indirect nature of this analysis; rather than measuring the amount of milk in the diet, analysis of fecal alkane content provided an estimate of the proportion of the diet made up by forage, not milk. Therefore, if males ingested more forage as well as more milk than females, there would be no detectable difference in the relative concentrations of fecal alkanes between genders. Although male calves did graze more often in instantaneous samples than female calves, the difference was small and did not reach significance. Whether it could account for the discrepancies between the results of the alkane analysis and behavioural observations is difficult to determine.

An additional means by which mothers may invest more in their male offspring is to allow them an extended period of nutritional dependence, relative to female offspring. Weaning dates were found to be later for males in zebu cattle (Reinhardt and Reinhardt 1981) and in northern elephant seals (Reiter et al. 1978). The slopes of regressions of alkane content on calf age provide an estimate of the rate of weaning in the Ministik population. This rate tended to be faster for female calves, and although this difference was not significant (perhaps due to the low power of the test), it suggests that natural weaning dates for males might be later than for females.

4.3.2 Growth rates

Gender differences in growth rates during the period of maternal investment have often been presented as evidence for gender-biased maternal investment (Kovacs and Lavigne 1986a, 1986b, Anderson and Fedak 1987, Kovacs and Lavigne 1992). Investigation of gender differences in growth of wapiti calves at Ministik has provided equivocal results. In agreement with findings for red deer (Clutton-Brock et al. 1982), Hudson et al. (1991) found growth rates higher for male than for female wapiti calves at Ministik. No gender difference was found in either the current study, or a study conducted at Ministik by Hudson and Adamczewski (1990). It is possible that sample sizes were responsible for this discrepancy; Hudson et al. (1991) analyzed growth rates of 89 calves, whereas only 12 and 20 calves were involved in the work done by Hudson and Adamczewski (1990) and the current study, respectively. This idea was confirmed by the calculation of the power of this test (see Section 3.3.2).

In many ungulate species, the weaning process may occur too gradually for offspring growth rates during this period to be attributed solely to levels of maternal investment (Pélabon et al. 1995). Wapiti calves begin to forage on their own at between 3 and 4 weeks of age, and as they mature, their activity levels may vary. Forage intake by offspring, as well as activity levels, should be considered before drawing conclusions about growth rates relating to maternal investment. The analysis of the time spent foraging, resting and active by calves showed no significant differences between genders for foraging and activity, however female calves did rest significantly more often than males ($p<0.04$). Even after taking into consideration levels of calf activity and foraging, this study revealed insufficient evidence to draw conclusions about growth rates in relation to maternal investment. At any rate, whether growth rates reveal bias in maternal allocation of resources or gender-related differences in allocation of nutrients to growth remains uncertain (Clutton-Brock 1991).

4.3.3 Contact maintenance

The only difference in proximity between mother-son and mother-daughter dyads occurred in the first calf age class, between 0-3 weeks of age. This may be the only stage in calf development where mother-calf proximity is crucial, owing to its important antipredation value to 'hider' species (Lent 1974). Mothers of males spent less time in close proximity to their very young offspring than did mothers of females. In the wild, mothers who spend too much time in close proximity to their hiding calves risk revealing their location to predators. In white-tailed deer, younger mothers maintained less distance between themselves and their fawns, and subsequently suffered higher levels of calf mortality (Ozoga and Verme 1986). Thus, one explanation for the observed patterns in proximity relates to mothers of sons making more of an attempt to reduce the risk of predation, at the expense of having to travel longer distances to nurse their calves. However, other explanations are feasible, including the possibility that mothers of males must travel further to find sufficient forage to meet the high demands of sons, and thus spend less time close to their calves than do mothers of females.

By synchronizing their behaviour with that of their calves, mothers may more easily maintain contact with them. Overall, there was no difference in how often mothers synchronized their behaviour to that of their male and female calves. Maternal level of nutrition played a major role, as mothers in the supplement group synchronized their behaviour with their resting and active calves more frequently than mothers in the pasture group, while the opposite was true for synchronizing behaviour with foraging calves. Shifting behavioural patterns in order to synchronize behaviour with that of calves could be energetically costly to mothers at a time when demands are high. Young calves may spend much of their time resting; a mother who rests while her calf rests is sacrificing time which could be spent foraging. Similarly, maintaining contact with an active calf requires an increase in energy expenditure. That mothers on a higher plane of nutrition could more often afford to rest and be active with their calves, while mothers on pasture alone synchronized behaviour mainly when their calves foraged, confirm that there are costs associated with this type of maternal care. Within nutritional treatments, gender differences did become apparent in the amount of time hinds spent resting with their calves. In the supplement group, where mothers were under fewer time and energy constraints due to the availability of feed, mothers rested more often with sons than with daughters. However, in the pasture groups, where presumably costs were exaggerated, mothers rested less with sons than with daughters. This could be the result of higher demands in this group on mothers of sons, who were investing more in terms of milk transfer, and were under more pressure to forage regardless of calf behaviour.

Calves contributed more than mothers to maintaining mother-calf proximity, as indicated by the positive mean value of the index for spatial transitions (Hinde and Atkinson 1970). There was a tendency for calves in the pasture group to contribute more to maintaining proximity than did calves in the supplement group, indicating that this type of activity may incur a cost to mothers. In addition, mothers of males tended to play a larger role in maintaining proximity than did mothers of females. Despite these differences, the fact that index values for both genders were positive (ie. the calf always contributed more than its mother) makes it unclear whether conclusions regarding maternal investment should be drawn. In studies of spatial relations in bison, Green (1992) found that calves were also primarily responsible for maintaining proximity with mothers, and concluded that spatial transitions may be a more important aspect of contact maintenance in primates than in ungulates.

No evidence for gender-biased maternal investment was provided by measures of contact interactions. Although vocalizations likely play an important role in contact maintenance (Green 1992), they were recorded too infrequently to be analyzed. Grooming was the only contact interaction analyzed, and no difference was found between the amount of time spent grooming sons and daughters. Mothers in the supplement group spent significantly more time grooming their calves than did mothers in the pasture group. This most likely reflects the different activity budgets of the two groups; hinds in the pasture group had to spend more time foraging, whereas hinds provided with supplemental feed could afford to allocate more time to grooming offspring.

In terms of the components of contact maintenance investigated, some evidence for male-biased investment was provided by mother-calf proximity and synchrony of behaviour. Mothers maintained more distance between themselves and their young sons, which could reduce risks of predation. In addition, when maintained on a high plane of nutrition, mothers synchronized their behaviour with sons more often than with daughters. There was also some evidence to suggest that mothers may play a larger role in maintaining proximity, through spatial transitions, with sons than with daughters.

4.4 Costs of reproduction

Barren hinds, hinds who calved but did not lactate and hinds who calved and lactated should represent a progression of increasing costs of reproduction. But the measurements of ADG in these three groups did not conform to this pattern. The group who should have been intermediate in weight gains consisted of the animals who had their calves taken away shortly after birth to be hand-reared, yet this group seemed to suffer higher costs than either of the other two groups. It is possible that the removal of calves could cause a great deal of stress to their dams, and have as much or more of a negative impact on weight dynamics as would the stress of lactation. If ADG reflects an animal's response to any type of stress, it becomes a poor predictor of reproductive cost alone.

An additional departure from predicted patterns arose from the lack of detectable difference in ADG between barren females and those who successfully raised offspring. These two groups of individuals should represent opposite ends of the spectrum in terms of reproductive cost. However, there may be some risk associated with assessing reproductive costs by comparing individuals who reproduce with those who don't. Clutton-Brock et al. (1983) found that individual differences in red deer may have caused reproductive costs to be underestimated when costs were assessed by comparing reproductive and non-reproductive animals.

If mothers of sons and daughters suffered different costs of reproduction, this was not apparent from their weight dynamics. There was no difference in the costs, as measured by ADG from calving to weaning, of raising male and female offspring. A mother's age and when she gave birth seemed to be more important in determining her weight change over the period of lactation; older mothers and mothers who gave birth relatively late in the season gained weight more slowly, regardless of calf gender.

Given that differences in ADG were not apparent between barren and reproductive hinds, or between mothers of males and females (despite apparent differences in both pre-and post-natal investment), it is possible that ADG is not the best index of reproductive cost in this population. There are, however, other ways in which reproductive costs could manifest themselves.

The best way to assess reproductive costs would be to measure directly the effects on hinds' future reproduction and survival. In red deer, mothers who raise sons face lower over-winter survival, as well as a higher probability of being barren the following year, than do mothers who raise daughters (Clutton-Brock et al. 1981). The latter is also true of bison (Wolff 1988). This type of direct measurement of cost is desirable to obtain, but was impractical for the research herd used in this study for two reasons. First, reproductive performance at Ministik is too high; in any given year very few mature females fail to reproduce. Therefore, attempting to measure the cost to females, in terms of whether or not they are able to reproduce the following year, would be ineffective. Similarly, measuring reproductive costs in terms of future survival is not suitable since adult mortality rates in captive wapiti are quite low.

Parasite load has been used as an indirect measure of reproductive cost in bighorn sheep (Festa-Bianchet 1989). Although Festa-Bianchet found no difference in future reproduction for ewes raising male and female lambs, there was indirect evidence for a higher cost associated with raising male lambs, in terms of a weakened immune system. Mothers of male lambs had significant increases in levels of fecal lungworm larvae relative to mothers of female lambs. Wapiti used for the current study are routinely treated to prevent parasites, and so this type of measure would not be appropriate in assessing reproductive costs.

Other common ways of assessing reproductive costs to mothers involve examining the timing of subsequent reproductive events. For example, the time it takes for a female to return to estrus after raising a calf may be used to estimate reproductive costs. In both bison (Wolff 1988) and red deer (Clutton-Brock et al. 1981), mothers who have raised male calves conceive later in the following rut than do mothers who have raised females. Similarly, in bighorn sheep, mothers raising males experienced a delay in returning to estrus relative to mothers of females (Hogg et al. 1992). Consequently, mothers gave birth later in years after they raised male offspring in red deer and bighorn sheep (Clutton-Brock et al. 1981, Hogg et al. 1992); late birth dates are maladaptive since peak lactation may not coincide with high forage quality (Oftedal 1985, Festa-Bianchet 1988b). The interbirth interval is another variable used to measure reproductive cost. Longer interbirth intervals following male offspring have been reported for African elephants (Lee and

Moss 1986). In the study population, close observation of the herd during the rut is impractical due to the dangerous nature of rutting stags, thus the timing of estrus was not often known. The interbirth intervals were easily calculated, however, there were no differences in lengths of intervals following male and female wapiti calves in this study.

Despite the findings that both pre- and post-natal maternal investment were biased towards males, higher costs associated with raising male offspring were not apparent. There is, however, one piece of information which indicates that mothers of males may suffer more than mothers of females. Mothers of sons spent more time grazing than mothers of daughters, suggesting that they had to compensate for the higher expenditure on their offspring. That this relationship was true only in the absence of supplemental feed may imply that reproductive costs are apparent only under stressed conditions, as proposed by Boyce and Perrins (1987). Perhaps even the conditions in the pasture group were not stressed enough to allow 'true' costs of reproduction, in terms of fertility and survival, to become apparent. Animal care protocol governing the management of the research herd prohibits allowing animals to suffer to the point where mortality, or even interruptions in reproduction, are likely.

According to the definitions of Clutton-Brock (1991), this study has provided evidence for male-biased maternal care, but not maternal investment, in wapiti. Parental care refers to any behaviour of parents which is likely to improve the fitness of their offspring; there are no implications with respect to cost. Parental investment relates to how parental care reduces any aspect of a parent's fitness. Some studies which have found evidence for male-biased maternal care have failed to find evidence for higher costs of males (Duncan et al. 1984, Kovacs and Lavigne 1986a, Trillmich 1986, Le Boeuf et al. 1989). Although some conclude that no biased investment exists if no costs can be revealed (ie. Le Boeuf et al. 1989), others have made the assumption that higher expenditure in offspring of one gender necessarily brings about higher costs (ie. Trillmich 1986). In this study, it is reasonable to conclude that conditions were not stressed enough to reveal the costs associated with gender-biased investment. Although mothers appeared to expend more on sons, both before birth and prior to weaning, they may have been able to compensate for this. In circumstances where managed populations have a nutritional plane above that expected for natural populations, it has been suggested that costs may translate into increased food intake rather than decreased body condition or reproductive performance (Clutton-Brock and Albon 1982). Mothers of males in the supplement group would have been able to compensate quickly by feeding on concentrates, thus no difference was observed in time spent grazing by mothers of males and females. In the pasture group, however, differences in the amount of time spent grazing by mothers of males and females were readily observed. It is possible that in natural populations demonstrating the same male-biased patterns of maternal care as those observed in this study, reproductive costs such as reduced fertility or survival of mothers raising sons would be exhibited.

4.5 Evaluation of study

When considering the results of this study, three potential weaknesses should be kept in mind. The first concerns the accuracy of the records of reproductive performance at the

Ministik Research Station. Over the years, several different people have been responsible for the collection and recording of this information. The information used in this study was obtained from several sources: original data sheets, compiled written records on file at the station, computer data sets compiled for other studies, daily journals kept by station managers and the station's annual reports. Although every effort was made to cross-reference between the different sources to verify information, it became apparent that there may have been some inconsistencies. To minimize the risk of errors, any pieces of information which were questionable were excluded from data sets. The drawbacks of using this data set, with its potential for errors, are outweighed by the benefits of the availability of information that would be difficult, if not impossible to obtain from a wild population.

The second problem arises from a possible lack of independence of data used for some analyses. Most of the wapiti females at Ministik gave birth in more than one year, thus several of the data sets (ie. birth weights, interbirth intervals, average daily gains) contain parameters measured for the same individual in different years. Treating multiple samples from one individual as independent may lead to an increased chance of committing a Type I error (rejecting a correct null hypothesis). According to Leger and Didrichsons (1994), the pooling of data collected from the same individual is valid if the variance within individuals is greater than the variance between individuals. In the case of the data set used to examine interbirth intervals preceding births of calves, a preliminary analysis showed that individual female identity had no significant effect on interval length ($p>0.99$), meaning that within-individual variance greatly exceeded between-individual variance. Pooling in this case is valid. Decisions regarding pooling for other data sets containing multiple measurements were made after considering inter- versus intra-individual variance as well as the possible consequences of pooling.

A related problem involves the collection of nursing bout data. There were only 28 mother-calf pairs from which to collect data, and over 600 instances of nursing were recorded, thus several measurements were made on the same individuals. No satisfactory way was found to use repeated-measures analyses, and at the same time include all necessary factors and covariates. A preliminary analysis was performed to determine whether this posed a serious problem: this involved an ANCOVA with bout length as the dependent variable, and included identity of the hind as a factor, along with calf age and calf gender as covariates. This analysis showed that although hind identity became a significant factor in determining bout length, there was no change in the effects of calf gender; nursing bout length was still significantly longer for male than for female calves. It would have been desirable to include hind identity in the final model, however Systat would not run the analysis if all the factors and covariates were included in the same model. Since including hind identity did not change the conclusions drawn with respect to the effects of calf gender, it does not appear that the multiple measurements posed a serious problem.

The third problem concerns two cases of allo-mothering among the animals used in the study. One female calf was deserted by her mother at birth, and immediately adopted by another hind who had given birth to a male calf on the same day. Another male was consistently nursed and groomed by both his mother and another hind (who also mothered her own female calf). This type of cross-fostering is not thought to be common in wild populations, but may arise often in captive herds due to the inability of parturient hinds to isolate themselves from the herd as they would in the wild. The adoptive mother in the first case successfully raised both calves through to weaning. In the second case, the adoptive mother's own calf was injured prior to the end of the study, and this pair had to removed from the herd, thus only nursing bout data, and not contact maintenance data were collected. All data collected from the adoptive mothers and their calves were closely examined; these hinds appeared to treat their adopted calves in the same way that other hinds treated their own calves. Because of the limited number of animals available for behavioural observations (and especially the small number of female calves), excluding these animals from the study would have presented a problem. Since the data fell into the ranges recorded for 'normal' calves and their mothers, they were included in the data sets used to investigate measures of pre- and post-natal investment. However, both the hinds and the calves differed from the rest of the herd in weight dynamics, therefore they were not included in data sets for calf growth rates or hind ADG. It is unlikely that including these animals in the study has caused a bias in the results.

4.6 Conclusions

Do wapiti mothers divide their investment equally between male and female offspring? According to Fisher (1930), investment in males and females must be equal, with sex ratios skewed towards offspring of the least expensive gender. If wapiti were behaving according to these principles, then the male-biased sex ratios found in this study would indicate that females are more costly to produce. In fact, the evidence that pre- and post-natal investment are biased towards males, together with the findings that mothers of males spent more time foraging, support the opposite idea - that males are more expensive. The possibility that mothers balance their male-biased pre-weaning investment with higher post-weaning investment in daughters cannot be ignored. This has been proposed for species where sons disperse and daughters share their mothers' home ranges (Clark 1978). However, sharing home ranges with daughters is not likely to constitute an important form of maternal investment in species in which females do not defend feeding territories (Clutton-Brock and Albon 1982). Clutton-Brock et al. (1981) dismissed the idea of female-biased post-weaning investment for red deer; this conclusion is also reasonable for wapiti. Fisher's theory of equal investment does not hold true for this research herd of wapiti. Instead, wapiti mothers appeared to bias investment towards males, both by adaptive modification of sex ratios (Trivers and Willard 1973) and by differential allocation of resources (Reiter et al. 1978, Maynard Smith 1980).

The conclusions may be summarized as follows:

- Wapiti mothers at Ministik did not appear to invest equally in male and female offspring, and instead seemed to bias investment towards sons.
- Overall, sex ratios at birth were significantly male-biased.
- Mothers in good condition produced more male than female offspring, while mothers in poor condition produced even sex ratios.

- Mothers invested more in male than in female calves pre-natally, as indicated by higher male birth weights, and the evidence for longer gestation periods for males.
- Mothers invested more in male than in female calves post-natally, primarily by allowing them longer nursing bouts, but also by providing them with better maternal care.
- Mothers who raised male calves spent more time grazing than mothers raising female calves, suggesting that they may have suffered higher costs of reproduction.

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APPENDIX 1 - Information recorded during two-hour instantaneous sample periods, at two-minute intervals.

Distance Classes (distance between mother and calf)	0 m 1-5 m 6-10 m 11-20 m 21-40 m >40 m
States of Hind / Calf Behaviour	**Foraging** - grazing, browsing, feeding on pellets, oats or hay, drinking water **Active** - walking, playing, grooming self, interacting with other animals, calves stealing milk from hinds other than their mothers **Resting** - animal is bedded (head up or down), or standing inactive (may be ruminating)
Categories of Dyad Behaviour	Both rest Hind rests, calf forages Hind rests, calf active Both forage Hind forages, calf rests Hind forages, calf active Both active Hind active, calf rests Hind active, calf forages

APPENDIX 2 - Information recorded during one-hour continuous, focal-dyad samples.

Variable	Information recorded
Spatial transitions:	
Approaches:	Number of movements by either mother or calf across a 5, 10 or 20m boundary which decrease the distance between the pair
Leaves:	Number of movements by either mother or calf across a 5, 10 or 20m boundary which increase the distance between the pair
Contact interactions	Amount of time spent by individuals grooming each other
	Number of times one individual nuzzles the other
	Number of times one individual vocalizes in the direction of, or while searching for, the other
Foraging	Amount of time spent grazing, browsing, feeding on pellets, oats or hay
	Amount of time spent ruminating

APPENDIX 3 - Means (± SE) for significant differences reported in the text for the analysis of proximity between mothers and their calves.

Distance class	Number of scans spent at this distance (mean ± SE)	
	supplement group (n=12)	pasture group (n=11)
< 10 m	24.0 ± 2.5	15.4 ± 1.7
< 20 m	37.8 ± 1.8	30.1 ± 1.0
> 20 m	23.1 ± 1.8	30.9 ± 1.0

APPENDIX 4 - Means (± SE) for significant differences reported in the text for the analysis of synchrony of behaviour.

Category of dyad behaviour		Number of scans during which this category of behaviour was observed (mean ± SE)	
		supplement group (n=12)	pasture group (n=11)
Both rest	overall:	35.3 ± 1.5	25.8 ± 2.1
	males:	37.8 ± 1.6	23.4 ± 1.9
	females:	31.9 ± 1.9	32.2 ± 4.1
Hind forages, calf rests	overall:	10.1 ± 1.1	16.6 ± 1.3
	males:		18.3 ± 1.1
	females:		12.1 ± 2.2
Both active	overall:	0.9 ± 0.2	0.3 ± 0.1
Hind forages, calf active	overall:	1.7 ± 0.3	0.8 ± 0.2
Both forage	overall:	6.0 ± 0.7	9.5 ± 1.1
	males:		10.1 ± 1.1
	females:		7.7 ± 2.7